



Spatial patterns of woody plant encroachment in a temperate grassland

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Abstract

Context Woody encroachment is the process whereby grasslands transition to a woody-dominated state. This process is a global driver of grassland decline and is ultimately the outcome of increased woody plant recruitment in grasslands. Yet, little is known about how recruitment distances structure spatial patterns of encroachment.

Objectives Here, we develop a recruitment curve to describe the scatter of woody plant recruitment around seed sources and examine how this structures spatial patterns of encroachment.

Methods We developed a recruitment curve for *Juniperus virginiana* using an encroachment dataset that captures spread from tree plantings into treeless grassland sites in the Nebraska Sandhills (USA). In addition, we used height classes of encroaching *J. virginiana* as subsequent time steps of an encroachment process to examine how the leading edge of encroachment expanded over time.

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Results The recruitment curve was characterized by a fat-tailed distribution. Most recruitment occurred locally, within 157 m of seed sources (95th percentile distance), while, sparse long-distance recruitment characterized the curve's tail. Expansion of the leading edge of encroachment was characterized by two features: (1) a slow moving, high density area near tree plantings and (2) rapid expansion of the distribution's tail, driven by long-distance recruitment in treeless areas.

Conclusion Our results show a high capacity for woody plant invasion of grasslands. Local recruitment drives transitions to woody dominance, while long-distance recruitment generates a rapidly advancing leading edge. Plans to conserve and restore grasslands will require spatially informed strategies that account for local and long-distance recruitment of woody plants.

Keywords Effective seed dispersal · Recruitment distance · Seed dispersal · Tree invasion · Woody encroachment · Woody transitions

Introduction

Grassland ecosystems across the world have experienced increases in the abundance and dominance of woody plants, many of which have transitioned to an alternative, woody dominated state (Van Auken 2000; Stevens et al. 2017; Rosan et al. 2019). This

process, referred to as woody plant encroachment, is associated with severe changes in the provisioning of grassland ecosystem services, including reduced food production (Fuhlendorf et al. 2008; Anadon et al. 2014), freshwater supply (Jackson et al. 2005; Zou et al. 2018), biodiversity (Chapman et al. 2004; Ratajczak et al. 2012), and increased risk of large wildfires (Donovan et al. 2020) and vector-borne diseases (Loss et al. 2021). While woody encroachment has been attributed to many different causes [e.g., altered fire and herbivory regimes, increased seed dispersal, climate change, and rising atmospheric CO₂ concentrations; Van Auken (2009)], it is the outcome of woody plant dispersal and recruitment. Either of these can limit the encroachment process (Brown and Archer 1988; Archer et al. 2017; Woods et al. 2019). During the Holocene for example, mesquite (*Prosopis* spp.) encroachment is believed to have been dispersal limited in North America prior to the introduction of domestic livestock, which increased seed dispersal and corresponds to a period of unprecedented encroachment (Brown and Archer 1988; Brunelle et al. 2014). Alternatively, disturbances like fire and herbivory can prevent woody plant recruitment despite an abundance of seed dispersal (Hoffmann 2000; Heisler et al. 2003; Allred et al. 2012). Ultimately, factors influencing recruitment such as fire and herbivory, climate, soil, and competition operate against a backdrop of dispersal-based limitations (Archer et al. 2017; Woods et al. 2019). That is, dispersal regulates opportunities for recruitment. Yet, seldom is dispersal examined as part of the encroachment process, a factor that constrains practitioners' ability to understand and manage encroachment as a spatial process.

One way to account for dispersal in the encroachment process is through quantification of recruitment curves. Recruitment curves describe the scatter of trees as a function of distance from the seed source. They closely mimic seed dispersal curves (Greene and Johnson 2000; McNamara et al. 2019) and almost always follow a characteristic form with an abundance of relatively short distance recruitment at one end of the curve and a paucity of long distance recruitment at the other (Clark 1998; Clark et al. 1999; Nathan et al. 2003). However, specific details of recruitment curves vary considerably and lead to variation in the patterns of adult plants. For instance, animal-dispersed species tend to have longer dispersal distances

compared to wind-dispersed species, which leads to differences in recruitment patterns at both local and broad scales (Clark et al. 2005; Bullock et al. 2017). From an encroachment perspective, rapid transitions from grassland to woodland are driven by the most abundant recruitment distances (Archer et al. 1988; Fuhlendorf et al. 1996); whether that distance is 1-m or 100-m has major implications on the risk of woodland transitions in grasslands. At broad scales, long distance recruitment dictates the speed at which woody species can invade intact grassland regions (Kot et al. 1996; Clark 1998; Nathan 2006). Recruitment curves therefore provide important information for understanding patterns of woody encroachment at multiple scales.

