



Flood dynamics dictate distributions of *Elaeagnus angustifolia* L. (Russian olive) on a riverine floodplain

Natalie M. West · Ann Marie Reinhold · Geoffrey C. Poole ·
Erin K. Espeland

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Abstract North American invasions of *Elaeagnus angustifolia* L. (Russian olive) are still expanding, and hydrochory could be increasing invasion impacts along rivers. Spatial association between riverine flood-inundation patterns and *E. angustifolia* distributions suggests a link between seed movement potential and invasion patterns in time and space. Using output from hydraulic inundation models, we mapped inundation zones associated with successive flood return intervals within 10.81 km² of the estimated 500-year floodplain of the Yellowstone River, Montana, USA.

Natalie M. West and Ann Marie Reinhold have contributed equally to this work.

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N. M. West (✉) · E. K. Espeland
USDA-ARS Pest Management Research Unit, Northern
Plains Agricultural Research Laboratory, Sidney,
MT, USA
e-mail: Natalie.West@usda.gov

A. M. Reinhold · G. C. Poole
Department of Land Resources and Environmental
Sciences, Montana State University, Bozeman,
MT, USA

A. M. Reinhold · G. C. Poole
Montana Institute on Ecosystems, Montana State
University, Bozeman, MT, USA

We then evaluated spatial relationships among inundation zones and *E. angustifolia* distribution. *Elaeagnus angustifolia* was highly spatially associated with frequent flood return intervals: 80% of *E. angustifolia* exists within a subset of the floodplain predicted to flood every 10 years or less, with the highest occupancy in the 1.5- to 5-year return zones. Within frequently inundated areas, floodplain occupancy of *E. angustifolia* was distributed in patterns consistent with likely areas of sediment deposition. Thus, existing predictions of invasion timelines are likely to improve with explicit consideration of dispersal opportunities associated with hydrochory during flooding. In particular, if hydrochory is a significant secondary dispersal mechanism, then seed immigration at flood intervals of 5 years or less could lead to substantially shorter invasion lags than currently predicted.

Keywords Hydrochory · Dispersal · Plant invasion · Flood frequency · River valley

Introduction

Riparian invasions of *Elaeagnus angustifolia* L. (Russian olive) are increasing across western North America with negative impacts on riparian plant communities, successional dynamics, and nutrient cycling (reviewed in Katz 2016; Katz and Shafroth

2003; Shafroth et al. 2010). This large-seeded, N-fixing, shrub or small tree is predicted to have a 30-year invasion lag (Lesica and Miles 2001), and invasion rates are assumed to be limited by dispersal and establishment at regional scales (e.g., due to associations with proximity to water and intentional plantings, McShane et al. 2015; Nagler et al. 2011). At fine spatial scales, however, *E. angustifolia* occupies a broad range of physical conditions and sites with various hydrodynamics and moisture availabilities (Katz and Shafroth 2003). *Elaeagnus angustifolia*'s dispersal dynamics remain understudied and, despite extensive riparian invasion, the role of waterborne seed transport and deposition (hydrochory) in invasion dynamics has not been explicitly evaluated. On the Yellowstone River floodplain in central Montana, USA, we posit that hydrochory is the dominant dispersal mechanism driving *E. angustifolia* distribution. Through targeted delivery of large numbers of propagules to locations with high water availability, propagule pressure from hydrochory may override establishment limitation to drive riparian invasion patterns (i.e., Nilsson et al. 2010). If so, the spatial distribution of *E. angustifolia* on the floodplain will mirror patterns of seed deposition via hydrochory rather than spatial variation in microsite suitability. Using remote sensing and hydrologic modeling data, we conducted a pilot study to detect a signature of hydrochory from spatial patterns of *E. angustifolia* occurrence and flood inundation frequency across the floodplain. We then incorporated key rates of propagule delivery (i.e., flood inundation frequencies) into a model of *E. angustifolia* stand recruitment to highlight potential impacts of hydrochory on invasion patterns.

