

Research article

Spatial patterns of plant invasiveness in a riparian corridor

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Abstract

Analysis of landscape-scale patterns of plant invasiveness can assist in interpreting spatial patterns of plant species richness. We investigated downstream variation in plant invasiveness in the riparian corridor of the free-flowing Vindel River in northern Sweden by introducing seeds of an alien species, *Helianthus annuus*, in 0.25 m² plots of natural vegetation from mountain headwaters to the coast and found a significant downstream pattern with middle reaches having the highest invasiveness. We related invasiveness to species richness, both on a reach scale (200-m long stretches of riverbank encompassing the experimental plots) and on the scale of experimental plots. We found no significant correlation between plant invasiveness and species richness, neither at the reach nor at the plot scale. The number of available soil substrates shows a significant positive quadratic relationship with location along the river and substrate fineness shows a near significant negative quadratic relationship with location along the river, with middle reaches having coarser substrates. Several studies have shown that plant species richness in riparian corridors often exhibits a quadratic pattern with highest species richness in the middle reaches of a river, similar to the pattern we found for invasiveness. Although species richness *per se* might not be a primary factor for invasibility, the same habitat conditions as those supporting plant species richness, can help in explaining large-scale patterns of plant invasion in riparian zones.

Introduction

Understanding how spatial patterns may regulate invasive spread of species has become an important goal of landscape ecology (With 2002). Two important reasons are that human transformation of landscapes has facilitated dispersal of some organisms, and that invasion by alien species can be a major cause of diversity loss (Vitousek et al. 1997; Wilcove et al. 1998; Mack et al. 2000). There are several examples of plant invaders that have reduced the number of native species (e.g. Alvarez

and Cushman 2002), and in many parts of the world invaders are controlled by humans at heavy expenses (Pimentel et al. 2000; Le Maitre et al. 2002).

Riparian corridors are considered as being the landscape elements that are most sensitive to plant invasion (DeFerrari and Naiman 1994; Stohlgren et al. 1999; Brown and Peet 2003). A major reason is that riparian corridors consist of an array of landscape elements (Ward et al. 2002) with a high frequency of open ground for colonization (Malanson 1993) and form dispersal networks

connecting different landscapes (Forman and Godron 1986). The hydrologic connectivity is a major cause for the high species diversity of river corridors (Ward et al. 2002), but also serves as a dispersal vector for alien invasive organisms. There are several examples of alien infestations that have caused severe problems in riparian corridors. One of the most well known is the invasion of salt cedar (*Tamarix* spp.) in North American watercourses. Well over half a million hectares of riparian land had been invaded by salt cedar by year 2000 (Zavaleta 2000). The trees of this genus use more water compared to the native trees, leading to reduced groundwater levels, elimination of natural vegetation, and reduced water flows in river channels (Di Tomaso 1998).

A key question landscape ecologists may ask about invasive species is what makes some ecosystems more invasible than others. Early work suggested that species richness was the key-controlling factor (Elton 1958). High species richness would then make communities more resistant to invasions and species-poor communities would be the easiest to invade. Later work has shown that patterns of invasiveness might be scale dependent (Brown and Peet 2003; Byers and Noonburg 2003). Brown and Peet (2003) found a positive relationship between species richness of exotic and native species in riparian areas at larger scales (100 m²), but the relationship graded into a negative relationship at increasingly smaller scales (0.10 m²). In small-scale experiments there is often a negative relationship between invasiveness and species richness (Tilman 1997; Knops et al. 1999; Stachowitch et al. 1999; Naeem et al. 2000; Prieur-Richard et al. 2000; but see Wardle 2001), whereas many comparative studies performed at larger scales find positive relationships (Planty-Tabacchi et al. 1996; Lonsdale 1999; Stohlgren et al. 1999; Levine 2000). Suggested mechanisms behind this discrepancy are that environmental and ecological factors covarying with diversity make more diverse communities more easily invaded (Levine and D'Antonio 1999; Levine 2000). Although diversity tends to reduce invasiveness at the scale of neighboring plants, other factors covarying with diversity may be more important for invasiveness (Levine 2000).

