

Disrupted connectivity in biotic and geomorphic patterns in stream-lake systems

Lina Polvi¹ and Lovisa Lind²

¹Umeå Universitet Teknisk-Naturvetenskaplig Fakultet

²Karlstad University

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Abstract

Ecological and geomorphic theory assume longitudinal connectivity; we test whether these concepts apply in a naturally disconnected stream network with mainstem lakes and coarse glacial legacy sediment. We determined downstream hydraulic geometry relationships for channel width and inventoried riparian vegetation in each new process-domain (rapids, slow-flowing, lakes) along a continuous ~10 km segment in two catchments in northern Sweden. Hydraulic geometry relationships for width were very weak, indicating that although channel width does increase in the downstream direction, there is very large local variation in width, within and among process domains. Riparian vegetation richness did not increase markedly downstream as expected in a connected stream network, and there are very weak relationships between riparian vegetation composition similarity among reaches and distance between reaches, indicating that hydrochory plays a minor role in metacommunity organization. Formerly continentally-glaciated catchments are thus highly fragmented and local factors steer geomorphic form and biotic organization.

Title Page

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Authors: Lina E. Polvi¹ & Lovisa Lind^{1,2}

¹Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden, lina.polvi@umu.se

²Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden, lovalind@gmail.com

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Tel: +46 90 786 6190

Mobile: +46 70 256 3446

E-mail: lina.polvi@umu.se

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Corresponding author: Lina Polvi, Umeå University, Department of Ecology & Environmental Science, Linnaeus väg 6, 907 36 Umeå, Sweden

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Abstract Page

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Main text

INTRODUCTION

At large spatial scales, a stream's geomorphic and ecological form and behavior can be predicted based on longitudinal trends (e.g., Downing et al., 2012). From a geomorphic perspective, at the catchment scale, the concept of downstream hydraulic geometry (DHG) shows that several channel form parameters, including width and depth, increase as a power function of bankfull discharge (Leopold & Maddock, 1953), which in turn increases with drainage area. Due to predicted decreases in slope and thus shear stress, bed material grain size should also decrease (Gasparini et al., 1999). Within stream ecology, Vannote et al., 1980 built on the idea of downstream hydraulic geometry by extending the idea of longitudinal patterns or adjustments from the “physical system of geomorphologists into a biological analog” (Vannote et al., 1980), developing the river continuum concept (RCC). The RCC predicts longitudinal patterns in multiple stream ecosystem factors, including the type of macroinvertebrates present, the ratio of photosynthesis to respiration and the relative amount of coarse and fine particulate organic matter, all of which are strongly coupled to the predicted increase in channel width. Furthermore, biodiversity (species richness) often shows a predictable downstream increasing trend towards the middle of the catchment due to dispersal effects and more favorable growing conditions (e.g., Nilsson et al., 1989, Dunn et al., 2011, Kuglerová et al., 2015).

Since the establishment of the DHG and RCC concepts, exceptions to unidirectional

downstream trends have been described, including the geomorphic process domain concept (Montgomery, 1999), the serial discontinuity concept (Ward & Stanford, 1995), patch dynamics (Townsend, 1989; Poole, 2002), the river wave concept (Humphries et al., 2014), and the mighty headwater hypothesis (Finn et al., 2011). However, these concepts of downstream trends, implying longitudinal connectivity, still form the basis for multiple assumptions and concepts within river science (e.g., Surian, 2002; Frings, 2008; Dunne & Jerolmack, 2020). For example, the amount of allochthonous material input into a stream tends to decrease with increased channel width due to the greater percentage of the channel covered by canopy compared to larger channels (Vannote et al., 1980, Doi, 2009). To study these changes, rather than measuring channel width and canopy cover, studies commonly rely on drainage area as a proxy (e.g., Jonsson et al., 2018). If these basic longitudinal gradients do not exist in a certain catchment, then we must re-examine which geomorphic and ecological processes drive longitudinal stream patterns. The serial discontinuity concept,

predicts local diversity to increase with increasing distance to dams (Ward & Stanford, 1995), and Green et al. (n.d.) found the same pattern for invertebrates but along a lake-stream system with lakes disrupting the continuity. However, geomorphic and ecological trends are often not examined simultaneously to explain organization of a stream network, even though they are intertwined with each other. Hence, the objective of this study was to examine whether geomorphic and ecological longitudinal trends, as defined by channel width and riparian vegetation richness and community composition, exist in a naturally disconnected catchment consisting of lakes and streams. By understanding the geomorphic and biotic longitudinal organization of a stream network, we can set expectations for recovery after stream restoration.

