Stream Structural Limitations on Invasive Communities in Urban Riparian Areas

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Urban riparian plant communities exist at the interface between terrestrial and aquatic habitats, and they are rich sources of species biodiversity and ecosystem services. The periodic floods that promote species diversity in riparian plant communities also increase their vulnerability to nonnative plant invasions. Plant invasions are constrained by seed and suitable habitat availability. However, how seed dispersal and establishment limitations interact to shape nonnative plant invasions in riparian communities is poorly understood. We use Stream Visual Assessment Protocol data to evaluate the hydrological and geomorphological parameters that influence the seeding and establishment of six common nonnative species in urban riparian habitats: garlic mustard, purple loosestrife, reed canarygrass, common reed, Japanese knotweed, and multiflora rose. To address this objective, we analyzed stream reach data collected during a basin-wide environmental assessment of the extensively urbanized upper Niagara River watershed. We found limited support for our prediction that propagule limitation constrains the distribution of nonnative riparian species, likely because these species are well established in the study area. Instead, we found that opportune stream reach characteristics better predict the distribution of the common invasive riparian species—most notably open tree canopy. Given that there is widespread investment in urban riparian forest restoration to improve water quality, increase stream-bank stability, enhance wildlife habitat and promote recreation, our data suggest that riparian forests may provide the additional benefit of reducing the abundance of some, but not all, invasive plants.


Key words: Novel community, seed limitation, Stream Visual Assessment Protocol, suitable habitat.
Management Implications

The progression from individual plant invasions to the establishment of widespread exotic communities requires that potential invaders are available and that there is suitable habitat in which they can establish. Nonnative riparian plant communities are widespread, particularly in urban areas, and often share common species. We evaluated the hydrologic and geomorphologic parameters that might influence the urban riparian distributions of six common nonnative riparian species in the urbanized upper Niagara River watershed: garlic mustard, purple loosestrife, reed canarygrass, common reed, Japanese knotweed, and multiflora rose. We found that four of these species are well established in the region so that seed availability did not appear limiting; instead, we found riparian canopy cover to be the strongest limiting factor on the invasive riparian communities. These data suggest that limiting the distribution of invasive species in urban riparian habitats requires a straightforward approach: restore riparian forests. Forest restoration in urban/riparian habitats is a widespread management goal expected to create many ecological benefits, including improved habitat and water quality. Still, the stream–forest interface is inherently edge habitat, and invasive species thrive along forest edges. Increasing forest canopy may reduce invasive species communities, but the widespread presence of well-established riparian invaders and the mitigating effects of stream-bank edge habitat suggest that full eradication is unlikely. Moreover, we also found conflicting species-specific associations and habitat responses, suggesting that managing individual invasive species may require specific interventions.

Urbanization and associated human activities alter hydrologic variability by influencing the frequency and duration of both high and low flows, and by increasing the temperature and nutrient enrichment of waters (Auble et al. 1994; Decamps et al. 1988; Engstrom et al. 2009; Nilsson et al. 1991; Paul and Meyer 2001; Rood and Heinz-Milne 1989; Walsh et al. 2014). High flow disturbs existing vegetation, and low flow promotes drought-tolerant upland species; both altered urban flow regimes allow the incursion of invasive riparian species (Groomman et al. 2003; Maskell et al. 2006; Pysek and Prach 1993).

In addition to shaping plant communities through flood disturbance and dynamic resource availability, streamflow often acts as the seed vector for those communities (Jansson et al. 2005; Merritt et al. 2010; Nilsson et al. 2010). Hydrochory (water dispersal) is a major source of propagule pressure for plants colonizing riparian habitats (Jansson et al. 2005; Leyer 2006; Merritt et al. 2010), dispersing seeds (or viable vegetative parts, e.g., Kowarik and Saumel 2008; Truscott et al. 2006) between riparian habitats at local and regional scales (Andersson et al. 2000; Gurnell et al. 2008; Jansson et al. 2005; Johansson et al. 1996; Merritt et al. 2010; Merritt and Wohl 2006; Vogt et al. 2006). Riparian plants often exhibit specific traits adapted to hydrochory, such as air cavities for increased flotation (Boedeltje et al. 2003; Nilsson et al. 2010), but many nonwetland plants primarily adapted to other dispersal modes (e.g., wind, bird) also move through water dispersal (Hampe 2004; Johansson et al. 1996; Nilsson et al. 2010; Saumel and Kowarik 2010). Streamflow not only transports seeds downstream, but also delivers them to different levels of the shoreline depending on flood stage and plant dispersal traits (Drezner et al. 2001; Merritt and Wohl 2002; Middleton 2000). Hydrochory also is a vector for riparian invasion by exotic plant species (Nilsson et al. 2010; Saumel and Kowarik 2010; Thomas et al. 2006; Truscott et al. 2006). Stream connectivity through hydrochory results in propagule pressure from large catchments so that downstream locations receive diverse species inputs, including invasive exotic species.