In the central Great Plains grasslands, *Juniperus virginiana* encroachment is leading a large-scale transition towards woody dominance (Briggs et al. 2005; Engle et al. 2008; Twidwell et al. 2013b). *Juniperus virginiana* is a fire-sensitive tree species whose high fecundity (Holthuijzen and Sharik 1985a), avian seed dispersal system (Holthuijzen and Sharik 1985a; Horncastle et al. 2004), rapid growth rates (Engle and Kulbeth 1992), and drought tolerance (Msanne et al. 2017) enable it to rapidly transform undisturbed grasslands to a woody-dominated state (Briggs et al. 2002; Fuhlendorf et al. 2008). Widespread fire exclusion in the Great Plains has removed the natural barrier to *J. virginiana* recruitment and thereby left dispersal as a key constraint of an impending transition to woody dominance (Briggs et al. 2005; Engle et al. 2008; Twidwell et al. 2013b; Wilcox et al. 2018). In a well-documented example, Ratajczak et al. (2016) showed that 56% of the Flint Hills tallgrass prairie region lacked fire-vegetation feedbacks required to prevent a transition to woodland, but remained in a tallgrass prairie state due to dispersal limitations (see also Collins et al. 2021). Research from North America's temperate forest region indicates that *J. virginiana* seed dispersal occurs up to 515 m from seed sources (Holthuijzen and Sharik 1985b); however, no studies have evaluated dispersal or recruitment distances in the Great Plains where dispersal appears to be the most limiting factor to this species invasion.

In this study, we develop a recruitment curve for *J. virginiana* to better understand the limiting role of dispersal in driving woodland transitions. Early afforestation experiments conducted in the treeless prairies of the Nebraska Sandhills provide a unique

opportunity to study the spatial patterns of encroachment. Tree plantings often represent the first seed sources present in Sandhills' landscapes and function as distinct nodes of encroachment (Fig. 1) (Donovan et al. 2018). We use a dataset capturing more than 70 years of encroachment from tree plantings into treeless prairie sites to (1) quantify a recruitment curve for *J. virginiana*, (2) distinguish between short (local) vs. long recruitment distances, and (3) characterize how the leading edge of woody encroachment, originating from tree plantings, develops and expands over time. Ultimately, these objectives advance scientific understanding of woodland transitions as a spatial process.

Methods

Study system

This study was conducted at two sites in the central Sandhills, of Nebraska, USA (Fig. 2). The Sandhills is a disturbance-dependent grassland region located in the central portion of the Great Plains temperate grassland biome, encompassing a 57,778 km² area of vegetated sand dunes (Johnsgard 2005). Despite early trends of woody encroachment in the Sandhills

(Roberts et al. 2018; Fogarty et al. 2020), the region remains one of the most intact grassland regions in the world (Scholtz and Twidwell 2022). Study sites were located at the Nebraska National Forest at Halsey (36,422 ha) and Samuel R. McKelvie National Forest (46,976 ha) (Fig. 2). These sites were designated as national forests in 1902 to serve as large-scale tree planting experiment and demonstration sites. Each site contains large, hand-planted forests and windbreaks surrounded by native mixed-grass prairie communities (Fig. 1). Tree plantings are primarily composed of *J. virginiana* and *Pinus ponderosa* and represent the first woody plants established at these sites. Since establishment, woody plants have spread from tree plantings into adjacent prairies with greater levels of encroachment at Nebraska National Forest at Halsey compared to the more arid prairies at Samuel R. McKelvie National Forest. Rates of encroachment in the Sandhills tend to increase with mean annual precipitation which explains the lower level of encroachment observed at Samuel R. McKelvie National Forest. The vast majority of encroachment consists of *J. virginiana*, at both sites and in the Sandhills as a whole, with some local instances of *P. ponderosa* spread alongside *J. virginiana*.

Mixed-grass prairie communities support an array of grassland-obligate species and are dominated