Background

Downstream hydraulic geometry can predict several aspects of stream properties including mean velocity and depth (Leopold & Maddock, 1953; Lee & Julien, 2006), however, channel width is most widely studied due to the ease of making remote or simple field measurements (e.g., Fisher et al., 2013; Dunne & Jerolmack, 2020). Longitudinal increases in channel width show a consistent scaling relationship with bankfull discharge, in that the exponent (b) commonly approximates 0.5 (Equation (1)); whereas, the coefficient (a) reflects local variations in streambank erosivity, controlled by sediment texture, vegetation type, flow regime, etc. (Anderson et al., 2004). Although downstream hydraulic geometry relationships are commonly well-developed in alluvial channels, strong downstream hydraulic geometry relationships are evident even in regions with external non-alluvial controls, such as in bedrock channels with local variations due to variations in bedrock erosivity (Montgomery & Gran, 2001), and in those with discontinuous colluvial input (Wohl & Wilcox, 2005). However, in cases where the substrate resisting forces exceed hydraulic driving forces, downstream hydraulic geometry relationships are not as well developed, such as in mountain streams with very coarse sediment relative to hydraulic forces (where the stream power to sediment size ratio ($/D_{84}$) $< 10,000 \text{ kg/s}^3$) (Wohl, 2004). Lakes can also contribute to overall poor DHG relationships, with higher width to depth ratios directly downstream of lakes, as a result of lakes trapping sediment (Arp et al., 2007). In cases where bankfull discharge data are unavailable, drainage area can be used a proxy for bankfull discharge (Equation (2) & (3)) (Soar & Thorne, 2001; Faustini et al., 2009). Because there may be additional factors to drainage area controlling bankfull discharge, DHG relationships using drainage area tend to show significantly more scatter, yet is still a powerful tool since only a digital elevation model is required as input data (Faustini et al., 2009). However, although drainage area-based DHG relationships are poor in some regions, in a review of regression coefficients for width vs. drainage area relationships (Eq. 3), all R^2 values exceed 0.24 and most > 0.6 ; exponent-values (beta), which should be less than b (commonly ~ 0.5) since the relationship between drainage area and discharge (Eq. 2) where the exponent-value (y) is commonly slightly less than 1 (Faustini et al., 2009), mostly ranged from 0.3-0.45.

$$w = aQ^b, \quad (1)$$

where w is bankfull width, a is a regional coefficient, Q is bankfull discharge, and b is a regional exponent (commonly ~ 0.5).

$$Q = xA^y, \quad (2)$$

where A is drainage area, and x and y are regional coefficients and exponents, and y is commonly slightly < 1 .

$$w = \alpha A^\beta, \quad (3)$$

where α and β are empirical parameters and β is commonly < 0.5 .

Moreover, adjustment of geomorphic parameters assume an alluvial channel where self-adjustment of channel form based on the current flow regime is possible (Leopold & Maddock, 1953, Phillips & Jerolmack, 2016). Therefore, semi-alluvial channels, which contain cohesive or coarse sediment deposited by non-fluvial geomorphic processes (Polvi et al., 2014; Pike et al., 2018; Polvi, 2021) could also contribute to poor-fitting relationships between geomorphic and ecological longitudinal patterns rather than fitting the established patterns from highly connected stream networks with alluvial channels.

Geomorphic and ecological longitudinal trends are intertwined with one another, depending on connectivity of flows and sediment in addition to ecological meta-communities, through migration of organisms and dispersal of seeds and propagules. Because hydrochory is dependent on longitudinal connectivity for dispersion, the organization of passively dispersing organisms (e.g., riparian vegetation), provides a natural test of functional connectivity. Through hydrochory, species accumulate downstream, which leads to higher species richness or densities downstream (e.g., Nilsson et al., 1989, Dunn et al., 2011, Kuglerová et al., 2015). In anthropogenically-fragmented catchments (e.g., due to dams), hydrochoric seed dispersal is interrupted, thus altering the biotic communities, causing proximal reaches on either side of a dam to form dissimilar riparian vegetation species compositions (Jansson et al., 2005). Although anthropogenic factors can create barriers in connectivity (e.g. dams) (Nilsson, 2005; Nilsson et al., 2010) and stream restoration has focused on increasing connectivity, many geomorphic and ecological engineering processes serve to create natural forms of longitudinal disconnectivity. These spatially and sometimes temporally intermittent barriers or buffers to flow, sediment and propagule fluxes, have received much less attention in the hydrochory literature and how they influence metacommunity organization. Once prevalent beaver dams and log jams cause widespread ‘leaky’ barriers (Wohl & Beckman, 2014), serving to trap sediment, carbon, and attenuate flows. Similarly lakes, which are widespread in northern latitudes (Messenger et al., 2016), particularly where Pleistocene glaciation has eroded bedrock and deposited moraine dams, can have substantial effects on stream topology and form and function of rivers where they are connected to stream networks (Gardner et al., 2019), such as the connectivity of sediment (Arp et al., 2007), seed dispersal (Su et al., 2019a, b), and diversity of invertebrates (Green et al., n.d.) .

