

Landscape configuration and flood frequency influence invasive shrubs in floodplain forests of the Wisconsin River (USA)

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Summary

1. Invasive species are present worldwide, yet predicting which invasive species will become problematic in which ecosystems remains an important ecological challenge. Floodplains are at particular risk for invasion, especially when subjected to anthropogenic disturbance.
2. We examined how components of flood regime, habitat quality and habitat configuration influenced the presence and abundance of three invasive shrubs in the floodplain of the Wisconsin River. Shrub taxa included two non-natives (*Lonicera* spp. and *Rhamnus* spp.) and one native (*Zanthoxylum americanum*). Observations of taxa presence and abundance were recorded in nine forested river reaches, spanning three physiographic regions. We also compared the productivity of *Z. americanum* across a flood control levee in one reach.
3. Physiographic region significantly predicted the presence and abundance of these three taxa, acting as a synthetic indicator of differences in climate, geography and topography. Invasion was greatest in regions where modifications to flood regime and land use were most pronounced. Physiographic region was excluded from subsequent analyses to assess more specific predictors of shrub distributions.
4. Habitat configuration and quality both predicted shrub taxa presence and abundance. Shrub taxa were most frequently observed and most abundant in small forest patches, near roads, and in sandy soil with low nutrient content. Edge habitats have many of these characteristics. Edges appear to be favoured by avian shrub dispersers and provide conditions suitable for invasive establishment.
5. Flooding influenced non-native and native invaders differently. Non-native taxa were observed less frequently and at lower abundances in frequently flooded areas, probably because of a sensitivity to flooding. However, the presence, abundance and productivity of the native invader increased with flooding. Anthropogenic modifications to the flood regime limited hydrologic connectivity and may have reduced the competitive advantage of flood-tolerant traits, which allowed the invasion of upland species.
6. *Synthesis.* In the floodplain of the Wisconsin River, anthropogenic modifications that created edge habitat and altered flood regime facilitated shrub invasions, whereas unfragmented forest and intact flood regime limited invasion. Large patches of floodplain forest, less regulated flooding regimes, and lower road densities may help reduce the spread of invasive shrubs in temperate floodplains.

Key-words: anthropogenic disturbance, exotic species, flood regime, landscape pattern, landscape ecology, land-use history, habitat quality, invasive species, riparian forest, soil nutrients

Introduction

Intentional and accidental introductions of non-native species into new ecosystems have been occurring for centuries. However, unprecedented global movements of people and goods are currently increasing the presence of non-native

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species world-wide (National Research Council 2002). Additionally, native invasives are becoming an increasing problem in many anthropogenically disturbed ecosystems (Stapanian *et al.* 1998). Invasive plants may endanger native biodiversity (Mack *et al.* 2000), alter ecosystem functions (Hooper *et al.* 2005) or change natural disturbance regimes (Mack & D'Antonio 1998). Progress has been made characterizing potential invaders (Rějmanek & Richardson 1996; Reichard & Hamilton 1997; Kolar & Lodge 2001) as well as habitats susceptible to invasion (Lonsdale 1999; Pyšek *et al.* 2003; Ohlemüller *et al.* 2006). However, accurately predicting which invasive species will become problematic in which habitats remains an important challenge in ecology (Hobbs & Humphries 1995; Prieur-Richard & Lavorel 2000; Lambrinos 2002).

The successful invasion of a species into a particular location requires dispersal, colonization and establishment (Kolar & Lodge 2001; Richardson *et al.* 2007). Dispersal success varies with the quantity of dispersing propagules (Von Holle & Simberloff 2005) and the landscape being invaded (With 2002). Habitat configuration, or spatial arrangement of landscape features, often affects dispersal patterns (With 2002; Hastings *et al.* 2005). Once a propagule has successfully dispersed, its successful establishment depends on the intensity of competition from established species (Keane & Crawley 2002; Daehler 2003) and habitat quality (Williamson & Fitter 1996). Habitat quality, or fine-scale site characteristics, can include soil attributes, land-use history, or topography (e.g. Dupré & Ehrlén 2002; Kolb & Diekmann 2004).

The aspects of habitat configuration important for dispersal vary with dispersal mechanism. Wind dispersed species exhibit larger dispersal ranges in unfragmented landscapes (With 2002). Seeds dispersed by animals often cluster around landscape features, such as hedgerows and edges frequented by animals (With 2002; Deckers *et al.* 2005). Edge habitat can act as a corridor for plant dispersal by providing suitable habitat for colonization throughout the landscape (Meekins & McCarthy 2001). Landscapes with a high density of edge habitat often experience high rates of invasion (Luken & Goessling 1995; Yates *et al.* 2004; Hansen & Clevenger 2005). Isolated patches within landscapes may gain some protection from invasion, particularly from dispersal-limited species (Quintana-Ascencio & Menges 1996; Bastin & Thomas 1999).

After successfully dispersing, seedling establishment is influenced by habitat quality (Williamson & Fitter 1996). Habitat quality is frequently characterized using soil characteristics (Honnay *et al.* 1999; Dupré & Ehrlén 2002; Kolb & Diekmann 2004) and land-use history (Jenkins & Parker 2001; Aragón & Morales 2003). Invasive species are often more common on sites with high nutrient concentrations (Lake & Leishman 2004) or sites where agriculture was recently abandoned (Jenkins & Parker 2001). Additionally, low vegetation density (Hutchinson & Vankat 1997) and high light availability (Luken & Mattimiro 1991) can result in larger invasive populations.

