

Vegetation patterns and processes in riparian landscapes

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Abstract

The objective of this study was to increase understanding of the processes structuring and controlling the species richness of riparian plant communities. In particular, I examined the unimodal relationship, found in many rivers, between plant species richness and location along the river corridor. The most important finding was that this pattern is dynamic and varies with time, most likely in response to large-scale flood disturbances. I also found that the sensitivity to flood disturbance varied with the environmental setting of the riparian reaches. Turbulent sections of the river retained high species richness, whereas tranquil reaches had significantly lower species richness in years following high and prolonged flooding, compared to a period without extreme flood events. Riparian soils along turbulent reaches are more resistant to oxygen depletion during floods, a factor which is likely to contribute to the maintenance of species richness.

The finding that the species richness pattern varied with time led me to ask which factors control plant diversity along riparian zones. I addressed this question by formulating three contrasting, although not mutually exclusive, hypotheses: (1) longitudinal patterns in riparian plant species richness are governed by local, river-related processes independent of the regional species richness, (2) riparian plant species richness is controlled by dispersal along the river, i.e., longitudinal control, and (3) the variation in riparian plant species richness mirrors variation in regional richness, i.e., lateral control. I found indications of all three types of control, although local factors seemed to fit most of the criteria. Riparian species richness was not significantly correlated to species richness in the surrounding upland valley. It was however significantly negatively correlated to soil pH, a local habitat factor of the reach. The fact that the species richness pattern varied in time, corresponding to the presence or absence of extreme flood events suggest that it is influenced by local disturbance regimes. The potential for control by longitudinal dispersal was found to be highest in the middle reaches of a river. Here, the similarity between upland and riparian vegetation was lowest, and invasibility (germination ability) was highest. Earlier work has shown that regulated rivers have an inverted species richness pattern compared to free-flowing rivers, with lowest species richness in the middle reaches. One potential mechanism behind this could be varying susceptibility to disturbance along the river. I tested this by experimentally disturbing the vegetation, applying the same level of disturbance along an entire free-flowing river. However, the response to experimental disturbance did not vary with location, likely because of a major flood disturbance preceding the experiment.

Key words: anoxia, disturbance, downstream patterns, flooding, invasiveness, plant species richness, resilience, riparian vegetation, spatial, temporal

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Sammanfattning

Syftet med denna avhandling är att öka förståelsen för de processer som strukturerar och kontrollerar artrikedomen av kärlväxter hos växtsamhällen längs älvstränder. Tidigare studier, både i Sverige och andra delar av världen, har visat att artrikedomen av kärlväxter längs fritt strömmande vattendrag ofta uppvisar högst artrikedomen längs dess mellersta delar. Ett flertal olika förklaringar till detta mönster har presenterats. Exempel är intermediär störning från översvämning, hög habitatheterogenitet, och rumslig variation i effekten av nedströmsspridning. I det senare fallet tänker man sig att frön och andra spridningsenheter ackumuleras längs älvens lopp, men i de nedre delarna är störningen allt för stor för maximal etablering.

Det viktigaste resultatet i denna avhandling är att nedströmsmönstret för kärlväxters artrikedomen varierar över tiden, mest troligt som resultat av storskalig och långvarig översvämning under vårflood. De data som finns i avhandlingen omfattar bl.a. tre upprepade inventeringar av 200 m långa älvstrandssträckor fördelade längs hela Vindelälvens lopp. Dessa är gjorda med 10-åriga intervall. Två av dessa inventeringar utfördes strax efter långvariga översvämningar av hela strandzonen (hela stranden översvämmad under 8 respektive 12 dagar), och en gjordes efter en period av mera "normala" vårflooder (hela stranden översvämmad under 1-3 dagar). Olika typer av älvstränder reagerade olika mycket på denna variation i översvämning. Stränder längs forsar uppvisade mindre känslighet och bibehöll hög artrikedomen under alla tre undersökningarna, medan stränder längs sel (lugnflytande sträckor) hade signifikant lägre artrikedomen efter perioder av långvarig översvämning. Strandjorden längs selsträckor är generellt sett finkornigare och homogenera än strandjorden längs forsar, vilket leder till att vattnet i den översvämmade strandjorden rör sig relativt snabbt i forsar men blir mer stillastående i sel. Detta leder i sin tur till att forsarna bibehåller syresättningen av jorden bättre än vad selen gör. Andelen rudrata arter (som associeras med mänsklig aktivitet och är störningsgynnade) är generellt sett låg längs Vindelälvens stränder. Efter långvariga översvämningar var däremot andelen sådana arter signifikant högre i selen än vad som kunde förväntas, troligtvis på grund av att översvämningarna öppnade upp luckor i vegetationen där dessa arter snabbt kunde etablera sig.

Upptäckten att nedströmsmönstret i artrikedomen var variabelt över tiden ledde till frågan vilka faktorer som kontrollerar kärlväxters artdiversitet längs älvstränder. Jag angrep denna fråga genom att ställa upp tre kontrasterande hypoteser (men där en inte utesluter en annan): (1) nedströmsmönster i kärlväxters artrikedomen kontrolleras av lokala, älvrelaterade processer, oberoende av den omgivande regionala artrikedomen, (2) älvstränders artrikedomen kontrolleras av vattenspridning längs älven (longitudinell kontroll), (3) älvsträndernas artrikedomen speglar det

omgivande landskapets artrikedom (lateral kontroll). Jag fann indikationer på alla typer av kontroll, men lokala faktorer motsvarade flest kriterier. Det fanns ingen signifikant korrelation mellan omgivningen och älvstrandens artrikedom, inte heller fanns det någon korrelation mellan artrikedomen på små (0,25 m² provytor) och stora (200 m långa älvsträckor) skalor inom älvstranden. Artrikedomen uppvisade också en relativt stark negativ korrelation med strandjordens pH som är en lokal faktor. Det faktum att nedströmsmönstret i artrikedom är variabelt över tiden tyder också på att lokala störningsregimer är viktiga för artrikedomen. Vissa fakta tydde på att nedströmsspridningen är viktig för artrikedomen. De mellersta delarna av älven hade lägst similaritet mellan älvstrandens och omgivningens växtsamhällen. Detta tyder på att effekterna av nedströmsspridningen (longitudinell kontroll) är störst i dessa delar. Jag kunde också visa att invaderbarheten (förmågan för en art att etablera sig) är högst i de mellersta delarna av älven. Även om det inte fanns någon korrelation mellan artrikedomen i omgivningen och på älvstranden var similariteten i artsammansättning generellt sett hög längs älven vilket tyder på att älvstrandens flora inte är unik utan i stort sett utgör en kondenserad variant av den omgivande artpoolen.

Tidigare arbeten har visat att reglerade älvar uppvisar ett inverterat mönster i förhållande till de fritt strömmande, med lägst artrikedom i de mellersta delarna. En möjlig förklaring till detta skulle kunna vara att känsligheten för störning varierar längs älven. Jag testade detta experimentellt genom att störa vegetationen längs en fritt strömmande älvs hela lopp. Jag fann dock inga indikationer på att känsligheten skulle variera längs olika delar av älven. En anledning till detta kan dock vara att systemet nyligen hade utsatts för storskalig översvämning och på så sätt redan formats efter störningskänslighet.

Resultaten i denna avhandling visar att det är viktigt att ta hänsyn till både rumsliga och tidsmässiga skalor då man tolkar artrikedom i ett så pass dynamiskt system som älvstränder utgör. De naturliga processer som formar systemet varierar både i tid och rum, och både skötsel och restaureringsprojekt bör ta hänsyn till denna dynamik för att uppnå och bibehålla hög ekologisk status.