We focused our study on two catchments in boreal northern Sweden that are heavily influenced by past continental glaciation, creating a stream network with multiple instream lakes and coarse till deposits (Nilsson et al., 2002; Polvi et al., 2014; Su et al., 2019a, b). The stream networks can be divided into three process domains, defined by Montgomery (1999) as zones with distinct geomorphic processes that structure ecological disturbances and thus organize biotic communities: rapids, slow-flowing reaches, and lakes (Nilsson et al., 2002; Su et al., 2019a, b) (Figure 1a). Rapids are steep (S_0 : 0.1-5%) gravel- to boulder-bed channels with coarse glacial legacy sediment (cobbles and boulders) and bedforms that do not conform to alluvial bedform-channel slope relationships, *sensu* Montgomery & Buffington (1997); slow-flowing reaches ($S_0 < 0.1\%$) are straight or meandering channels flowing through peat or fine sediment with wetland vegetation riparian zones; lakes have inlets and outlets and are lined with either fine sediment or coarse till. Within our study catchments, we examined the longitudinal distribution of process domains along nearly the entire mainstem channel, evaluated how channel width changes downstream and examined how riparian vegetation communities change along the channel in each new process domain. Our aim was to determine whether these glaciated, boreal stream networks fit established patterns of geomorphic and ecological longitudinal changes. We test the functional geomorphic and ecological connectivity of these catchments with high-resolution spatial data of riparian vegetation communities and channel width.

MATERIALS AND METHODS

Study location and study setup

Our study was located in the boreal region of northern Sweden in two catchments of similar size ($\sim 350 \text{ km}^2$): Hjuksån and Bjurbäcken (*ån* and *bäcken* both mean ‘stream’/ ‘creek’), both of which are tributaries of the free-flowing Vindel River that in turn flows into the Ume River $\sim 30 \text{ km}$ upstream of its outlet in the Baltic Sea (Figure 2). In addition to glaciation shaping the catchment through numerous mainstem lakes and large amounts of coarse glacial sediment, the landscape is divided into two regions—above and below the former highest coast-line (FHC). The FHC divides areas that have been only affected by glaciation and contains undisturbed glacial sediment from areas that have been under sea level after glaciation and affected by deltaic processes and subsequently uplifted by post-glacial isostatic rebound (Fredén, 1994). Hjuksån catchment ($64^\circ 25' \text{N}$, $19^\circ 45' \text{E}$, alt. 245 m) is located nearly entirely below the FHC, whereas Bjurbäcken ($65^\circ 6' \text{N}$, $18^\circ 4' \text{E}$, alt. 320 m) is completely above the FHC. The upland vegetation in the study area is dominated by boreal forest with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and the riparian vegetation is

dominated by deciduous trees, tall herb, and graminoid communities.

We started collecting geomorphic and ecological data directly downstream of the furthest upstream lake, encompassing 18 process domain reaches in Bjurbäcken and 20 process domain reaches in Hjuksån catchment. Geomorphic data were collected along the entire mainstem channel of Bjurbäcken and Hjuksån, starting below the upstream lake, to the tributary junction with the Vindel River. Riparian vegetation data were collected starting at the same point and ~18 km downstream in Bjurbäcken and ~9 km downstream in Hjuksån.

Geomorphic study

In order to obtain a large set of data points, active channel width was measured using current orthophotos with GIS software (ArcMap 10.5, 2017). Active channel width was measured between the channel banks, perpendicular to the downstream direction, every 50 m. Several other geomorphic factors were also recorded, including the process domain as identified from the orthophoto, the surficial geology, and proximity to glacial features (e.g., eskers, moraines). Surficial geological deposits were recorded in four different categories (bedrock, peat, subglacial and deltaic fine sediment (including postglacial clay, silt and sand and subglacial sands), coarse till). Using a 2-m digital elevation model, we determined the channel slope and the drainage area at each measured transect, the latter of which was used as a proxy for bankfull discharge. We then plotted the power relationships between drainage area and channel width for all transects and each process domain separately to determine whether the stream networks conform to expected downstream hydraulic geometry relationships.

To predict channel width we used multiple regression models, based on drainage area distance downstream from lake, channel slope, proximity to glacial feature, and type of surficial geology deposits (categorical). Selection was based on lowest AIC with backward-step selection. The relationship between channel width and drainage area were analysed using power regressions. Multiple linear regressions were used to determine logged values of power regression. All statistical analyses were performed in R studio version 3.6.0 (R Core Team, 2021).

