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Rangelands in a fragmented grass-dominated landscape are vulnerable to tree invasion from roadsides

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Abstract Roadsides can be vectors for tree invasion within rangelands by bisecting landscapes and facilitating propagule spread to interior habitat. Current invasive tree management in North America's Great Plains focuses on reducing on-site (i.e., interior habitat) vulnerability through on-site prevention and eradication, but invasive tree management of surrounding areas known to serve as invasion vectors, such as roadsides and public rights-of-ways, is sporadic. We surveyed roadsides for invasive tree propagule sources in a central Great Plains grassland landscape to determine how much of the surrounding landscape is potentially vulnerable to roadside invasion, and by which species, and thereby provide insights into the locations and forms of future landcover change. Invasive tree species were widespread in roadsides. Given modest seed dispersal distances of 100–200 m, our results show that roadsides have potential to serve as major sources of rangeland exposure to tree invasion, compromising up to 44% of rangelands in the study area. Under these dispersal distances, funds spent removing trees on rangeland properties may have little impact on the landscape's overall vulnerability, due to exposure driven by roadside propagule sources. A key implication from this study is that roadsides, while often neglected from management, represent an important component of integrated management strategies for reducing rangeland vulnerability to tree invasion.

Keywords Invasion · Rangeland · Woody encroachment · Juniperus virginiana · Gleditsia triacanthos · Elaeagnus umbellata

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Introduction

Invasion of North America's Central Great Plains (CGP) by woody species reduces native biodiversity and ecosystem function, and is compounded by fragmentation from human development such as roads interacting with broader landscape features (Mellor et al. 2013; Richardson et al. 2014; Riitters et al. 2018). Invasive tree management is therefore a priority for CGP natural resource managers. For example,

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the Natural Resource Conservation Service (NRCS) in Nebraska spent $8.6 million on cost-share removal and prescribed burning on the removal and control of problematic and invasive woody plants, primarily eastern redcedar (*Juniperus virginiana*) between 2004 and 2013 (Simonsen et al. 2015). *J. virginiana* is a rapid grassland colonizer in the CGP that spreads from windbreaks and shelterbelts (Donovan et al. 2018) via mammal and bird dispersal (Horncastle et al. 2004), leading to transformation of soils and loss of multiple ecosystem services (Mellor et al. 2013). Other regional invasive woody species include honey locust (*Gleditsia triacanthos*) and autumn olive (*Elaeagnus umbellata*). *G. triacanthos* is an open canopy generalist that spreads easily via vertebrate dispersed seeds (Ferreras et al. 2015) and suckering (Schnabel et al. 1998) within ruderal habitat across temperate to sub-tropical climates (Romero et al. 2021). *E. umbellata*, an invasive of eastern U.S. forests, is a less documented but incipient invader in Nebraska and the CGP that is attractive to generalist bird species (Kohri et al. 2011) and spreads partially due to roadside influences (Flory and Clay 2009). These species all produce large, fleshy fruits and seeds of high food value to vertebrates, which have the potential to spread seeds over large distances (Allan 1959; Holthuijzen and Sharik 1985a; Coulson et al. 2014).

Despite research indicating that roadsides are generally a contributor to invasive woody species spread (Gelbard and Belnap 2003; Coulson et al. 2014; Riitters et al. 2018), there is less information about the distribution of specific species within linear human-maintained habitats such as roadsides, and how roadside management may impact roadside woody species distribution in contrast to overall landscape distribution. Additionally, management of woody invasives often emphasizes interior habitats while neglecting surrounding areas, such as windbreaks and roadsides (Donovan et al. 2018). However, linear landscape features such as trails and riparian forest corridors harbor invasive propagules and facilitate invasion into remaining interior habitat (Gelbard and Belnap 2003; Lockwood et al. 2005; Nemec et al. 2011). Roadside invasive species have the potential to reduce the resilience of regional ecosystem services including cattle production, public recreation, hunting, and wildlife habitat, yet generalized understanding of management in these contexts is limited (Richardson et al. 2014).

In this study, we explore the potential for roadsides to function as a source of invasion risk in interior habitats. The study area is a relatively intact rangeland landscape embedded within the broader Corn Belt region of the Midwestern US. Our objectives are to (1) document the abundance and density of invasive woody species along roadsides, and (2) model the extent of interior habitat exposure to roadside propagule sources based on seed dispersal scenarios.

