Incipient woody plant encroachment near native tree plantings signals heightened vulnerability for an intact grassland region

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RESEARCH ARTICLE

Incipient woody plant encroachment signals heightened vulnerability for an intact grassland region

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Abstract

Question: What constrains *Juniperus virginiana* encroachment in semi-arid grasslands: precipitation-based constraints on establishment or dispersal-based constraints on spread?

Location: Sandhills grassland, Nebraska, USA.

Methods: We tracked juvenile and adult stages of *J. virginiana* encroachment using field sampling and remote sensing across a network of 40 sites spanning a wide precipitation gradient (399–655 mm). Regional patterns of encroachment were then used to assess the relative support for precipitation-based constraints on establishment versus dispersal-based constraints on spread in a region transitioning to a more encroached state.

Results: Woody encroachment was widespread and we found no evidence that low precipitation precludes encroachment in the Sandhills. Instead, encroachment patterns were best described by proximity to planted propagule sources. However, levels of encroachment were highly variable. Encroachment density was low at more arid sites that lacked nearby stands of planted *J. virginiana*, and encroachment tended to increase with proximity to plantings and higher mean annual precipitation, suggesting that both variables play a role in the rate of encroachment.

Conclusion: Our results indicate that woody encroachment is constrained by dispersal in the Sandhills and that planted propagule sources increase grassland vulnerability to encroachment, regardless of mean annual precipitation. This may be true for other intact grassland regions where barriers to woody plant establishment have been altered or overcome. A key implication is that programs and policies need to consider encroachment risks from planted propagule sources and how to manage them to avoid fragmentation of intact grasslands.

KEYWORDS
Afforestation, dispersal-limited encroachment, *Juniperus virginiana* L., mean annual precipitation threshold, propagule pressure, Sandhills, shifting baseline, tree invasion, vulnerability, woody plant encroachment

1 | INTRODUCTION

Globally, correlations between woody cover and precipitation in grassy ecosystems are used to inform predictions of woody encroachment potential (Bond et al., 2003; Sankaran et al., 2005; Staver et al., 2011; Scholtz et al., 2018). Above precipitation thresholds, disturbance regimes are hypothesized to be needed to maintain grassland dominance and prevent encroachment, while, little to no encroachment is expected below these thresholds (Bond et al., 2005; Sankaran et al., 2005; Bond, 2008; Scholtz et al., 2018). Global vegetation models predict that over one-half of the world's C_4 grasslands would transition to a woodland or forest state in the absence of fire, while little or no encroachment was predicted for more arid grassland regions (Bond et al., 2005). The corresponding rationale has been that grasslands in locations below precipitation thresholds are immune to woody plant transitions (Bond et al., 2003; Bond et al., 2005; Scholtz et al., 2018), do not require fire to maintain grass dominance (Sankaran et al., 2005; Higgins et al., 2007; Scholtz et al., 2018), and are ideal sites for introducing trees without the consequences of encroachment (Zon, 1935; Grünzweig et al., 2003; Bastin et al., 2019).

However, grassy ecosystems around the world are exhibiting shifting baselines that depart from historical analogues (Stevens et al., 2016; Stevens et al., 2017; Rosan et al., 2019; García Criado et al., 2020). Woody encroachment in these systems has been attributed to various environmental change drivers, including altered fire and herbivory regimes (Fuhlendorf et al., 2008; Rosan et al., 2019), rising atmospheric CO_2 concentrations (Moncrieff et al., 2014), land use changes (Brown & Archer, 1988; Rosan et al., 2019), altered temperature and precipitation regimes (García Criado et al., 2020), nitrogen deposition (Köchy & Wilson, 2001), and tree planting (Richardson et al., 1994; Donovan et al., 2018). These changes question the validity of long-standing assumptions that trees are at equilibrium with their resources in more arid grasslands and motivate alternative explanations of the factors that limit encroachment.