Ecological study

For each new process domain reach, we identified all vascular plants in the riparian zone between the summer low water mark and the edge of the riparian zone (as defined by the dominance of *Vaccinium myrtillus* (bilberries)). The identification of plant species followed the taxonomy in Krok and Almquist (2013). In the following cases, two or more species were treated as one taxon: *Carex juncella* + *Carex nigra*, *Callitriche* spp. (difficult to identify in the absence of floral characters), *Hieracium* spp., *Taraxacum* spp. (apomictic), *Sparganium* spp. (common with hybrids). All vegetation inventories took place in June-August 2016. For large lakes, we only inventoried riparian plants found in the first and last 300 m along the shoreline. We calculated richness (number of species) and species density for each reach/lake and determined community composition. We used regression analyses to study the relationship between changes in species density and richness with geographical distance downstream. We also examined whether there were relationships between community similarity, using Jaccard's index, and distance between reaches to determine whether hydrochoric dispersal is a potential control on riparian metacommunity organization. All statistical analyses were performed in R studio version 3.6.0 (R Core Team, 2021).

RESULTS

Weak downstream hydraulic geometry relationships

Along the mainstem of Bjurbäcken, over 1300 measurements of channel width and drainage area were made with drainage areas ranging from ~50- 360 km², and along the mainstem of Hjuksån, ~900 measurements were made with drainage areas ranging from ~8 to 360 km². As expected, when lake widths are included, downstream hydraulic geometry relationships between drainage area and channel width, as defined by a power relationship, are extremely poor, with one catchment even showing an overall decrease in channel width. When lakes are excluded, the relationships remain poor but weakly positive. When lakes are excluded in Bjurbäcken, located above the FHC with coarser glacial sediment, there is still a very weak relationship

with an R^2 of 0.08 with an exponent (β -value) of 0.34 (Figure 3). When only focusing on rapids, the R^2 value increases to 0.30, and the β -value is 0.56. In Hjuksån, located below the FHC, the power relationship excluding lakes is stronger than in Bjurbäcken with an R^2 value of 0.43 and a β -value of 0.68, and the relationship with only rapids even decreases in explanatory power to an R^2 of 0.42 and a β -value of 0.39 (Figure 3). The two catchments show opposing directions of explanatory power for the two reach types: Hjuksån has stronger explanatory power for slow-flowing reaches ($R^2 = 0.57$), whereas Bjurbäcken has very low explanatory power for slow-flowing reaches ($R^2 = 0.04$).

Significant multiple linear regression models including combinations of factors of downstream distance from a lake and categorical variables of surficial geology types were found for both catchments, increasing explanatory power of width predictions, in particular in the Hjuksån catchment. Downstream distance from a lake was only a significant factor in Hjuksån (below the FHC), where increased distance downstream from a lake decreases predicted channel width. Furthermore in the Hjuksån catchment, for both rapids and slow-flowing reaches combined, the surficial geology types of coarse glacial till and bedrock lowered channel width, whereas deltaic and fine subglacial sediment increased channel width. The relationship for only rapids contained peat as the only significant surficial geology type, which increases channel width. Exponent (β -) values ranged from 0.51-0.65, and R^2 -values ranged from 0.47-0.69, where the relationship for only slow-flowing reaches was the strongest. In the Bjurbäcken catchment, the downstream distance from a lake was not a significant factor, but various combinations of surficial geology types were significant factors. The presence of peat or coarse till decreased the predicted width, while the presence of bedrock had opposite effects for relationships of only rapids (decreasing channel width) compared to slow-flowing reaches (increasing channel width). Even with the additional explanatory parameters, the drainage area-width relationships for Bjurbäcken were very poor with very low R^2 -values, ranging from 0.10 to 0.33, where the relationship for rapids had the highest explanatory power. Exponent (β) values were much lower in Bjurbäcken, than for Hjuksån, at 0.18 to 0.26, indicating a more gradual increase in channel width with increasing drainage area.

Low connectivity of riparian vegetation communities

There are no statistically significant trends in richness of vascular riparian plants with downstream distance in Hjuksån with all the reaches combined or for each process domain separately. In Bjurbäcken, there was a significant relationship between richness and distance downstream for all reaches combined ($p = 0.003$, $R^2 = 0.43$) with a slope indicating two new species per kilometer; however, there are no significant relationships for each process domain, separately. However, to control for the large difference in area between the different reaches we focus our results on species density. We found an increase in cumulative species richness (Figure 4) but a negative relationship between species density of vascular riparian plants with downstream distance in Hjuksån with all the reaches combined ($R^2 = 0.21$, $p = 0.0471$, $\text{mean} = 0.05$) (Figure 4a-b); however, there are no significant relationships in Bjurbäcken or for each process domain separately in Hjuksån (Bjurbäcken: $R^2 = 0.009$, $p = 0.694$, $\text{mean} = 0.06$). In examining relationships of reach similarity (in terms of riparian vegetation species composition) by distance between reaches, a few relationships can be found. There are significant relationships when all process domains are combined for both Hjuksån ($p = 0.003$, $R^2 = 0.05$) and Bjurbäcken ($p > 0.001$, $R^2 = 0.09$) (Figure 4 c-d). There is also a significant relationship between riparian vegetation similarity and distance between reaches for lakes in Hjuksån ($p = 0.002$, $R^2 = 0.176$) and for rapids in Bjurbäcken ($p < 0.001$, $R^2 = 0.226$) (Table 2).