Methods

We evaluated the Yellowstone River floodplain within the USDA-Agricultural Research Service Fort Keogh Livestock and Range Research Laboratory, Custer County, Montana, USA (Fig. 1). Within the conterminous United States, the Yellowstone River is the longest temperate river unaffected by mainstem impoundments (White and Bramblett 1993). The river has an annual snowmelt-driven flood pulse, which usually occurs in June (Chase 2013). The flood pulse drives channel migration and associated erosion and deposition of floodplain sediments. *Elaeagnus*

angustifolia was likely introduced to the region in the 1950s and spread onto the Yellowstone floodplain at Fort Keogh by the 1960s (unpublished data).

We defined the active floodplain as the portion of our study area predicted to be inundated during a 500-year flood event, based on hydraulic inundation modeling conducted by the US Army Corps of Engineers (USACE). Using the Hydrologic Engineering Center's River Analysis System (HEC-RAS) software, the USACE (2016) estimated floodplain inundation extent for flood return intervals of 1.5-, 2-, 5-, 10-, 20-, 50-, 100-, 200-, and 500-year, corresponding to discharges of: 1170; 1339; 1747; 2008; 2299; 2560; 2789; 3030; and 3313 m³ s⁻¹, respectively (Chase 2013). We generated a raster map (2.5 m by 2.5 m cell size) of "inundation zones" (Fig. 1a) where each cell value reflected the smallest modeled flood return interval at which the cell is inundated by water. Thus, *on average*, the 2-year inundation zone is flooded once every 2 years, the 5-year inundation zone is flooded once every 5 years, etc. We excluded main and side channels perennially inundated or scoured regularly enough to preclude vegetation establishment by masking portions of the floodplain predicted to be wet during a 968 m³ s⁻¹ flow event (approximately a 1.05-year flood event; areas inundated by water, on average, 19 out of 20 years).

We used a digital map created from aerial imagery (Combs and Potter 2011) of presence versus absence ("occupancy") of *E. angustifolia* along the Yellowstone River to characterize the spatial distribution of *E. angustifolia*. We converted "presence" polygons to a raster of *E. angustifolia* occupancy (2.5 m by 2.5 m cell size) and cross-tabulated occupied and unoccupied raster cells by floodplain inundation zone (Fig. 1b; Table S1). We conducted a Pearson's Chi-squared test to assess whether the distribution of *E. angustifolia* occupancy was independent of inundation frequency. The spatial data sets we used are freely available from the Yellowstone River Corridor Geographic Information Clearinghouse (2018). Geoprocessing tasks were conducted in R (R Core Team 2019) using the "sp" (Pebesma and Bivand 2005; Bivand et al. 2013) and "raster" (Hijmans 2019) packages, with geospatial data visualized and Fig. 1 generated with ArcGIS Desktop 10.6.1.

Additionally, we used an existing empirically-derived heuristic model (Lesica and Miles 2001; "baseline") to illustrate impacts of additional seed