Riparian ecosystems are characterized by hydrologic connectivity. Connectivity is comprised of longitudinal, or

downstream, connectivity, and lateral connectivity, or hydrologic transport onto the floodplain (Middleton 2002). Floodplains are also noted for their vulnerability to invasive species (Deferrari & Naiman 1994; Meekins & McCarthy 2001; Brown & Peet 2003). Longitudinal hydrologic connectivity in river-floodplain ecosystems can disperse seeds downstream (Richardson *et al.* 2007), and lateral hydrologic connections can alter soil nutrients, generate bare substrate, and stress established plants (Naiman & Décamps 1997). These conditions can also promote establishment of native species. However, high spatial and temporal heterogeneity resulting from flood events provides many opportunities for establishment (Sousa 1984), and may explain why native and invasive species frequently co-occur in riparian areas (Planty-Tabacchi *et al.* 1996). Floodplain communities comprised of flood-adapted species may be resistant to invasion, because these species are unlikely to experience stress during flooding (Hobbs & Huenneke 1992; Alpert *et al.* 2000; Daehler 2003). However, when flood regimes are altered by dams and levees, established flood-tolerant species may lose their competitive advantage over invaders (Hobbs & Huenneke 1992). Additionally, the presence of dams may affect dispersal success and hence the likelihood of invasives colonizing new sites (Planty-Tabacchi *et al.* 1996; Jansson *et al.* 2000). These anthropogenic modifications to flood regimes are common in river floodplains world-wide (Vitousek *et al.* 1997; Nilsson *et al.* 2005).

In this study, we investigated how habitat configuration, habitat quality and flood regime influence the presence and abundance of shrub taxa in the floodplain of the Wisconsin River, USA. We sampled three invasive shrubs, two non-native taxa and one native upland species. Additionally, we examined the productivity of the native invasive shrub in a subset of the floodplain. Specifically, we addressed the following question: How do habitat configuration, habitat quality, and flood regime influence the presence, abundance and productivity of invasive shrubs? We expected that invasive taxa *presence* would be closely related to successful dispersal, whereas invasive taxa *abundance* and *productivity* would be closely related to successful establishment. Therefore, we hypothesized that habitat configuration would best predict invasive taxa presence, and habitat quality would best predict invasive taxa abundance and productivity. Lastly, we expected that flooding would facilitate invasive taxa presence through seed dispersal, but might limit their abundance and productivity because of the conditions (e.g. anoxia) that can accompany flooding.

Methods

STUDY AREA

The Wisconsin River is a sandy, braided channel that flows c. 700 km to its confluence with the Mississippi River and drains a watershed of 31 805 km² (Durbin 1997). Discharge varies among river reaches, largely due to the presence of dams. Discharge averages 200 m³ s⁻¹ among reaches (Freeman *et al.* 2003), but can surpass 1000 m³ s⁻¹ in typical spring floods (Gergel 2002). The watershed includes three physiographic regions defined by soil and parent

material (Martin 1965), which result in unique vegetative (Turner *et al.* 2004) and hydrologic (Freeman *et al.* 2003) characteristics within each region. The river headwaters located in the Northern Highland region are steeply graded (Martin 1965) and include 27 dams (Freeman *et al.* 2003). Soils in this region are silt and silt loam deposited over glacial till, and drainage is poor (Hole 1976). In the Central Plain region, the river grade flattens and fewer tributaries are present (Martin 1965). Dams limit longitudinal connectivity, and levees and setback levees restrict lateral flooding in some reaches (Gergel 2002). Agricultural and urban land is more prevalent than in other regions (Freeman *et al.* 2003). Sandy soil predominates, although lacustrine silt and clay from a large, glacial lake are also present (Hole 1976). In the unglaciated Western Upland region, the river becomes broad, shallow and slow moving (Martin 1965). Longitudinal and lateral hydrologic connections occur throughout this region, as no dams or levees are present (Freeman *et al.* 2003). Forested floodplain is comprised of large forest patches dominated by flood-tolerant tree species (Turner *et al.* 2004). Soft sandstones and limestones predominate (Durbin 1997), and soils are coarse and well drained (Hole 1976).

Vegetation composition in the Wisconsin River floodplain has shifted in the past several decades (Turner *et al.* in press), reflecting changes in hydrology (Gergel *et al.* 2002; Dixon 2003), herbivore abundance (Hale 2004), land use (Bürgi & Turner 2002), and disease (Schnitzler *et al.* 2005). After 1950, overall understory density and the density of invasive shrub species have both increased (Alsum 2003; Hale 2004). The increased density of thorny shrubs, including *Rhamnus* spp. and *Zanthoxylum americanum*, may be related to large increases in the deer population, because thorny species are not readily browsed (Milewski *et al.* 1991). The construction of dams also altered flood regimes in this time period and may have contributed to changes in vegetation composition (Hale 2004).

STUDY SPECIES

We studied three invasive shrub taxa in Wisconsin River floodplain forests: *Z. americanum*, *Lonicera* spp. and *Rhamnus* spp. *Z. americanum* is native to upland forests in Wisconsin, USA (Wisconsin State Herbarium 2007), and the other two taxa are native to Asia (Batcher & Stiles 2000; Converse 2004).

Three non-native *Lonicera* species are prevalent in Wisconsin, and all are distinguished from native *Lonicera* taxa by their bush, rather than vine, forms. Individual non-native species of *Lonicera* were not identified in this study because hybridization is common, making species difficult to distinguish in the field. Non-native *Lonicera* observations may include the common *L. morrowii* and *L. tatarica*, both introduced in the late 1800s, as well as their hybrid *L. bella*, and *L. maackii*, a recently introduced species (Wisconsin Department of Natural Resources 2005a). *Lonicera* spp. grow rapidly, increasing height and producing additional stems until becoming reproductively mature, typically at around 5 years of age (Deering & Vankat 1999; Batcher & Stiles 2000). Seeds are primarily dispersed by birds (Nyboer 1992), although mammals may also be dispersers (Vellend 2002).