DISCUSSION

We found longitudinal trends in geomorphic and ecological parameters to be very weak in these naturally disconnected study catchments, which contains disparate channel types that segment the stream. Our study also finds the geomorphic difference between the catchments to be visible in the riparian vegetation along the different catchments.

Downstream hydraulic geometry relationships of width- drainage area power functions explain at most 57% of variability in width for slow-flowing reaches in Hjuksån, and a minimum of only 4% of variability in width for slow-flowing reaches in Bjurbäcken. Combining all reach types, only 8% of variability in width is explained

in Bjurbäcken and 43% of variability is explained in Hjuksån. According to Faustini et al. (2009), all of these regressions classify as ‘poor’ fits, except for slow-flowing reaches in Hjuksån; and the power relationships in Bjurbäcken have poorer fits than for any region in the conterminous United States (Faustini et al., 2009). In the Hjuksån catchment, located below the FHC, which contains more fine deltaic sediment in addition to coarse glacial sediment, there are slightly stronger downstream hydraulic geometry relationships for all reach types, indicating potential for self-adjustment in response to the current flow regime as seen in alluvial channels (Singh et al., 2003; Wohl, 2004). The fact that rapids and the catchment above the FHC show poorer DHG relationships, fits with Wohl’s (2004) observations from coarse mountain streams, where low ratios of the stream power to D_{84} lead to poor DHG fits. Exponent (β -) values, which describes the spatial rate at which width increases with increased drainage area, typically range 0.2-0.4 (Faustini et al., 2009). Combined reaches and slow-flowing reaches in Bjurbäcken fall within that range (0.34 and 0.26, respectively) in addition to rapids in Hjuksån (0.39); however, the remaining reach types have fairly large β -values (ranging 0.56- 0.75) (Figure 3), indicating a fairly rapid downstream increase in channel width, potentially caused by a y -value >1 (Equation (2)), due to the more dendritic drainage basin in Hjuksån compared to a more linear drainage basin in Bjurbäcken (Figure 2) and greater connections to groundwater (Burgers et al., 2014).

The presence of lakes in the Hjuksån catchment, containing finer sediment and thus having more alluvial characteristics, create wider channels directly downstream of the lake than if the reach was further downstream of a lake (Table 1). Lakes are serving to reset the longitudinal sediment conveyor belt by trapping fine sediment, increasing width: depth ratios directly downstream of lakes (Arp et al., 2007). In the Sawtooth Mountains region of Idaho, US, channel shape recovered by 50% within 1.0-1.8 km downstream of lakes and required up to 10-20 km to recover by 90%. Given the high spatial density of lakes in catchments in northern Sweden, channels may never recover and thus never reach a non-lake influenced equilibrium form. In addition to the significant effect of lakes, several surficial geology types, reflecting erosivity of streambanks affect the drainage area- channel width relationship, where the coarse till has a narrowing effect and fine deltaic, and subglacial sediment has a widening effect (Table 1). Peat has a widening effect on rapids but a narrowing effect on slow-flowing reaches, likely because the intrinsic cohesivity of clay in peat will decrease lateral erosion but compared to coarse till found in rapids the presence of peat will allow greater erosion. Likewise, bedrock has a narrowing effect in rapids and the slow-flowing reaches in Hjuksån but a widening effect in slow-flowing reaches in Bjurbäcken; bedrock outcrops found in slow-flowing reaches are smoothly rounded features composing the bed or small parts of the banks, whereas bedrock in rapids will lead to high slopes that naturally form narrower channels or make up streambanks that will hinder any lateral erosion. In general, the low R^2 values and generally low β -values reflect the low ability for semi-alluvial channels to adjust their channels to the contemporary flow regime (Polvi, 2021).

The positive relationships between increased distance between reaches and reach similarity indicates low connectivity between reaches in terms of hydrochoric seed or propagule dispersal. However, models like linear regressions are sensitive to outliers and therefore these models are significant but with a very weak R^2 . We therefore interpret these results a lack of connectivity since reaches closer to each other are less similar than reaches that are further apart. The geomorphic trend of weak longitudinal relationships with lakes is also mirrored in the ecological data by a slight trend in decrease in longitudinal species density of riparian vegetation in Hjuksån, and no significant relationships in Bjurbäcken.