Contents

List of papers	1
Introduction	2
The riparian zone.....	2
Riparian zones in boreal rivers.....	3
Disturbance and its role for riparian zones.....	4
Species richness distribution in free-flowing rivers.....	6
Species richness distribution in regulated rivers.....	7
Objectives	7
Control of diversity.....	8
Temporal variation in species richness patterns.....	8
Sensitivity to disturbance.....	9
Methods	10
Study site.....	10
Flood history.....	11
Vegetation surveys.....	13
Environment.....	14
Invasion experiment.....	14
Disturbance experiment.....	15
Summary of the papers	15
Control of species richness.....	15
Temporal variation in species richness patterns.....	16
Sensitivity to disturbance.....	18
Conclusion	20
Implications for river management	22
Further perspectives	22
Acknowledgements	23
References	23
Tack	30

List of papers

This thesis is a summary of the following papers, which will be referred to in the text by their Roman numerals.

- I B. Malm Renöfält, D. M. Merritt and C. Nilsson. Connecting variation in vegetation and streamflow: the functions of large floods for riparian plant diversity and composition in boreal rivers. Submitted manuscript.

- II B. Malm Renöfält, R. Jansson and C. Nilsson. Spatial patterns of plant invasiveness in a riparian corridor. *Landscape Ecology*, in press. Published as “Articles in Advance” at: <http://www.kluweronline.com/issn/0921-2973/contents>, prepublication date: 09/08/2004.

- III B. Malm Renöfält, C. Nilsson and R. Jansson. Spatial and temporal patterns of species richness in a riparian landscape. Submitted manuscript.

- IV B. Malm Renöfält and C. Nilsson. Longitudinal variation in vegetation responses to disturbance in a riparian corridor along a boreal river. Manuscript.

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Introduction

Studying biodiversity is a central and common theme for many ecologists. Much of this work has attempted to understand the ecological concept of biodiversity maintenance (Schluter & Ricklefs 1993). Understanding the control of diversity is not an easy task. Finding correlations between environmental factors and biodiversity may be easy, but understanding the causal relationships between diversity and these factors can be extremely difficult (Huston 1994). Environmental factors may not only be related to diversity, but also strongly interrelated, and their relative importance might change in space and time. This makes it difficult and maybe impossible to fully understand diversity controls and threats.

Disturbance and spatial heterogeneity (along with several other factors) are brought forward as important controlling agents (e.g. Ricklefs & Schluter 1993; Huston 1994). The overarching hypothesis about disturbance is the “intermediate disturbance hypothesis” which predicts that diversity peaks at intermediate levels of disturbance (Connell 1978). Many studies have supported this hypothesis (e.g. Huston 1979; Sousa 1979), although others have shown both negative (e.g. Englund 1991; Wilson & Tilman 1991) and positive (e.g. Tilman 1983; Philips *et al.* 1994) linear relationships between diversity and disturbance. Spatial resource heterogeneity is theorized to promote high diversity (Ricklefs 1977; Grime 1979; Tilman 1982; Tilman & Pacala 1993; Palmer 1994) although other hypotheses and studies suggest that it is the average supply of the most limiting resource that determines diversity (e.g. McArthur & Wilson 1963; Rozenzweig & Abramsky 1993; Stevens & Carson 2002). However, it is a real challenge to identify and understand both disturbance regimes and heterogeneity, especially on larger scales.

The riparian zone

Rivers play a central role in almost all landscapes in the world. They often intersect large regions and connect a multitude of landscape elements. The structural and functional attributes of riverscapes include longitudinal resource gradients, floodplain dynamics, interactions with groundwater and a set of multiple disturbance regimes (Ward 1998). The riparian zone is defined as the interface between aquatic (continuously inundated) and terrestrial (rarely inundated) areas of the river corridor. Naiman & Décamps (1997) defined interfaces as areas that have resources and control energy and material flux. These attributes make the riparian zone vital to the health of the surrounding aquatic and terrestrial ecosystems. The contribution to surrounding ecosystems is a central function of the riparian zone but, as Simberloff & Cox (1987) point out, it also “constitutes an important habitat of its own right”. Riparian zones are “hotspots” of diversity, often superseding that of the surrounding landscape (e.g. Nilsson *et al.* 1989; Tabacchi *et al.* 1990; Junk

& Piedade 1993; Goebel *et al.* 2003), and places where important ecological and geomorphologic processes occur (Gregory *et al.* 1991; Naiman & Décamps 1997).

Rivers also belong to one of the most degraded ecosystems in the world, as a result of human exploitation (Petts 1984). Currently, humans use more than half of the world's run-off (Postel *et al.* 1996) for varying purposes, such as irrigation and hydropower production, and 59% of the world's 292 largest river systems are fragmented and regulated by dams (Nilsson *et al.*, submitted manuscript). This human intervention has disrupted the natural flow regime, either by changing the magnitude and frequency of floods, altering timing and/or duration of floods or by altering the rate of change between various discharges (Poff *et al.* 1997). These changes strongly affect organisms that live in the river and riparian zone.

The increasing development pressure and altering land use continue to threaten riparian and riverine organisms. During recent decades scientists have brought forward an accumulating body of evidence that a river's natural flow regime is vital to the health of the system (i.e., Poff *et al.* 1997; Richter & Postel 2004), and the analysis of how different flows affect and drive various processes has achieved more and more attention among scientists. Global warming and its associated changes in the global water cycle possess an additional threat to riverine systems (IPCC 2001). Magnitude, frequency and seasonality of floods are all expected to be altered as global temperature rises. The most important effects predicted for northern Scandinavia are an increase in annual average runoff and a change in the timing of the flow through the year (e.g. Hulme *et al.* 1999). A larger ratio of precipitation during winter will fall as rain. This will lead to increased runoff in winter and, as there is less snow to melt, spring runoff will decrease. Furthermore, the summer flow will be much more variable because of rainstorms. These forecasted changes concur with the trend observed during the last few decades, with increased winter, summer and autumn flows, and decreased spring runoff (Bergström & Carlsson 1993; Peterson *et al.* 2002). Large floods rejuvenate the riverine systems in many ways (Richter & Postel 2004), but it is not known what will happen if they become more frequent and unpredictable.