One alternative hypothesis is that sparse woody cover observed in many semi-arid grasslands is at levels far below their maximum potential, and the lack of encroachment reflects dispersal limitations rather than establishment-based constraints. Given interests in afforestation programs for reducing atmospheric CO_2 concentrations and concerns over the risks to other ecosystem services when trees spread from plantings into grassy ecosystems (Bond et al., 2019), frameworks are needed to distinguish between dispersal- and establishment-based constraints on encroachment. The unified framework for biological invasions provides such an approach (Blackburn et al., 2011). The invasion framework uses demographic transitions to categorize different points in the invasion process and differentiates between establishment- and spread-based constraints on a species' invasion. Dispersal becomes a primary limiting factor of spread as barriers to establishment are overcome (e.g., due to altered disturbance regimes, rising atmospheric CO_2 concentrations, etc.). Under this framework, no encroachment or the establishment of only juveniles signals a potential establishment barrier and is one line of evidence that current woody plant distributions reflect maximum woody plant potential. In contrast, self-sustaining establishment and spread of adult and juvenile trees signals an ongoing encroachment process. In these regions, woody plant abundance is below its maximum potential but has been geographically limited due to the lack of establishment opportunities (i.e., dispersal).

Here, we implemented a regional-scale study to determine whether the distribution of woody plants in the Sandhills grassland of Nebraska, United States, reflects precipitation-based constraints on establishment or dispersal-based constraints on spread in a region transitioning to a more encroached state. Trees were historically sparse in the Sandhills and limited to steep riparian slopes (Pool, 1913); however, cultivation of regionally native *Juniperus virginiana* L. beginning in the early 20th century has resulted in the introduction of woody propagule sources throughout the Sandhills (Pool, 1953). The long-standing hypothesis is that sparse woody cover in more arid portions of the Sandhills reflects a soil moisture barrier to establishment that constrain non-cultivated, self-propagating woody populations (Zon, 1935; Clements, 1936). This hypothesis forms the basis for a lack of policy adaptation, because of an expectation that mean annual precipitation below 508 mm (often approximated as west of the 100th meridian by natural resource agencies; NSTC, 2019) precludes woody encroachment (Clements, 1936). In this study, we test this hypothesis against the alternative, dispersal-limited hypothesis based on the distribution of juvenile and adult *J. virginiana* encroachers across a wide precipitation gradient in the Sandhills. In addition, we assess the relative importance of moisture and propagule availability variables for explaining encroachment patterns. The Sandhills' history of tree planting across a wide precipitation gradient provides a unique perspective on the risks of introducing woody propagules in grasslands and has important implications for other grassland regions.

2 | MATERIALS AND METHODS

2.1 | Study system

This study was conducted in the 57,778 km^2 Sandhills prairie ecoregion located in Nebraska, United States (Figure 1). The Sandhills is among the planet's largest intact grasslands and is also the largest sand dune complex in the Western Hemisphere (Johnsgard, 2005; Scholtz & Twidwell, 2022). Soils in the Sandhills are remarkably uniform, well drained, and sandy (78%–98% sand content; Soil Survey Staff, USDA-NRCS). Differences in soil moisture are largely driven by mean annual precipitation (Sridhar et al., 2006), which increases along a west to east gradient (399–655 mm, respectively) with an overall mean of 527 mm (WorldClim; Fick & Hijmans, 2017) (Figure 1). Seventy percent of precipitation occurs during the growing season (Burzlaff, 1962). Average annual temperature is 9°C, with monthly low and high temperatures of −4.2 and 22.9°C, respectively (HPRCC, 2020). The primary land use in the Sandhills is cow–calf