Spread of exotic plant species is common and worldwide, but only few studies have explored landscape level patterns of invasiveness that go

beyond noting that ecosystems are differently invaded. Planty-Tabacchi et al. (1996) investigated longitudinal patterns of plant invasiveness in the riparian corridors of the French Adour River and the North American McKenzie River and found that the proportion of alien plant species increased downstream. Nilsson et al. (1989) found the same pattern for ruderal plants in the riparian corridors of the free-flowing Torne and Kalix Rivers in northern Sweden. Nilsson et al. (1989, 1991a) also found that total riparian plant species richness was quadratically related to downstream position along free-flowing rivers in northern Sweden, with richness at its highest in the rivers' middle reaches, i.e., the inland region between the mountains and the coast. This pattern has subsequently been found also in several other rivers (Planty-Tabacchi et al. 1996), but there are also examples of contrasting results. For example, Gould and Walker (1997) found that species richness increased linearly downstream in the Canadian, north-flowing Hood River.

Nilsson and Jansson (1995) suggested four mechanisms for the quadratic distribution of species richness: (1) early post-glacial immigration in the middle reaches during a high coastal stage when present upstream and downstream reaches were unavailable for colonization (because of glacial ice cover and inundation, respectively), leaving remnant relict populations until present, (2) downstream dispersal by water resulting in an accumulation of propagule species further downstream, but the potential species richness is not realized because of too much substrate disturbance in the lower reaches, (3) intermediate disturbance in the middle reaches when the river transits from little eroded, morainic substrates to easily eroded riverine and lacustrine sediments, and (4) maximum heterogeneity in the middle reaches because of an overlap between morainic and sedimentary substrates. While the first hypothesis could be specific for the recently glaciated Scandinavia, the last three hypotheses should be more generally applicable, even when morainic soils are lacking.

Jansson et al. (2000) supported the role of dispersal by showing that free-flowing rivers exhibited continuous changes in the riparian flora downstream, whereas impounded rivers exhibited discontinuities in riparian species composition likely caused by the dams acting as barriers. In four dammed rivers in northern Sweden, where a

positive quadratic pattern of species richness likely occurred prior to damming, there was a negative quadratic pattern with species richness at its lowest in the mid reaches (Nilsson and Jansson 1995). Plant propagules are unlikely to pass dams, and their species richness in stranded drift was lower in a regulated than in a free-flowing river (Andersson et al. 2000a). In order to contribute to the local species pool of a reach, species need not only disperse but also establish. According to a landscape ecological framework, the invasion of new species occurs in several stages, (1) introduction, (2) colonization (germination), (3) successful establishment (survival and reproduction), (4) dispersal to new sites, (5) spatially distributed populations; which may lead to (6) invasive spread (With 2002). We measured the variation in the second stage of this process in relation to the spatial distribution of various environmental and biotic factors in the riparian corridor and evaluated whether the results could contribute to the understanding of the longitudinal patterns of species richness in entire rivers.

By following species richness data from the Vindel River over two decades we have observed species richness patterns in this specific system to be temporally variable depending on the magnitude of flood disturbance (B. M. Renöfält, C. Nilsson and R. Jansson in review). After a decade with only low to moderate flooding, species richness exhibited a hump-shaped pattern with the middle reaches having most species. The period of relative stability that preceded this pattern suggests that the hump-shaped pattern corresponds to the maximum species richness allowed by the local environment. In surveys made following large floods species richness decreased considerably downstream along the river, and mean species richness was lower than after a period with low to moderate flooding.

Deutschewitz et al. (2003) showed that species richness patterns for native as well as alien plants are promoted by similar factors and several studies have shown that alien plant species richness follows the pattern of native species richness (Levine 2000; Stadler et al. 2000; Sax 2002). We used *Helianthus annuus*, which is a non-native species in the northern boreal flora, to test invasiveness in the Vindel River corridor. We asked specifically (1) how does invasiveness in riparian corridors relate to species richness at different scales, and (2) does

invasiveness exhibit any specific trends downstream?

Methods

Study area

We worked along the Vindel River, which is a free-flowing river in northern Sweden (Figure 1). The river originates in the Scandinavian mountain range on the border between Norway and Sweden and empties in the Gulf of Bothnia. In other words, it intersects a cross section of the entire northern Swedish landscape, from the mountains to the coast. The river is 455 km long and joins the Ume River about 30 km from the coast, forming an 8th order river. The Vindel River system exhibits a pristine (non-regulated) water-level regime including spring flooding in mid June due to snowmelt and a subsequent lowering of the water level during the summer and winter, with some minor increases during the autumn. Natural discharge of the Vindel River at the confluence with the Ume River varies between 16 and 1787 m³s⁻¹, with an annual mean of 200 m³s⁻¹ (data from 1911–2000, Swedish Meteorological and Hydrological Institute). The range of flood height, relative to the summer low-water level is between 1.2 and 4.6 m in the studied portions of the main channel (Sundborg et al. 1980). Riverbank width ranges from 6.6 to 150.0 m in the main channel. Bank substrate is dominated by morainic deposits along the upper reaches of the main channel and by fine sediments along the lower reaches.