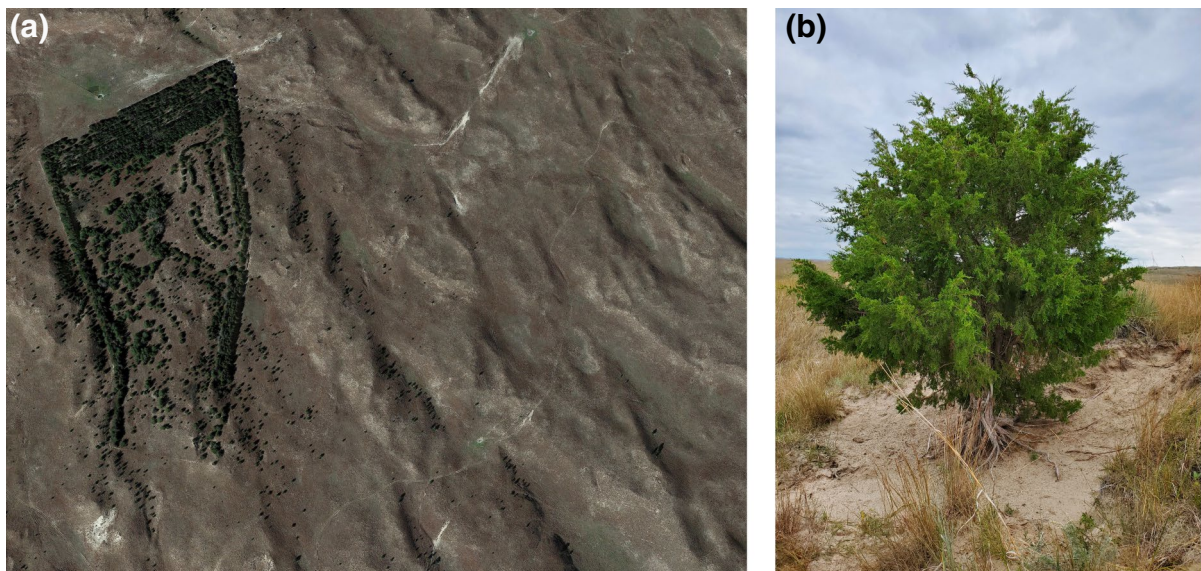
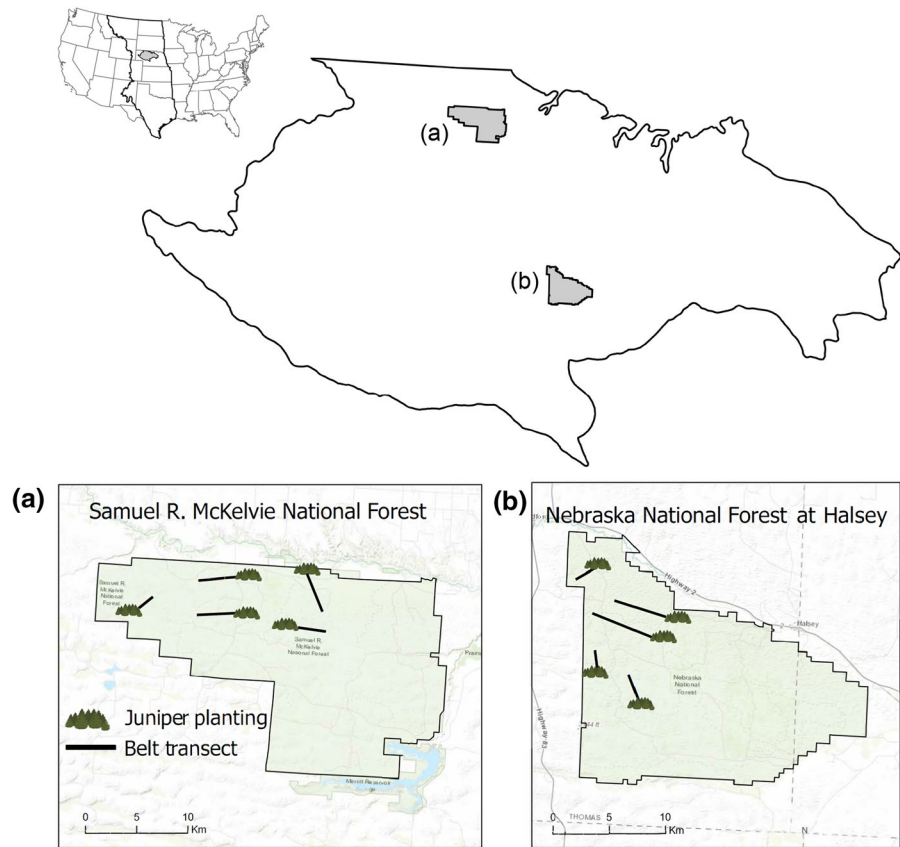


Fig. 1 Example of **a** *J. virginiana* encroachment around a tree planting and **b** an encroaching *J. virginiana* in the Sandhills, NE USA (satellite imagery is from Google Earth)

Fig. 2 Map of studies sites **a, b** and transects used to examine spatial patterns of woody encroachment in the Sandhills ecoregion of the central Great Plains



by prairie sandreed (*Calamovilfa longifolia*), little bluestem (*Schizachyrium scoparium*), sand bluestem (*Andropogon hallii*), and switchgrass (*Panicum virgatum*). Management has focused on fire exclusion tactics to protect tree plantings from fire (Stubbendieck and Tunnell 2008) as well as livestock grazing with a common stocking rate of 0.3 animal unit months (AUM) per hectare. However, more recent management has focused on grassland diversity by incorporating prescribed fire and tree removal within targeted areas (not included in this study). The climate at these sites is semiarid continental, with mean annual precipitation of 556 and 495 mm and mean annual temperature of 16.7 and 17.3 °C for Nebraska National Forest at Halsey and Samuel R. McKelvie National Forest, respectively (Fick and Hijmans 2017; HPRCC 2020). Soils at both sites are dominated by Valentine fine sand and consist of deep, excessively drained soil (Soil Survey Staff, USDA-NRCS).