Poorly developed downstream hydraulic geometry relationships with regards to channel width, combined with low support for connectivity between riparian vegetation communities in semi-alluvial stream-lake systems, indicate that these are highly fragmented catchments where local factors steer geomorphic form and biotic communities. All rivers are part of a landscape context with varying degrees of connectivity between segments and reaches. Previous work has shown that dispersal is strong in well-connected areas compared to isolated headwaters, and patterns of connectivity among sites in a network can affect population dynamics (Swan & Brown, 2017). Hence, biodiversity has often been shown to increase towards the middle of the catchment (Nilsson et al., 1989; Kuglerová et al., 2015). However, stream networks in northern Fennoscandia are commonly naturally fragmented and consist of three types of process domains (rapids, slow-flowing reaches and lakes), which all differ in morphology and hydraulics that influence their capacity to facilitate

the plant dispersal (Su et al., 2019a, b). In a connected stream network, one would expect a downstream increase in species richness density (Andersson et al., 2000; Kuglerová et al., 2015). However, in our naturally fragmented river system we found the opposite pattern, with a reduction in species density with increasing distance downstream. These differences in patterns can partly be explained by the high spatial resolution and that our study was conducted continuously along two streams, in comparison to previous studies with lower spatial resolution and discontinuity in sampling (e.g. Nilsson et al., 1994; Andersson et al., 2000; Kuglerová et al., 2015). The increased spatial resolution and sampling continuity allowed us to find an overall reduction in species density, as a function of the lack of hydrochory due to the presence of numerous lakes (Su et al., 2019a, b). Lakes trap ~80% of seeds during the spring flood and only allow downstream transport if the lake outlet is aligned with the wind direction (Sarnecki et al., 2014; Su et al., 2019a). In a connected stream network, we would also predict higher similarity between reaches close to each other; however, in our disconnected systems we did not find such a relationship. Su et al. (2019b) showed that these three process domains have differing plant species communities, and thus seed banks may therefore provide a local source for metacommunity control, or perhaps diversity depends mostly on local site conditions (Green et al., n.d.), and not connectivity.

Rather than longitudinal controls of increasing discharge (as a function of drainage area) and inter-reach connectivity on channel width and riparian vegetation communities, our results indicate that our study catchments are driven by local-scale geomorphic and ecological controls. These local-scale controls, such as surficial geology (presence of coarse glacial sediment) and local seed banks and source populations, are therefore more important in recovery of stream processes and communities than connectivity of flows, sediment, and propagules between reaches in responding to disturbances, which include habitat restoration. Therefore, passive ecological recovery, with recolonization by hydrochory, is not as likely in disconnected stream networks, and thus manual planting of riparian vegetation may be necessary. Similarly, geomorphic recovery through channel adjustment based on the current flow regime is unlikely in disconnected networks with semi-alluvial process domain segments; thus, physical channel manipulation should play a larger role in stream restoration. In addition, interactions between channel width and riparian vegetation communities throughout the catchment may serve to further shape reach morphology and riparian zones (Anderson et al., 2004).

With weak downstream hydraulic geometry relationships, traditional stream ecology concepts, which assume increasing width as drainage area increases, may not apply. Geomorphic relationships with channel size have also been used to model nutrient uptake in river networks (Ensign & Doyle, 2006). Thus, given the abundance of lakes in northern latitudes (Messenger et al., 2016), this study can have widespread implications on the understanding of fluvial processes and stream ecosystems in boreal, and (sub)arctic regions. For example, we may not be able to rely on past cornerstones of river science, such as downstream hydraulic geometry and the river continuum concept, in certain catchments in understanding river dynamics, designing stream restoration projects, and predicting responses of communities after restoration or other natural disturbances. Furthermore, disconnected fluvial systems with abundant lakes may also be analogous to pre-anthropogenic stream networks that contained abundant log jams and beaver dams, which create various degrees of natural disconnectivity (Wohl & Beckman, 2014; Green et al., n.d.). These naturally occurring discontinuities should be distinguished from anthropogenic dams that are nearly complete barriers to propagule, sediment and water fluxes. Natural fluvial disconnectivity features buffer fluxes and allow transport in temporal pulses and through leaky barriers; thus, lakes can provide a model for how beaver dams and log jams, which are temporally and spatially heterogeneous, affect functional connectivity of processes affecting geomorphic form and ecological communities.

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TABLES & FIGURES

Table 1. Multiple linear regression models (selected based on lowest AIC with backward-step selection) to predict channel width based on drainage area, distance downstream from lake and type of surficial geology. Surficial geology variables are categorical (1 or 0). All models: $p < 0.0001$ and all parameters have p -values < 0.05 .

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image1.emf available at <https://authorea.com/users/474987/articles/564575-disrupted-connectivity-in-biotic-and-geomorphic-patterns-in-stream-lake-systems>

Table 2. Relationship between downstream position (order of reach) and species richness and density for each process domain type and all reaches combined (catchment); relationships for similarity are presented between all sites and the geographical distance (in meters) between them. P-values < 0.05 are shown in bold with their corresponding R^2 values.