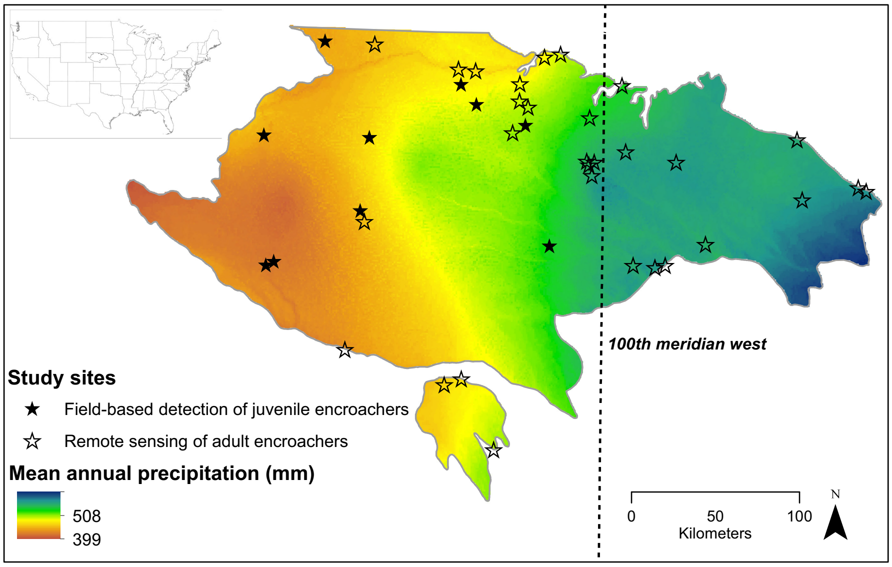

FIGURE 1 Mean annual precipitation gradient in the Sandhills of Nebraska, USA. Stars denote the distribution of 40 public land sites where encroachment by adult *Juniperus virginiana* was inventoried with remote sensing. Solid stars show a subset of 10 sites west of the 100th meridian west that were also sampled for juvenile *J. virginiana* encroachers (<1.6 m in height).

livestock production with a common stocking rate of 0.3 animal unit months (AUM) per hectare (Schacht et al., 2011). Dominant grass species in the Sandhills include *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Calamovilfa longifolia* (Hook.) Scribn., *Eragrostis trichodes* (Nutt.) Alph. Wood, and *Bouteloua hirsuta* Lag. Fire was historically common in the Sandhills and included both anthropogenic and lightning-ignited fires (Axelrod, 1985). Mean fire return intervals ranged from four to eight years prior to European settlement (Guyette et al., 2012); however, fire exclusion policies since settlement have greatly reduced fire occurrence (Twidwell et al., 2020). From 1984 to 2017, only 2% of the Sandhills area burned by large fires (MTBS Project, 2019).

The Sandhills has not experienced the level of encroachment that has occurred in recent decades throughout the southern and eastern portions of the Great Plains (Engle et al., 2008). Yet, the abundance of woody plants has increased due to encroachment by *J. virginiana* and, to a much lesser degree, *Pinus ponderosa*, a native tree species associated with more localized increases in abundance (Steinauer & Bragg, 1987; Donovan et al., 2018; Fogarty et al., 2020). Despite being regionally native to the Great Plains and eastern North America, non-cultivated *J. virginiana* were rare in the Sandhills and largely restricted to steep riparian slopes during the early 20th century (Pool, 1913). Key life-history traits allowed this fire-sensitive, non-resprouting species to persist within a biome characterized by 5000–8000 years of frequent anthropogenic-driven fire ignitions (Axelrod, 1985): (1) A broad abiotic affinity, allowing germination and growth in a range of typically inhospitable environments; (2) prolific seed production — mature trees can produce 87,000-1,592,000 seed-bearing cones annually (Holthuijzen & Sharik, 1985); (3) potential for long-distance seed dispersal by birds (Fogarty et al., 2022); (4) a lifespan potential of 500 years (Therrell & Stahle, 1998); (5) drought tolerance (Eggemeyer et al., 2006); (6) volatile oils that make *Juniperus* spp. unpalatable to most herbivores (Launchbaugh et al., 1997); and (7) dense canopies that displace herbaceous fuels near the canopy (Engle et al., 1987). However, these same traits, coupled with reduced fire occurrence, have allowed *J. virginiana* to encroach previously uninhabitable grasslands. Moreover, tree-planting programs promoting the establishment of shelterbelts have assisted in the regional expansion of *J. virginiana*, resulting in increased grassland exposure to seed dispersal (Briggs et al., 2002; Fogarty et al., 2022; Hanberry, 2022).

2.2 | Description of study sites

We selected 40 public land properties to study encroachment across the aridity gradient of the greater Sandhills ecoregion (Figure 1). Public lands are distributed across the Sandhills and were among the earliest sites to introduce *J. virginiana* propagules (Pool, 1953), thereby guaranteeing long-term exposure to seed dispersal from established stands. We excluded portions of public land sites that occurred outside of the Sandhills ecoregion. Public lands in the Sandhills range in area from 13 to 46,876 ha; five are greater than 4500 ha. Most sites were wildlife management areas, state recreation areas, or state parks owned by the Nebraska Game and Parks Commission (35 sites), the remaining five sites were national wildlife refuges owned by the US Fish and Wildlife Service (three sites), and national forests and grasslands owned by the US Forest Service (two sites).

