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RESEARCH ARTICLE

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Landscape features control river's confluences water quality and tributary fish composition

Rachel E. Bowes[1,2] | Eva Bergman[1] | Serena Donadi[3] | Larry Greenberg[1] | Leonard Sandin[4,5] | Lovisa Lind[1]

[1]Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden

[2]Department of Biological Sciences, Emporia State University, Emporia, Kansas, 66801, USA

[3]Department of Aquatic Resources (SLU Aqua), Swedish University of Agricultural Sciences, Stockholm, Sweden

[4]Norwegian Institute for Water Research (NIVA), Oslo, Norway

[5]Norwegian Institute for Nature Research (NINA), Trondheim, Norway

Correspondence
Rachel E. Bowes, Emporia State University, 1 Kellogg Circle, Emporia, Kansas 66801, USA.
Email: rebowes.ecology@gmail.com

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Abstract

Rivers networks represent hierarchical dendritic habitats within terrestrial landscapes and differences in connectivity and land use influence dispersal, and consequently biodiversity patterns. We, therefore, measured variation in water chemistry and fish abundance and related these to a number of landscape characteristics (e.g., wetland, urban, wooded, and agricultural) in the River Klarälven and its 30 permanently flowing tributaries. We hypothesized that these environmental attributes would differ between tributary and main stem habitat and that these differences would be driven by landscape attributes including land use. We found considerable intertributary variation in temperature and nutrient levels, and between the tributaries and the main stem. Generally, water temperature was lower in the tributaries, whereas nutrient levels were higher in the tributaries. The lower water temperature has implications for coldwater fishes, and we found two fishes, burbot and lamprey, associated with coldwater tributaries. We also found an inverse relationship between water quality and anthropogenic land use. Protecting tributaries with low anthropogenic impact will likely become increasingly important with ongoing global warming as they can function as thermal refugia for coldwater fishes. Hence, this study underscores the need to evaluate water courses at regional scales to identify spatial refuges and ensure connectivity.

KEYWORDS
fish diversity, landscape, tributary, water quality

1 | INTRODUCTION

Rivers cover a small fraction of the world's surface area, but support a disproportionately high amount of global biodiversity (Dudgeon et al., 2006). Rivers and their surrounding areas also carry out important ecosystem services, for example, processing of organic matter and preventing pollutants reaching downstream areas (Hanna et al., 2018; Malmqvist & Rundle, 2002). Thus, they have many system-wide functions and serve as transport vectors for sediments, organic matter, nutrients, and species (Limburg et al., 2001).

Rivers systems are composed of a hierarchical network of channels, which form a branching, complex fractal grid within the catchment (Perkins & Reiss, 2010), where local habitat patches are spatially linked (Gothe et al., 2013). At the catchment scale, land use, topography, geographic setting, distance from source, and stream discharge strongly influence, for example, nutrient input and water temperature

(Allan, 2004; Caissie, 2006), whereas quality and quantity of riparian vegetation and amount of groundwater and tributary inflow are key variables at the reach scale (Dodds & Oakes, 2008; Kelleher et al., 2012; Loicq et al., 2018).

As river systems are inherently heterogeneous, water temperature and chemistry vary within the network across space and time (Buffam et al., 2007; Vatland et al., 2015). Water quality at the downstream endpoint of a watershed reflects the diverse and complicated ecological, hydrological and biogeochemical functions and interrelationships within the entire catchment. Several studies have shown that stream water chemistry can be both an important indicator and an integrator of diverse ecosystem processes (Bormann & Likens, 1967; Likens & Bormann, 1995; Likens, 2004). First and second-order tributaries (headwater streams) make up a great majority of the total river length within a river system (Downing et al., 2012) and their importance for the physical, chemical, and biological functions of the entire river network is apparent as these small streams tend to be more spatially and temporally variable compared to larger channels (Wohl, 2017). At the same time, each tributary within the river network potentially has its own "water chemical fingerprint" (Buffam et al., 2007), and the variation in water chemistry in headwaters within a single catchment can be as large as the variation in a statistically representative sample of many river systems across a large boreal forest region (Temnerud & Bishop, 2005). Within the stream network, tributary confluences or "nodes" can be described as landscape "hotspots," which are affected by both natural and human-induced environmental factors (Rice et al., 2006). Hotspots are areas that in comparison to the surrounding areas, show disproportionally high chemical reaction rates (Mclain et al., 2003).

Tributaries and headwaters can serve as spawning and rearing areas for fish, providing unique habitats for permanent resident species and migrating species, and refugia habitats from extreme environmental conditions (e.g., flow and temperature; Wohl, 2017). As tributaries vary in terms of nutrient content and water temperature, they affect nutrient cycling in the rivers they flow into, and quantifying this variation among tributaries provides insight into the physiochemical environment of entire river systems (Kiffney et al., 2006). This is especially true for water temperature as this is a critical variable shaping river and stream ecosystems and is a highly sensitive "master" variable of water quality (Hannah et al., 2008), and affects the physiology and metabolism of organisms (Abram et al., 2017).

Land use changes strongly influence water chemistry since rivers and streams serve as recipients of inorganic and organic substances, including pollutants, from the surrounding landscape. In general, water quality is good in unfragmented forest patches with little intervention from human land use (Lee et al., 2009). Changes in thermal regimes can, for example, alter rates of nutrient cycling, change dissolved oxygen concentrations (Caissie, 2006), affect stream metabolism, alter biochemical reactions, productivity, biogeochemical cycling, organic matter decomposition, and ecosystem dynamics (Demars et al., 2011). Humans strongly influence water temperature and nutrient inputs into stream ecosystems, mainly through land use (e.g., tree removal in the near-stream zone; Kovach et al., 2018), water regulation, and damming (Heggenes et al., 2018). Changes in water temperature are fundamentally important in freshwater environments as c. 99% of all freshwater organisms are ectotherms (Falfushynska et al., 2016), and for fish species such as salmonids, thermal regimes exert strong effects, for example, on developmental rates and migration (Kavanagh et al., 2010).