Riparian zones in boreal rivers

The present Swedish rivers are of a relatively recent origin. They were totally reshaped during the latest glaciation, which ended 8,000-12,000 yrs ago. The continent began to rebound as the inland ice cap melted off. This has resulted in a relatively distinct boundary between unsorted glacial substrates (till) and lacustrine sedimentary deposits above and below the former highest coastline. Boreal rivers

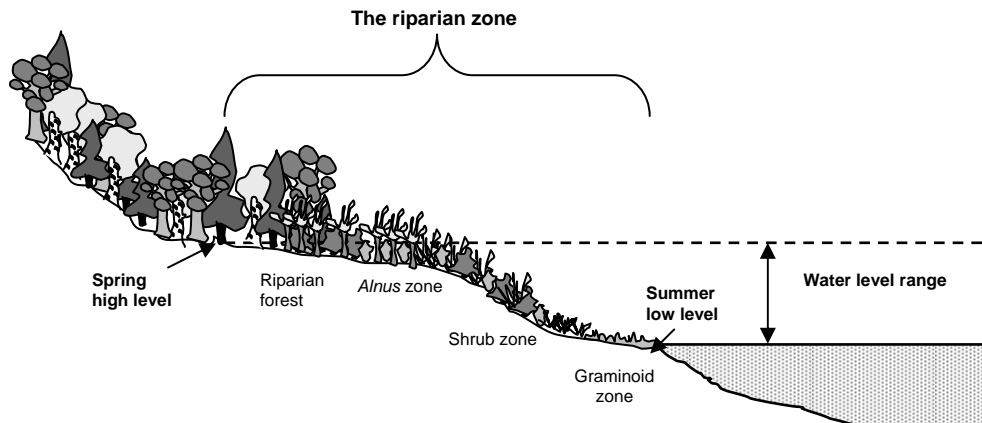


Figure 1. The riparian zone in boreal rivers.

have two major types of river reaches; turbulent (rapids) and tranquil (slow-flowing). Turbulent reaches typically have channels with coarse material such as bedrock, boulders, stones and gravel. The flow is fast and turbulent and sedimentation is low. Tranquil reaches, on the other hand, have a slower, more laminar flow, with higher sedimentation rates (but sedimentation in boreal rivers is still generally low as compared to alluvial rivers), which results in a much finer channel material containing a larger proportion of sand and silt (Nilsson 1999).

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 at the lower parts (Fig. 1). This zonation reflects the ability of the vegetation to cope with inundation (Bloom & Voesenek 1996; Bloom 1999). On a species level, an average riverbank along the main channel of the Vindel River 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*.

Disturbance and its role for vegetation in riparian zones

The high diversity within the riparian zone is first and foremost ascribed to its dynamic nature; a feature mainly associated with variation in flood disturbance (Naiman *et al.* 1993). Both the impact of the floodwater itself, and associated debris flows create a shifting mosaics of landforms. In boreal rivers, ice-jams cause flooding (Church 2002), and moving ice scars the substrate as well as the vegetation (Filip *et al.* 1989; Nilsson *et al.* 1993). As a consequence, riparian species richness will vary in space and time (Ward 1998). Rivers differ widely among each other in their geomorphologic response to flooding depending on their geological and geographical conditions. Depending on channel gradient and structure, channel geomorphology and sediment load, the ecological responses to

flooding will also vary within a river (e.g. Bornette *et al.* 1998; Palik *et al.* 1999; Bendix & Hupp 2000).

A natural flooding regime generally enhances riparian plant species richness by offering a variety of habitats and dampening the effects of competitive exclusion by highly competitive species (Naiman & Décamps 1997; Poff *et al.* 1997). Several studies have shown that species richness of riparian plants peaks at intermediate levels of flood frequency (i.e. Pollock *et al.* 1998; Chapin *et al.* 2002), as postulated by the “Intermediate Disturbance Hypothesis” (Connell 1978).

It is, however, difficult to distinguish positive from negative disturbances in a system that has developed and is maintained by natural, seasonal variation in the physical environment. Pickett & White (1985) defined disturbance as “any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment”. This definition was modified by Resh *et al.* (1988) to include only events that exceeded a predictable range in the frequency of occurrence or intensity of disturbance. Both of these definitions view disturbances as discrete events. Sparks *et al.* (1990) further refined the definition to include “graded changes in controlling factors that eventually exceed critical thresholds and cause effects similar to those of a discrete disturbance”. According to their definition disturbance in a river—floodplain system is defined as “an unpredictable event that disrupts structure or function at the ecosystem, community or population level”. The papers included in this thesis adopt this latter view.

Large floods provide several ecosystem functions to the river and its surrounding riparian zones (Richter & Postel 2004), but if the vegetation in riparian zones is flooded for a longer time or the discharge is extreme in magnitude, large floods may actually reduce species richness (Lewis *et al.* 1987; Stromberg 1993; Smith *et al.* 1998). Extreme floods may scour and uproot riparian forests and understorey vegetation, saturate soils thus altering the physical environment for organisms living within the flooded zone, and change sediment transport and redistribution of material within the riparian corridor (Friedman & Auble 1999). Extreme flooding during the growing season will exert a greater influence on vegetation than autumn and winter flooding because it affects plant growth and development (Newbold & Mountford 1997; Johansson & Nilsson 2002).

In addition, extreme floods affect soil conditions. Unsaturated soils have the same oxygen pressure as the atmosphere. When soils become waterlogged oxygen is rapidly depleted, gas exchange is obstructed by up to 10,000 times, and soil oxygen is further reduced by plant uptake through roots, soil animals, and microbial processes. Changes in the soil physical-chemical properties that accompany reducing conditions are best reflected in the oxidation-reduction potential (ORP). As oxygen levels decrease, anaerobic reduction processes begin. The reduced ions produced in the rhizosphere in this process may be toxic to some

plants. Depending on temperature and respiration activity, depletion of oxygen may take hours to days (Pezeshki 1994).

Species richness distribution along free flowing rivers

The longitudinal composition and richness of organisms living in river ecosystems are highly variable and several attempts have been made to understand if they vary in any predictable fashion. The “River Continuum Concept” (Vannote *et al.* 1980) predicted that diversity is highest in the middle reaches of large rivers, basically as a result of large environmental heterogeneity. This work mainly addressed macroinvertebrates. However, Nilsson *et al.* (1989, 1991a) showed that this was also the case for riparian plant species richness in free-flowing boreal rivers in northern Sweden. Similar patterns have been found in French and North American rivers, suggesting that the pattern might have some generality (Planty-Tabacchi *et al.* 1996). Nilsson & Jansson (1995) suggested four mechanisms for the quadratic distribution of species richness:

- 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.
- 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.
- Intermediate disturbance in the middle reaches when the river transits from little eroded, morainic substrates to easily eroded riverine and lacustrine sediments.
- 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. Planty-Tabacchi *et al.* (1996) suggested that the hump-shaped pattern of natural plant species richness found in the French and North American rivers was a result of intermediate disturbance in the middle course of the rivers. However, Gould & Walker (1998) found a lineary decreasing pattern, going from high altitudes towards the coast in the north-flowing Hood River in Arctic Canada. They also found that species richness correlated very strongly with soil pH, and more specifically a high within-site variation in soil pH, indicating that local habitat factors are important. Pollock *et al.* (1998) showed that species richness within a reach was positively correlated with the spatial heterogeneity in the variation of microsite flood frequencies indicating that variation in topography of the reach was beneficial for species richness.

Species richness distribution in regulated rivers

Longitudinal patterns of vascular plant diversity differ between regulated and free-flowing rivers in northern Sweden (Nilsson & Jansson 1995). Although the total species richness does not differ, reach species richness is lower in the regulated rivers. Regulated rivers exhibit an almost inverted downstream pattern compared to free-flowing ones, with lowest species richness in the middle reaches. Consequently, Nilsson & Jansson (1995) suggested that the difference could depend on four factors: (1) the persistence of former soil and vegetation varies along the river, (2) habitats for relict populations of plants have been destroyed, (3) dispersal of plants has been reduced following fragmentation of the river corridor, and (4) changed disturbance regimes resulting from regulation. They rejected the first hypothesis, as they did not find any difference in substrate heterogeneity between regulated and free-flowing rivers. The second hypothesis cannot be tested, but it is likely not valid for the reasons mentioned above. The third hypothesis has been supported by later work, showing that fragmentation of rivers by dams results in a disrupted floristic composition between impoundments (Jansson *et al.* 2000). The distribution of propagules is also hampered in rivers fragmented by dams (Andersson *et al.* 2000). The fourth hypothesis is difficult to test. One possibility is to try to quantify changes in different types of disturbances, for example flooding (frequency, duration and timing), mechanical scarring and litter deposition, on a longitudinal scale along regulated rivers, and compare them with free-flowing references to test if disturbance regimes in some regions have changed more than others. Another explanation could be that some regions of the river are more sensitive to disturbances, thereby losing more species.