2.3 | Sampling

2.3.1 | Remote-sensing detection of adult encroachers

At each study site, we used satellite and aerial imagery repositories from ArcGIS and Google Earth (1993–2016) to determine the distribution of adult *J. virginiana* encroachers. All sites <4500 ha were exhaustively inventoried (35 of 40 sites) using a series of 500-m wide belt transects that spanned the entire length of the site. From the five remaining large sites (>4500 ha), one site (Crescent Lake National Wildlife Refuge) was exhaustively inventoried to ensure that adult encroacher presence/absence was accurately recorded because trees were extremely rare at this site; the other larger sites were randomly surveyed over an area corresponding to the same sampling effort as smaller sites (at least 5% of the total terrestrial area of each larger public land site). This resulted in equivalent search efforts across all sites. Remote sensing captured individuals at least 1.6 m tall (based on supplemental field verification), which corresponds with general size classes of *Juniperus* spp. in the Great Plains associated with sexual maturity (Owensby et al., 1973; Fuhlendorf et al., 1996). We also used satellite image repositories to digitize all planted *J. virginiana* located within or nearby public land sites.

2.3.2 | Field detection of juvenile encroachers

To determine the extent of the incipient stage of the encroachment process, we conducted a large-scale field inventory study in June 2018 in the western Sandhills to detect the distribution of juvenile encroachers (individuals <1.6 m that go undetected from remote-sensing imagery and generally below size classes required for sexual maturity) (Figure 1). We selected a subset of 10 sites for field inventory. These sites included the most arid public lands where soil moisture is expected to function as a barrier to non-cultivated, self-propagating woody plants. Surveys were conducted following a purposive (i.e., non-random) sampling protocol used for identifying rare plant species (Palmer et al., 2002; Chiarucci et al., 2018) to search for the occurrence of juvenile encroachers.

At each site, we established a minimum of three 100-m^2 plots in areas deemed high candidates for encroachment (e.g., in areas with adult *J. virginiana*, planted stands, and based on previous research of the region; Donovan et al., 2018). Search efforts were consistent among all sites. At each site, plots were surveyed using a series of 20 5-m wide belt transects that spanned the entire 100-m length of the plot area. Field surveyors searched within the herbaceous layer for seedlings as well as individuals above the herbaceous layer but undetectable by remote-sensing imagery (individuals <1.6 m in height). The presence and height was recorded for all juvenile *J. virginiana* encroachers less than 1.6 m in height.

2.4 | Statistical analysis

Response variables recorded for each of the 40 study sites consisted of the presence (binary outcome) and density of adult encroachers. Of these sites, adult encroachers were only absent from two. Therefore, statistical analyses were conducted to investigate correlates of encroacher density. Adult encroachment data contained a single outlier; further investigation of this site showed that high *J. virginiana* densities were due to rapid re-encroachment following tree removal, which is associated with higher tree densities compared to the initial encroachment process (Fogarty et al., 2021). We therefore removed this site from statistical analyses.

Linear models were used to describe the effects of moisture and propagule availability on the density of encroaching adults (Box–Cox-transformed to meet normality assumptions) across a network of 39 sites in the Sandhills. Several measures of moisture availability have been used to describe soil water limitations on trees, and we considered several of these measures: mean annual precipitation (MAP) (WorldClim; Fick & Hijmans, 2017), effective rainfall (ER) (CGIAR-CSI; Trabucco & Zomer, 2018), and aridity index (AI) (CGIAR-CSI; Trabucco & Zomer, 2018). Because these predictor variables are highly correlated, we only used the variable that had the highest correlation (r) with the response variable in further analyses. We also used proximity to planted *J. virginiana* stands (J.PROXIMITY) as a predictor variable to examine the role of propagule availability on the density of encroaching adults. *J. virginiana* has a male:female sex ratio around 1:1 and planted stands are known propagule sources (Stoeckler & Slabaugh, 1965; Vasiliauskas & Aarssen, 1992; Fogarty et al., 2022). In the Sandhills, planted *J. virginiana* stands (e.g., shelterbelts) are common, often represent the sole propagule source for a site, and have been shown to contribute to encroachment (Donovan et al., 2018; Fogarty et al., 2022). Proximity to planted *J. virginiana* was calculated in ArcGIS as the mean Euclidian distance of a site's terrestrial area (divided in 30-m^2 grid cells) to the nearest planted *J. virginiana* stand, following the methods of Benson (2013).