With ongoing global warming, the amount of (cold) thermal refugia within a river network could decrease, and a large-scale study in the U.S. predicted a reduction by as much as 36% of coldwater habitats with climate change (Mohseni et al., 2003). A decrease in thermal refugia in river networks will have strong negative effects on future aquatic biodiversity, especially in combination with increased nutrient inputs associated with changing land use (intensification of agriculture) and decreased river network connectivity (Doherty et al., 2021). Moreover, connectivity (ecological and hydrological), that is, the degree to which matter (water, solutes, sediment, and organic matter) and organisms can move among patches in a landscape or ecosystem, strongly influences the resistance and resilience of rivers to natural and human-induced disturbances (Crook et al., 2015).

How environmental conditions in a tributary influence the heterogeneity of the downstream channel has been partly answered by a study of Kiffney et al. (2006). Here, we mainly focus on how landscape features influence the water chemistry of the tributaries, and thereby the main stem, and fish abundance. Given the importance of rivers for biodiversity and the influence of land use on water quality, we ask if tributaries are potentially important refugia for organisms and thereby for conservation efforts. Specifically, we ask: (1) what are the differences in chemical characteristics and temperature between the main stem and tributaries, (2) which landscape characteristics are related to the chemical characteristics of tributaries, and (3) are tributaries and their confluences potentially important for fish as refugia?

2 | METHODS

2.1 | Study area

The 460 km long river Klarälven (59° 23′ 0″ N, 13° 32′ 0″ E), with a catchment area of 11,820 km^2, flows through Norway and Sweden and empties into Lake Vänern in Karlstad, Sweden. The mean annual outlet discharge to Lake Vänern is 162.5 m^3/s, and the mean annual high water discharge is 690 m^3/s (www.smhi.se). The area has a temperate to subarctic climate, with mild winters and cool summers. The majority of the surrounding landscape is forested (68%–94% forested land use in tributary watersheds), followed by agricultural land (0%–37%). The river is home to endemic populations of landlocked Atlantic salmon (*Salmon salar*) and brown trout (*Salmo trutta*), which have been affected by industrial activities, timber floating, and intensive fishing (Greenberg et al., 2021; Piccolo et al., 2012). The river has been regulated by hydropower since the early 1900s, and there are currently 11 hydropower stations, 2 in Norway, and 9 in Sweden, along the river. The northern most hydropower stations in Sweden are Höljesdammen power plant in Höljes, Sweden (130 MW) and Edsforsen

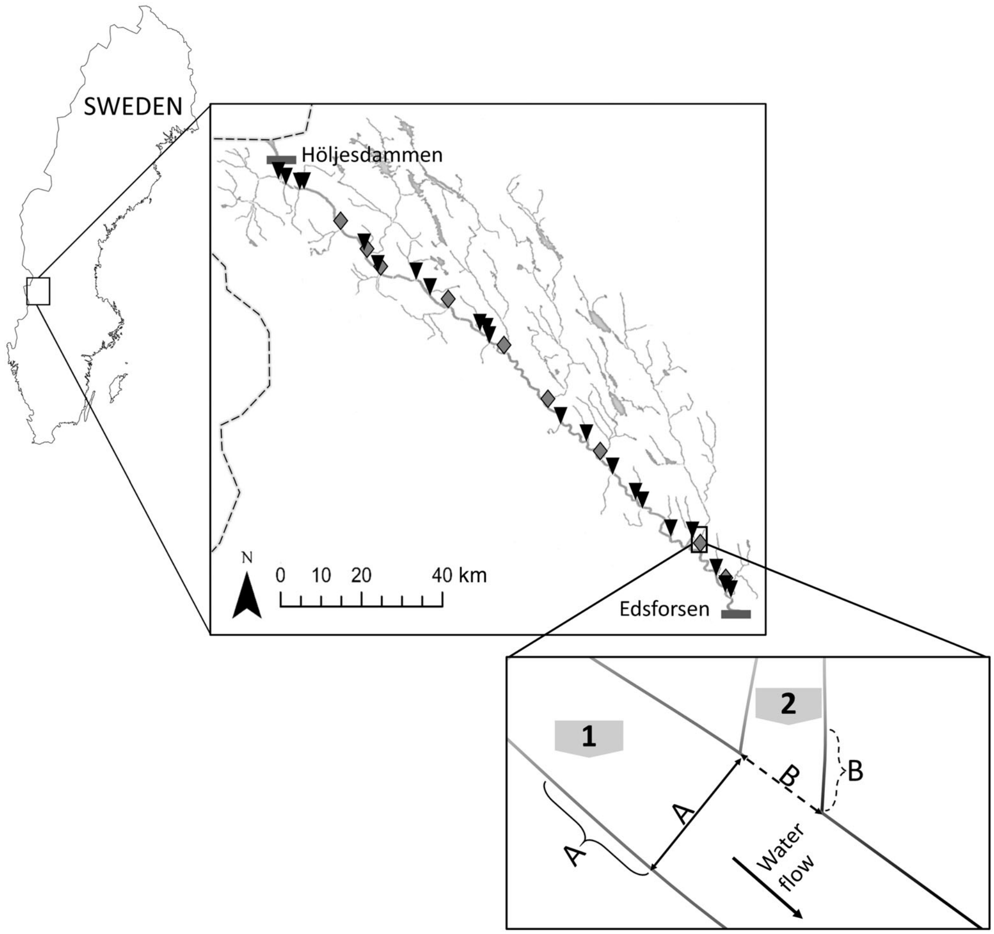

FIGURE 1 Map of study area, Klarälven, and sampling schematic at each of the tributary junctions. Map sources: Esri, HERE, Garmin, FAO, NOAA, and USGS. Every permanent registered tributary (represented by triangles and squares on the map; 30 in total, data from the Swedish Meteorological and Hydrological Institute) was sampled in the Klarälven between Höljesdammen and Edsforsens (labeled and represented by gray bars in the map) in Sweden in August 2019. Water chemistry and physical characteristics data were collected at two locations at each of the 30 tributary junctions. The gray squares also indicate that electrofishing had been conducted at these sites. Distance A is the main channel width at that site, which varied across the entire study area with of range of 38–230 m and mean of 122.13 ± 52.29 m (SD). Distance B is the tributary mouth width at that particular site, which also varied significantly across all sampled tributaries ranging from 3 to 110 m with mean of 20.51 ± 20.65 m (SD).

power plant in Edebäck, Sweden (9 MW; Figure 1). We sampled all the 30 permanent tributaries (according to the Swedish Meteorological and Hydrological Institute [SMHI]) in Klarälven between these two impoundments, extending over a distance of ~115 km (Figure 1).