The annual growing season on land (numbers of days with mean temperatures exceeding +5 °C) ranges from < 140 days at the headwaters to nearly 170 days at the mouth of the river (Ångström 1974). The catchment area comprises 12,654 km², 5% of which are lakes. The riverbank vegetation along the Vindel River is distinctly vertically zoned at any given location, going from forest communities at the top, to shrub vegetation to herbaceous communities (Nilsson 1999). On a species level, an average riverbank along the main channel may show the following sequence of dominants (from top to bottom): *Pinus sylvestris*, *Vaccinium vitis-idaea*, *Alnus incana*, *Calluna vulgaris*, *Molinia caerulea*, *Salix lapponum*, *Carex juncella* and *Ranunculus reptans*. The riverbank

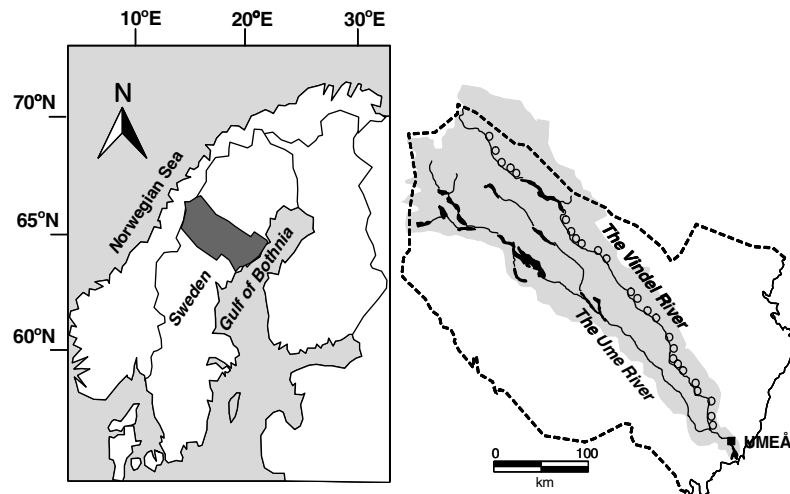


Figure 1. The Vindel River in northern Sweden. The map of Scandinavia to the left shows the study area in gray. Circles indicate the location of the 25 studied river reaches.

flora is composed of species indigenous to Sweden, i.e., exotics or aliens are almost absent. Working in a system virtually free from exotics or alien species requires precautions when choosing which species to introduce. We therefore designed the experiment to be certain not to become vectors of a new invasion.

Fieldwork

Fieldwork started in mid June in 1997, immediately after the spring flood had receded. Twenty-five river reaches were located at more or less equal distances from headwaters to mouth in the Vindel River (Figure 1). All reaches were located in the tranquil part of the transition area from turbulent to tranquil water. In this area current velocity slows down, and slackwater and eddies often occur. It represents the habitat where most water-borne propagules are deposited (Merritt and Wohl 2002), and where invasion is most likely to occur. Each site was 80-m long with four 0.5×0.5 m plots evenly distributed. All plots were located in the *Alnus incana* zone, or at corresponding levels. This zone corresponds to an elevation band within the riparian zone with approximately equal flooding conditions throughout the river. One hundred seeds of *Helianthus annuus* were sown in each plot. Seeds were sown in mid June, just after the recession of the spring flood peak. This time

corresponds to the time when the majority of dispersal by hydrochory occurs in this system. Additional dispersal sometimes occurs during autumn flooding but except for species germinating in autumn, these seeds are redistributed during next year's spring flood. Each plot was watered with 10 L of river water directly after sowing. To minimize competition among introduced species, only one exotic, *Helianthus annuus*, was introduced. It is an annual, non-native species that is not part of the riparian flora. Although this species is listed as an invasive weed in the US (USDA 2004), earlier experience of *Helianthus annuus* in dispersal experiments (Andersson et al. 2000b) has shown that this species exhibits traits that assure a safe invasion experiment. Even though it readily germinates on riverbanks in northern Sweden, it is far from flowering or producing seeds during its short, single growing season and therefore does not spread. We also knew that the seedlings do not survive winter. The seedlings are large with a characteristic shape and are thus easy to identify. Sowing of the plots was repeated in two subsequent years, 1997 and 1998.