Candidate models were created to test for both singular and additive effects of moisture and propagule availability on the density of adult encroachers (TREE.DENSITY; Box–Cox transformed). Model support was compared using Akaike's Information Criterion corrected for small sample sizes (AIC_c) with model assessments based on ΔAIC_c values (values 0–2 indicate strong relative support) and AIC_c weights. Variable effect size was assessed using averaged parameter estimates, standard errors, and confidence intervals. All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018) with the *geoR* (Ribeiro et al., 2020), *AICcmodavg* (Mazerolle, 2017), and *bbmle* (Bolker & Team, 2017) packages.

3 | RESULTS

Contrary to predictions that mean annual precipitation would preclude woody encroachment at more arid grassland sites, encroaching woody plants were detected at the most arid sites that contained nearby propagule sources (Figure 2). We detected juvenile and adult *J. virginiana* encroachers far below the perceived mean annual precipitation threshold of 508 mm (Figure 2). Adult encroachers were observed on 38 of 40 sites and across a wide range of mean annual precipitation conditions (from sites with 425 to 605 mm). This study estimated a total of 269,729 adult encroachers across the 40 public land sites, of which 46,899 occurred below the hypothesized mean annual precipitation threshold (Appendix S1). The two sites that did not exhibit encroachment

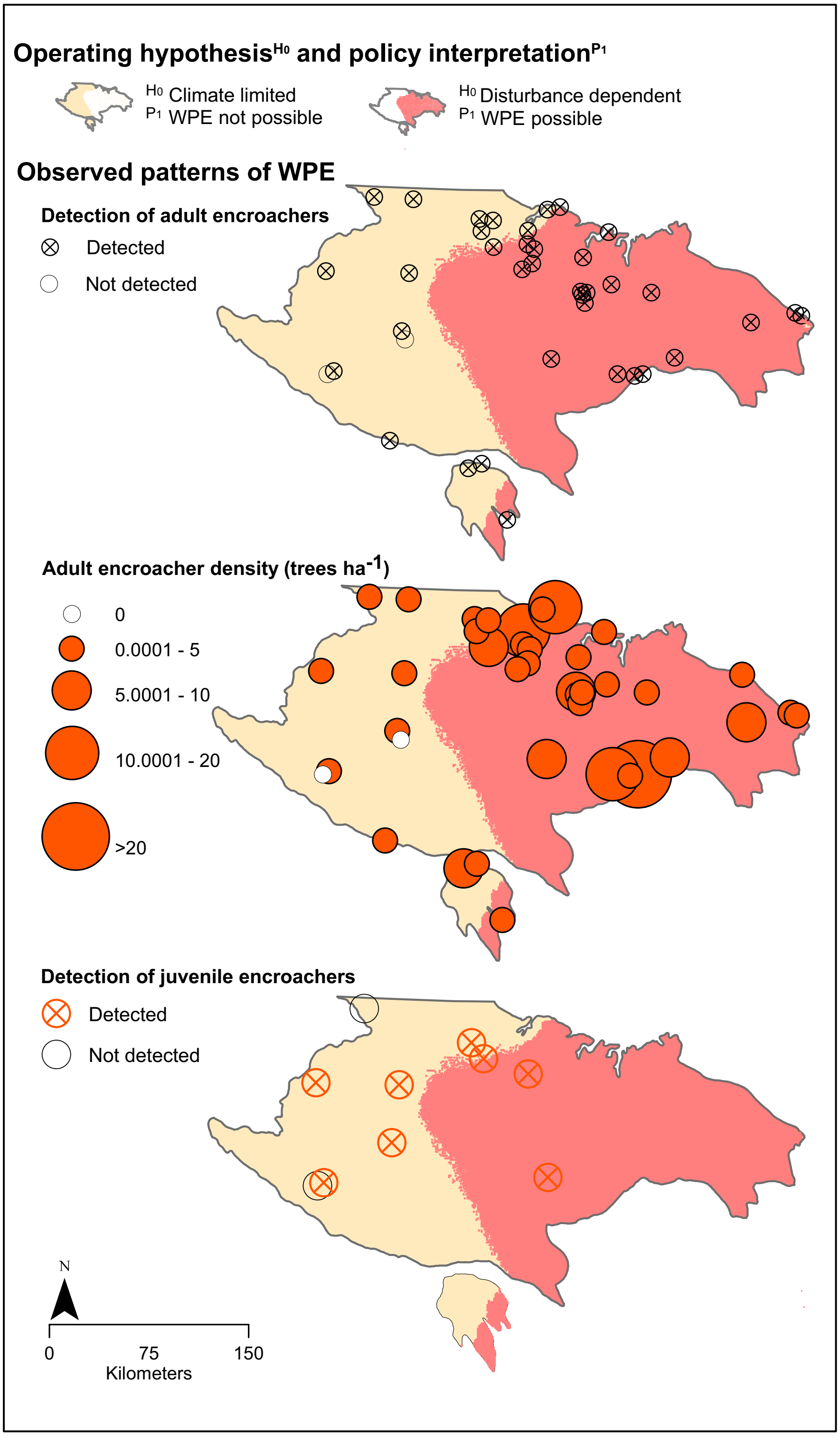

FIGURE 2 Operating hypothesis showing climate-limited portion of the Sandhills (tan) from disturbance-dependent portion (pink) and associated interpretations of woody plant encroachment (WPE) compared to observed patterns of *Juniperus virginiana* encroachment in the Sandhills, Nebraska, USA. Adult encroachment data reflect encroachment from 1993 to 2016 detected using satellite image repositories. Juvenile encroachment data reflect the presence/absence of *J. virginiana* <1.6 m in height and were collected in the field in 2018.

by adult *J. virginiana* did not contain on-site propagule sources and on average were 1.3 and 4.2 km from the nearest planted propagule source (Appendix S1). All other sites were located in areas with nearby propagule sources and contained adult encroachers (Appendix S1). Twenty-three sites contained planted *J. virginiana* propagule sources.

Juvenile and adult encroachers were detected on the most arid site (425 mm mean annual precipitation) with nearby stands of planted *J. virginiana* (Crescent Lake National Wildlife Refuge). We detected juvenile encroachers on seven of 10 sites in the more arid portion of the Sandhills where field sampling occurred (Figure 2). Of the three sites where we did not detect juvenile encroachers, two sites (Shell Lake WMA and Valentine NWR) had low densities of adult encroachers, while one site (Crescent Lake WMA) that was 4.2 km from the nearest *J. virginiana* propagule source did not exhibit encroachment by juvenile or adult *J. virginiana* (Appendix S1).