Study design, sampling, and analysis

We investigated the spatial patterns of woody encroachment using 10, 100-m wide belt transects that extended from a treeless grassland area to the nearest *J. virginiana* planting that served as a seed source for spread (Figs. 1 and 2). Transects were established by randomly generating a point within candidate treeless areas (identified based on previous research at the study sites) and then drawing a line to the nearest *J. virginiana* planting using ArcGIS. This approach was used to ensure that all transects captured a wide range of distances from *J. virginiana* seed sources, which resulted in transects of different lengths. We considered areas ‘treeless’ that were at least 515 m from the nearest detectable tree using imagery from Google Earth (Visser et al. 2014). This distance reflects the maximum seed dispersal distance for *J. virginiana* based on available research (Holthuijzen and Sharik 1985b) and was used to minimize the occurrence of *J. virginiana* seed sources near the transect end point. *J. virginiana* plantings were used

as transect starting points because they represent the first seed sources introduced in these landscapes and transects were designed to capture the leading edge of *J. virginiana* encroachment. All transects were at least 1.3 km in length and contained no previous woody plant management (based on management histories provided by U.S. Forest Service staff). Each study site contained five transects that ranged from 1.3–5.5 km in length and started at large *J. virginiana* plantings established from 1950 to 1982 (Fig. 1). Transects were independent sample units and were located a minimum of 1.7 km from other transects (Fig. 2).

Prior to sampling encroaching *J. virginiana*, we recorded the location, height, and sex of planted *J. virginiana* located near the transect starting point (Fig. 1). Encroaching *J. virginiana* were then sampled using 10, 10-m wide belt transects nested within larger, 100-m belt transects. Transects were navigated using GPS units that contained transect maps. Characteristics recorded for each *J. virginiana* consisted of location, height, and sex (female, male, or unknown). Sex was determined based on the presence/absence of seed or pollen cones. Height was measured using a telescoping measuring pole and was used as a proxy for tree age because it is strongly correlated with *J. virginiana* age in semi-arid grasslands (Engle and Kulbeth 1992), can be consistently and quickly measured across a wide range of tree sizes, and avoids challenges of other measurements (e.g., diameter at breast height) that are not conducive to multi-stemmed, low stature trees such as *J. virginiana* in the Sandhills' semi-arid climate. *J. virginiana* located outside of 100-m belt transects were also sampled when they were the closest seed source to a tree within the transect [following Debain et al. (2007)]. This was done to ensure that the nearest seed source was recorded for all trees located within transects. Search effort was consistent among all transects. Field sampling occurred in August and September of 2020.

A recruitment curve was developed based on the scatter of *J. virginiana* around planted and encroaching seed sources. *J. virginiana* were considered seed sources to smaller encroaching *J. virginiana* when they represented the closest seed bearing tree or were of reproductive height (> 1.5-m; Owensby et al. 1973 and based on supplemental field data) and lacked pollen cones. This included planted *J. virginiana* as well as encroaching individuals that met the above criteria.

J. virginiana is dioecious with considerable variation in seed production among years, and unlike pollen cones, seed cones are often removed by birds during the growing season (Holthuijzen and Sharik 1985a). We therefore considered taller trees that lacked pollen cones as potential seed sources (given the preceding criteria were met). These criteria were conservative and were used to avoid over estimation of long-distance recruitment events that are rare, however, these assumptions will undoubtedly under estimate some recruitment distances (Nathan and Muller-Landau 2000). The Euclidean distance between seed sources and encroaching *J. virginiana* was calculated using ArcGIS.