Several environmental characteristics were quantified in the 200-m reach encompassing the experimental plots, with plots located in the center. These include river margin width (mean width of five measurements equally distributed along the reach), height (in the middle of the reach), percent cover of substrate types [classified

using the Wentworth grain sizes clay, silt, sand, gravel, pebbles, cobbles, and boulders (Chorley et al. 1984), supplemented by peat and bedrock (see Nilsson et al. 1991b for further details), substrate heterogeneity (number of substrates per reach), substrate fineness [Φ values calculated by weighing \log_2 -transformed values of mean particle size by percentage composition of the river margin substrate (Wright et al. 1984, Nilsson et al. 1989)], and percent cover of plants (herbs, graminoids and dwarf shrubs vs. shrubs and trees).

Plots were analyzed in mid August. The number of *Helianthus* seedlings was counted both years, whereas the presence and percent cover of all other species were determined in 1998 only. In mid August, frost nights are getting relatively common and we did not want to risk the seedlings to die before the inventory. Therefore, all counted *Helianthus* seedlings were in the cotyledon-stage. None of the seedlings had produced a second set of leaves, probably due to climatic conditions and none of them survived until the next growing season. Plant species composition of the 200-m reach encompassing the experimental plots was also recorded in 1998. The definition of species follows the taxonomy in Krok and Almquist (1994) with a few exceptions where two or more species difficult to separate were treated as one taxon.

Data analysis

Location along the river was measured on maps as the distance from the headwater, and plot invasiveness was measured as the number of *Helianthus* seedlings per plot. Reach invasiveness was calculated as the total number of seedling emergence per reach. Vegetation cover of the plot was obtained by combining the total cover of individual species < 0.5 m in height within a plot (therefore, cover values can exceed 100%), and dominance was calculated by dividing cover of the most dominant species by total cover of the plot (May 1975).

Relationships between invasiveness and species richness, both on plot and reach scales, were analyzed using Spearman's rank correlation with no prior assumptions of dependence and

independence. On the plot scale, invasiveness, percent cover of vegetation, and dominance of the plot, were also tested by Spearman's rank correlation analysis. All analyses were repeated for both years except for the vegetation cover of each plot, which was estimated only in 1998.

Downstream patterns of invasiveness in the river margin (total sum and variance in seedling emergence per reach) were explored by LOWESS regression (Trexler and Travis 1993). The main objectives of a LOWESS regression are to smooth noisy data and reveal general underlying patterns, not necessarily linear in nature. It is done by a series of locally-weighted least-square regressions around a moving focal point. Since LOWESS regression does not provide an estimate of the strengths and significance of the relationships, we also used polynomial regression to test the relationships. The relationships between invasiveness and environmental variables on a reach scale (substrate features, river margin height and area, and percent cover of vegetation) were tested using Spearman's rank correlation. Relationships between these environmental variables and location were explored with LOWESS regression and tested using linear and polynomial regressions. All statistical analyses were made using the SPSS statistical software package version 11.0, except for LOWESS regression where we used Sigmaplot, version 7.0.

Results

Invasiveness and species richness

Reach scale

Invasiveness was correlated between years 1997 and 1998 ($r = 0.59$, $p = 0.002$, Spearman's rank correlation coefficient), indicating consistency in response between years. We found no significant correlation between invasiveness and species richness, neither for 1997 nor 1998 or for both years combined (Figure 2).

Plot scale

We did not find any statistically significant correlation ($p > 0.05$) between plant invasiveness and plant species richness at the plot scale in 1997 or in 1998 (Figure 3a). The total cover of vegetation and the dominance in the plot were not correlated with

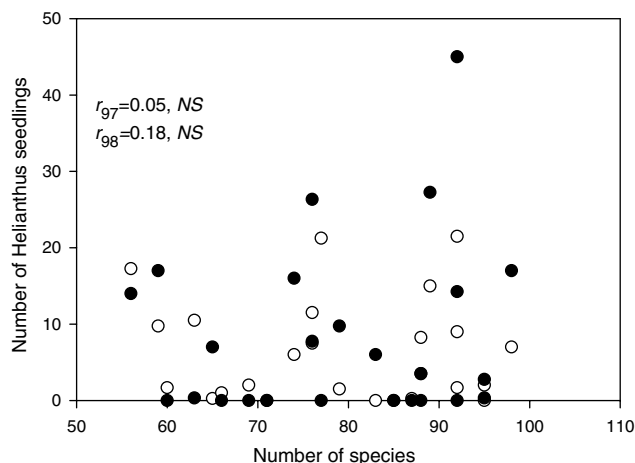


Figure 2. Relationships between reach invasiveness (total number of seedlings per reach) and reach species richness in the Vindel River in northern Sweden. \circ = 1997, \bullet = 1998. Invasiveness and reach species richness were not significantly correlated ($p > 0.05$).