2.2 | Tributary characteristics data collection

Water chemistry and physical characteristics data were collected at two sampling locations at each of the 30 tributary junctions during the month of August 2019. The first sampling location was in the main channel of the Klarälven, one main channel width upstream of each of the 30 tributary junctions (Figure 1: Distance A). The second sampling location was one tributary mouth width upstream within the tributary (Figure 1: Distance B). This sampling design was chosen, so that the difference in water chemistry in the main channel and tributaries could be assessed without water from the other source confounding the sample. At each of the two sampling locations (Figure 1: #1 in the main stem, #2 in the tributary) we collected the following: date and time of sampling, air temperature (°C), main channel width, tributary mouth width (used to determine the sampling site in the tributary), and tributary sampling site transect width, measured with a range finder (m). At each tributary sampling site, we measured depth and water velocity profiles using a handheld current meter for discharge measurements (OTT HydroMet C2). Ten equally spaced depth and velocity profiles were taken (measuring the velocity [cm/s] at 0.2, 0.6, and 0.8 × the depth) in a single transect within each tributary. At each sampling location (main channel and tributary), in situ measurements of water temperature (°C), conductivity (μs/cm), dissolved oxygen (% and mg/L), turbidity (NTU), and pH were measured using a YSI Professional Plus handheld multiparameter meter (YSI Instruments, Yellow Springs, OH, USA). Measurements were taken in the water column, avoiding the surface and bottom water layers. This depth varied with overall depth of the tributary, generally around 0.50 m, below the surface. Since the main channel depth was generally >2 m, samples in the main channel were taken from a boat at a depth of ~0.5 m. Additional depth- and width-integrated stream water samples were collected at each sampling location (in the main channel and tributary) for subsequent water chemistry analyses. Water samples were taken according to a standardized protocol, bottled and immediately sent to the Geochemical Laboratory in the Department of Aquatic Sciences and Assessment at Swedish University of Agricultural Sciences (SLU; https://www.slu.se/en/departments/aquatic-sciences-assessment/laboratories/vattenlabb2/) to be analyzed within 24 h of collection. All measurements of basic water properties were performed as per standard Swedish standardized and accredited methods. Analyses included: conductivity (μs/cm), dissolved oxygen (% and mg/L), pH, Alkalinity/Acidity (mekv/L), filtered absorbance (Abs F 420/5; 420 nm), total organic carbon (TOC; mg/L), total nitrogen (TNb μg/L), NH_4 (N μg/L), $NO_2 + NO_3$ (N μg/L), PO_4 (P μg/L), total phosphorous (P μg/L), SO_4 (IC mekv/L), Cl (mekv/L), F (mg/L), Ca (mekv/L), Mg (mekv/L), Na (mekv/L), K (mekv/L), and Si (mg/L). In situ measurements (in the main channel and tributary) of chlorophyll *a* were taken from five randomly selected locations using a UniLux chlorophyll *a*, single wavelength miniature fluorimeter, with a dynamic range 0–100 μg/L and a detection limit of <0.01 μg/L chlorophyll *a*.

2.3 | Landscape characteristics data collection

The landscape characteristics examined in this study were derived from digital data obtained for each tributary watershed. The data consisted of mapped polygons of land use and land cover, impervious surface area, soils, and elevation from the Swedish Meteorological and Hydrological Institute (SMHI) and Esri GIS: land use data (% cover: forest, agriculture, urban [i.e., buildings], pavement [i.e., roads and parking lots], lakes/streams, and moorland), 10 m riparian buffer classification category (bare, mixed cover, fully forested; visual estimates based on aerial photos in Google Earth), slope, watershed area (km^2), tributary length (km), number of dams in the tributary, average annual discharge (m^3/s), and average August 2019 discharge (m^3/s). For land use variables, the arcsine transformation was calculated as two times the arcsine of the square root of the proportion.

2.4 | Electrofishing data

The dataset was extracted from the Swedish Electrofishing RegiSter (SERS), conducted by electrofishing from 1951 to 2014 (Sers, 2013). We used electrofishing data from the Klarälven tributaries from years 2000–2016. Surveys were done according to the European standard (EN 14011:2003). These procedures allow standardization of sampling methods for descriptions of fish communities. The surveys had a median sampling area of 188 m^2, with half of the surveys within 106–300 m^2. Most surveys (73%) were done in the recommended time of the year, that is, August or September. Fish density was expressed as the estimated number of individuals per 100 m^2. We selected only streams included in the Swedish Meteorological and Hydrological Institute (SMHI) Vattenwebb (https://www.smhi.se/data/hydrologi/vattenwebb), where the whole stream width was electrofished. Moreover, we selected only tributary sites that were located within 1 km of the tributary mouth and included in our chemical surveys (one of the 30 permanent tributaries of the Klarälven between Höljes and Edsfors, Sweden). In total, this created a sub-dataset with nine tributaries, each with multiple sampling events/years. The nine tributaries included in the electrofishing analyses encompassed most of the environmental gradients (e.g., temperature and fluvial geomorphology) seen across all 30 tributaries (Figure 4b).