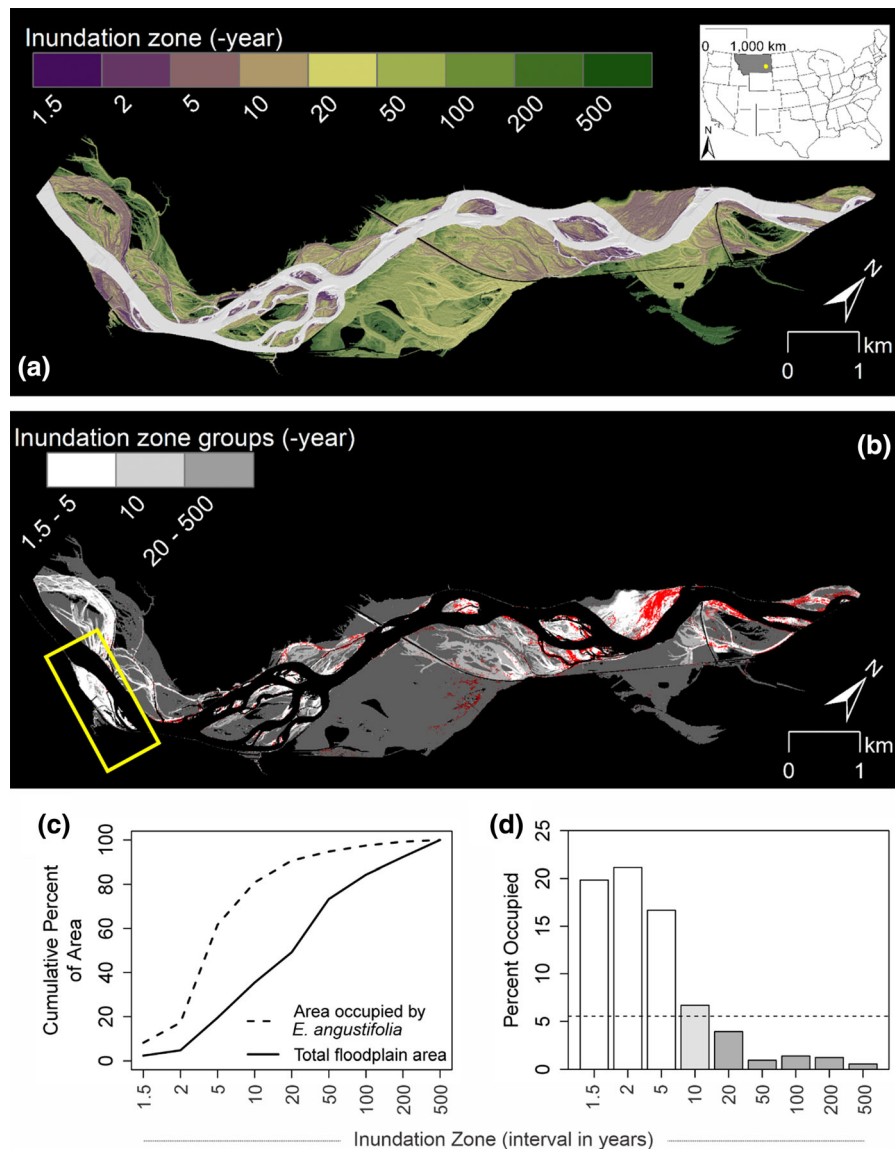


Fig. 1 Spatial distribution of inundation zones and *E. angustifolia*, Yellowstone River floodplain within the Fort Keogh Livestock and Range Research Laboratory, Custer County, Montana, USA (star in inset in upper right). **a** Flood inundation zone map: the color of each pixel indicates the most frequent flood return interval at which that pixel is predicted to be inundated; **b** *Elaeagnus angustifolia* occupancy (red) plotted beneath the 1.5- to 5-year inundation zones (white), the 10-year inundation zones (light grey), and the 20-year and greater

inundation zones (dark grey). **c** Cumulative percent of floodplain area occupied by *E. angustifolia* (total occupied area = 0.60 km²) and total floodplain area (total area = 10.81 km²) plotted by inundation zone; **d** Percent of floodplain occupied by *E. angustifolia* within each inundation zone: dashed horizontal line denotes percent occupancy of *E. angustifolia* in the study area as a whole; bar colors reflect inundation zones grouped in **b**. The yellow box on **b** denotes location of side channel enlarged in Fig. 3

deposition on *E. angustifolia* stand development. The baseline scenario assumed founding by a single individual with no immigration, density-dependence in recruitment, or age-dependent change in fecundity. We created another scenario that included propagule

immigration at the midpoints of key flood return intervals (1.5-, 5-, 10-year intervals: 3-, 5-, and 7-year midpoints) identified in the spatial analysis. We projected populations to 45 years post-founding for both scenarios and compared total number of trees and

mature trees at 10, 20, and 30 years (three generations). Model details, code, and an R script are provided as supplementary material.