invasiveness, but there was a tendency that only plots with less than 100% plant cover (i.e., presence of bare soil) and relatively low dominance had high establishment of *Helianthus* seedlings (Figures 3b and c). The species composition of plots was variable but plots with low establishment and high dominance were predominantly covered with graminoid species, such as *Deschampsia cespitosa*, a common tussock-forming grass along the Vindel River.

Invasiveness and location

The LOWESS regression revealed approximately the same longitudinal pattern of plant invasiveness in the two subsequent years (Figure 4a), with the number of emerging *Helianthus* seedlings being higher in the middle reaches of the river. In both 1997 and 1998 there was a statistically significant quadratic relationship between invasiveness and location (1997: $R^2 = 0.29$, $p = 0.0244$, 1998: $R^2 = 0.30$, $p = 0.0217$), also found when data from 1997 and 1998 were pooled ($R^2 = 0.25$, $p = 0.0012$).

We also tested downstream patterns of variance in invasiveness along the river (variance in number of seedlings per site) and found a weak, but significant quadratic relationship ($R^2 = 0.14$, $p = 0.0342$, data for both years pooled) with the middle reaches being more variable in establishment (Figure 4b).

Environmental variables

We investigated downstream patterns of environmental variables and found a positive quadratic relationship ($R^2 = 0.26$, $p = 0.038$) between substrate heterogeneity and location with middle reaches being the most heterogeneous. Substrate fineness exhibited a nearly significant negative quadratic relationship ($R^2 = 0.22$, $p = 0.068$) with the middle reaches having the coarsest substrate (Figure 5).

River margin width exhibited a strong linear increase downstream ($R^2 = 0.44$, $p = 0.0004$); an extreme outlier, where the upper part of the riparian zone consisted of a large, flat mire, was excluded from the data set. None of the other environmental variables [height of river margin, vegetation cover (trees and shrubs vs. herbs, graminoids and dwarf shrubs)] showed any significant relationship with location along the river ($p > 0.05$). The only environmental variable that showed any significant relationship with invasiveness was river margin width, which was negatively correlated with invasiveness in 1998 (Table 1).

Discussion

We did not find any significant correlation between invasiveness and species richness, neither on the reach nor on the plot scale (Figures 2 and 3). However, it is debated whether species richness