Boat electrofishing was performed in the upper and middle sections of the Klarälven River in 2012–2013 and 2017–2018 by the Norwegian Institute for Nature Research as described in Museth et al. (2015). An electrofishing boat of the CATRAFT type, equipped with a 7.5 kW generator, was used for sampling. The details of the sampling are presented in Vänerlaxens Fria Gång report (Gustafsson et al., 2015). Sampled fish were counted, measured, and identified to species (trout and salmon were identified as among +0, and older fish). To compare the relationships between sensitive and insensitive fish species found in the main channel versus the tributaries, we used the classification of the Swedish VIX index (Beier et al., 2007). We also classified the fish species into those expected to have an expanding range in northern Europe versus species with expected decreasing ranges (with increasing temperatures and decreased oxygen concentrations; Lehtonen, 1996).

2.5 | Statistical analyses

Paired sample *t*-tests of the different water chemistry variables were used to test for differences between the main channel and the 30 tributaries. These results were visualized with interquartile box plots (Minitab Statistical Software).

Predictor variables were standardized, *Z*-scores were calculated for all explanatory variables, so that all variables were on the same scale for the multidimensional analyses and ordinations. Variation in water chemistry and fish species abundance was related to landscape characteristics by using principle component analysis to reduce the number of landscape characteristics, respectively. The broken-stick method (Jackson, 1993) was used to evaluate the number of components to be retained for further analysis. Hence, variables with the strongest loadings along significant primary components were retained for further analysis, reducing the number of significant landscape characteristics for the tributary water chemistry to 14, and for fish species abundance in the tributaries to 13. After this, canonical redundancy analyses (RDA) was used to identify the relationship between the reduced number of landscape characteristics and tributary chemistry and fish abundance, respectively (Rao, 1964). This canonical technique relates a matrix of response variables (*Y*) to a corresponding matrix of landscape characteristics s (*X*) (Legendre &

Legendre, 1998). Resulting scores are correlations between the tributary chemistry or fish abundance and the landscape characteristics, and they are displayed in correlation triplots with axes scaled by adjusting the scores to the variance in chemistry or fish abundance (ter Braak, 1990). The additional contribution of each landscape characteristic to the RDA model was evaluated by Monte Carlo permutation tests during forward selection of the explanatory variables at the 5% significance level (499 permutations). All multivariate analyses were performed using the CANOCO program (Version 4.5; ter Braak & Smilauer, 2002).

To test the contribution of the landscape variables (including land use in the watershed for each tributary and the categories lakes/streams, urban, forest, agriculture, moorland, wetland, pavement, as well as watershed areas, distance to hydropower plant, tributary length, time of day, slope, tributary discharge, air temperature, and number of tributary dams) to explained variation in the tributaries' physical and chemical parameters, we performed multiple linear regression models in R (Version 4.0.4, R Studio Team, 2020). Response variables were temperature, total nitrogen, total phosphorous, chlorophyll *a*, filtered absorbance and TOC. Total nitrogen, total phosphorous, and chlorophyll *a* were log transformed to meet normality assumptions. Collinearity between predictors was checked by calculating the variance inflation factor for each predictor, using a threshold value of two, and Spearman's rank correlation coefficients. Urban and agricultural land use were highly correlated (Spearman's rank correlation coefficient $= 0.71$, $p < 0.001$), and given their ecological importance in explaining tributary water properties we decided to include them in separate models. Forest land use was collinear with agricultural land use (Spearman's rank correlation coefficient $= -0.42$; $p < 0.022$), hence, agricultural land use was not included in the "urban model." Lakes and stream land use were collinear with forested land use (Spearman's rank correlation coefficient $= -0.38$; $p < 0.037$), hence lakes and streams were included in the "agricultural model." Wetlands and moorland land use were collinear with both agricultural and urban land use; hence, they were excluded from the analyses as they were deemed less ecologically significant than urban and agricultural land use. Finally, we excluded stream slope from the agricultural model because of collinearity (Spearman's rank correlation coefficient $= -0.66$, $p < 0.001$). These were the final model in order to test the contribution of the different landscape variables:

$y \sim$ Tributary length $+$ time of day $+$ agriculture $+$ lakes and streams.

$y \sim$ Tributary length $+$ slope of the tributary $+$ time of day $+$ urban $+$ forested.

3 | RESULTS

Although all the tributaries were located within the same main channel watershed (River Klarälven; Figure 1), there was large variation in the chemical characteristics measured in the tributaries. Tributaries differed significantly in their chemical characteristics when compared to sites located immediately adjacent but in the main channel (Figures 2 and 3). Mean temperature of the tributaries was 14.51°C ± 1.52 (SD), and mean temperature of the main channel was 16.53°C ± 0.84 (Paired $T_{29} = -8.20$; $p < 0.001$). Tributaries had significantly higher TOC (Figure 2; TOC, mg/L; main channel TOC $= 8.948$, tributary TOC $= 19.140$, Paired $T_{29} = 7.53$, $p < 0.001$), total nitrogen (Tot-N, µg/L; main channel Tot-N $= 265.4$, tributary Tot-N $= 468.8$, Paired $T_{29} = 6.42$, $p < 0.001$), total phosphorous (Tot-P, µg/L; main channel Tot-P $= 8.29$, tributary Tot-P $= 20.85$, Paired $T_{29} = 2.01$, $p = 0.05$), chlorophyll *a* (Chl *a*, µg/L; main channel Chl *a* $= 8.134$, Tributary Chl *a* $= 12.046$, Paired $T_{29} = 2.42$, $p = 0.022$), and brownness of the water as measured by filtered absorbance at 420 nm (Abs F420/5, 420 nm; Paired $T_{29} = 6.83$, $p < 0.001$) when compared to the adjacent main channel sites.