The density of adult encroachers was best explained by proximity to planted *J. virginiana* and mean annual precipitation (Table 1). Proximity to planted *J. virginiana* was the only predictor variable included in both top models ($\Delta AIC_c < 2$) (Table 1). Densities of *J. virginiana* tended to be higher on public land sites that were in close proximity to planted *J. virginiana* stands (mean = 3.6 trees ha^{-1}) compared to sites with proximities greater than 2 km from planted *J. virginiana* (mean = 0.2 trees ha^{-1}) (Table 2, Figure 3). Among the moisture availability variables considered, mean annual precipitation had the strongest correlation with the density of adult encroachers, although this variable only received strong support when considered alongside proximity to planted *J. virginiana*. Densities of encroaching adults tended to be higher on sites with greater mean annual precipitation, whereas densities were relatively low on more arid sites (Figures 2, 3). However, the relationship between mean annual precipitation and density was highly variable (95% confidence interval overlapped zero; Table 2) and more arid sites often had encroachment densities similar to more mesic sites when propagule sources were nearby (Figure 3).

4 | DISCUSSION

Globally, low abundances of woody plants in arid and semi-arid grassland ecosystems have been interpreted as evidence that these areas have little to no potential for woody encroachment (Bond et al., 2003, 2005; Sankaran et al., 2005; Lehmann et al., 2014; Scholtz et al., 2018). However, our results show no support that sparsely distributed woody plants in the Sandhills are reflective of establishment-based constraints. Instead, our results support an alternative hypothesis that the distribution of woody plants in the Sandhills reflects dispersal-based constraints on spread in a region below its maximum woody plant potential (Collins et al., 2021; Hanberry, 2022). Even at the most arid sites, well below proposed precipitation thresholds, we found juvenile *J. virginiana* as well as demographic transitions to adult trees when planted propagule sources were nearby. These results are supported by ecophysiological studies that have shown juvenile and adult *J. virginiana* to be well suited to survive in the Sandhills' semi-arid conditions (Eggemeyer et al., 2006; Bihmidine et al., 2010; Msanne et al., 2017).