Results

We found strong evidence for a spatial relationship between *E. angustifolia* distribution and flood inundation zones in our study area ($P < 2.2e-16$, $X^2 = 131,190$, $df = 8$, critical value = 15.51; Fig. 1 and Table S1). *Elaeagnus angustifolia* occupancy was highly spatially associated with the portions of the floodplain inundated at relatively frequent return intervals (Fig. 1b); 62% of the *E. angustifolia* occurrence was within the 1.5 to 5-year inundations zones (19% of total floodplain area) and 91% of *E. angustifolia* occurrence was within the 1.5 to 20-year inundation zones (49% of total floodplain) (Fig. 1c).

Percent occupancy (Fig. 1b, d) was greatest in the 1.5- to 5-year inundation zones (white), intermediate in the 10-year inundation zone (light gray), and lowest in the 20-year and greater inundation zones (dark gray).

Simulation results showed that incorporating additional immigration substantially increases *E. angustifolia*'s projected invasion potential. Seed immigration intervals of 7, 5, and 3 years—frequent return interval midpoints—would increase the number of mature trees by a factor of 1.5, 2.0, and 2.5 after 20 years (N_{base} : 2 vs. N_{approx} : 3, 4, and 5) and a factor of 1.8, 2.1, and 3.1 after 30 years (N_{base} : 8 vs. N_{approx} : 14, 17, and 25, Fig. 2a). Extrapolating from the baseline model, in which mature trees would have constituted approximately $\frac{1}{4}$ of the hypothetical population, projected increases in total stand count would be 1.5, 1.9, and 2.7 times (N_{approx} : 54, 67, and 98) greater than the baseline (N_{base} : 36) at 30 years (Fig. 2a).

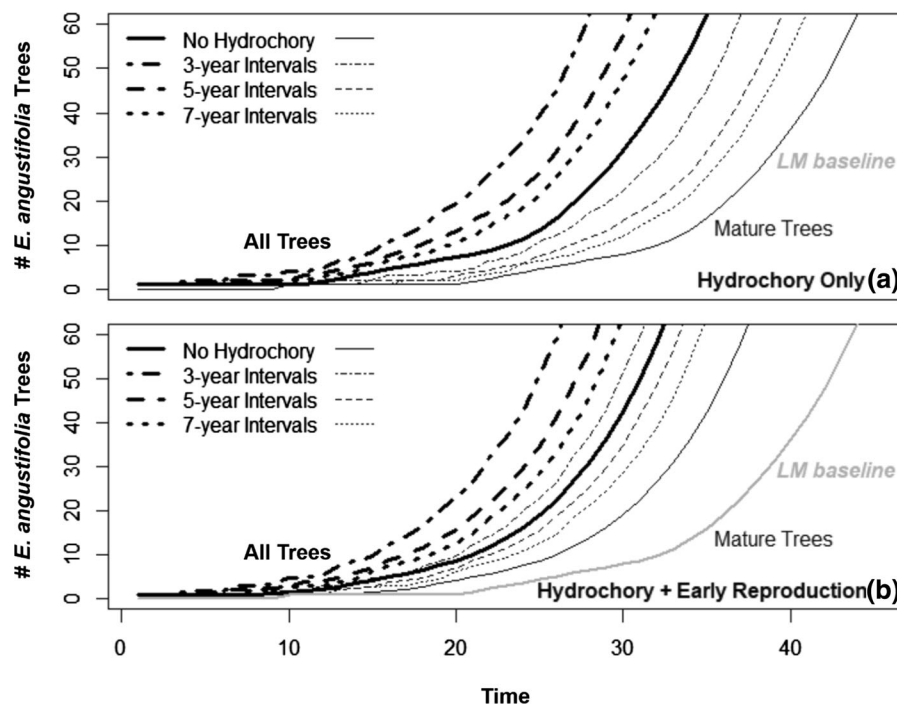


Fig. 2 Projected total number of *E. angustifolia* trees (thick lines) and of mature *E. angustifolia* trees (thin lines) over time with and without immigration (e.g., associated with hydrochory). The baseline model (“No hydrochory”—solid lines) is based on Lesica and Miles (2001, “LM baseline”). Hydrochory is incorporated into models modified from LM baseline as immigration of a single additional propagule at 3- (dotdash), 5-