Canonical RDA showed that the landscape characteristics, specifically land use of the tributaries' watersheds, explained 60% of the variation in the tributary water chemistry data (Figure 4). An overall permutation test of significance showed that the canonical R^2 between tributary chemistry and landscape characteristics was highly significant ($p = 0.004$). The first two canonical axes explained 53.6% and 0.19% of the variation in the chemical data, respectively. Fourteen landscape characteristics had significant influence on the chemical characteristics: land use of the tributary´s watershed (forested, pavement, lakes and streams, wetlands, urban, agriculture, and moorland), length of the tributary, discharge of the tributary, slope of the tributary (from source to mouth), number of dams/impoundments in the tributary, tributary watershed area, location of the tributary in relation to Edsforsen power plant in the main channel (i.e., "distance" in Figure 4), and air temperature at time of sampling. From the RDA, one can postulate that many nutrients (Tot-P, PO_4, NH_4, Na, Cl, conductivity, and Tot-N) and chlorophyll *a* have similar landscape level drivers. Specifically, higher levels of anthropogenic land use (urban, agriculture, and moorland) cause an increase in nutrients. On the other hand, the larger the tributary (length, discharge, and watershed area) or the more forested the watershed, the lower the nutrient levels in the tributary. It is difficult to draw any conclusions about the second (vertical) axis of the RDA, with its very low eigenvalue (0.19%).

Multiple regression analyses showed that agricultural land use was often the factor contributing the most to the explained variation in the tributaries' physical and chemical parameters. Specifically, in the agricultural model, agricultural land use had a positive effect on temperature ($p = 0.014$), total nitrogen ($p = 0.010$), total phosphorous ($p = 0.002$), and chlorophyll *a* ($p = 0.051$; Table S1). Tributary length had a negative effect on total nitrogen ($p = 0.015$). In the urban model, urban land use had a positive effect on total phosphorus ($p = 0.003$) and a positive trend for temperature ($p = 0.054$). Total phosphorus was negatively affected by tributary length ($p = 0.013$) and slope ($p = 0.048$, Table S2). None of the explanatory factors considered was found to influence TOC and filtered absorbance 420.

Fifteen fish species/taxa (the two age classes of brown trout (*Salmo trutta*) and salmon (*Salmo salar*), 0+ and older fish, were considered as separate taxa for each species) were found in the Klarälven River system, either caught using boat electrofishing in the main stem (13 taxa), wade electrofishing in the main stem (8 taxa) or wade

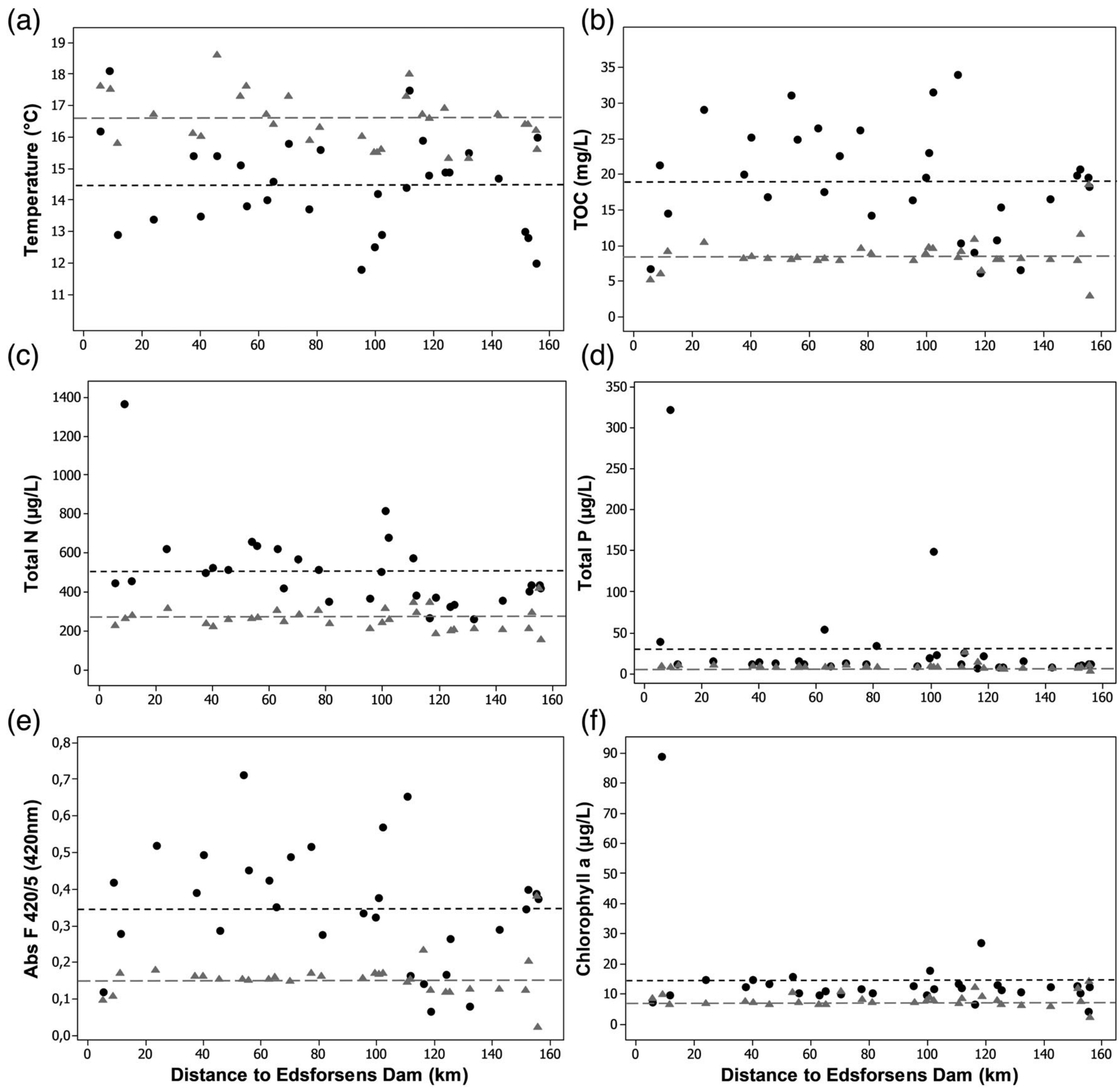

FIGURE 2 Variability in a subset of measured variables among tributaries (black circles) and in the main channel (gray triangles). X-axis is the distance of the tributary mouth from the downstream dam (Edsforsens) in the main channel of the Klarälven (river miles). Water flows from Höljesdammen toward Edsforsens. Black dotted line indicates the mean across all tributaries for that variable, gray dashed line refers to the mean across all main channel sites. (a) Temperature of the tributaries and main channel. (b) Total organic carbon (TOC) in the tributaries and main channel. (c) Total nitrogen (N) in the tributaries and in the main channel. (d) Total phosphorous (P) in the tributaries and main channel. (e) Brownness of the water as measured by filtered absorbance at 420 nm in the tributaries and in the main. (f) Measured chlorophyll *a* in the tributaries and main channel.