Body

We selected a 6278-ha area centered around Spring Creek Prairie, a relatively large rangeland preserve in southeastern Nebraska owned by the National Audubon Society that serves as a key hotspot for regional biodiversity preservation (for full site description and photographs, see Supplementary Information S1 and S2). Next, we chose ten 500-meter transects that corresponded to roadside margins within the region by distributing randomly generated coordinates along unpaved road line features in ArcGIS Pro 2.8.0 and selecting 10 transect starting points. The prevailing road pattern in the Denton Hills is a one-mile cardinally oriented road grid aligned with Public Land Survey System section boundaries; therefore, we randomly assigned a direction to each survey starting point, resulting in ten 500-meter transects that were oriented either east-west or north-south. From each sampling point, researchers walked 500 m in the chosen random direction, searching for and counting individual trees between the right side of road and adjacent private land borders (henceforth called right-of-way (ROW)).) We sampled three species, eastern red cedar (*Juniperus virginiana*, JUVI), honey locust (*Gleditsia triacanthos*, GLTR), and autumn olive (*Elaeagnus umbellata*, ELUM). To determine average ROW width and roadside acreage along each transect (Supplementary Information S3), we measured the distance in meters from the road edge to the edge of the ROW at six evenly spaced points along each transect. We identified the edge of the ROW as the location either directly under telephone lines or at the private property fence, whichever was closer to the road edge. Mean ROW width and standard error was 5.8 ± 0.14 m.

To calculate sampled roadside area for determining sampled invasive tree densities (objective 1), we

Table 1 Tree species counts across transects ($n = 10$)

Species	*n*	Mean	SD	Median	Range
Juniperus virginiana	10	23	21.6	22	0–70
Gleditsia triacanthos	10	7.7	10.7	2.5	0–26
Elaeagnus umbellata	10	0.3	0.9	0	0–3
All species	10	31	25	29	0–74

Table 2 Tree species densities (trees/ha) across transects (n = 10)

Species	*n*	Mean	SD	Median	Range
Juniperus virginiana	10	81.6	77.5	78.2	0–253.8
Gleditsia triacanthos	10	27.8	39.4	9	0–100.3
Elaeagnus umbellata	10	0.9	2.9	0	0–9.3
Total	10	110.3	87.9	109.4	0–268.3

took the average ROW width per transect and multiplied by 500 m (transect length). We also estimated total roadside area in the Denton Hills in hectares by taking the average ROW width from all 10 transects and multiplying by the length of public roads within the study area (Allen et al. 1997, Supplementary Information S3).Information3 To determine the density of roadside invasive trees (Objective 1), we calculated the individual species abundance per hectare and all tree species combined per hectare, plus summary statistics for abundance and densities. We computed these analyses in R 4.1.1 (R Core Team 2021). Count data and summary statistics are reported in Table 1 and Supplementary Information S4, and tree densities and summary statistics are reported in Table 2. Since the count and density data were not normally distributed (Shapiro-Wilks tests yielded $P < 0.001$), with a low sample size ($n = 10$), we report median values, which are more meaningful than mean values, alongside other summary statistics (Tables 1 and 2).

J. virginiana was the most prevalent invasive woody species (per transect median count: 22, median density: 78.2 trees/ha), followed by *G. triacanthos* (median count: 2.5, median density: 9 trees/ha) and *E. umbellata* (median count: 0, median density: 0 trees/ha) (Tables 1 and 2). Median count for all species combined was 29 (Table 1), and total median density for all species combined was 109.4 trees/ha (Table 2).

To quantify the landscape within the study area vulnerable to tree invasion from roadsides, we assumed that roads were potential propagule sources (Coulson et al. 2014). Using the 2019 National Land Cover Database (NLDC), we calculated coverage of forests and rangeland within the study area boundary. From the 2019 NLCD land cover data, we selected the categories of "Herbaceous" and "Hay/Pasture" as rangeland, and "Shrub/Scrub", "Mixed Forest", "Evergreen Forest", and "Deciduous Forest" as forest. All other categories (such as developed acreage, crop fields, and wetlands) were excluded due to their negligible value as habitat for the invasive tree species in question. Forests and rangeland comprise 3,764 ha within the study region, including 3,347 ha of rangeland and 417 ha of forest (Fig. 1).

We buffered roads within the study area by 100, 200, 500, and 1000 m. *J. virginiana* seed dispersal has been documented at 100 m (Holthuijzen and Sharik 1985b) with 515 m the theoretical maximum dispersal distance for the species (Holthuijzen and Sharik 1985c); though recent data suggest *J. virginiana* seeds can disperse up to 1000 m (Fogarty et al. *unpublished results*). *E. umbellata* disperses up to 300 m (Kohri et al. 2011), and additionally *G. triacanthos* seeds are spread by cattle (Ferreras et al. 2015), suggesting the possibility of similar dispersal distances given the high local prevalence of ranching. Additionally, buffering by dispersal distances greater than 1000 m would have led to overlapping coverage within the study area, due to the density of roads (Fig. 1). After buffering, we clipped the forests and rangeland land cover layers by each road buffer and calculated the total areas for each within the study region. This represents the area and percentage of the total of each cover class that is vulnerable to roadside invasion for each scenario of seed dispersal (Fig. 2). These analyses were completed in ArcGIS Pro 2.8.0.

based on documented *J. virginiana* seed dispersal distance, since this species was the most abundant in our sampling, is well established across the study region, and can be effectively controlled with established proactive methods including haying and prescribed fire (Simonsen et al. 2015).