Invasive plants typically disperse downstream (e.g., Love et al. 2013; Nakayama et al. 2007), but many riparian invaders also disperse upstream, suggesting alternate, possibly anthropogenic, dispersal modes (Osawa et al. 2013). Anthropogenically altered landscapes commonly host many exotic plant species that invade riparian areas (Chytry et al. 2008; Osawa et al. 2013). For example, roadsides provide suitable habitat and roadways provide a dispersal corridor for many invasive plants (Christen and Matlack 2009; Flory and Clay 2009; Mortensen et al. 2009; Warren et al. 2011a). In turn, invasive plants spread from roads to adjacent riparian areas (Al-Chokhachy et al. 2013; Menuz and Kettenring 2013; Watterson and Jones 2006).
The objective of this research was to evaluate the hydrological, geomorphological, and plant community characteristics that correspond with the distribution of six common invasive exotic riparian plant species in the eastern Great Lakes region. Investigating species invasions requires an assessment of both establishment and seed limitations (Eschtruth and Battles 2011), and little is known about the strength of each in promoting riparian invasion (Chytry et al. 2008). Whereas direct measurements, such as soil moisture and seed production, closely link with ecological dynamics, these measures often are impractical at a basin-wide scale with “snapshot” survey data. Instead, proximate data, such as tree canopy cover as a proxy for reduced sunlight and temperature, are reasonable for applied assessment. We analyzed stream reach data collected as part of a basin-wide environmental assessment of the extensively urbanized upper Niagara River watershed in western New York State and tested whether invasive plant presence and richness appeared limited by habitat (establishment), availability (dispersal), or an interaction between the two. Given that propagule pressure and anthropogenic disturbance generally overwhelm habitat limitations in invasive species (Chytry et al. 2008; Von Holle and Simberloff 2005; Warren et al. 2012), we expected greater invasive species occurrence in riparian reaches close to roads with greater flooding and shallow bank slopes.

Materials and Methods

Study Sites. The study sites were located in the Niagara River Greenway, which is defined by municipal boundaries in Erie and Niagara counties in western New York State, USA (NRGC 2007) (Figure 1). The Greenway extends from the town of Porter, where the Niagara River enters Lake Ontario, through several municipalities located along the Niagara River, to the city of Buffalo in the southernmost portion of the Greenway. Greenway land use is mixed with the largest portion being classified as residential development (31%), followed by agricultural (17%) and vacant (17%) (NRGC 2007). Our study sites included 348 reaches in 12 streams in the Greenway. A standard reach length of 61 m (200 ft) was used and reaches represented the combinations of vegetation, stream morphology, and hydrologic regime found throughout the Greenway. Five streams, Fish, Gill, Cayuga, Bergholtz, and Bull, were located in Niagara County. The remaining seven streams were located in Erie County and included the following creeks: Tonawanda, Ellicott, Two Mile, Woods, Gun, Big Six Mile, and Spicer.

Survey Methods. The Natural Resources Conservation Service (NRCS) Stream Visual Assessment Protocol (SVAP) (NRCS 1998, 2009) was used to collect stream condition data during the summer 2013 field season. The SVAP is a qualitative multidisciplinary assessment used to perform rapid visual assessment of several elements of overall stream corridor conditions. The SVAP has been used to assess streams throughout the United States, and several studies demonstrate agreement between the SVAP and other qualitative assessment methods (Hughes et al. 2010; McQuaid and Norfleet 1999). Moreover, field crew training reduces observer bias and improves the precision and accuracy of qualitative assessment methods (Bjorkland et al. 2001; Hannaford et al. 1997; Ward et al. 2003). A trained three-person field crew scored SVAP elements in each stream reach, including channel condition, riparian zone, bank condition, water appearance, nutrient enrichment, pools and canopy cover. These elements were scored using an element description and scoring matrix (see NRCS 1998, 2009).

Study Species. The stream assessment database included the presence or absence of six invasive riparian plant species: Alliaria petiolata (Bieb.) Cavara & Grande (garlic mustard, hereafter “Alliaria”), Lythrum salicaria L. (purple loosestrife, hereafter “Lythrum”), Phalaris arundinacea

Figure 1. Map of the upper Niagara River watershed (western New York) with municipal boundaries and stream reaches.
Data Analysis. We examined covariation among invasive species presence in urban riparian areas using principal component analysis (PCA) using the “prcomp” method and “scale” option (standardizes all variables to unit length) in the R statistical package (R Development Core Team 2015). For binary data, PCA places the descriptors in multidimensional space at the square root of their complements (Borcard et al. 2011). We excluded two species, *Polygonum* and *Rosa*, because there were not enough presence replicates for a meaningful analysis. These species were included, however, in community species richness and descriptive statistical analyses.