Mean annual precipitation, in tandem with propagule availability, is therefore more likely associated with the rate of encroachment in the Sandhills, rather than the potential for encroachment to occur. Rates of encroachment tend to decrease with mean annual precipitation (Fuhlendorf et al., 2008; Stevens et al., 2016) and moisture-limited systems are therefore expected to require longer periods of time for woody plants to spread before providing evidence of a maximum potential (Archer et al., 1988; Wakeling et al., 2012; Collins et al., 2021). This process may require decades to millennia as barriers to establishment and spread are overcome. For instance, the introduction of domestic livestock dispersal agents in southwestern US grasslands is associated with a 200-year period of unprecedented encroachment (Brunelle et al., 2014). Based on these findings, differentiating slow rates of encroachment (i.e., ecosystems in transition) from evidence of a maximum potential would alter existing vulnerability models and predictions of the extent of grassland loss this century (Bond et al., 2005; Scholtz et al., 2018; Bastin et al., 2019; Wonkka et al., 2019). Globally, encroachment is widespread across a broad precipitation gradient (Stevens et al., 2017) and has already exceeded its proposed maximum potential in some moisture-limited regions elsewhere in the world (e.g., South Africa: Stevens et al., 2016; Brazil: Rosan et al., 2019).

Our finding that encroachment was strongly associated with proximity to planted propagule sources indicates that propagule availability plays an important role in limiting encroachment and that *J. virginiana* planting has increased encroachment pressure in ecosystems like the Sandhills where non-cultivated woody plants are rare. This finding complements those of a recent assessment that documented a rapid range expansion of *J. virginiana* in the western Great Plains aided by tree plantings, particularly shelterbelts (Hanberry, 2022). These are important findings because *J. virginiana* is extensively planted in the Great Plains (Ganguli et al., 2008) and tree-planting programs have been, and continue to be, rationalized based on the benefits provided by shelterbelts (Zon, 1935; Brandle et al., 2004). Yet, *J. virginiana* is among the most notorious encroaching species in North America and is associated with severe social-ecological consequences in grasslands (Briggs et al., 2002; Twidwell et al., 2013; Bielski et al., 2017; Zou et al., 2018), which should be considered as risks of introducing propagule sources. Similar examples can be found globally where native and non-native woody species are viewed as inconsequential to grassy ecosystems but then encroach later on (Richardson & Rejmánek, 2011; Nackley et al., 2017). A key lesson from invasion biology is that propagule pressure and residence time drive woody invasion (Richardson et al., 2015). While

TABLE 1 Model selection results for models used to describe the density of adult encroachers (Box–Cox-transformed) on public land sites from 1993 to 2016 in the Sandhills, Nebraska, USA

Model	K[a]	ΔAIC_c[b]	ωi[c]
TREE.DENSITY ~ J.PROXIMITY+MAP	4	0.0	0.60
TREE.DENSITY ~ J.PROXIMITY	3	0.9	0.39
TREE.DENSITY ~ MAP	3	9.6	0.01
NULL	2	16.9	<0.001

[a]Number of parameters in the model.
[b]Difference in AIC_c value among model and the most strongly supported model.
[c]AIC_c Weight — relative strength of support for model.

TABLE 2 Parameter estimates ($\beta \pm$ SE) and confidence intervals (CI) from top supported models used to describe the density of adult encroachers (Box–Cox-transformed) on public land sites from 1993 to 2016 in the Sandhills, Nebraska, USA

Predictor	$\beta \pm$ SE	Lower CI (2.5%)	Upper CI (97.5%)
J.PROXIMITY	−0.0011 ± 0.0003	−0.0016	−0.0005
MAP	0.0096 ± 0.0054	−0.0013	0.0205