We found that roadsides have a high potential to contribute to rangeland and forest vulnerability, even at the conservative dispersal distance estimates of 100–200 m. At these lower distances, 24–44% of rangeland and 16–38% of forest in the study area is

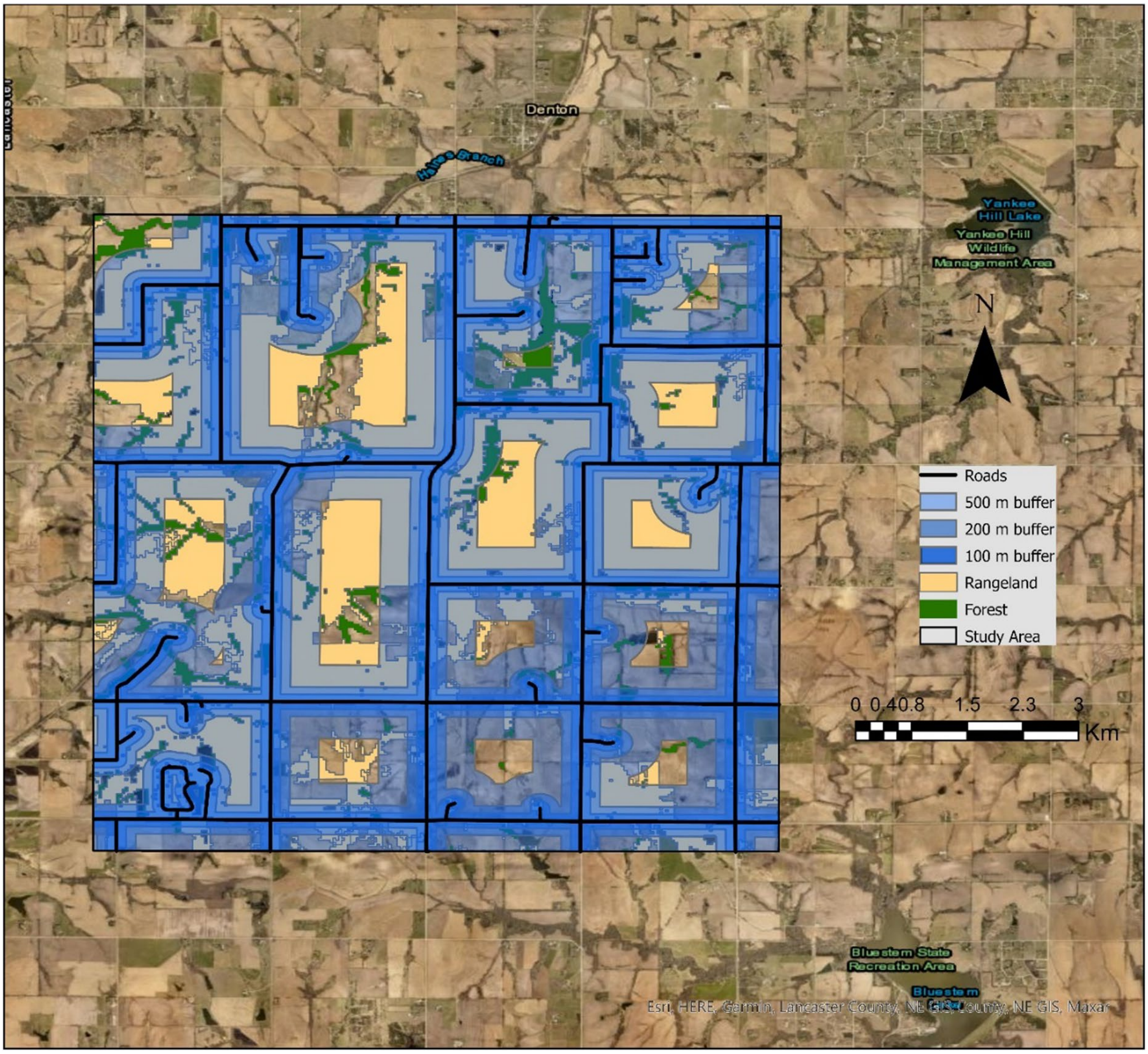

Fig. 1 Study area map indicating landscape vulnerability to tree invasion from roadsides under the three most conservative dispersal estimates. Buffer units are in meters (m). The 1000 m buffer is not shown due to it covering virtually the entire study area and largely obscuring the underlying land cover classes

exposed to roadside propagule sources from invasive trees (Fig. 2). These numbers increase to 84–99% and 73–93% of rangelands and forests, respectively, under 500–1000 m seed dispersal scenarios.