Objectives

The broad aim of this thesis was to increase understanding of the processes structuring and controlling the species richness of riparian vascular plant communities. The work was based on wide temporal and spatial scales of species richness surveys and experimental designs to explore sensitivity to disturbances. The work in the thesis can be formulated in three main objectives:

- How is riparian vegetation controlled on a landscape scale?
- Are spatial patterns of plant species richness stable through time?
- How do various reaches of a river react to similar disturbances?

Control of diversity

I approached this question by exploring three contrasting (although not mutually exclusive) hypotheses (Table 1): (1) longitudinal patterns in riparian plant species richness are governed by local, river-related processes independent of the regional

species richness, (2) riparian plant species richness is controlled by dispersal along the river, i.e., longitudinal control, and (3) the variation in riparian plant species richness mirrors variation in regional richness, i.e., lateral control. I specifically tested for (1) correlations between local, riparian and upland diversity, (2) correlations between riparian species richness and environmental factors, and (3) temporal variation in riparian diversity patterns. (**III**, with additional results from **I** and **II**.)

Temporal variation in species richness patterns

I evaluate the four hypothesis postulated by Nilsson & Jansson (1995, see above), asking how their relative importance concurred with the results (**I-III**).

Intermediated disturbance—If intermediate flood disturbance is an important factor behind the hump-shaped species richness pattern, what happens when the disturbance gradient is shifted to a more extreme situation (**III**)?

Downstream dispersal—The role of downstream dispersal is hypothesized to be largest at intermediate reaches of the river. In paper **II** I ask if the outcome of a dispersal event, the germination stage, varies along the river, thus being a possible factor behind longitudinal species richness patterns. Paper **III** evaluates the importance of downstream dispersal by comparing similarity in species composition between riparian reaches and adjacent upland plots. If the effect of downstream dispersal (additional contribution of species) is higher in some areas, this could be reflected in lower similarities between upland and riparian vegetation in those areas.

Postglacial relict populations—If a relict population contributes to a higher species richness in middle reaches, this would be consistent through years. I evaluate this hypothesis mainly in paper **III**.

TABLE 1. Summary of three expected diversity patterns depending on whether riparian plant species richness is primary controlled by (1) lateral, regional processes, (2) longitudinal, regional processes by means of dispersal along the river corridor, or by (3) local habitat-related processes.

	Primary control of diversity		
	Local habitat factors	Longitudinal dispersal	Lateral dispersal
Correlation between local, riparian and upland diversity	No	No	Yes
Correlation between riparian species richness and environmental factors	Yes	No	No
Temporal variation in riparian diversity patterns	Yes	Yes	No

Habitat heterogeneity—I ask if species richness correlates with any measurements of habitat heterogeneity, mainly number of available substrates, but also site variation in soil pH. I also discuss longitudinal patterns in habitat heterogeneity (**II** and **III**) as being potentially important for optimized species richness.

Finally, I try to conceptualize their relative importance over a longer time period, using different flooding scenarios.

Sensitivity to disturbance

Extreme floods—Paper **I** addresses the issue of extreme floods, by asking how large (or more specifically how long-lasting) flood events would affect species richness. I also ask whether the sensitivity to flood stress and disturbance varies between different types of river reaches by comparing the effects on morphologically and hydraulically distinct reaches: tranquil and turbulent. The environmental differences between tranquil and turbulent reaches offer different conditions for plants during floods. Since the initial effect of inundation of plants is through the root system, I hypothesize that the hydrological connectivity of the substrate and thus the oxygen availability in flooded soils and the sensitivity of the riparian vegetation would differ between the two types of reaches which could be reflected in differing sensitivity to flood disturbance.

Invasive species—Invasive species is a major problem, facing river systems of the world (DeFerrari & Naiman 1994; Stohlgren *et al.* 1999; Brown & Peet 2003). It is also one of the major causes of diversity loss (Vitousek *et al.* 1997; Wilcove *et al.* 1998, Mack *et al.* 2000). Therefore, it is important to increase the understanding of factors influencing invasiveness of a system. I address the topic in paper **II**. Boreal riparian systems are virtually free from exotic species. The climatic conditions and relatively short growing seasons make these systems suitable for safe large-scale invasiveness studies with a carefully chosen target species. Previous work has often related sensitivity to invasions to existing species richness. Two rather contrasting views have been presented; (1) high species richness buffers against invasions and, (2) high species richness facilitates invasions. I asked specifically; (1) how does invasiveness in riparian corridors relate to species richness at different scales, and (2) does invasiveness exhibit spatial patterns?

Varying sensitivity—As mentioned above, several hypotheses have been suggested to why impounded rivers have lowest species richness in the middle reaches, whereas their free-flowing counterparts peak in species richness in the corresponding reaches. Paper **IV** addresses the fourth hypothesis formulated by Nilsson & Jansson (1995), by testing if the susceptibility of riparian vegetation to disturbance varies along the river. My main hypothesis was that vegetation along a

free-flowing river responds differently in different reaches to the same type and intensity of disturbance. I tested this hypothesis by evaluating the effects of mimicked natural disturbances, scouring, litter deposition, and grazing, on river reaches located along the entire Vindel River, both on species composition and species richness. I also tested the effect on functional species groups, thus separating between trees+shrubs, dwarf shrubs, herbs and graminoids.

Methods

Study site

The work included in this thesis was conducted in the Vindel River and its adjacent river valley (Fig. 2). The river originates in the mountains forming the border between Norway and Sweden, and empties in the Ume River, approximately 30 km from the coast, where it forms an 8th order river, with a total length of 455 km.

The range of flood heights, 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 on the same sites ranges from 6.6 to 150 m in the main channel. Bank substrate is dominated by morainic substrates along the upper reaches of the main channel and by fine sediments along the lower reaches. The annual growing season on land ranges from <140 d at the headwaters to nearly 170 d at the mouth of the river (Ångström 1974).

The catchment area comprises 12 654 km², 5% of which are lakes. Forests dominate the upland part of the catchment. Biogeographically, the catchment area ranges from alpine vegetation, to subalpine birch forest, to boreal coniferous forest.

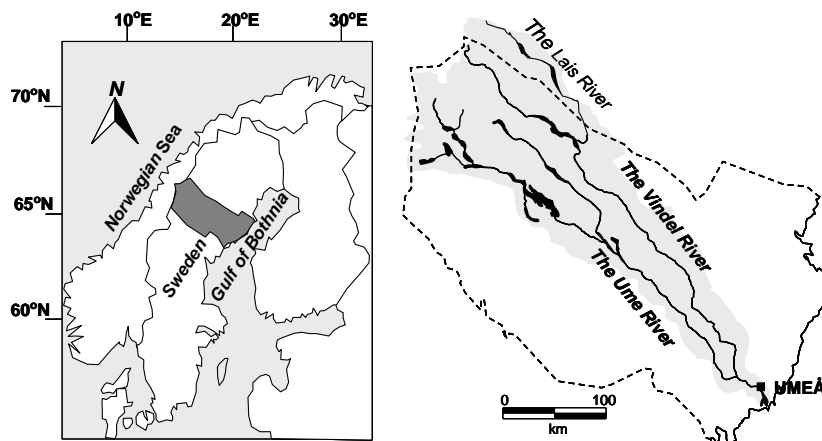


Figure 2: The location of the Vindel River.

Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate the coniferous forest. The broad-leaf component mainly consists of birch (*Betula* spp.) and aspen (*Populus tremula*). Goat willow (*Salix caprea*), grey alder (*Alnus incana*) and rowan (*Sorbus aucuparia*) occur as single trees or small stands. Marshlands and small lakes are common elements in the landscape. The catchment is sparsely populated (0.4-2.3 inhabitants km⁻²) and agricultural land is scarce (<10%).

Flood history

The hydrograph of a boreal river shows highest discharges in spring, as a result of snowmelt. Spring flood peaks usually occur in June and water levels are then subsequently lowered throughout the year, with some occasional minor increases in autumn as a result of rainfall. The water level regime in the Vindel River is pristine (free-flowing), but historically the river and its tributaries were extensively used for timber floating. This has resulted in a simplification of the riverbed, and structures that facilitate timber transport are still present in the channel. Natural discharge in the Vindel River at its confluence with the Ume River varies between 16 and 1800 m³s⁻¹, with an annual mean of 200 m³s⁻¹ (Swedish Meteorological and Hydrological Institute). The variation in annual flows between years is relatively small, but the inter-annual variation in flood peaks and duration can vary considerably (Fig. 3). Expressed by a coefficient of variation, the variation in mean annual flows was 15.9% for the period 1911—1988.

I used discharge data from two different gauging stations in the Vindel River, one situated in the upper and another in the lower part, to calculate maximum discharge and duration of flow that equals flooding of the entire river margin (Swedish Meteorological and Hydrological Institute, Fig. 3). Discharges exceeding 1000 m³s⁻¹ (which would represent flooding of the entire river margin in the lower part of the river, Fig. 3c) and 800 m³s⁻¹ (which would represent flooding of the entire river margin in the upper part of the river, Fig. 3d) occur approximately every second to third year but each event rarely lasts more than a couple of days. During the spring flood in 1978, discharge exceeded 1000 m³s⁻¹ during 9 d at the lower gauging station, and 800 m³s⁻¹ during 8 d at the upper gauging station.

During the 1980s, discharges rarely exceeded levels that flooded the entire riparian zone, and flood peaks did not last for more than a few days. In 1995, the Vindel River exhibited the largest flood on record. Discharge exceeded 1800 m³s⁻¹ at both the upper and lower gauging stations (accurate levels could not be measured in the lower part, since water levels exceeded the capability of the gauging station, hence the level given for 1995 in Fig. 3b is an underestimate of the

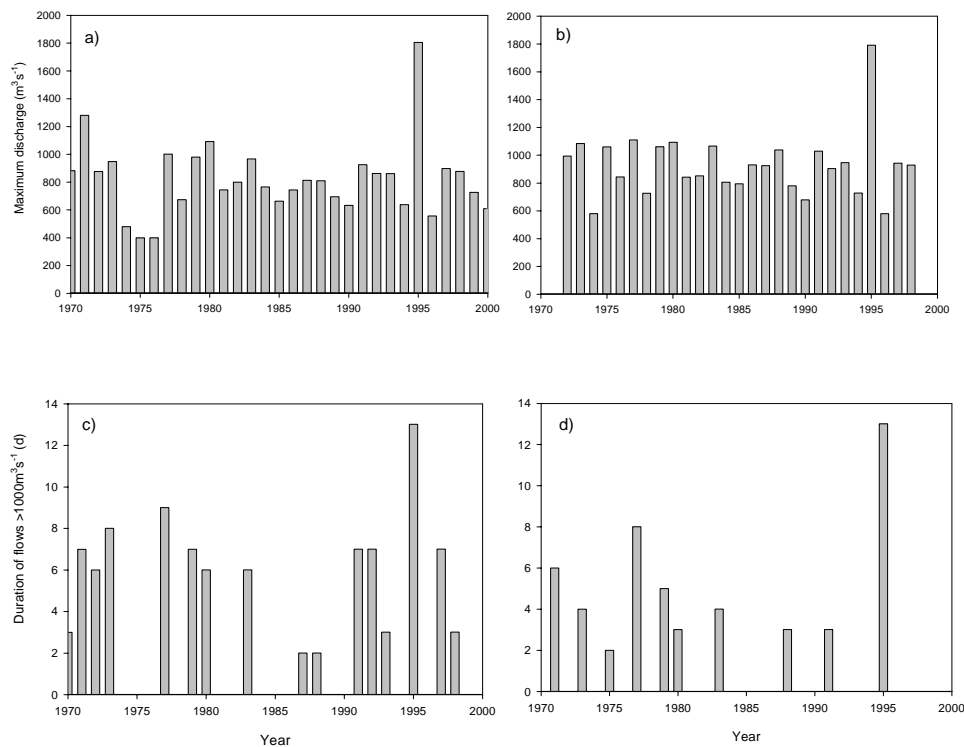


Figure 3: Discharge in the Vindel River, 1970–2000. Maximum discharge for: (a) upper part of the river, (b) lower part of the river. Duration of discharge (days) flooding the entire riparian zone for: (a) upper parts of the river (discharge $>800\text{m}^3\text{s}^{-1}$), (b) lower parts of the river (discharge $>1000\text{m}^3\text{s}^{-1}$).

true discharge), which is twice the normal mean maximum discharge of the lower part, and discharges exceeded $1000\text{m}^3\text{s}^{-1}$ and $800\text{m}^3\text{s}^{-1}$, respectively for 13 d (Figs 3c and d).

Vegetation surveys

Reach scale— I used reach scale riparian vegetation data collected at three occasions under a two-decade period; 1978, 1988 and 1997/98. All of these were used in papers **I** and **III**. In papers **II** and **IV**, I used the reach scale data collected in 1998. Each site consisted of a 200-m long reach spanning the entire width of the river margin that is regularly flooded during the growing season. This equals the entire area between the spring flood maximum, i.e., the highest level attained at least once every 2 yr, and the summer low level (Fig. 1). The spring high-water level was judged equivalent to the lower end of continuous occurrences of flood-intolerant species such as *Vaccinium myrtillus*. Deposition of water-transported

drift material and erosion of sediment and organic matter also helped determining the high-water level. Upland vegetation is generally species-poor compared to riparian zones, making the exact delimitation of the riparian zone less critical. Two persons recorded all vascular plant species growing within this reach independently, and species lists were combined. I also estimated the percentage cover of trees + shrubs (individuals of woody species >0.25 cm) and dwarf shrubs (< 0.25 cm) + herbs. This was made by eye independently by two persons; final cover values were reached by consensus. The 1997/98 data were as follows:

Plot scale—(III) Small-scale diversity was measured in four 0.25 m² plots situated in each of the 25 river turbulent reaches. These plots were all situated in the zone of *Alnus incana*, or at corresponding levels.

Upland—(III) Upland species richness was assessed in 25 plots with a size of 3.75 km² (1.5 x 2.5 km). These data were collected in 1996. To adequately assess plant species richness I adopted a strategy maximizing that all types of plant habitats were found and investigated. Two persons inventoried each plot by walking along a total of eight, equally wide line transects, arranged perpendicular to the short edge of each plot. Species lists were then combined. This strategy enabled the investigators to scan all plant habitats and to concentrate their efforts on species-rich communities.