A preliminary analysis of recruitment distances at Nebraska National Forest at Halsey and Samuel R. McKelvie National Forest indicated high levels of overlap in recruitment curves between sites (Fig. S1). We therefore pooled recruitment data across sites for all further analyses to provide a general pattern of recruitment distances across a range of conditions in the Sandhills (Holthuijzen and Sharik 1985c; Stewart et al. 1998; Greene and Johnson 2000; McNamara et al. 2019). A candidate set of three probability density functions were used to quantify *J. virginiana* recruitment curves: lognormal, Weibull, and negative exponential. Each are simple decay functions commonly used to model dispersal (Greene et al. 2004; Hirsch et al. 2012). Lognormal and Weibull are considered fat-tailed distributions in comparison to the negative exponential function which has a constant decay rate (Nathan et al. 2012; Table 1). Fat-tailed probability density functions refer to leptokurtic distributions that exhibit a high degree of positive skew relative to a normal distribution and have a higher chance of extreme events. We used the

Table 1 Candidate set of probability density functions use to describe the scatter of recruitment around seed sources and *J. virginiana* plantings

Name	Probability density function ^a
Lognormal	$f(x) = \frac{1}{\sqrt{2\pi\sigma x}} e^{-\frac{(\ln(x)-\mu)^2}{2\sigma^2}}$
Weibull	$f(x) = \frac{a}{b} \left(\frac{x}{b}\right)^{a-1} e^{-\left(\frac{x}{b}\right)^a}$
Exponential	$f(x) = \lambda e^{-\lambda x}$

^aterms: μ mean, σ standard deviation, a shape parameter, b scale parameter, λ rate

‘*optim*’ function in R (R Core Team 2018) to identify parameter values for each probability density function that maximized the likelihood of our data (Hirsch et al. 2012). Once model parameters were optimized, we compared the relative support for each model using Akaike’s Information Criterion corrected for small sample sizes (AIC_c) and selected the top model based on the lowest ΔAIC_c score. Goodness-of-fit was assessed by comparing predicted and observed recruitment distances using a Kolmogorov-Smirnov test. We used the cumulative distribution function and high percentile recruitment distances to distinguish between average, short-distance recruitment vs. rare, long-distance recruitment characteristic of the distribution’s tail (Nathan et al. 2003).

The leading edge of encroachment was characterized based on the distribution of encroaching *J. virginiana* around tree plantings. Spatial expansion of the leading edge over time was examined indirectly using *J. virginiana* height classes to represent subsequent time steps in the encroachment process. *J. virginiana* height and age are strongly correlated, with trees reaching a height of 1-m around 5 years of age (Owensby et al. 1973; Engle and Kulbeth 1992). *J. virginiana* recruitment data was therefore subset in to five height classes to represent time steps of woody encroachment: t_1 =individuals ≥ 5 m; t_2 =individuals ≥ 4 m; t_3 =individuals ≥ 3 m; t_4 =individuals ≥ 2 m; t_5 =individuals ≥ 1 m. The onset of seed production typically starts when *J. virginiana* are about 1.5 m in height between the ages of 6–11 [depending on regional differences in growth rate (Owensby et al. 1973; Engle and Kulbeth 1992)]. Time steps therefore captured additional dispersal from tree plantings as well as the expansion of seed sources as part of the encroachment process. The distribution of encroaching *J. virginiana* around tree plantings was quantified for each time step ($t_1 - t_5$) using probability density functions (using the same functions and AIC_c -based selection approach outlined above). This allowed us to track the spatial expansion of a woody encroachment leading edge over time. Specifically, we tracked how the 50th, 75th, 90th, 98th, and 99th percentile distances from the tree planting changed across subsequent time steps to characterize expansion of the leading edge.

Results

We sampled a total of 961 encroaching *J. virginiana* across 10 transects. The average height of encroaching *J. virginiana* was 1.9 m and ranged from 0.03 to 7.75 m compared to an average height of 6.75 m for planted *J. virginiana* (range 3.19–11.5). All planted stands contained mature, seed bearing *J. virginiana*, representing 49% of trees in sampled tree plantings (male:female ratio=0.95). Most encroaching *J. virginiana* lacked cones (75%), although, among mature trees with cone development the male to female ratio was 1.0.

Recruitment distances ranged from 0.1 to 966.6 m from the nearest seed source with a median and mean distance of 11.4 and 40.1 m, respectively. The recruitment curve was best described by a lognormal probability density function ($\mu=2.527$ and $\sigma=1.538$; Table 1). Predicted and observed recruitment distances were not significantly different (Kolmogorov-Smirnov test; $D=0.03$, $P=0.1647$), indicating that *J. virginiana* recruitment distances followed a lognormal distribution. The recruitment curve followed a characteristic fat-tailed distribution: recruitment density was highest near seed sources (1.2 m) and then rapidly declined with increasing distance