Given that species presence and richness generally increase with habitat area (Preston 1962), we included riparian extent (habitat area, m$^2$) to account for community saturation (i.e., larger habitat patches invariably contain greater species richness). We included flooding (m, channel depth at bank-full — channel depth at lowflow) as a predictor of hydrochorous seed movement (Boedeltje et al. 2004; Greet et al. 2012). Flooding also can create suitable plant recruitment conditions by eroding stream banks and depositing seeds at different distances from shore, and seed deposition decreases with bank steepness (Greet et al. 2011; Kronvang et al. 1997; Soomers et al. 2010), so we included bank slope (m, channel depth at bank-full/channel width at bankfull) as a predictor of seed recruitment. Increased nutrients and roadways generally benefit invasive rather than native species (Menuz and Kettenring 2013), so we also included nutrient status (index) and riparian distance to road (m). Because invasive plants generally are shade-intolerant (Bazzaz 1979), including most of our study species (Table 1), we also included riparian overstory canopy cover (index). The nutrient status and canopy cover indices were based on observer ratings at a scale of 1 to 10. The nutrient status index included water color, algal growth, and aquatic plant density. The canopy cover index was based on categories of percentage of tree shading.

The stream field data were autocorrelated and unbalanced by stream, and the response variables were presence/absence and counts. We used a generalized linear mixed model (GLMM) approach to accommodate the study design with stream (n = 17) as a random effect and riparian extent, flooding, bank slope, nutrient status,
Results and Discussion

*Lythrum* was the most common invasive plant found in our surveys (62.5% of all stream reaches). *Phragmites* (50.0%), *Phalaris* (31.9%), and *Alliaria* (27.7%) were less common, and *Polygonum* (6.9%) and *Rosa* (2.8%) were uncommon. Overall, 63.9% of the stream reaches were occupied by at least one of the invasive species. Plotting the four most common species on a biplot graph indicated that the first two principal components (PC1 and PC2) adequately explained correlation among plants (68% of the variation) (Figure 2). *Alliaria* and *Phalaris* positively covaried along PC1 (43% of the variance) whereas *Lythrum* and *Phragmites* negatively covaried along PC2 (25% of the variance). The two plant groupings along PC1 and PC2 were orthogonal, indicating no relationship between them.

The best-fitting invasive presence model (based on AIC selection) retained all of the stream/riparian variables, but the slope values for flooding, nutrients, and distance to road did not differ significantly from zero. The likelihood of occurrence of invasive plant species increased significantly with riparian extent (coefficient [coef.] = 0.657, SE = 0.210, z = 3.143, P = 0.002) and a significant canopy cover by slope interaction term (coef. = 2.729, SE = 1.025, z = 2.663, P = 0.008) indicated that invasive species presence decreases significantly with canopy cover and increases with steeper banks, but neither has an effect where both are greatest (Figure 3). Similar to the presence model, the best-fitting invasive richness model also retained all of the stream/riparian variables, but none of the slope values differed from zero except canopy cover. Invasive species richness decreased significantly with canopy cover (coef. = −0.096, SE = 0.028, z = −3.459, P = 0.001) (Figure 4).

All stream/riparian variables best predicted *Lythrum* presence, but only the slope for increased riparian extent and decreased canopy cover differed significantly from zero (riparian extent, coef. = 0.699, SE = 0.240, z = 2.910, P = 0.004; canopy cover, coef. = −0.300, SE = 0.061, Z = −4.966, P < 0.001). Only decreased canopy cover predicted the presence of *Phragmites* (coef. = −0.235, SE = 0.106, z = −2.215, P = 0.027). Distance to road, flooding, riparian extent, and canopy cover best predicted *Phalaris* presence, but none of the slope values differed significantly from zero. Only increased canopy cover predicted the presence of *Alliaria* (coef. = 0.345, SE = 0.175, z = 1.977, P = 0.048).

Invasive riparian plant communities appeared far more establishment- than seed-limited along the urban streams measured here. The invasive plants were more likely to
In larger riparian areas, but increased tree canopy cover reduced their presence and community diversity along the streams. We found weaker evidence for dispersal limitations on the invasive plants.