electrofishing in tributaries (10 species) (Table 1). The most common species caught by boat electrofishing in the main stem were grayling (*Thymallus thymallus*), salmon 0+, and trout (>10% of the caught individuals). The most commonly caught fish by wade electrofishing in the main stem were bullhead (*Cottus gobio*), common minnow (*Phoxinus phoxinus*), and trout 0+, and in the tributaries bullhead, trout, and burbot. The lamprey (*Lampetra sp.*) was the only species found exclusively in tributaries, albeit in very low numbers, whereas five species were found only in the main stem (perch (*Perca fluviatilis*), common dace (*Leuciscus leuciscus*), European whitefish (*Coregonus sp.*), common chub (*Leuciscus cephalus*), and ide (*Leuciscus idus*)).

Six of the fish taxa were classified as sensitive according to the Swedish VIX index (Beier et al., 2007) and one was classified as insensitive (perch only found in the main stem; Table 1). One sensitive taxon was only found in tributaries (lampreys, which were rare), three were common in the main stem (grayling, salmon, and trout 0+), whereas two sensitive taxa were common both in the main stem and tributaries (bullhead and trout). Two species, burbot (*Lota lota*, only common in tributaries) and trout (common both in tributaries and the main stem) were both classified as sensitive, whereas four taxa with a shrinking range were found only in the main stem (Grayling, Trout 0+, Salmon 0+, and Minnow). One uncommon species with a shrinking range (European whitefish) was exclusively found in the main stem.

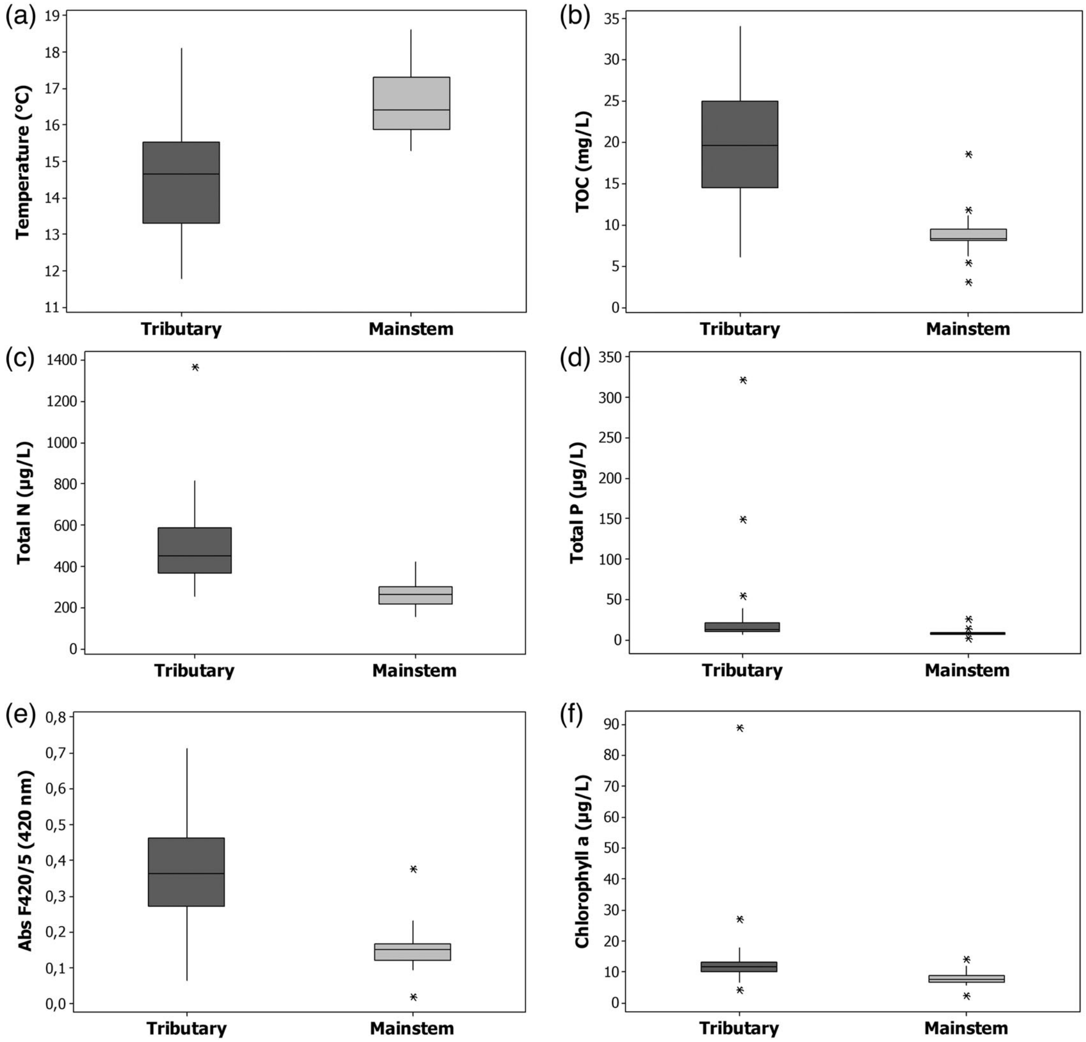

FIGURE 3 Interquartile box plots of chemical variables in the tributaries (dark gray) as opposed to the main channel sites (light gray). (A) Mean temperature ($p = 0.000$). (B) Mean total organic carbon (TOC) ($p = 0.000$). (C) Mean total nitrogen (Tot-N) ($p = 0.000$). (D) Mean total phosphorous (Tot-P) ($p = 0$ 0.05). (E) Brownness of the water as measured by filtered absorbance at 420 nm ($p = 0.000$). (F) Mean measured chlorophyll *a* ($p = 0.022$). The *p*-values through paired samples *t*-test.