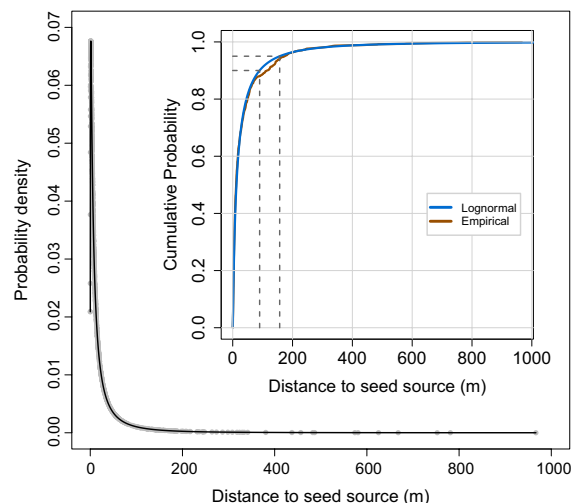


Fig. 3 Recruitment curve (black) characterizing the scatter of encroaching *J. virginiana* around a seed source. The inset plot shows the cumulative probability of recruitment as a function of distance from a seed source. Dashed lines mark the 90th and 95th percentile distances and denote a break between average vs. rare, long-distance recruitment distances

Table 2 Percentile distances of *J. virginiana* recruitment calculated from lognormal and empirical distribution functions

Model	90th percentile distance (m)		95th percentile distance (m)	
	Estimate	95% CI ^a	Estimate	95% CI ^a
Lognormal	89.9	78.8–102.2	157.1	134.8–181.5
Empirical	113.8	94.3–145.5	173.0	148.7–196.9

^a95% confidence intervals calculated using the bootstrap technique

until recruitment eventually became sparse at longer distances (Fig. 3). A breakpoint distinguishing average, short-distance recruitment vs. rare, long-distance recruitment was identified based on the cumulative distribution function between the 90th and 95th percentile distances (Fig. 3), which showed that 95% of recruitment is expected to occur within 157.1 m of a seed source (see Table 2 for 95% confidence intervals and comparison with observed data). Recruitment beyond this distance from a seed source characterized the recruitment curve's tail (Fig. 3).

The spatial distribution of encroachment around tree plantings was positively skewed and was best described by a Weibull probability density function ($a=0.678$ and $b=516.324$; Table 1). *J. virginiana* distance from plantings ranged from 1.8 to 5292.8 m with a median and mean of 261.6 and 688.5 m, respectively. Encroachment density was greatest near tree plantings and then rapidly declined until *J. virginiana* became sparse (Fig. 4). Development and expansion of a leading edge of encroachment from tree plantings was best described by a series of Weibull and lognormal functions (corresponding to height classes [$t_1 - t_5$] used to represent subsequent time steps of encroachment from a tree planting). Two main features characterized changes in the leading edge over time: (1) A slow moving, high density area near the tree planting and (2) a rapidly advancing tail (Fig. 4). This dynamic is evidenced by changes in percentile distances from tree plantings between time steps (Fig. 4). Little movement of the 50th, 75th and 90th percentile distances between time steps shows an area of high encroachment density near tree plantings. While, relatively rapid expansion of the 98th and 99th percentile distances represents spatial advancement of the distribution's tail, an area of low recruitment probability. One exception occurred between

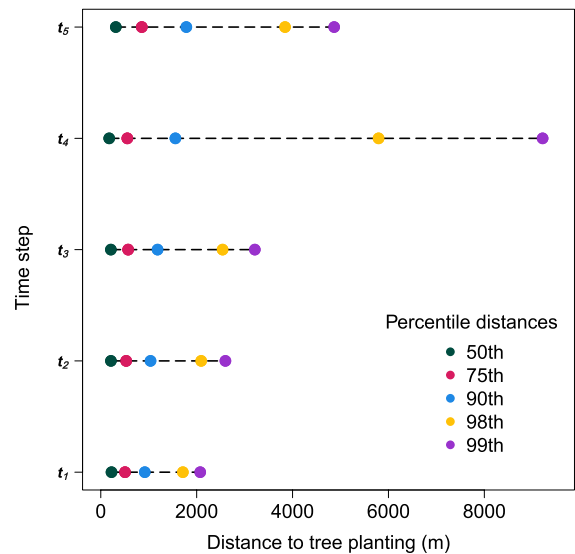


Fig. 4 Percentile distances from tree plantings calculated from the distribution of encroaching *J. virginiana* around tree plantings over five subsequent time steps (represented by height classes: $t_1 \geq 5$ m; $t_2 \geq 4$ m; $t_3 \geq 3$ m; $t_4 \geq 2$ m; $t_5 \geq 1$ m). 98th and 99th percentile distances from tree plantings show changes in the encroachment distribution's tail compared to the 50th, 75th, and 90th percentile distances representing high density encroachment

time steps $t_4 - t_5$, in that the 98th and 99th percentile distances declined. This result appears to be an artifact due to a lack of long-distance recruitment data needed to characterize further expansion of the distributions tail beyond distances sampled in this study. Consequently, an abundance of local recruitment in time step t_5 resulted in an artificial contraction of the distribution's tail.