(dashed), and 7- (dotted) year intervals. **a** Model projections with hydrochory at identified return intervals—maintains original demographic parameters; **b** Model projections with hydrochory, but with a percentage of the 5–6-year (5%) and 7–9-year (40%) age classes also achieving reproductive maturity (class percentages from Fig. 2 in Lesica and Miles 2001). The baseline curve is colored gray in **b**

Discussion

The non-random association between *E. angustifolia* occupancy and flood return interval suggests that inundation dynamics are an important determinant of the fine-scale spatial distributions of *E. angustifolia* on the Yellowstone River floodplain. Our simulations further demonstrate that failing to consider this association risks underestimating *E. angustifolia*'s invasion potential. We offer two parsimonious explanations linking inundation frequency with *E. angustifolia* occupancy. First, frequently inundated sites may release *E. angustifolia* from establishment limitation by providing suitable microhabitats (e.g., higher soil moisture) for germination and growth. Second, hydrochory may deliver seeds repeatedly to frequently-flooded depositional areas, imposing high propagule pressure. Both mechanisms are likely co-occurring. Distinguishing whether one is a primary driver requires a nuanced look at *E. angustifolia* distribution within frequently inundated zones.

Specifically, if water availability drives *E. angustifolia* establishment, and propagule pressure is governed by a process other than hydrochory (e.g., vertebrates, within-stand recruitment), we would expect a relatively uniform or haphazard spatial distribution of *E. angustifolia* across frequently inundated portions of the floodplain. In contrast, if hydrochory imposes propagule pressure across the floodplain with uniformly low microsite limitation, we would expect dense patches of *E. angustifolia* in frequently inundated areas where sediment deposition occurs (e.g., on point bars, on the downstream side of mid-channel bars, and in side channels abandoned by the river and reforested over time). Overall, the occurrence of *E. angustifolia* on our study site is consistent with the latter pattern—well-defined, concentrated patches in frequently inundated areas consistent with zones of sediment deposition. In fact, concentrated patches of *E. angustifolia* now dominate all but one of the reforested side channels on the study site. The exception is a side channel that was bifurcated by a large dike in the 1970s (Fig. 3). During reforestation, the dike prohibited hydrochory by eliminating flow through the side channel. In the absence of hydrochory, *E. angustifolia* was detected at only two locations (12.5 m²) in the side channel. Both the overall pattern and the exception are consistent with propagule pressure via hydrochory operating as

the primary spatial driver of *E. angustifolia* invasion, with establishment limitation then operating after seeds are deposited.

Immigration at frequencies suggested by our analysis (e.g., 3-, 5-, and 7-year returns) would increase invasion intensity and shorten management time-windows for invasion control. The only published empirical approximation of invasion rate (Lesica and Miles 2001) suggests a 30-year demographic lag between a single colonization and exponential increase of mature *E. angustifolia*. However, this baseline model excluded immigration and did not address the accumulated stand invasion. Using 30 years as a rule-of-thumb risks underestimating invasion and misallocating control efforts. Our estimated model impacts are conservative. We add only one additional recruit per inundation event, likely an underestimate of fluvial influence on propagule pressure, and demographic processes contributing to invasion lags may change over time (i.e., Yokomizo et al. 2017). For instance, shorter generation times, in the absence of density dependence, may further decrease invasion lags (i.e., Fig. 2b). Lesica and Miles (2001) used a 10-year gap to consistent reproduction, but reported flowering in earlier age classes. Scott et al. (2018) suggested reproduction along the Escalante River could occur at five years or less, and we detected flowering three years post-establishment in our study area (unpublished data). Realistic predictions of future invasions and timelines require more data on how *E. angustifolia* demography and dispersal interact in riparian systems. Eradicating nascent invasions within the range of the earliest flood return intervals identified, e.g., 3–5 years, may be required to reduce recruitment from flood deposits and new seed input from residents.