	Similarity		Richness		Species density		Species density
	p	R^2	p	R^2	p	R^2	R^2
Bjurbäcken							
Slow-flowing	0.132	0.039	0.063	0.59	0.894	0.004	0.004
Rapid	<0.001	0.226	0.211	0.290	0.183	0.392	0.392
Lake	0.686	0.007	0.146	0.739	0.638	0.131	0.131
Catchment	<0.001	0.092	0.003	0.429	0.694	0.099	0.099
Hjuksån							
Slow-flowing	0.059	0.044	0.774	0.013	0.673	0.027	0.027
Rapid	0.794	0.002	0.508	0.158	0.149	0.555	0.555
Lake	0.002	0.176	0.284	0.361	0.430	0.216	0.216
Catchment	0.003	0.052	0.532	0.023	0.047	0.212	0.212

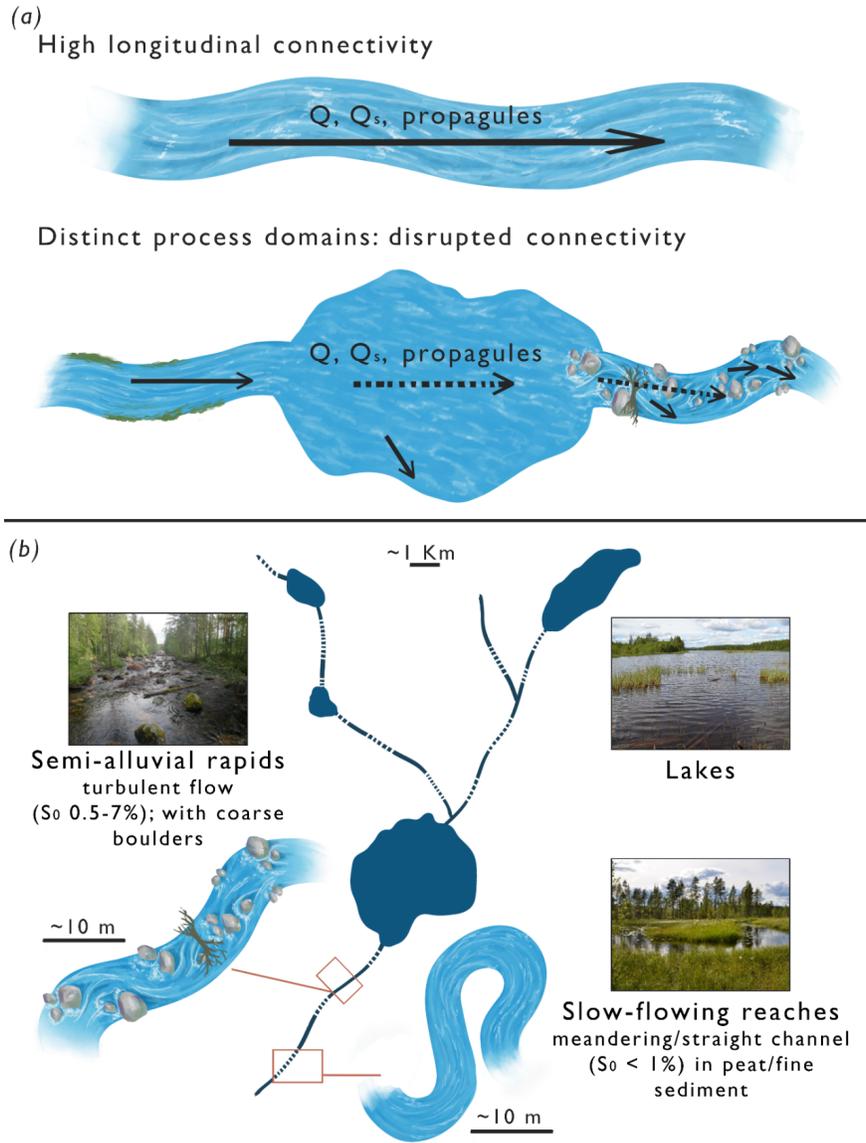


Figure 1. (a) Conceptual diagram of disrupted connectivity of flow (Q), sediment (Q_s) & propagules (seeds and other revegetative plant parts). Solid arrows indicate high connectivity & dashed arrows indicate higher potential for disconnection. (b) Conceptual diagram of stream networks with three distinct process domains: rapids, slow-flowing reaches & lakes.