Rhamnus cathartica and *R. frangula* are thorny species introduced in the late 1800s, and both species are currently increasing their range (Wisconsin Department of Natural Resources 2005b). *R. cathartica* and *R. frangula* were not identified separately, although *R. cathartica* was more frequently observed. *Rhamnus* spp. exhibit rapid growth and individuals reach seed bearing age quickly (Converse 2004). The berries are dispersed by many species of birds and small mammals (Catling & Porebski 1994). Adult plants can

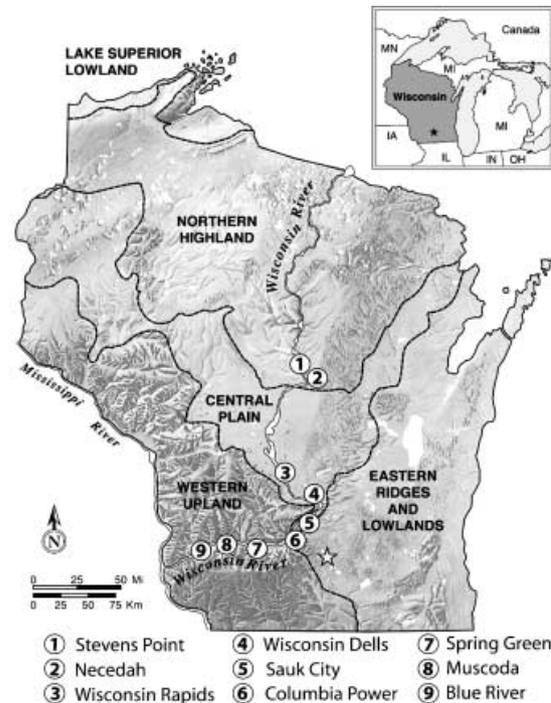


Fig. 1. Map of the region showing the Wisconsin River, physiographic regions (after Martin 1965) and numerically labelled study reaches. Reaches 1 and 2 are located in the Northern Highland, reaches 3–6 are located in the Central Plain, and reaches 7–9 are located in the Western Upland.

tolerate moderately wet soils (Stewart & Graves 2004), although germination rates decline when seeds are submerged (Archibold *et al.* 1997). *Rhamnus* spp. often reach high densities in riparian areas (Reinartz & Kline 1988; Possessky *et al.* 2000).

Z. americanum is native to forests of the central and eastern United States. This thorny species is typically found in upland habitats (Immel 2001), but can also occur in riparian areas (Hale 2004). It can tolerate poor soils and occasional flooding. *Z. americanum* fruits are dispersed by birds, and perhaps small mammals (Immel 2001), but vegetative reproduction is common and can produce dense thickets (Reinartz & Popp 1987).

STUDY DESIGN

We examined the presence and abundance of these shrub taxa in 100-year floodplain forests, as delineated by the US Federal Emergency Management Agency (FEMA) maps. Sampling was conducted between 1999 and 2001 in nine reaches ranging from Steven's Point in the north to Blue River in the south (Fig. 1). Reaches were selected to include forested areas and to avoid dams, reservoirs and urban areas. Within each reach, 10–18 transects (*c.* 560–800 m in length and separated by at least 400 m) were randomly established in the floodplain perpendicular to the river. Sample plots (10 × 20 m) were established at 125-m intervals along each transect, with an average of five plots per transect. The number of plots sampled within each reach varied from 47 to 75, with an average of 62 plots per reach. A total of 561 plots were sampled over 3 years. In each plot, shrub presence and abundance were measured. Additionally, the productivity of *Z. americanum* was measured in plots located in one reach. Variables indicating habitat quality, habitat configuration

Table 1. Description of the environmental variables used in this study, grouped into the categories used in interpretation of results

	Description	Source
Habitat quality variables		
Inorganic soil nutrients (Factor 1)	Derived in factor analysis, represents pH, Ca, Mg, P and K, higher factor values indicate higher concentrations	This study
Soil texture (Factor 2)	Derived in factor analysis, represents the percentages of sand, clay and silt. Higher values indicate more silt and clay and lower sand content.	This study
Soil organic matter and total nitrogen (Factor 3)	Derived in factor analysis, represents soil organic matter and total nitrogen. Higher factor values indicate larger quantities.	This study
Forest canopy cover	Percent cover, estimated at 10 m above shrub canopy.	Miller <i>et al.</i> (2004)
Land-use history	Land-use history of plots from 1930 to 1990. Ordinal variable with 1 = continuously forested; 2 = unforested in the 1930s, forested in the 1960s and 1990s; 3 = unforested in the 1930s and 1960s, forested in the 1990s.	Freeman <i>et al.</i> (2003)
Habitat configuration variables		
Physiographic region	Northern Highland, Central Plain or Western Upland (see Fig. 1)	Martin (1965)
Forest patch area (ha)	Area of the forest patch	This study
Distance to road (m)	Lateral distance to the nearest paved road	This study
Flood regime variables		
Distance to river (m)	Lateral distance to the main channel	This study
Relative elevation (m)	100-year flood elevation subtracted from plot elevation, lower negative values indicate wetter plots	Digitized from FEMA maps
Location in relation to setback levee	Categorical variables indicating whether a plot is separated from the main channel by the levee	This study

and flood regime were also recorded for each plot (Table 1). Details of these measurements are presented below.

SHRUB PRESENCE AND ABUNDANCE

The presence and absence of each shrub taxon was recorded in each plot; a taxon was considered present when an individual of any size was observed inside the plot. The abundance of each taxon was then determined using belt transects. Two 10 m × 2 m belt transects (located at metres 5 and 15 along the 20-m plot edge) were established in each plot, and the number of individuals ≥ 0.5 m high and rooted within the belt were recorded by taxon. The 0.5-m height threshold was selected because most shrubs were at least this tall (K. I. Predick & M. G. Turner, personal observation) and because we wanted to avoid the high year-to-year variation in seedlings that could confound analysis of data collected over three field seasons. Annual variation in flood timing and magnitude is associated with substantial variability in the establishment and survival of woody seedlings on floodplains (Streng *et al.* 1989; Jones & Sharitz 1998). Shrubs ≥ 0.5 m tall represent individuals that successfully established within the plot, and would thus be a relatively conservative estimate of abundance. Counts were summed for the two belt transects in each plot (i.e. 40 m² sampled area) and reported as stems m⁻².