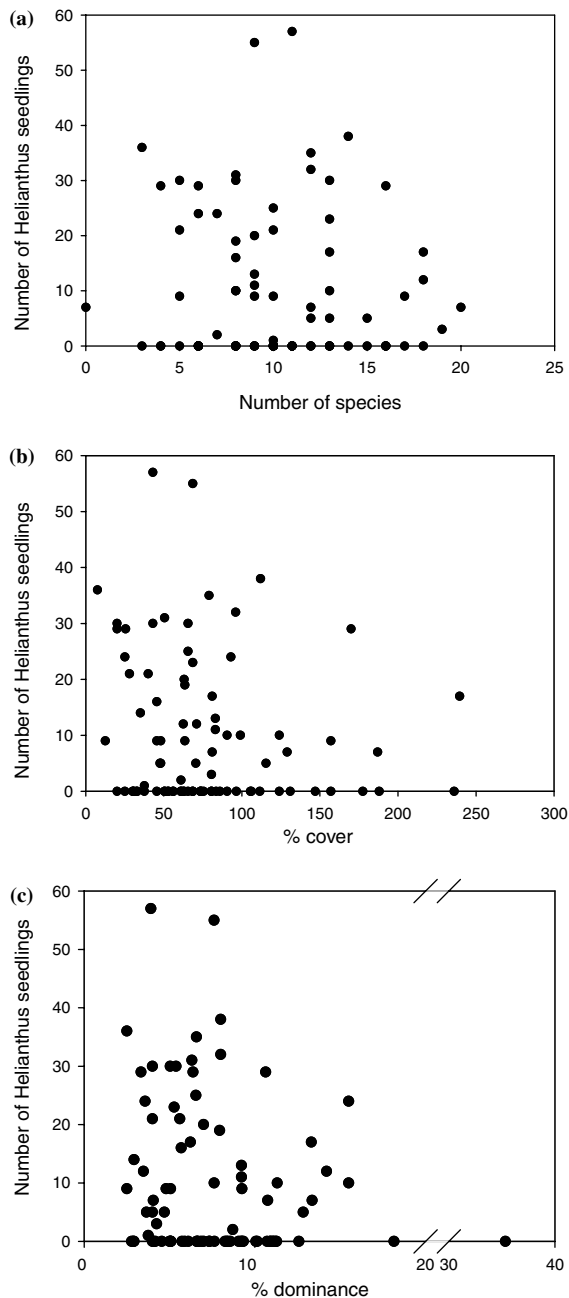


Figure 3. Relationships between number of *Helianthus annuus* seedlings and (a) species richness, (b) plant cover, and (c) relative plant dominance at the plot level. We found no significant correlations between invasiveness and these variables (Spearman's rank correlation, $p > 0.05$).

is a good predictor of invasiveness (Wardle 2001). Models and experimental studies often confirm the theory that diverse communities are more resistant to invasion (Tilman 1997; Naeem et al. 2000),

whereas the majority of large-scale observations show that more diverse systems have more exotic species (Lonsdale 1999). Light and nutrient availability are important for plant establishment. Planty-Tabacchi et al. (1996) found that sites with young immature vegetation were more easily invaded by alien species than sites with older, more mature vegetation. However, they concluded that the alder flats of the Hoh River in the western US, even though containing mature vegetation, held many alien species because seedling establishment was facilitated as a result of increased light availability after defoliation in autumn. Although we found no significant correlation between plot invasiveness and plot species richness, cover or dominance, high values of invasiveness were obtained only for plots with open space and relatively low dominance (Figure 3). Levine (2000) suggested that the effect of diversity arises at the germination/seedling stage because establishing seedlings are vulnerable to shading. It is, however, hard to evaluate the importance of shading in our study because most plots had bare soil and low dominance. Nutrient availability would certainly be one important factor for successful establishment. However, all of the germinated *Helianthus* seedlings were at the cotyledon stage, still living on endosperm resources. Competition for nutrients is thus not a likely explanation for our results.

The Vindel River intersects an entire landscape gradient from mountains to coast and exhibits a pattern of species diversity in its riparian corridor that is similar to other major free-flowing rivers in northern Sweden (Nilsson et al. 1989). Later observations have shown that this pattern is temporally variable (B. M. Renöfält, C. Nilsson and R. Jansson in review, but we advocate that the pattern that develops during a period with low disturbance from flooding (a positive quadratic pattern) is the best expression of the optimal local environmental conditions for diversity in the river. We used invasion experiments to explore whether these assumed optimal conditions in the local environment would also result in higher seed germination and establishment in the middle reaches, and found the same type of positive quadratic relationship (Figure 4a). In other words, those reaches that become inhabited by most species during relatively stable conditions also offered the best conditions for germination. We will discuss the quadratic downstream patterns of plant