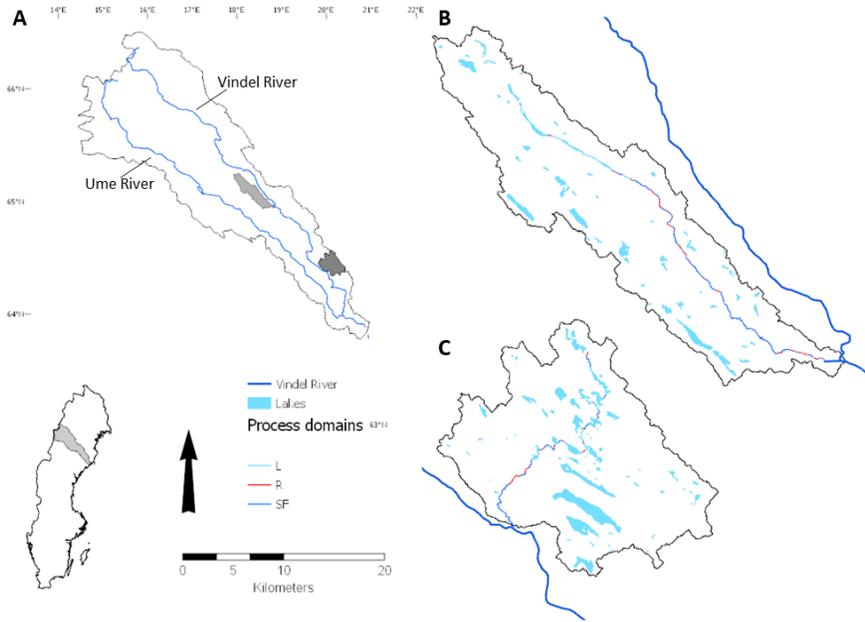


Figure 2. (a) Location of Bjurbäcken and Hjuksån catchments (drainage areas $\sim 350 \text{ km}^2$) along the Vindel River (Bjurbäcken in light grey and Hjuksån in dark grey) in the Ume River catchment. The location of Ume River catchment shown in grey within map of Sweden (bottom left). Maps of sub-catchments (b) Bjurbäcken and (c) Hjuksån show process domain reaches demarcated along the mainstem. All lakes within catchments (on both mainstem and tributaries) shown as light blue. The mouth of both rivers (Bjurbäcken and Hjuksån) are at the Vindel River. Scale bar applies to sub-catchment maps.

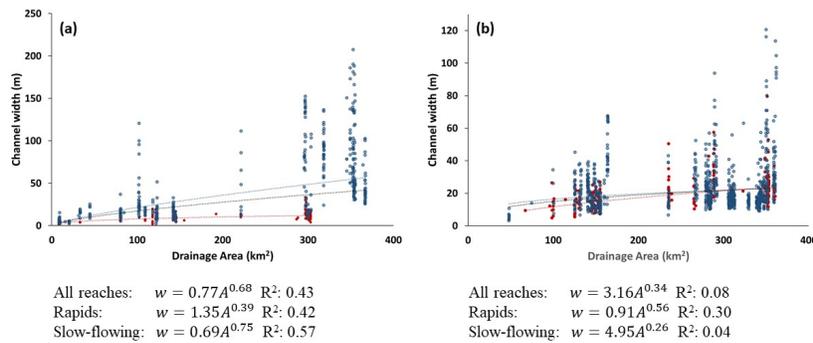


Figure 3. Relationship between channel width and drainage area for rapids (red) and slow-flowing reaches (blue) with corresponding power regressions (black line shows trend for combined reach types) for (a) Hjuksån and (b) Bjurbäcken.

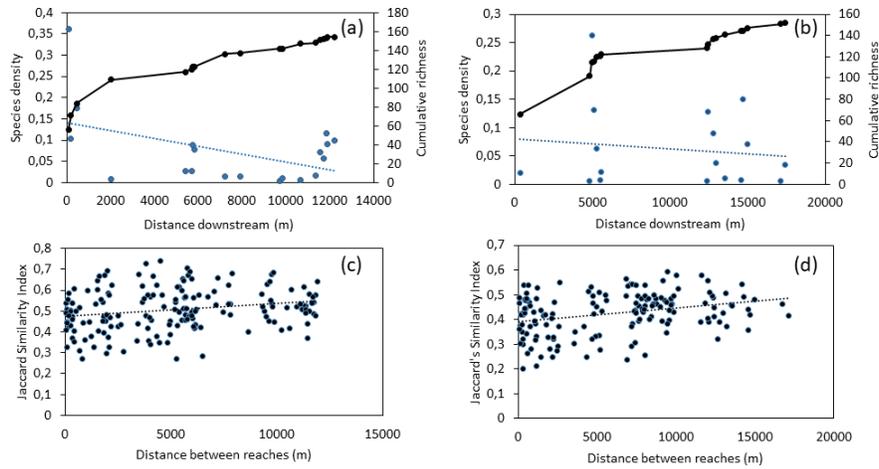


Figure 4. Relationships between species density (richness/area) and distance downstream (blue points & line) and cumulative richness (black line) for (a) Hjuksån and (b) Bjurbäcken. Species density regressions: Hjuksån ($p = 0.0471$, $R^2 = 0.21$), Bjurbäcken ($p = 0.694$, $R^2 = 0.009$). Relationships between similarity between vegetation communities and distance between all reaches for (c) Hjuksån and (d) Bjurbäcken. Linear regression: Hjuksån ($R^2 = 0.05$, $p = 0.003$), Bjurbäcken ($R^2 = 0.092$, $p < 0.001$).