Z. AMERICANUM PRODUCTIVITY

In 2001, a subset of plots in the Wisconsin Dells reach (reach 4 in Fig. 1) was sampled for *Z. americanum* productivity. Setback levees bisect the floodplain in this reach, providing a natural experiment on the influence of overbank floods on shrub growth. Levee construction occurred about a century ago and excluded areas outside the levee from active flooding (Gergel 2002). We focused on *Z. americanum* because it was the most abundant shrub taxon in this reach.

Z. americanum annual above-ground net productivity (ANPP) was measured in 29 plots in the Wisconsin Dells reach, 15 inside the levee and 14 outside the levee. Plots were located along transects sampled by Gergel *et al.* (2002), 12 of which overlapped with plots used in the present study. A 25-m² circle was placed in the centre of each plot, and the stem diameter of each *Z. americanum* individual in that area was measured and used to predict its above-ground productivity. ANPP for each plot was determined by summing the predicted productivity of each measured individual in the plot.

Above-ground productivity was estimated using an allometric equation created for *Z. americanum* shrubs using dimension analysis techniques (Whittaker & Woodwell 1968; Hughes *et al.* 1987; Etienne 1989). The allometric equation was constructed from 40 shrubs collected from both sides of the levee and representative of the range of sizes present in the floodplain. All destructively sampled individuals were located outside of sample plots. Three characteristics (canopy width, canopy height and stem diameter at 10 cm) of each individual were measured in the field for evaluation as potential predictors of above-ground biomass. Each individual was then harvested and the current year's growth (stems, leaves and berries) was removed and oven dried at 60 °C for 24 h. The total dry mass produced by each shrub was regressed against the morphological measurements recorded in the field. Stem diameter alone was an excellent predictor of shrub productivity (adj. $R^2 = 0.93$). The allometric equation generated to estimate shrub production was

$$s = 0.37d - 0.98 \quad (\text{eqn 1})$$

where s = square root [dry mass of biomass produced (g)] and d = stem diameter at 10 cm.

HABITAT QUALITY VARIABLES

Habitat quality was characterized using soil properties, canopy cover, and land-use history. Three soil samples were collected from the top 20 cm of the soil surface at random locations in each plot.

Table 2. Results of factor analysis performed on soil data collected from 497 sampling plots in floodplain forest along the Wisconsin River. Values are factor scores generated using varimax rotation. Factor scores were used in subsequent statistical analyses. Boldface values indicate the highest loading for each variable

Variable name	Factor 1	Factor 2	Factor 3
	Inorganic soil nutrients	Soil texture	Soil organic matter and total nitrogen
Organic matter (%)	-0.004	0.168	0.954
pH	0.837	-0.019	-0.140
Phosphorous	0.786	0.237	-0.098
Potassium	0.558	0.365	0.157
Calcium	0.808	0.126	0.375
Magnesium	0.837	0.256	0.132
Total nitrogen	0.088	0.112	0.943
Sand (%)	-0.201	-0.962	-0.123
Silt (%)	0.177	0.907	-0.007
Clay (%)	0.177	0.720	0.350

The three samples were combined, dried, and analysed for pH, calcium, magnesium, phosphorous, potassium, nitrogen, percent organic matter, and percent sand, silt and clay at the Wisconsin Soil and Plant Analysis Laboratory, Madison, WI. Due to missing samples or analyses, complete soils data are only available for 497 of the 561 total plots. Canopy cover was determined at nine 5-m radius subplots located in the centre of the sampling plot and 20 m and 40 m from the centre along the four cardinal directions. The percentage canopy cover was estimated at two canopy heights (10–20 m and above 20 m), and estimated cover for both heights was combined then averaged across the nine subplots (Miller *et al.* 2004). The land-use history of each plot was determined from digital orthophotos created from aerial photographs taken in the 1930s, 1960s and 1990s (Freeman *et al.* 2003). In this study, we used the number of historic time periods a plot was unforested to indicate land-use history. Plots that were forested in each historic time period were coded as one, while plots that were agricultural land in the 1930s, but forested by the 1960s, were coded as two. Lastly, plots that were not forested until the 1990s were coded as three. All plots were forested by the 1990s, but those coded two or three had reverted from agricultural land use. So, our land-use history metric increased as agricultural land use was more recent.

HABITAT CONFIGURATION VARIABLES

Habitat configuration variables included physiographic region, forest patch area, and the distance to the nearest road. Our sample plots spanned three physiographic regions, as defined by Martin (1965) and described above. We used physiographic region as a synthetic representation of the geological, climatic and topographic characteristics of each plot. Data for forest patch area and the distance to the nearest road were generated using a geographical information system (GIS) based on plot locations recorded using a global positioning system (Freeman *et al.* 2003).

FLOOD REGIME VARIABLES

Flood regime was represented by the shortest distance to the main channel and the relative elevation of each plot. The distance from each plot to the channel was determined using a GIS (Freeman *et al.* 2003). Relative elevation provides an indication of how susceptible each plot is to inundation. It was calculated by subtracting the 100-year flood elevation from the plot elevation, so plots with lower values are more likely to flood. Elevation was estimated using a 0.6-m

digital terrain model or by extrapolating from topographic maps (Turner *et al.* 2004).