Discussion

Dispersal regulates opportunities for woody plant recruitment and plays a key role in the vulnerability of grassy ecosystems to woody encroachment. The aim of this study was to evaluate how recruitment distance structures spatial patterns of encroachment. Our results show a high capacity for *J. virginiana* invasion of intact grassland ecosystems. The recruitment curve was characterized by a fat-tailed distribution with an abundance of local recruitment within ~200 m of seed sources (>95% of observed and predicted recruitment; Table 2), followed by farther, infrequent

recruitment that characterized the curve's tail. This recruitment curve is generally consistent with those described for invasive trees (Kot et al. 1996; Lewis 1997; Debain et al. 2007) and demonstrates how short- and long-distance recruitment play distinct, yet complementary, roles in driving woodland transitions in grasslands.

In the absence of disturbances, an abundance of local recruitment contributes to strong, destabilizing feedbacks that drive rapid woodland transitions (Langevelde et al. 2003; Twidwell et al. 2013a; Ratajczak et al. 2014). In this process, local recruitment begets local recruitment, thereby rapidly increasing woody plant abundance as grasslands near seed sources transition to woody dominance (Archer et al. 1988). On the other hand, infrequent, long-distance recruitment does little to directly increase abundance; however, these events play an important role in the spatial expansion of woody plants into grassland. Long-distance recruitment in treeless areas create new nodes of encroachment where infilling between nodes can occur over time. Studies from other regions indicate that infilling is promoted via two reinforcing pathways: (1) as woody plants develop they provide vertical structures that attract birds and thereby increase the probability of additional avian seed deposition (McDonnell and Stiles 1983; Archer et al. 1988; Prather et al. 2017), and (2) as woody plants mature and develop seed, local recruitment further promotes infilling.

In addition to creating new nodes of encroachment, a higher chance of long-distance recruitment is attributed to plant invasions that may accelerate over time, rather than travel at a constant rate of spread, depending on the shape of the recruitment curve's tail (Clark 1998). Results from this study provide two lines of evidence that the leading edge of *J. virginiana* encroachment may accelerate over time. First, the *J. virginiana* recruitment curve quantified in this study is consistent with fat-tailed distributions that can lead to accelerating invasions (Kot et al. 1996; Lewis 1997; Clark et al. 1999; Liu and Kot 2019). Second, expansion of the leading edge of encroachment advanced more quickly from one time step to the next (as evidenced by the 98th and 99th percentile distances of the leading edge from time steps $t_1 - t_4$), until the leading edge presumably exceeded what our sampling approach could represent. Nonetheless, our results demonstrate a high capacity for invasion.

In fact, most studies, including this one, are likely to underestimate the speed of the leading edge due to the challenges of capturing long-distance recruitment events that are rare (Nathan 2006). In regards to woody encroachment, these results help explain how *J. virginiana* has become so pervasive in a grassland biome following fire exclusion. In addition to this species' capacity for invasion, tree planting programs assist the invasion process by functioning as mass, long-distance recruitment events that establish new nodes of seed dispersal, often far from other seed sources (Ganguli et al. 2008; Roberts et al. 2018; Donovan et al. 2018). A recent assessment shows that over the last 28 years, tree planting contributed to an approximate 54 million ha range expansion of *J. virginiana* in the western Great Plains region (Hanberry 2022).

The recruitment curve developed here allows for an improved understanding of encroachment patterns and helps explain dispersal-driven time lags between changes in fire regimes and associated woodland transitions in Great Plains ecosystems (Wells 1970; Twidwell et al. 2013b; Ratajczak et al. 2014, 2016; Collins et al. 2021). Rates of encroachment are ultimately dependent on seed production, the location of seed sources, dispersal, seedling establishment, recruitment to adult size classes, and plant growth rates. Yet, studies assessing rates of encroachment seldom consider these factors and often reflect encroachment rates that are dependent on the local conditions of a site (e.g., Briggs et al. 2002; Fogarty et al. 2021; Fuhlendorf et al. 1996). The recruitment curve provided here helps bridge gaps between dispersal and recruitment and can be used to inform a more generalized understanding of rates of *J. virginiana* encroachment. For instance, grasslands often lack fire-vegetation feedbacks required to prevent woodland transitions but remain in a grassland state temporarily due to dispersal limitations (Ratajczak et al. 2016). The recruitment curve provides a basis to better understand the lifespan of such grasslands based on their proximity to seed sources. We expect rates of encroachment to be most predictable within ~200 m of seed sources, where recruitment is most common. At farther distances, the intrinsic variability associated with fat-tailed distributions indicates that encroachment rates will be more stochastic (Lewis 1997).