Discussion

Coordinated invasive tree management between properties (i.e., interior habitats) and surrounding ROWs could reduce the vulnerability of rangelands and forests to invasion and reinvasion. Roadsides are reservoirs for non-native species, and are permeable corridors for species dispersal within the surrounding landscape (Flory and Clay 2009; Nemec et al. 2011; Soper et al. 2019). While state and interstate transportation departments actively manage for invasive woody species on state highways, many rural roads in the CGP are managed by counties or private landowners and receive sporadic invasive tree management, if any (for example, some are mowed regularly and some are not). The presence of permanent

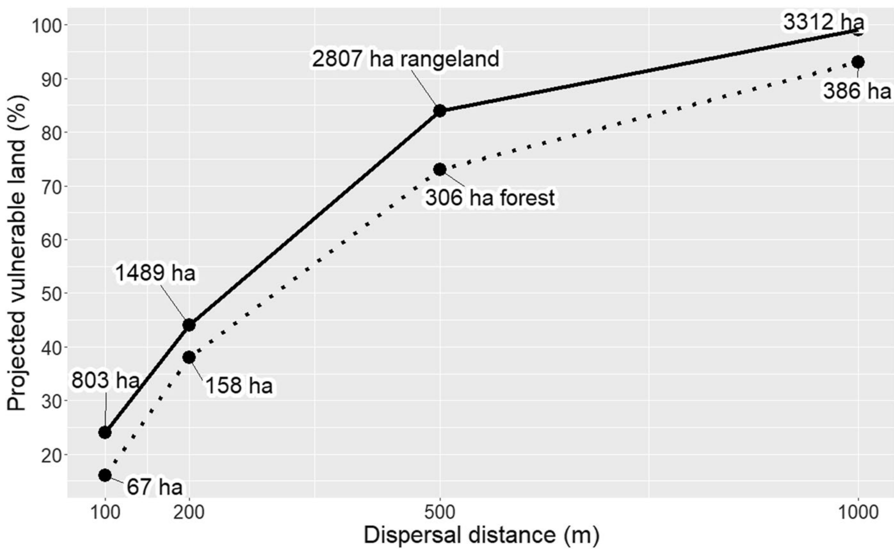

Fig. 2 Percentage of rangeland (solid line) and forest (dotted line) within the 6278-hectare (ha) study area vulnerable to tree invasion, based on four dispersal distance scenarios. Numbered points indicate the hectares of each land cover type impacted by each dispersal scenario

pasture fencing delineating ROW edges in the CGP may further reduce the likelihood of invasive tree removal, either from counties deferring to pasture fencing owners, or private owners simply choosing not to remove trees from fence lines. Regardless, our results indicate that the longevity of rangeland and forest management treatments could be compromised by roadside propagule sources. This is supported by other research indicating that woody invasives such as *E. umbellata* may become more common if seed dispersal to interior habitat and mature forests continues (Flory and Clay 2009), and linear propagule reservoirs persist on landscapes (Holthuijzen and Sharik 1985c).

This interpretation of our results stems from one of the fundamental tenets of invasion biology, landscape ecology, and systems thinking—that ecological systems do not exist in isolation and therefore, context (i.e., surroundings) matters. Under our seed dispersal scenarios, management treatment effects may be short-lived if invasive trees are removed only from interior pastures and not ROWs, ROW boundary fence lines, or other linear landscape features, because a significant portion of the local landscape is within potential seed dispersal distance of ROWs that harbor propagule sources (Lockwood et al. 2005). However, coordinated management efforts that consider interior pastures, ROWs, and ROW fence lines are more likely to reduce landscape vulnerability to invasion and reinvasion. In other words, landscape vulnerability to tree invasion depends not only on management of focal habitats, but on whether or not management is able to remove sources of seed exposure from neighboring lands.

Our dispersal scenarios show that roadsides have potential to drive rangeland exposure across a majority of the study landscape suggesting that roadsides, while often neglected, are an important component of the landscapes overall vulnerability to tree invasion. We further demonstrate the potential for the long-term efficacy of conservation action to be affected, in part, by the degree of coordination with management of rangelands and adjacent roadways. Rangelands are globally threatened by woody species invasions; therefore, management should be strategically and spatially targeted based on components that drive risk and vulnerability, including exposure from public ROW.

The CGP contains remnants of unique, rangeland-dominated landscape with high susceptibility to tree invasion, which continues to occur throughout the state of Nebraska (Fogarty et al. 2020), North America, and the world (Nackley et al. 2017). We recommend that systemic invasive tree management on interior properties and public ROWs be coordinated with landowners for increased treatment efficacy, reduced landscape vulnerability, and enhanced resilience in the delivery of ecosystem goods and services, including cattle production, public recreation, hunting, and wildlife habitat.

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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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