STATISTICAL ANALYSES

Sampling year was an insignificant predictor of shrub taxa presence and abundance, so data among years were lumped in all analyses. Potential colinearity among the independent variables was evaluated by computing Pearson correlation coefficients. Excluding the soils data, correlations among all pairs of variables were low ($r < 0.20$), so we considered them sufficiently orthogonal for use in multiple regression analyses. However, there were significant correlations among the soil variables. Therefore, we used multivariate data reduction methods (factor analysis with varimax rotation; SAS Institute 1996) to reduce the number of soil variables. The factor analysis produced three orthogonal factors (Table 2), corresponding to inorganic soil nutrient concentrations, soil texture, and soil nitrogen and organic matter, which were used in the multiple regression analyses.

Variables influencing the presence of each shrub taxon were evaluated using stepwise logistic regression. Two models were constructed for each taxon, one including all plots ($n = 561$) but no soil variables, and the other using the subset of plots ($n = 497$) with soil data. Logistic models were assessed using a likelihood ratio test and Hosmer and Lemeshow goodness-of-fit test (Hosmer & Lemeshow 2000). The significance of independent variables in the model was determined using a likelihood ratio test with $P \leq 0.05$. Taxon abundance was analysed using stepwise multiple regression, and models again were constructed both with and without the soil variables. Variables were retained when $P \leq 0.05$. Because physiographic region was a significant predictor of invasive shrubs (results presented below), we used one-way ANOVA to determine how the more specific independent variables differed among the three regions. With respect to the detailed measurements of *Z. americanum* in the Wisconsin Dells reach, shrub presence was compared across the levee with a two-tailed Fisher's exact test, whereas above-ground productivity was compared across the levee using a *t*-test.

Results

Of the three shrub taxa surveyed, *Z. americanum* was observed most frequently. It was present in 34% of the plots, with an average density of $0.97 \text{ stems m}^{-2} \pm 1.85 \text{ SE}$ in those plots. The other two taxa were less prevalent and reached

Table 3. Results of one-way ANOVA describing how habitat configuration and quality variables differ among three physiographic regions (Fig. 1). $n = 497$ for the three soil factors and $n = 561$ for all other variables; d.f. = 2. Variables are defined in Table 1

Variable	<i>F</i>	<i>P</i>	Comparison among regions*
Inorganic soil nutrients factor	96.3	< 0.0001	W > C > N
Soil texture factor	61.6	< 0.0001	N > W > C
Soil OM and N factor	13.8	< 0.0001	(N = C) > W
Land-use history	3.9	0.2479	NS
Forest canopy cover	7.3	0.0007	(W = N) > C
Forest patch area	17.4	< 0.0001	C > (W = N)
Distance to road	13.4	< 0.0001	N > W > C
Distance to river	15.2	< 0.0001	(C = W) > N
Relative elevation	5.2	0.2063	NS

*W = Western Upland, C = Central Plain, N = Northern Highland; NS = non-significant.

much lower densities when present. *Rhamnus* spp. occurred in 13% of plots ($0.48 \text{ stems m}^{-2} \pm 1.38 \text{ SE}$) and *Lonicera* spp. were only present in 8% of plots ($0.29 \text{ stems m}^{-2} \pm 0.94 \text{ SE}$).

PHYSIOGRAPHIC REGION

In the logistic regression models, physiographic region was the best predictor of presence for each taxon ($P < 0.0001$ for all taxa), and it also was a significant predictor of the abundance of *Z. americanum* and *Rhamnus* spp. ($P < 0.001$ for both taxa). *Z. americanum* was most likely to occur in the Central Plain and was less likely to occur and least abundant in the Western Upland ($P < 0.05$). Both *Rhamnus* spp. and *Lonicera* spp. were also more likely to be present in the Central Plain than in the other regions ($P < 0.0001$ for each taxon). *Rhamnus* spp. were also more abundant in the Central Plain region than in both other regions ($P < 0.05$).

Results of ANOVA revealed significant differences in habitat configuration and quality variables among the regions, except for relative elevation and land-use history (Table 3). The Central Plain, where invasive shrubs were most abundant, was characterized by very sandy soils with moderate soil nutrient concentrations. The Central Plain also had significantly lower canopy cover than the other two regions, despite having larger forest patch sizes; distance to roads was also lower. In contrast, the Northern Highland was characterized by soils high in silt and clay but low in nutrient concentrations; distance to roads was greater, whereas distance to the river was lower than the other two regions (Table 3). The unglaciated Western Upland had the greatest soil nutrient concentrations and the lowest soil organic matter and total nitrogen, but the other habitat variables were intermediate among the regions. Thus, physiographic region appeared to function as a synthetic variable in explaining shrub composition, but did not provide information about the specific drivers of shrub presence and abundance. Therefore, physiographic region was excluded from subsequent stepwise regression analyses to assess more specific predictors of shrub presence and abundance.

INVASIVE TAXA PRESENCE

Variables related to habitat configuration, habitat quality and flood regime were all important in predicting the presence of shrub taxa (Tables 4 and 5). In logistic regression analyses that included the plots with soils data (Table 4), *Z. americanum* was more likely to be found on sandy soils with low nutrient content and organic matter. Habitat configuration was also important, as this species was observed more frequently near roads. Lastly, *Z. americanum* presence was positively influenced by flooding, with presence more likely near the river. *Rhamnus* spp. were more likely to be observed in sandy soils, with low percentages of silt and clay. The presence of

Table 4. Results of stepwise logistic regression models, including soil variables, of the presence of three shrub taxa in the Wisconsin River floodplain. Significant variables from each model are grouped into the categories used in interpretation of the results, and the sign of their relationship is indicated; d.f. = 1. Variables are defined in Table 1