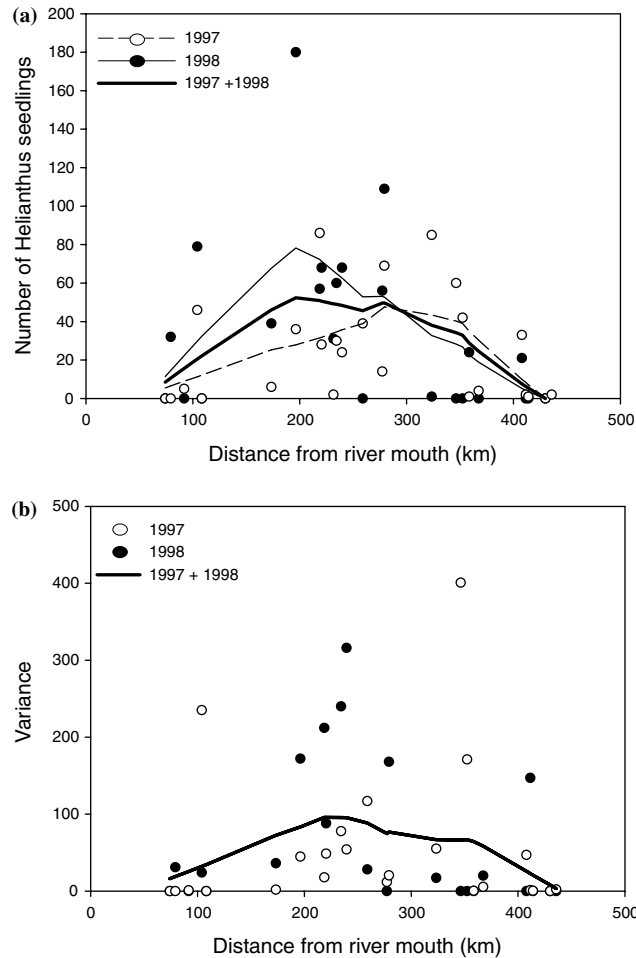


Figure 4. Downstream patterns of (a) invasiveness (total number of seedlings per reach) and (b) variation in invasiveness, along the Vindel River in northern Sweden. Lines are LOWESS curves ($f = 0.5$). Both invasiveness and variance in invasiveness showed a significant positive polynomial relationship to location (invasiveness 1997: $R^2 = 0.29$, $p = 0.024$, invasiveness 1998: $R^2 = 0.30$, $p = 0.022$, invasiveness 1997+1998: $R^2 = 0.25$, $p = 0.0012$, variation in invasiveness 1997+1998: $R^2 = 0.14$, $p = 0.034$).

invasiveness and species richness along the riparian corridors of the Vindel River, exploring possible, underlying mechanisms. We base our discussion on the four hypotheses presented by Nilsson and Jansson (1995).

The hypothesis explaining downstream patterns of species richness as resulting from dispersal assumes that the number of propagule species increases downstream, but that the potential for high species richness cannot be realized in the lower reaches because of low habitat heterogeneity and high disturbance (Nilsson and Jansson 1995). Hence, establishment conditions also need to be accounted for. We kept the dispersal factor constant by adding a similar number of seeds to each

plot, but invasiveness still varied, presumably due to variation in some environmental factor(s). In reality, however, dispersal often exhibits downstream variation (Andersson and Nilsson 2002), and seed addition experiments (Levine 2001; R. Jansson, personal observation) have shown that riparian vegetation is unsaturated, suggesting that seed limitation is an underlying factor for diversity patterns in rivers. Our results suggest that conditions for germination also need to be considered when evaluating the role of dispersal. In 1997, an additional flood due to heavy rainfall followed the spring flood immediately after seeds were sown onto the plots. Several plots were re-flooded, which probably removed seeds and

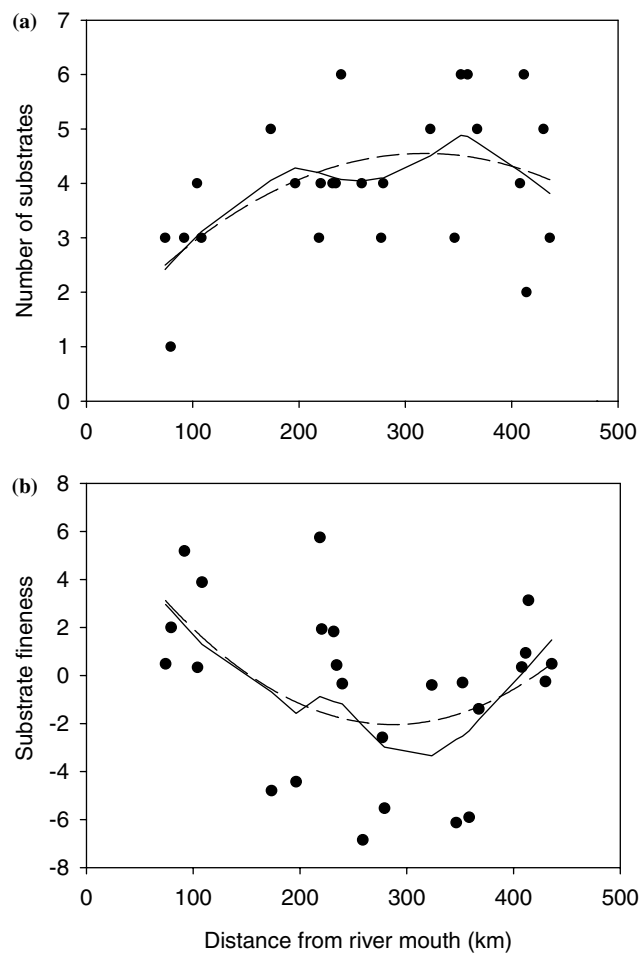


Figure 5. Patterns of (a) substrate numbers and (b) substrate fineness along the Vindel River in northern Sweden. Thin lines are LOWESS curves ($f = 0.5$), and dotted lines are regression lines. Substrate numbers were quadratically related to downstream location ($R^2 = 0.26$, $p = 0.038$); substrate fineness was not ($R^2 = 0.22$, $p = 0.068$).