The best-fit models for invasive species presence and richness retained all stream parameters. The strongest limitation on invasive species presence and richness was imposed by tree canopy cover—likely a proxy for light availability and temperature (Warren 2010a,b). Although some invasive species tolerate shade and invade beneath forest canopy (Martin et al. 2009), invasive species generally are shade-intolerant, including the species studied here (Dommanget et al. 2013; Marlor et al. 2014; Phillips-Mao et al. 2014). Lythrum and Phragmites presence decreased significantly in our plots with greater canopy coverage, but Alliaria presence actually increased. Alliaria appears a poor competitor where increased light promotes native species cover (Phillips-Mao et al. 2014) and unlike most invasive species, it may benefit from increased canopy cover. Interestingly, approximately 75% of riparian areas lack forest cover in the United States (Innis et al. 2000; Palmer et al. 2007; Wohl et al. 2007). Urban and riparian forest restoration are major management initiatives throughout the United States (Oldfield et al. 2013; Sweeney and Czapka 2004). Benefits associated with these projects typically include improvements in water quality and wildlife habitat, erosion control, and recreation (Sweeney and Newbold 2014). The results presented here suggest that a reduction in the occurrence of invasive riparian plants also might be a potential benefit from urban riparian forest restoration.

We expected that riparian extent, flooding, and distance to road would indicate seed limitation, the latter two as seed vectors, but only riparian extent showed any influence on invasive presence, and invasive plants species were more likely to occur in larger riparian areas. Our data also indicated that suitable riparian habitat for invasive plants was delineated by canopy cover. The weak evidence for seed limitation may be due to the indirect proxies, but it is not necessarily surprising considering that all of the six riparian species recorded in the basin-wide assessment are longstanding invaders, all first recorded in the region 65 to 180 yr before the assessment. Eschtruth and Battles (2011) found propagule pressure more limiting than habitat for three riparian invasive species, but all were recent invaders—the stage at which seed limitation would be expected. Moreover, the research was conducted in a natural...
area, which might be expected to contain fewer invasive species than the urban area where our data were collected. Finally, anthropogenic disturbance makes habitat more suitable for invasive species (Chytry et al. 2008), and urban stream systems are far more altered than those found in natural areas (Maskell et al. 2006; Paul and Meyer 2001; Pysek and Prach 1993).

The two species exhibiting the greatest tree canopy intolerance were *Lythrum* and *Phragmites*, but these also were the two species least likely to occur together—suggesting that shade intolerance did not fully explain their distribution. *Lythrum* generally is an upland species, most common in roadside ditches, whereas *Phragmites* is more strongly associated with waterways, suggesting that a better measurement of soil moisture, hydrologic regime, or both may be required to explain why they did not coexist. *Alliaria* and *Phalaris* generally occurred together, but neither appeared terribly limited by the environmental variables measured here, except that *Alliaria* increased with tree canopy coverage. Both species are passively dispersed (Coops and Van der Velde 1995; Nuzzo 1991) and may have riparian distributions more defined by dispersal than habitat limitations.

An intriguing pattern found in our data is that steep bank slopes offset the negative effects of increased tree canopy cover on the presence of invasive riparian species. Given that streamflow variability increases seedling colonization on gradual, but not steep, sloping stream banks (van Leeuwen et al. 2014), the effect does not seem to be greater colonization. The negative impact of canopy cover very likely is due to shading, and steeper slopes change the angle of solar irradiation, increasing understory light availability and temperature (Cantlon 1953; Warren 2010b). This finding underscores the need for riparian restoration plans to acknowledge potentially complex interactions between resource availability, riparian plant community structure, and fluvial geomorphology.

We linked a qualitative stream assessment with riparian species invasion—essentially linking habitat structure and ecological patterning. Hence, we used proximate data collected as part of applied stream assessment to explain theoretical controls on plant distributions. Other studies also have demonstrated agreement between SVAP assessment methods and biota, such as macroinvertebrates (de Jesus-Crespo and Ramirez 2011; Hughes et al. 2010), but we did not find any literature linking SVAP with riparian vegetation. An excellent step in building upon our approach would be the collection of vegetation abundance data, either percentage of cover or biomass. Presence/absence data limits our ability to assess the strength of establishment and seed limitations on the individual invasive plants. The binary analysis also makes it difficult to project trends and responses as the models linearize binary data in a statistically, but not intuitively, meaningful manner. Abundance data would not only allow inference about the strength of establishment and seed limitations on the invasive plants, but also give insight into the nonnative impacts on community and ecosystem processes.

Seed dispersal and the availability of suitable habitat determine species invasion. We found little evidence that long-established invasive species are dispersal-limited in urban riparian habitats, and habitat structure appeared the best predictor of invasive community richness. Still, although canopy coverage strongly limited the invasive communities, *Alliaria* increased with canopy; although the invasive community appeared more habitat- than dispersal-limited, *Alliaria* and *Phalaris* appeared more dispersal- than habitat-limited. *Lythrum* and *Phragmites* did not co-occur, whereas *Phalaris* and *Alliaria* generally did. These results suggest that managing habitat structure may influence invasive communities as a whole, but managing individual invasive species may require specific interventions. Moreover, management activities that suppress a specific invasive species might promote another.

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