Species	Variable	Variable category	Wald chi-square statistic	<i>P</i>
<i>Z. americanum</i>	– soil texture	Habitat quality	17.4	< 0.0001
	– inorganic nutrients	Habitat quality	8.6	0.0033
	– soil organic matter	Habitat quality	14.5	0.0001
	– distance to road	Habitat configuration	7.9	0.0050
	– distance to river	Flood regime	12.2	0.0005
Observations (present/absent) = 492 (200/292), Nagelkerke's $R^2 = 0.21$, percentage concordant = 72%				
<i>Rhamnus</i> spp.	– soil texture	Habitat quality	16.5	< 0.0001
	– distance to road	Habitat configuration	6.1	0.0134
	+ relative elevation	Flood regime	4.0	0.0446
Observations (present/absent) = 492 (92/399), Nagelkerke's $R^2 = 0.10$, percentage concordant = 67%				
<i>Lonicera</i> spp.	– soil texture	Habitat quality	21.1	< 0.0001
	+ land-use history	Habitat quality	5.9	0.0151
	– patch area	Habitat configuration	4.9	0.0266
	+ relative elevation	Flood regime	5.1	0.0241
Observations (present/absent) = 492 (55/437), Nagelkerke's $R^2 = 0.16$, percentage concordant = 74%				

Table 5. Results of stepwise logistic regression models, without soil variables, of the presence of three shrub taxa in the Wisconsin River floodplain. Significant variables from each model are grouped into the categories used in interpretation of the results, and the sign of their relationship is indicated; d.f. = 1. Variables are defined in Table 1

Species	Variable	Variable category	Wald chi-square statistic	<i>P</i>
<i>Z. americanum</i>	– distance to road	Habitat configuration	9.1	0.075
	– patch area	Habitat configuration	6.2	0.0131
	– distance to river	Flood regime	14.0	0.0002
Observations (present/absent) = 556 (233/323), Nagelkerke's $R^2 = 0.08$, percentage concordant = 62%				
<i>Rhamnus</i> spp.	– distance to road	Habitat configuration	6.1	0.0129
	+ distance to river	Flood regime	9.7	0.0018
Observations (present/absent) = 556 (101/455), Nagelkerke's $R^2 = 0.05$, percentage concordant = 62%				
<i>Lonicera</i> spp.	+ land-use history	Habitat quality	34.3	0.0114
	– distance to road	Habitat configuration	5.9	0.0154
	+ distance to river	Flood regime	4.5	0.0349
	+ relative elevation	Flood regime	5.5	0.0193
Observations (present/absent) = 556 (61/495), Nagelkerke's $R^2 = 0.08$, percentage concordant = 66%				

Table 6. Results of stepwise regression models, including soil variables, of the presence of three shrub taxa in the Wisconsin River floodplain. Significant variables from each model are grouped into the categories used in interpretation of the results, and the sign of their relationship is indicated; d.f. = 1. Variables are defined in Table 1

Species	Variables	Variable category	<i>F</i>	<i>P</i>
<i>Z. americanum</i>	– soil texture	Habitat quality	14.2	0.0061
	– inorganic nutrients	Habitat quality	17.2	0.0026
	– land-use history	Habitat quality	8.7	0.0309
	– distance to road	Habitat configuration	8.3	0.0355
	– patch area	Habitat configuration	8.8	0.0302
Sample size = 200, $R^2 = 0.12$, d.f. (model/error) = 5/194				
<i>Rhamnus</i> spp.	– distance to road	Habitat configuration	4.8	0.0311
Sample size = 93, $R^2 = 0.04$, d.f. (model/error) = 1/91				
<i>Lonicera</i> spp.	–	–	–	–

Rhamnus spp. also increased nearer roads. Finally, flooding appeared to inhibit the presence of this taxon, as it was more likely to be observed on high relative elevations, where flooding is less frequent. *Lonicera* spp. were also observed most frequently in sandy soils. The presence of this taxon also increased in smaller forest patches and on sites with more recent land-use disturbance. Similar to *Rhamnus* spp., the presence of *Lonicera* spp. declined with flood frequency, and occurrences were more likely on higher relative elevations.

In the logistic models constructed with the larger data set from which soils were excluded, different habitat configuration and flood regime variables were significant, but trends were consistent with models that included soils (Table 5). Without soils, the presence of *Z. americanum* was additionally predicted by small forest patches. In *Rhamnus* spp., the variables representing flood frequency changed, although the relationship to flooding was consistent. Presence of this taxon still increased in areas less likely to flood, but this was predicted by distance from the river rather than relative elevation. The presence of *Lonicera* spp. increased closer to roads and the relationship with land-use history remained, although patch size was no longer

significant. The flood intolerance of *Lonicera* spp. was still indicated by an increased presence on sites with higher relative elevations and at distances farther from the river.

INVASIVE TAXA ABUNDANCE

Multiple regression analyses including the soils data revealed that both habitat quality and configuration were important predictors of *Z. americanum* abundance (Table 6). The abundance of this species increased in sandier soils with low inorganic nutrient concentrations. *Z. americanum* was also more abundant in relatively undisturbed, smaller patches and nearer to roads. These variables comprised the best fit regression model for this species (adj. $R^2 = 0.12$). *Rhamnus* spp. were also more abundant closer to roads (Table 6), but *Lonicera* spp. abundance was not predicted by any of the variables we measured.