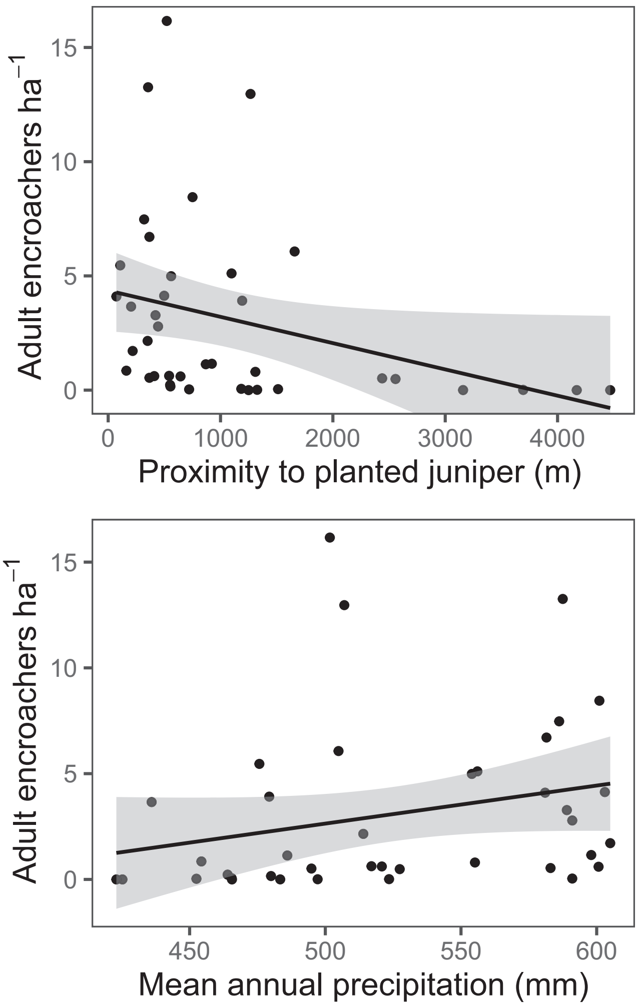

FIGURE 3 Relationship between the density of adult encroachers and (top) proximity to planted *Juniperus virginiana* and (bottom) mean annual precipitation. Shaded bands are 95% confidence intervals. Encroachment data were collected from 39 public land sites in the Sandhills, Nebraska, USA, and reflect encroachment from 1993 to 2016 detected from satellite image repositories.

this is consistent with the general patterns observed in the Sandhills, it is in contrast to assumptions of equilibrium between regionally native woody plants and climate and the notion that tree-planting programs can disregard the risks of encroachment in moisture-limited systems (Grünzweig et al., 2003; Bastin et al., 2019).

Regional assessments that consider both establishment and spread as limiting factors are needed to better understand the extent to which the world's remaining grassland regions are vulnerable to woody encroachment. Consistent trends of encroachment by adult plants are expected in systems where trees are far below their maximum potential (e.g., the Sandhills), including systems with slow rates of encroachment. These systems are vulnerable to encroachment and require disturbance (e.g., fire) to prevent increases in woody plant abundance. Assumptions of equilibrium between woody plant distributions and climate are expected to under-predict encroachment potential in these systems and lead to unexpected trajectories of grassland loss (e.g., Stevens et al., 2016). Grass-woody systems at equilibrium (or dynamic equilibrium) with climate are expected to exhibit relatively stable woody plant communities with no consistent trends of recruitment-based encroachment (as opposed to canopy expansion) (Browning et al., 2008). In the Sandhills, widespread encroachment by juvenile and adult *J. virginiana* indicates a lack of barriers to establishment and signals heightened grassland vulnerability to encroachment. Given widespread encroachment documented in this study, beyond a priori expectations, future studies on demographic bottlenecks across environmental gradients will provide important information for understanding the relative changes in vulnerability across the Sandhills grassland.

5 | CONCLUSIONS

Confusion over the roles of climate and disturbance on the distribution of grassy ecosystems have proven to have long-standing consequences for grassy ecosystems worldwide (Veldman et al., 2015; Pausas & Bond, 2018). A misunderstanding of the drivers that sustain grasslands has led to a disregard of the potential for encroachment to occur and its consequences. The debate over the potential for encroachment to occur in the Sandhills stems from a view that a climate climax drives as the primary determinant of grassland distribution (Clements, 1936; Borchert, 1950). Here, we found no evidence that a precipitation threshold precludes encroachment in the more arid portions of the Sandhills. Instead, our findings show that propagule sources play an important role in grassland vulnerability to encroachment, regardless of mean annual precipitation. This may be true in other intact grassland regions where barriers to encroaching woody plants have been altered. Key implications are that (1) tree-planting programs should no longer be implemented under the notion that spread will not occur; (2) policies and programs need to consider the location of propagule sources and how to manage them to prevent encroachment from fragmenting intact grasslands; and (3) future research that improves our scientific understanding of the extent to which the world's remaining grasslands are vulnerable to woody encroachment will be increasingly important for conservation in light of the global changes and pressures affecting these ecosystems.

AUTHOR CONTRIBUTIONS

Dillon T. Fogarty and Dirac Twidwell conceived the ideas and designed methodology; Dillon T. Fogarty collected the data; Dillon T.

Fogarty analyzed the data; Dillon T. Fogarty and Dirac Twidwell led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data are provided in Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Woody encroachment and environmental attributes from network of 40 public land sites.

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