We also found that there was large differences in diversity and richness of fish between different tributaries (Figure S1).

Canonical RDA showed that land use of tributary watershed explained 48% of the variation in fish species abundance ($p = 0.0320$; Figure 5). Trout 0+, burbot, minnow, and pike (*Esox lucius*) showed a similar response pattern, being positively correlated with the percent of lakes/streams, and negatively correlated with tributary length and percent agriculture in the watershed catchment. Salmon 0+, grayling and sculpin were generally positively correlated with the percent of wetlands in the catchment and mainly negatively correlated with tributary slope, forested, watershed area, pavement and number of tributary dams. In contrast, salmon 1+ showed a weakly positive correlation with watershed area, pavement, and tributary slope and forested land use. Trout 1+ was positively correlated with distance to Edsforsen hydropower station, and percent areal coverage of lakes/streams in the watershed, and negatively with tributary discharge and tributary length. The lamprey was positively correlated with watershed area, tributary length, and tributary discharge.

4 | DISCUSSION

We found that landscape features drive trends in stream water chemistry and fish species abundance. As such, large-scale patterns of landscape features may provide new insights into various biogeochemical and ecological processes. Correlation analysis and principal components analysis were used to determine representative variables, which accounted for most of the variation in each data set. We show that stream network architecture influences the distribution of fish species assemblages and water chemistry, something that is also supported by earlier studies (Grenouillet et al., 2004).

Small streams only cover a small portion of the world's surface area, but they play important ecological and biochemical roles within

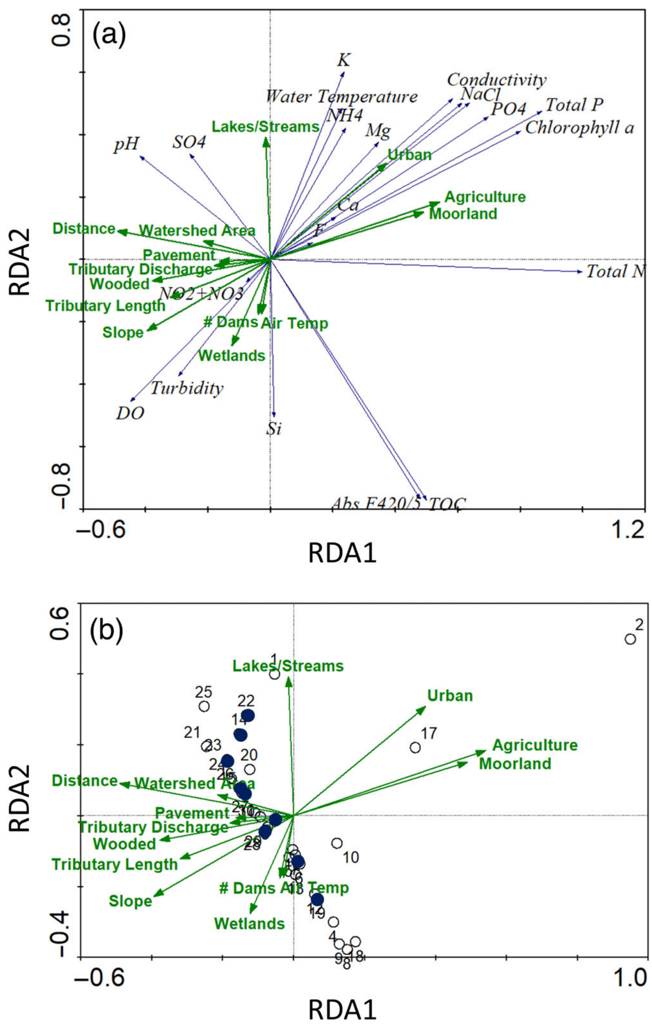

FIGURE 4 (a) Tributary chemistry and landscape variables redundancy analyses (RDA) triplot. (b) Circles indicate individual tributary samples with blue dots representing the sites that also have associated electrofishing data from the Swedish Electrofishing RegiSter. Bolded green arrows correspond to the significant environmental variables (14), and nonbolded blue arrows correspond to the measured chemical characteristics in the tributaries. For chemical data, eigenvalues: axis 1 = 0.536, axis 2 = 0.019; p-value 0.0040 (F-ratio = 11.09; number of permutations = 499). [Color figure can be viewed at wileyonlinelibrary.com]

the landscape (Kuglerová et al., 2017). Here, we focused on one large river watershed and found considerable variation across the different tributaries and between the tributaries and the main stem. Numerous studies have, for example, found that tributary streams are important sources of drifting invertebrates, detritus (Pond et al., 2016; Wipfli & Gregovich, 2002), nutrients (Kiffney et al., 2006), sediment (Benda, Andras, et al., 2004; Benda, Poff, et al., 2004; Rice et al., 2001), and large wood (Kiffney et al., 2006). We found tributary stream water nutrient levels to be higher than in the main stem. Hence, the main stem can often be quite nutrient poor and the tributaries therefore contribute with nutrients (Kiffney et al., 2006). The relative importance of tributaries on the water chemistry of the main stem depends on the volume of water in the tributary in relation to the main stem, but we also found that slope and tributary length, and amount of forest in the watershed influenced main stem water chemistry. For example, the larger the tributary and the more forestry the watershed (hence with little agricultural land use), the lower the nutrient levels. A previous study looked at the nutrient input from the tributaries to the main channel (Kiffney et al., 2006), but they did not include land-use cover in their analysis (because all tributaries were in forested landscapes), which is an important aspect for understanding the influence of different tributaries on the main stem, and of their relative importance. Furthermore, upstream land use can be more influential in larger streams while in smaller streams local land use and local environmental factors might be more important (Buck et al., 2004; Gothe et al., 2013), which could be another reason for the differences we observed in nutrient levels between the main stem and the tributaries.