When the influence of soils was excluded from the analysis, patch area and land-use history remained significant predictors of *Z. americanum* abundance, but canopy cover became important (Table 7). Increased canopy cover was associated with reduced abundance of *Z. americanum*. *Rhamnus* spp. were still more abundant closer to roads, although this model

Species	Variables	Variable category	F	P
<i>Z. americanum</i>	– land-use history	Habitat quality	6.2	0.0134
	– canopy cover	Habitat quality	4.6	0.0340
	– atch area	Habitat configuration	4.9	0.0286
Sample size = 233, $R^2 = 0.06$, d.f. (model/error) = 3/229				
<i>Rhamnus</i> spp.	– distance to road	Habitat configuration	6.0	0.0163
Sample size = 101, $R^2 = 0.05$, d.f. (model/error) = 1/99				
<i>Lonicera</i> spp.	–	–	–	–

Table 7. Results of stepwise regression models, without soil variables, of the presence of three shrub taxa in the Wisconsin River floodplain. Significant variables from each model are grouped into the categories used in interpretation of the results, and the sign of their relationship is indicated; d.f. = 1. Variables are defined in Table 1

Table 8. Results of stepwise logistic regression models, including soil variables, of the presence of three shrub taxa in the Wisconsin Dells reach (reach 4 in Fig. 1) of the Wisconsin River floodplain. Significant variables from each model are grouped into the categories used in interpretation of the results, and the sign of their relationship is indicated; d.f. = 1. Variables are defined in Table 1

Species	Variable	Variable category	Wald chi-square statistic	P
<i>Z. americanum</i>	– levee	Flood regime	11.5	0.0007
	– distance to river	Flood regime	12.5	0.0004
Observations (present/absent) = 67 (38/29), Nagelkerke's $R^2 = 0.64$, percentage concordant = 92%				
<i>Rhamnus</i> spp.	– patch area	Habitat configuration	11.4	0.0008
Observations (present/absent) = 67 (19/48), Nagelkerke's $R^2 = 0.27$, percentage concordant = 75%				
<i>Lonicera</i> spp.	+ land-use history	Habitat quality	5.6	0.0179
	– distance to road	Habitat configuration	4.9	0.0274
Observations (present/absent) = 67 (11/56), Nagelkerke's $R^2 = 0.28$, percentage concordant = 79%				

explained only a small amount of the observed variation (adj. $R^2 = 0.04$). *Lonicera* spp. abundance was again not predicted by any of the independent variables.

ABUNDANCE AND PRODUCTIVITY ACROSS A FLOOD CONTROL LEVEE

In evaluating the effect of the flood-control levee in the Wisconsin Dells reach, our analyses showed that *Z. americanum* was more likely to occur inside the flood control levee than outside, and at distances closer to the river (Table 8). The levee did not have a detectable influence on the presence of either *Rhamnus* spp. or *Lonicera* spp., which were predicted in this reach (Table 8) by variables very similar to those identified in the analyses using all nine reaches.

The average density of *Z. americanum* in the Wisconsin Dells reach was 1.46 stems m^{-2} (± 5.85 SE), *c.* three times greater than *Lonicera* spp. and *Rhamnus* spp. It was the only taxon with a density sufficient for analysing the effect of the setback levee. *Z. americanum* was more abundant ($P < 0.05$) inside the flood-control levee (36.4 ± 7.1 stems m^{-2}) compared with outside the levee (8.7 ± 6.1 stems m^{-2}). Where *Z. americanum* was present, its ANPP also was significantly higher ($P < 0.0001$) inside the levee (111.6 ± 1.9 g m^{-2} year $^{-1}$) compared with outside the levee (2.7 ± 65.6 g m^{-2} year $^{-1}$). Additionally, *Z. americanum* ANPP increased as relative elevation declined. Therefore, although typically considered an upland shrub, flooding appeared to increase the presence, abundance and growth rate of *Z. americanum*.

Discussion

PHYSIOGRAPHIC REGION

Physiographic region was a strong predictor of the presence and abundance of each shrub taxon, and its influence was consistent with the results based on the more detailed predictors of habitat quality and configuration. In particular, the positive association between invasive shrubs and sandy soils and proximity to roads is consistent with their increased frequency in the Central Plain. Physiographic region appeared to act as a synthetic, broad-scale indicator of the suite of factors controlling invasive shrub dispersal and establishment. Regional-scale factors have also been correlated with species composition in other studies (Larson *et al.* 2001; Dupré & Ehrlén 2002; Spyreas *et al.* 2004), and there is some evidence that broad-scale factors may predict invasive species richness better than fine-scale factors (Ohlemüller *et al.* 2006). However, fine-scale site characteristics have also been excellent predictors of invasive species distribution (e.g. Honnay *et al.* 1999; Kolb & Diekmann 2004). We conjecture that relationships are observed between species distributions and both broad- and fine-scale variables, because broad-scale variables create spatial patterns in processes that control vegetation composition at finer scales. This suggests a hierarchical link between the broad- and fine-scale processes that influence invasive species distribution.

Invasive shrub taxa were observed most frequently, and at the highest abundances, in the Central Plain, whereas

frequency and abundance were lowest in the downstream Western Upland. In contrast to our observations, river systems often display a longitudinal pattern in which invasive or ruderal species abundance increases downstream (Nilsson *et al.* 1989; Tabacchi 1995; Planty-Tabacchi *et al.* 1996; Renöfält *et al.* 2005). The downstream increase is usually attributed to anthropogenic land uses and hydrologic modifications becoming more pronounced (Planty-Tabacchi *et al.* 1996). The greater invasion frequency in the Central Plain may still reflect a gradient of human influence, as anthropogenic modifications to flood regime were most prominent there, and distance to roads was lowest (Table 3). The Central Plain also had lower canopy cover (Table 3) and light conditions may have been more favourable to the invasive shrubs. The less-modified Western Upland, which has extensive floodplain forests, no dams or levees, and includes the Lower Wisconsin Scenic Riverway, may be more resistant to invasion.

While this study did not consider the location of non-native species introduction, we believe that the distribution we observed among physiographic regions is not primarily caused by the location where these species were introduced. Non-native taxa have been present in the area for over a century, and multiple introductions are likely to have occurred (Wisconsin Department of Natural Resources 2004a; 2004b). All three taxa are also bird dispersed, suggesting that dispersal distances are likely to be substantial. Additionally, the non-native taxa (*Rhamnus* spp. and *Lonicera* spp.) exhibited similar distributions among physiographic regions as the native invasive species (*Z. americanum*).