Environment

Environmental characteristics of the reach—(I--IV) At each of the 200-m long reaches I noted a number of environmental characteristics. River-margin height was recorded for all data sets. River margin width (mean width of five measurements equally distributed along the reach), area (mean reach width × reach length) and percent cover of substrate types were recorded for the 1988 and 1997/98 datasets. Substrate types were 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). Values of mean substrate fineness were calculated by weighing log₂-transformed values of mean particle size by percentage composition of the river margin substrate (Wright *et al.* 1984; Nilsson *et al.* 1989). The locations of all reaches were measured as the distance from the source of the Vindel River.

Soil pH—(III) To evaluate the variation in soil pH along the river I sampled soil from the 25 turbulent river reaches representing the 1998 data. I used a 25 mm diameter manual soil auger and samples represent a soil depth of 5—20 cm depending on the depth of organic material. On each of these reaches, three soil samples were taken from the *Salix*, the *Alnus*, and the upper riparian forest zones, respectively. Each of those three samples was bulked from three sub samples, situated 0.5 m apart.

ORP and hydraulic connectivity—(I) ORP was measured in 2001. Ninety-six calibrated platinum tipped electrodes were installed at six sites along the river. Four sets of paired probes were randomly placed along 200 m long transects chosen to represent tranquil reaches and turbulent reaches. Probe tips were inserted to a depth of 15 cm and left in place for the remainder of the measurement period. ORP was measured to the nearest mV using an Orion portable pH meter five times during July in each of these sites immediately following the recession of peak flows. Reach-average hydraulic conductivity was calculated for tranquil and turbulent reaches from the 1997/98 data using the Kozeny-Carmen Bear equation (Freeze & Cherry 1979; Domenico & Schwartz 1998, see I). Particle size distributions were developed from substrate data gathered during field surveys.

Invasion experiment

(II) Twenty-five river reaches were located at more or less equal distances from headwaters to mouth in the Vindel River (Fig. 2). All reaches were located in the tranquil part of the transition area from turbulent to tranquil water. It represents the habitat where most waterborne propagules are deposited (Merritt & Wohl 2002), and where invasion is most likely to occur. Each site was 80-m long with four 0.5 x 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 corresponding to the time when the most dispersal by hydrochory occurs in this system. Each plot was watered with 10 L of river water directly after sowing. Sowing of the plots was repeated in two subsequent years, 1997 and 1998.

Plots were analysed 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.

Experimental disturbance

(IV) The experimental disturbance was performed on approximately the same 25 river reaches as the experimental invasion. Each of the reaches was located in the transition area between turbulent and tranquil water. The vegetation in this area is subjected to a similar disturbance regime all along the river. Four replicates of study blocks were located along a 100 m stretch in the upper turbulent section and four others along a 100-m long stretch of the slow-flowing section. Blocks in the turbulent section consisted of three randomly arranged plots; two types of mimicked natural disturbance, scouring and grazing, and a control plot. Blocks in the tranquil section consisted of one type of experimental disturbance, litter deposition, and a control plot.

Scouring was mimicked by raking (10 replicate strokes with a metal garden rake were used at each site), grazing was mimicked by cutting all aboveground vegetation approximately 1 cm above ground level, and litter deposition was carried out by evenly distributing sun-dried litter on top of the emerging vegetation. A follow-up of the disturbance treatments was made in mid August. The experiment was conducted during two subsequent years, 1997 and 1998.

Summary of the papers

Control of species richness

I found evidence for all the three hypotheses on how riparian plant diversity is controlled (Table 1), but most evidence indicated that local processes were most important.

Local control: First, I found no significant correlation between riparian and upland species richness. Secondly, I found a relatively strong negative relationship between riparian plant species richness and soil pH, a local attribute of the reach. This is consistent with the results by Gould & Walker (1987), although they found a positive relationship between soil pH and species richness, whereas I found a negative relationship. Thirdly, the longitudinal pattern in species richness differed between tranquil and turbulent reaches, presumably as a result of differences in the disturbance regime or local habitat factors. Fourthly, the longitudinal pattern in species richness along the riparian corridor varied temporally, suggesting control by local processes, such as flood disturbance. The temporal variation will be further discussed below.

Lateral control Some results support the hypothesis of a lateral, regional control of local, riparian species richness. First, downstream patterns of plant species richness were similar for both riparian and upland areas, both for natural and ruderal species in two out of three occasions (**III**, Figs 3 and 4). Secondly, the high similarities between riparian and upland floras indicate that the flora of riparian reaches is essentially a subset of the upland flora of the river valley (**III**, Table 2). However, large floristic similarities between riparian and upland areas are expected if riparian richness is locally controlled, given that riparian zones harbour a large proportion of the regional species pool.

Longitudinal control Similarity between riparian and upland floras was lowest in the middle reaches, where the role of downstream dispersal has been hypothesized to be highest (Nilsson & Jansson 1995). If riparian zones in the middle reaches receive many colonizing species from upstream areas, riparian—upland similarities should decrease. The pattern was analogous for both tranquil and turbulent reaches (**III**, Fig. 5b), and there was no difference in similarity between tranquil riparian reaches vs. upland, and turbulent riparian reaches vs.

upland (t-test, two tailed probability, $t=0.20$, $df=25$, $P>0.05$). This indicates that downstream dispersal has similar effects on both tranquil and turbulent reaches.

Temporal variation in species richness patterns

As Richter & Postel (2004) have pointed out, in order to maintain a healthy ecosystem, a river is dependent on the whole flow spectrum. This makes it dynamic over longer time periods. This is easily comprehensible for alluvial rivers, where erosion and sedimentation can shift the whole river channel over large areas and where large floodplains get flooded and species communities shift accordingly. Boreal rivers usually have a more stable channel and the riparian areas are restricted to less erosive material. On a smaller scale, it is easy to imagine that the spatial configuration of species richness is largely variable. Flood erosion may cause entire populations to go extinct at some places, whereas the creation of new habitats, such as gravel bars, may open up possibilities for new communities to establish. This will result in a mosaic pattern of diversity distribution. On larger landscape scales, diversity would be expected to be more stable, depending on climate gradients, geology and other more consistent factors and vary in a predictable manner.

As mentioned earlier, the species distribution of vascular plants along boreal riparian zones has shown to peak at intermediate reaches (Nilsson *et al.* 1991a, Nilsson *et al.* 1989). In contrast to previous studies, I found that species richness decreased linearly towards the coast in two out of three surveys (III, Fig. 4). The downstream pattern found in natural species richness in the 2 yr following long-lasting floods resembled the pattern found in the surrounding landscape. In a period without long-lasting floods species richness was highest in the inland parts of the river corridor. This led me to ask what caused these temporal differences.

I evaluated the four hypotheses postulated by Nilsson & Jansson (1995, *see above*) by exploring whether they are consistent with the results in my other studies. Two questions that need to be addressed are (1) why species richness increased most in the middle reaches of the river in the absence of major disturbance events, and (2) why this pattern was absent in years following major disturbance events.

Intermediate disturbance—The hypothesis about intermediate disturbance could potentially answer both questions. The longitudinal gradient of the river could be viewed as a disturbance gradient. In 'normal' years with moderate floods, which increase in magnitude and duration along the river, riparian zones in the middle reaches, where substrates turn from stable, morainic substrates to unstable sediments, are intermediately disturbed by flooding, which favours high diversity. During extreme events with long-lasting, high floods, this gradient is compressed towards the extreme end of the disturbance spectrum, where diversity decreases with disturbance intensity (Fig. 4).