affected the germination result negatively. The mean number of germinated seeds was lower in 1997 than in 1998 ($p = 0.039$, Wilcoxon's signed

Table 1. Relationships between invasiveness and environmental variables in riparian plots of the Vindel River in northern Sweden. Values are Spearman's correlation coefficients for 1997 and 1998. Significant correlations are boldfaced. $N = 25$ per test

Environmental variables	1997	1998
River margin width	-0.17 NS	-0.49*
River margin height	0.11 NS	-0.19 NS
Substrate heterogeneity	0.16 NS	0.21 NS
Substrate fineness	-0.36 NS	-0.25 NS
Cover of trees and shrubs	0.07 NS	-0.11 NS
Cover of herbs, graminoids and dwarf shrubs	-0.32 NS	-0.28 NS

* $p < 0.05$.

rank test), indicating that seeds may have been washed away from the plot or that germination ability was reduced. The fact that the 1997 and 1998 downstream patterns of invasiveness were correlated although hydrologic conditions differed indicates that the pattern may be relatively robust.

The intermediate disturbance hypothesis is another alternative. We have observed (B. M. Renöfält, C. Nilsson and R. Jansson in review) that downstream patterns of species richness in riparian corridors are temporally variable, most likely as a result of infrequent, large-scale disturbances such as extreme flooding. After a decade with relatively moderate flooding intensity, species richness exhibited a quadratic pattern along the river corridor. In contrast, during seasons immediately following extreme flooding, species richness

declined linearly downstream and attained a pattern similar to that of the surrounding regional diversity. These responses could explain why we did not find any significant correlation between reach species richness and invasiveness. In 1995, there was an extremely high and long-lasting spring flood in the Vindel River resulting in lower species richness per reach compared to the preceding more stable years (B. M. Renöfält, D. M. Merritt and C. Nilsson in review). If the middle reaches of the riparian corridor were more easily invaded by new species than other reaches, species richness in these areas would increase during relatively stable periods, supporting the hypothesis. However, since we sowed the *Helianthus* seeds after the flood peak their germination should not be directly affected by flood disturbance. The indirect effect of flooding disturbance, i.e., how it affects substrate features, cannot be discarded.

Habitat heterogeneity has been suggested as a general key factor promoting high diversity. Gould and Walker (1997) found a strong relationship between species richness and environmental heterogeneity in a Canadian arctic river. We found no correlation between neither substrate heterogeneity nor substrate fineness and invasiveness. However, in the Vindel River we found the same quadratic pattern for substrate heterogeneity as for plant species richness and plant invasiveness. Substrate fineness exhibited an inverse quadratic pattern with the middle reaches consisting of a coarser substrate (Figure 5). The lack of correlation between invasiveness and substrate heterogeneity might be an effect of scale as the plots in which invasiveness was measured may not have occurred in all types of substrates found at the reach scale. The fact that variance in invasiveness is highest in the middle reaches reflects the fact that middle reaches had a higher frequency of plots beneficial for invasion (Figure 4b). This could be due to substrate heterogeneity or some factor related to it, such as soil moisture. This makes it difficult to reject the hypothesis about habitat heterogeneity without further evaluation. The hypothesis about early post-glacial invasion is difficult to evaluate using the present results. However, we applied equal invasion pressure all along the river and the pattern of invasibility still varied, indicating that that the pattern is a result of contemporary processes rather than historic factors. The same species richness pattern has

been found also in rivers with different glacial histories (Planty-Tabacchi et al. 1996). This leaves habitat heterogeneity as the most likely factor explaining the pattern of plant invasiveness along the river. Since habitat heterogeneity is basically a result of disturbance, this factor cannot be discarded either.

There is now ample evidence that seed supply (i.e., invasion stage 1 – introduction – With 2002) can effect species composition (Zobel et al. 2000; Foster and Tilman 2003). The results of this study indicate that early stages in establishment [i.e., colonization (germination) according to With 2002] can help explaining species richness patterns in boreal rivers. These two stages are limiting for further successful establishment of a species on a landscape scale. The results also indicate that species richness *per se* is not a primary factor for invasiveness in the boreal riparian landscape, but rather that it is the spatial variation in factors such as habitat heterogeneity and disturbance patterns that affects invasiveness.

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