HABITAT CONFIGURATION AND HABITAT QUALITY

We hypothesized that habitat configuration would influence shrub dispersal, and thus predict shrub presence. Habitat configuration did influence the presence of each shrub taxon, with presence more likely in smaller forest patches and nearer to roads. Patch edges and roadways cause many well-known edge effects, including altered microclimate (Saunders *et al.* 1991; Harper *et al.* 2005) and species compositions that differ from patch interiors (Matlack 1994; Forman & Alexander 1998). Edges can act as corridors for invasive dispersers (Trombulak & Frissell 2000), such as birds (Hansen & Clevenger 2005). Shrub taxa in this study are all bird dispersed, which may contribute to the importance of edge habitat in their distribution. Bird species associated with edge habitat were the most abundant avian populations in our study sites (Miller *et al.* 2004).

We also expected that habitat quality would have a large effect on shrub establishment and predict shrub abundance. Soil characteristics were clearly important. For example, across all nine reaches, *Z. americanum* was more abundant in sandy soils with low nutrient content. Floodplains are wetter and more nutrient rich than the uplands (Naiman & Décamps 1997), so this species was more abundant where floodplain soil was more similar to upland soil. However, in the Wisconsin Dells reach, located within the sandy Central Plain,

Z. americanum was associated positively with flooding. These results suggest that controlling factors may act hierarchically. *Z. americanum* was also more abundant on less-disturbed sites, suggesting that historic, agricultural land use may limit its establishment. The legacy of agricultural land use can both limit and facilitate invasions depending on life-history characteristics of the invader (Honnay *et al.* 1999; Jenkins & Parker 2001).

Thus, we found some support for our hypotheses that habitat configuration would strongly influence shrub presence, whereas habitat quality would strongly influence shrub abundance. However, counter to these predictions, habitat quality variables (particularly soil characteristics) were also important predictors of shrub presence. Additionally, habitat configuration was often a significant predictor of shrub abundance; indeed, the sole predictor of *Rhamnus* spp. abundance was its proximity to roads, an aspect of habitat configuration. Overall, we found that similar combinations of habitat configuration and quality variables predicted both the presence and abundance of invasive shrubs. This suggests that habitat quality and configuration are related, perhaps through a predictable spatial pattern of patches suitable for invasive shrubs, such as habitat edges. Edge habitats provide dispersal corridors for invasive taxa along with suitable locations for establishment, thereby leading to a positive association between the presence and abundance of invasive taxa and the configuration and quality of edge habitat.

FLOOD REGIME

We hypothesized that floods would increase invasive presence, by acting as dispersal vectors, but limit abundance and productivity by stressing plants. However, we found that flooding increased the presence, abundance and productivity of *Z. americanum*, but decreased the presence and abundance of both non-native invaders. The different response among taxa is likely to be due to differences in their life-history characteristics. *Lonicera* spp. and *Rhamnus* spp. do not tolerate flooded conditions (Batcher & Stiles 2000; Stewart & Graves 2004). *Z. americanum* is also flood sensitive, but its ability to reproduce vegetatively and resprout from stems (Kurz 1997) may allow it to survive in active floodplains.

Anthropogenic modifications to the flood regime are likely to be responsible for the successful establishment of *Z. americanum* in active floodplains. It seems counterintuitive that the presence, abundance and productivity of a native upland species would be increasing. However, this species has become more regionally abundant in floodplains during the past 50 years, concurrent with anthropogenic modifications to flood regime (Hale 2004). Dams reduce longitudinal connectivity and limit the riverine dispersal of seeds (Jansson *et al.* 2000; Middleton 2002). Our results suggest that riverine dispersal of *Z. americanum* is not important, because the widest distribution of this species occurred in the region where dams are most abundant. However, dams also reduce flow, extend the duration of spring floods, and increase flow later in the growing season (Krug & House 1980; Dixon &

Turner 2006). These changes to flow regime have probably reduced the competitive advantage of flood-tolerant traits (Hall & Harcombe 2001; Hale 2004) and limited recruitment of species adapted to a different flood regime (Middleton 2002). In other studies, changes to flood regime (Richardson *et al.* 2007) and other disturbance regimes have also resulted in increased invasion (Sher & Hyatt 1999).

Conclusions

Our models predicted the presence of invasive shrubs, but explained little of the variation in their abundance, particularly for *Rhamnus* and *Lonicera* spp. Estimates of seed source location, the magnitude of propagule influx, introduction history, more direct measures of flood history, or inclusion of species richness, would probably increase the predictive power of our models. A limited number of observations may also constrain our explanatory power, as both of the non-native taxa were present on less than 15% of the plots surveyed and we observed densities of less than 1 stem m⁻² for each taxon, far lower than the densities observed in other habitats (Reinartz & Kline 1988; Luken & Goessling 1995). The limited presence and low abundance of invasive shrubs suggest that we were studying the early phases of invasion. Our results suggest that invasive species distributions can be characterized when invasive populations are small or while an invasion is in progress. Models that can predict invasive species distribution at the beginning of an invasion are especially useful for successful management of invasive species (National Research Council 2002), even though their predictive power may be limited compared with models generated from larger invasive populations. Re-sampling of these plots in the future could be especially informative regarding conditions that may facilitate the expansion of invasive shrubs, or conversely, the conditions that may impede their spread.

We conclude that anthropogenic alterations to the landscape and flood regime are facilitating shrub invasions in the Wisconsin River floodplain. Historic land-use and contemporary landscape patterns were both influential. Past agricultural land use, forest fragmentation, and the creation of edge habitat (i.e. small forest patches, locations near roads), increased the presence of invasive shrub species. Alterations to the flood regime also promoted expansion of a native, upland invasive species in the active floodplain. The lower Wisconsin River, associated with extensive floodplain forest and unregulated flow, appeared to have some protection from invasion. Our results suggest that large patches of floodplain forest, less regulated flooding regimes, and lower road densities, may help reduce the spread of invasive shrubs in temperate floodplains.

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