My results show that mean reach species richness is temporally variable and suggest that long-lasting floods reduce local plant species richness in the riparian corridor but that vegetation can recover between major flood events. The extreme floods of 1978 and 1995 (Fig. 2) strongly disturbed the river corridor, resulting in significantly lower species richness per reach in 1997/98 and 1978 than in 1988 (**I**, Fig. 3). Such effects of flood disturbance should increase downstream the river as the magnitude and duration of floods increase. This would cause more extinction of plant populations, potentially explaining the negative downstream trends in riparian species richness.

Downstream dispersal—Downstream dispersal has been proposed as an explanation for the hump-shaped pattern found in 1988, when species increased along the river with a maximum in the middle reaches, where after the sediments become too easily disturbed to allow for all colonizing species to establish (Nilsson *et al.* 1994). Lower similarities between the riparian corridor and the surrounding upland in the middle reaches are consistent with downstream dispersal being an important process for the species composition of the riparian zone (**III**, Fig. 5). Also invasiveness could be a potential explanation for this pattern. The results of the experimental study of invasiveness showed that middle, inland reaches of the river were more easily invaded than mountain or coastal areas (**II**, Fig. 4). Dispersal was kept constant in this experiment and it was performed after the recession of the peak in spring flood, excluding any direct effects of flood disturbance or variability in dispersal. In the absence of large disturbance events downstream dispersal might build up species richness in areas more susceptible to invasions. Neither the dispersal hypothesis, nor the invasiveness hypothesis could however explain the linear decrease found in 1978 and 1997/98.

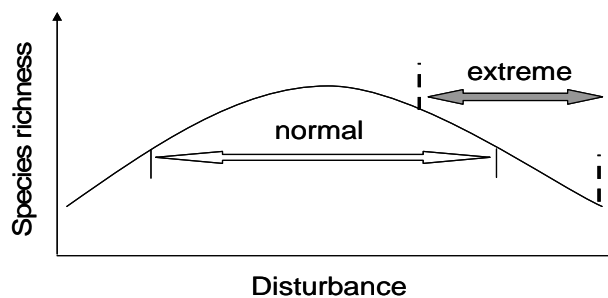


Figure 4. Conceptual relationship between species richness patterns and level of disturbance. The unfilled arrow represents the “normal” situation in the river. The shaded arrow represents extreme flooding situations.

Postglacial relict populations—The hypothesis about postglacial relict populations can be rejected on the ground of that the area with maximum richness found in 1988, harbouring relict populations according to the hypothesis, was considerably less species rich only 10 yr before (**III**, Fig. 4).

Habitat heterogeneity—This thesis offers few insights about the hypothesis on habitat heterogeneity. Species richness was most strongly related to soil pH (**III**, Table 2), but I found no evidence for a relationship between pH and any measure of heterogeneity. However, downstream patterns in site variation in pH exhibit the same hump-shaped pattern as found for species richness in 1988, and by Nilsson *et al.* (1991, 1994, 1995). Also, the number of available substrates was highest in the middle reaches of the river (**II**, Fig. 5a), but I found no correlation between species richness and number of available substrates.

Sensitivity to disturbance

Extreme floods — One potential environmental factor that differs between turbulent and tranquil reaches is the ability to withstand anoxia during long-lasting floods. If soils are anoxic over longer time periods, toxic irons will be produced. The intensity of soil redox potential has considerable influence on plant functioning and growth, although the critical intensity is species specific (Pezeshki & DeLaune 1998). However, “as a rule, the majority of plants succumb more quickly to flooding than to desiccation” (Larcher 2003). I tested how the riparian soils in tranquil and turbulent reaches, respectively, reacted to flooding and found that they differed significantly in their susceptibility to anoxia (**I**, Fig. 5). Hydraulic connectivity, which may reduce the risk of oxygen depletion through physical and microbial processes if a hydraulic gradient exists to increase turnover of shallow groundwater, differed significantly between turbulent and tranquil reaches, with considerably higher conductivity in the turbulent reaches (**I**, Fig. 6). These results indicate that reduced oxygen depletion in some habitats might be an important factor maintaining plant life during long floods and waterlogging of the soil.

Invasibility — Invasibility was highest in the middle reaches of the river in both years (**II**, Fig. 4). I could not find any significant correlations between invasibility and any environmental variables of the reach, except for river margin width (**II**, Table 1). The number of available substrates showed a similar downstream pattern as that of invasibility, and substrate fineness showed an inverse pattern to that of invasiveness (**II**, Fig. 5). I did not find any significant correlation between invasiveness and species richness, neither on the reach nor on the plot scale (**II**, Figs 2 and 3). However, it is debated whether species richness 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). My results 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.

Exotic species are virtually absent from the boreal riparian flora. However, a small percentage of the species are so-called ruderals (classification following Lid *et al.* 1987). Ruderal species have the same strategy as some of the invasive species, with high numbers of readily dispersed seeds and rapid colonisation rates. Looking at temporal variation in ruderal species in tranquil and turbulent reaches, respectively, showed that ruderal species richness in turbulent reaches remains relatively low and stable between years, whereas tranquil reaches are more variable, with a higher amount of ruderal species after flooding years (**I**, Table 2). In the years following long-lasting flooding, ruderal species were significantly underrepresented in turbulent reaches compared to what could be expected based on the total amount of ruderals these years. In a period of more normal flooding, the overall number of ruderal species was low. This implies that extreme flooding creates favourable conditions for opportunistic species to colonise in tranquil reaches, possibly due to plant mortality as a result of anoxia (**I**). Large floods create gaps in the vegetation, thereby allowing vegetation to rejuvenate but also paving the way for opportunistic, new species, including aliens to colonise (Menges & Waller 1983). It also implies that turbulent reaches have inherent mechanisms to withstand colonisation of ruderal species.

Downstream variation in sensitivity to disturbance — I did not find any support for the main hypothesis that middle reaches of the river are less resistant to disturbance. Such a support would have brought me closer to an explanation of the processes producing the inverted pattern of species richness found in regulated rivers (Nilsson & Jansson 1995).

One factor that interferes with the interpretation of this study is that the hump-shaped pattern of species richness along the river has turned out to be more unstable than previously believed (**III**, Fig. 4). Therefore, the responses of the mimicked disturbance might have been hampered because the system was too recently disturbed.

Graminoids resisted disturbance, except in the case of litter deposition (**IV**, Table 3). Many of the graminoids along the riparian zone were tuft-forming grasses and sedges resistant to scouring, such as *Deschampsia cespitosa*, *Molinia caerulea* and *Carex nigra+juncella*. These tufts were very resistant to raking. Graminoids also have a unique ability to grow after they have been subjected to grazing or cutting since grass leaves grow primarily from the base.

Although there was no longitudinal variation in the response to disturbance on the reach scale, I found a relationship between the effect of disturbance and the species richness on the plot scale (0.5 x 0.5 m). As predicted for the reach scale,

species-rich plots were less resistant to mimicked disturbance. In both years, the absolute species loss was highest for plots with high species richness and for almost all treatments. This could seem reasonable because they had more species to lose. However, the results indicate that species-rich plots lost proportionally more species as a result of denudation and grazing (IV, Fig. 3). I do not know whether this could be translated into how species-rich reaches react to disturbance. Although reach-scale and plot-scale species richness exhibited the same monotonically decreasing downstream pattern after the 1995 flood, they were not correlated, most likely due to a relatively large variation at the smaller scale (III).