Our results suggest that recruitment occurs farther from seed sources compared to studies conducted in

the eastern portion of *J. virginiana*'s range. In southwest Virginia, USA, the maximum seed dispersal distance along a fence line was predicted to be 515 m (Holthuijzen and Sharik 1985b); while, a separate study suggested that *J. virginiana* recruitment in abandoned pastures was possible up to 88 m from seed sources (Holthuijzen and Sharik 1985c). There are multiple of explanations for why we observed greater recruitment distances. First, differences in study design and context. Our study was designed to capture long-distance recruitment events within an intact grassland landscape using transects that were up to 5.5 km in length and that ended at treeless sites. Holthuijzen and Sharik's (1985a, 1985b) studies were conducted in pastures embedded within a forested landscape using transects that were no more than 290 m from seed sources. Our design was therefore more likely to capture long-distance recruitment events. Second, avian disperser communities are expected to substantially differ between Nebraska's Sandhills and southwestern Virginia. Birds are the primary dispersal agent for *J. virginiana* seeds (Phillips 1910; Holthuijzen and Sharik 1985a; Horncastle et al. 2004) and their habitat requirements and movement patterns therefore play an important role in recruitment patterns (Chavez-Ramirez and Slack 1994; Levey et al. 2005). The avian disperser community in the eastern portion of *J. virginiana*'s range is dominated by woodland species (e.g., yellow-rumped warbler, American robin, cedar waxwing) (Holthuijzen and Sharik 1985a); while, in the Great Plains, grassland birds (e.g., sharp-tailed grouse, eastern meadowlark; Adams and Thornburg 2010) are expected to be common dispersers, although surprisingly little is known about avian disperser communities in the Great Plains. We hypothesize that disperser communities with grassland birds increase dispersal distance into grassland environments due to these species preference for treeless habitats (Cunningham and Johnson 2019). For instance, grassland birds may be more likely to move into treeless areas after foraging on juniper cones.

We expect results from this study to be generally applicable to other grassland regions experiencing *J. virginiana* encroachment with differences in avian disperser communities being a major source of variation. Future research is needed to describe avian disperser communities across regional and woody cover gradients to better understand how these

differences influence encroachment patterns. Moreover, our recruitment curve was developed based on an ongoing encroachment process with multiple seed sources contributing to spread and is therefore most applicable to similar instances of encroachment where multiple seed sources exist on the landscape. In this approach, recruitment distances are described based on the nearest seed source (Greene and Johnson 2000; Debain et al. 2007; McNamara et al. 2019). This assumption is consistent with those made in seed dispersal studies as well as remote sensing and management applications that consider the most proximate seed sources (Brown and Carter 1998), but undoubtedly results in relatively conservative recruitment distances (Nathan and Muller-Landau 2000). Nonetheless, these findings advance understanding of encroachment as a spatial process and the roles of short- and long-distance recruitment in driving woodland transitions.

Implications

Juniperus virginiana is among the most well documented encroaching woody plants in North America (Briggs et al. 2005; Engle et al. 2008; Nackley et al. 2017), yet its behavior has confounded one community after another as it encroaches new areas. Research on landowner perception of encroachment illustrates that communities tend to underestimate risk during the early stages of encroachment when propagule sources are limited and then lack the capacity to manage the problem as encroachment quickly worsens (Morton et al. 2010; Harr et al. 2014). Insights from this study on the role of short- and long-distance recruitment help explain this phenomenon. In the early stages of encroachment seed sources are sparse and recruitment is driven by rare, long-distance dispersal, leading communities to potentially underestimate future management challenges as local dispersal becomes pervasive and dominates the recruitment process. Based on an improved understanding of encroachment as a spatial process, several considerations relevant to landscape management and planning follow: (1) Defending grasslands from encroachment requires control measures implemented at regular intervals that account for local recruits within ~200 m of seed sources as well as early detection, rapid response approaches to

account for long-distance recruits. (2) Approaches that account for long-distance recruits are critical to the maintenance of large, treeless tracts of grassland, especially those that lack frequent fire. (3) Small treatments that reduce woody cover but remain within range of local recruitment from other seed sources do little to reduce a site's exposure to encroachment and are expected to be short-lived in the absence of repeated follow-up treatments (Fogarty et al. 2021). (4) Reducing grassland exposure to encroachment will require targeted removal of *J. virginiana* that serve as local seed sources to relatively intact grassland sites. (5) Introduction of seed sources into treeless areas greatly increases grassland exposure to encroachment. Tree planting programs should therefore consider the location of introduced seed sources within a broader landscape context and the risks of short- and long-distance recruitment to nearby areas.

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Author contributions DTF, RBP and DT: conceptualized and designed the research. DTF and RBP: performed fieldwork. DTF and RBP: conducted data analyses. DTF and RBP: wrote the paper and all authors critically reviewed/revised the manuscript and agreed on the submission.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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