Disentangling seed and establishment limitations requires further experimental and observational studies. Seed addition experiments and seedbank excavation in different inundation zones will be necessary to evaluate the strength of propagule limitation. *Elaeagnus angustifolia* benefits from open germination sites and ample water availability, especially under deep shade, and floods that expand dispersal distances might dilute local processes (e.g., granivory) influencing stand recruitment (Katz and Shafroth 2003; Nilsson et al. 2010). Nevertheless, *E. angustifolia* is invasive in many parts of the world (e.g., Busso et al. 2013; Enescu 2018), invades multiple terraces and

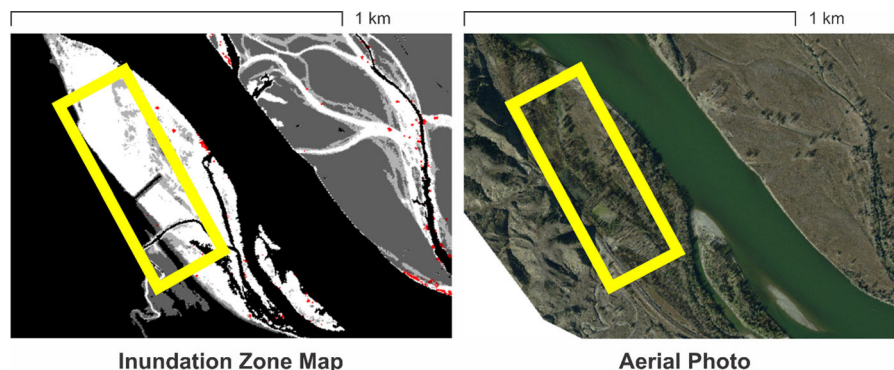


Fig. 3 *Elaeagnus angustifolia* occupancy within a diked side channel (yellow box) on the Yellowstone floodplain. Left panel: *E. angustifolia* occupancy (red) within the inundation zones

light conditions (Shafroth et al. 2010; Scott et al. 2018), has a persistent soil seedbank (415 seeds/m² (Brock 2003); Katz and Shafroth 2003), and can survive up to 15 years on precipitation alone (Reynolds and Cooper 2010). Further, dense local stands may change channel morphology and deposition, facilitating further invasion (i.e., Merritt and Wohl 2002; Scott et al. 2018). Existing hydrochory data are mainly anecdotal (e.g., Heinrich 2015; Pearce and Smith 2001). Quantifying interactions among dispersal, seed, and microsite limitation will help inform effective management decisions to limit the spread of *E. angustifolia*.

Preemptive management to reduce invasion can target propagule abundance (decreasing propagule availability in the landscape) or microsite availability (decreasing establishment likelihood). Control options along rivers are generally limited to costly and time-consuming tree removals critical to controlling local seed sources on the floodplain because we lack control mechanisms to decrease transport within rivers other than reducing near-river seed sources. Recognizing that additional seed deposition would be high in frequently inundated portions of the floodplain, managers can prioritize vulnerable areas, assuming less frequent flooding intervals are tied to slower rates of invasion or re-invasion. On our study site, vulnerable areas would be associated with return intervals of 5-years or less (19% of the floodplain). More detailed evaluation of dispersal via hydrochory will inform predictions of *E. angustifolia* riparian invasions and associated management strategies.

described in Fig. 1b (white = 1.5- to 5-year return intervals). Right panel: aerial photo of vegetation cover in the same side channel

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