Conclusion

I propose that species richness patterns in the riparian corridor change in response to the dynamics of flood disturbance. Whereas regular, moderate flooding is required to sustain high diversity in riparian ecosystems (Pollock *et al.* 1998), severe flooding is suggested to lower diversity throughout the riparian corridor by causing extinction of plant populations, as shown by the lower line in Fig. 5a, representing the 1997/98 species richness data (the year with lowest diversity). In years with relatively moderate floods, species richness may increase. This is shown by the upper curve, representing the downstream pattern of species richness in 1988 (Fig. 5a). Reaches situated in the middle of the river corridor have an intrinsic potential to accumulate most species. The mechanism could be that these reaches are intermediately disturbed by floods, harbour maximum habitat heterogeneity, receive high diversity of colonizing diaspores, reflected in a higher dissimilarity in species composition between upland and riparian vegetation (Fig. 5c), or because they are easily invaded (Fig. 5b), or a combination of these factors.

I further propose that the resistance to disturbance may vary between different regions of the river and with the environmental settings of a reach. Turbulent river reaches were more resistant to extended flooding. They had better aerated soils during flooding, thereby reducing the risk for potentially damaging anoxia. Ruderal species numbers responded to the prolonged floods, showing succeeding peaks in numbers in the tranquil reaches but not in the turbulent ones. I also found that the same region of the river that harboured maximum diversity in the period with only low to moderate flooding was the same region that was most easily invaded by an alien exotic species. This implies that factors that promote high natural diversity may also facilitate invasions by alien species.

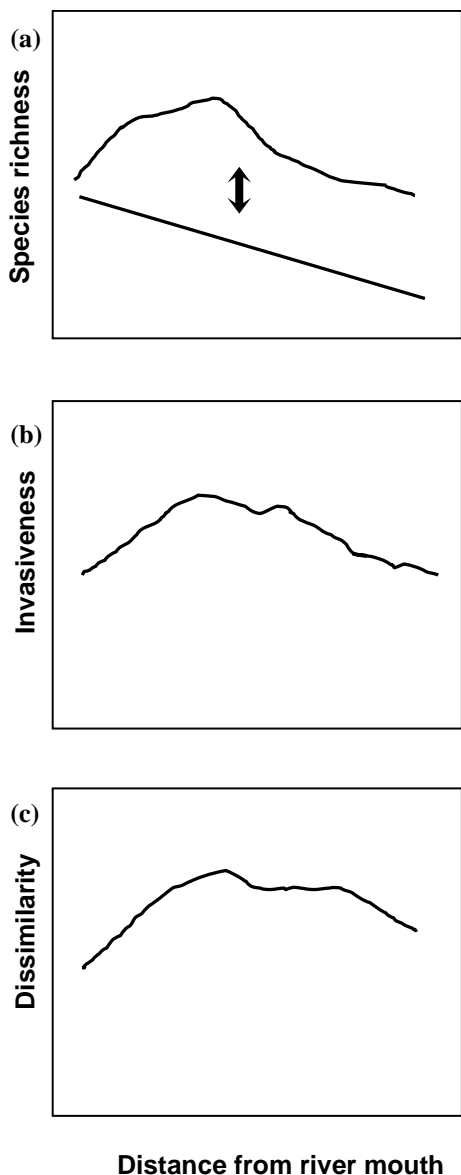


Figure 5. Conceptual figure showing (a) the range of variation in species richness [curves represent original species richness patterns from 1988 (upper curve, LOWESS regression) and 1997/98 (lower curve, linear regression)], (b) invasibility (curve represents pooled invasibility values from 1997 and 1998. LOWESS regression), and (c) dissimilarity between upland and riparian vegetation (curve represents dissimilarity data from 1997/98, LOWESS regression), along the Vindel River.

Implications for river management

My results suggest that it is necessary to incorporate both spatial and temporal scales in the interpretation of the dynamics of riverine plant diversity. In order to maintain healthy riparian zones, it is important to consider intra- and interannual flows and how the environmental responses to variation affect diversity. These results coincide with the growing notion among scientists that a river needs its entire flow spectrum to maintain ecological health. This is in stark contrast to how most of the world's larger river systems have been managed up to the present day

situation. As Richter & Postel (2004) put it; “rather than flowing to the rhythms of the hydrological cycle, they are turned on and off like elaborate plumbing works”. At best, only a minor fraction of the flow (often not even corresponding to base flow) is maintained for ecological purposes. However, some progress is being made. Richter & Postel (2004) put forward the South African 1998 National Water Act as a landmark in international water policy. The act states that “the quantity, quality and reliability of water required to maintain ecological functions on which humans depend shall be reserved so that the human use of water does not individually or cumulatively compromise the long-term sustainability of aquatic and associated ecosystems”. Also the European Water Framework Directive (EC 2000) incorporates a more holistic view on freshwater management, where ecological health is recognised as an ultimate goal.

The results further suggest that resistance and resilience of the riparian vegetation vary with the geomorphological setup of specific river reaches. The spatial and temporal scopes of human impact may therefore affect different parts of a river differently. I found that turbulent reaches resisted flood disturbance better than the tranquil reaches. If the forecasted effects of climate change make floods more unpredictable and more severe, these reaches may serve as refugia for plant diversity. Unfortunately, river exploitation worldwide has dramatically reduced the number of turbulent river reaches (dam construction in such reaches) or simplified their bed morphology (channelization). The areas along rivers that harbour the highest species diversity and should be the targets for protection have been those most hardly hit by schemes of river development. Restoration efforts made within the last decade, such as dam removal and channel widening, can thus prove to be useful tools in the rehabilitation of turbulent river reaches and of the resilience of entire rivers

Restoration efforts should consider and reflect the dynamic nature of these systems. These include the actual restoration, the post-restoration monitoring and the setting of goals. It is preferable to avoid “snap-shot” evaluations, but rather do continuous long-term follow-ups. Setting very specific goals without regarding the dynamics of a system (or allowing for it in the first place) may lead to a “failure” to meet these goals. A more flexible approach could be to follow restoration trajectories based on best available knowledge about the system, to evaluate if a system is moving towards a desired state.

Further perspectives

One obvious question in ecology is of course how general our findings are, especially when those findings stem from *in vivo* experiments and observations with a myriad of factors present, which are very difficult to control. The more generality that can be ascribed to observed patterns and processes, the better it is

thought to be. The truth is of course that nature is complex, and so many factors differ in space and time from one place to another. This is especially true for large scales. One way to test the generality of some of the findings included in this thesis would be to perform controlled experiments, including a number of target species, and test how they react to disturbances at various environmental settings in a selection of river ecosystems.

It is also desirable to attain a more thorough knowledge about how local riparian habitat factors vary along a free-flowing river, and how they interact with natural disturbances such as floods, draughts and erosion. This might add some further understanding to how species richness is maintained and what drives the dynamism of the system.

If longitudinal variation in the sensitivity to disturbance does not explain the responses following regulation, what then causes the patterns along regulated rivers? Some questions that need answering are:

- How has the disturbance regime changed, and what types of disturbances have been introduced or altered in the regulated system?
- Do they act similar all along the river or does the degree of disturbance vary?
- If some regions of the river are more strongly affected by regulation, how does this affect recruitment of new plants?
- How does the disruption of dispersal affect the local flora of the reach, and will the effect be stronger in some regions?

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