We found large variation in water chemistry of the tributaries, which mainly shows that the land use gradient (forested to urban/agriculture) drives many of the trends in water chemistry in the tributaries. Previous studies have also demonstrated that land use patterns have important effects on river water quality and aquatic ecosystems within a watershed (Fitzpatrick et al., 2007; Lee et al., 2009; Rothwell et al., 2010). The alteration of land use by human activities, such as expanding agricultural and residential land use, is one of the biggest environmental changes facing society (Turner et al., 2021). Thus it is not surprising that land use and land cover change are strongly correlated with multiple water chemistry parameters in our study, and in others (Hunsaker & Levine, 1995; Lee et al., 2009). Generally, agricultural land use has a strong influence on nutrient levels, both nitrogen and phosphorus, in river water (Buck et al., 2004; Woli et al., 2004), and we also see an increase in nutrients with increasing agricultural land use. Agricultural areas often lack a forested buffer zone adjacent to the stream, which results in higher water temperatures, and explains the positive relationship between temperature and abundance of agricultural land. We also found a positive relationship between urban land use cover and phosphorus levels, and industrial and urban land uses have also previously been associated with organic pollution, heavy metals, and nutrients (Kang et al., 2010; Li et al., 2017). The agricultural intensity also influenced fish species composition (Sutela & Vehanen, 2010), and we found the abundance of several fish species (minnow, trout 0+, pike, and burbot) to be negatively correlated with agricultural area. Sutela and Vehanen (2010), however, also showed that some species, such as perch and roach, are favored as agricultural intensity increases.

We also found the water temperature to be lower in the tributaries than in the main stem, which could be explained by for example a higher degree of shading (Kiffney et al., 2003), and/or a higher relative importance of groundwater (Kurylyk et al., 2015). The lower water temperature in tributaries compared to the main stem may create important thermal refuges (Brewitt et al., 2017). Generally, lower temperatures in the tributaries have implications for the protection of coldwater fish that are dependent on thermal refuges (Brewitt et al., 2017; Petty et al., 2012), especially in a future climate as river temperatures continue to rise (Jeong et al., 2013). Preserving and

TABLE 1 Fish rankings in main stem (M) and tributaries (T), caught by boat (2012–2018), or wade electrofishing (2000–2019).

		Main stem (boat)	Main stem (wading)	Tributaries (wading)				
English name	Scientific name	Percentage ind	Percentage ind	Percentage ind	Only M/T	Common in M/T	Sensitive/ insensitive	Extending/ shrinking
Grayling	*Thymallus thymallus*	54%	0%	<1%	–	M	S	S
Bullhead	*Cottus sp.*	7%	54%	43%	–	M/T	S	–
Trout	*Salmo trutta*	17%	4%	21%	–	M/T	S	S
Trout 0+	*Salmo trutta*	3%	17%	9%	–	M	S	S
Salmon	*Salmo salar*	<1%	3%	6%	–	–	S	S
Salmon 0+	*Salmo salar*	17%	2%	3%	–	M	S	S
Minnow	*Phoxinus phoxinus*	0%	10%	5%	–	M	–	S
Burbot	*Lota lota*	<1%	2%	10%	–	T	–	S
Perch	*Perca fluviatilis*	<1%	9%	0%	M	–	I	–
Pike	*Esox lucius*	<1%	0%	2%	–	–	–	–
Common dace	*Leuciscus leuciscus*	<1%	0%	0%	M	–	–	–
European whitefish	*Coregonus sp.*	<1%	0%	0%	M	–	–	S
Common chub	*Leuciscus cephalus*	<1%	0%	0%	M	–	–	–
Ide	*Leuciscus idus*	<1%	0%	0%	M	–	–	–
Lamprey	*Lampetra sp.*	0%	0%	<1%	T	–	S	–

Note: Classification of sensitivity based on the Swedish VIX index (Beier et al., 2007). Classification of expanding range in Northern Europe versus species with expected shrinking ranges based on Lehtonen, 1996.

restoring these thermal refuges might be an important instrument for maintaining coldwater species. Hence, lampreys, which are associated with coldwater streams, were exclusively found in the tributaries (Degerman & Sers, 1992; Trigal & Degerman, 2015). Burbot were also more common in tributaries than in the main stem and have been found to be a cold-stenothermic species, which are negatively impacted by high water temperatures (Stapanian et al., 2010). We also compared how many sensitive species (Beier et al., 2007) and species predicted to have decreasing ranges with increased temperatures (Lehtonen, 1996) were found in the main stem versus in tributaries. Here, we found no consistent pattern as we found three sensitive species were common in the main stem, one sensitive species was common in the tributaries and two were common in both the main stem and in the tributaries. Similarly, for the species with a predicted shrinking distribution, there was no consistent pattern, with four species in the main stem, one species in the tributaries and one species found both in the main stem and tributaries predicted to shrink. This was contrary to our expectation, where we expected specific cold water sensitive fish assemblages in (some of) the tributaries compared to the main stem. Instead, the data suggest that the assemblage structure in the tributaries is a nested subset of the assemblage composition of the main stem. This pattern is consistent with earlier observations, where similar patterns have been explained by the fact that larger streams have higher fish abundances and thus the species are less likely to go locally extinct, whereas smaller streams contain lower abundances and therefore exerts a larger extinction risk, which is related to higher nestedness (Taylor & Warren Jr, 2001). Miranda et al. (2018) explained that this pattern of nestedness may reflect fish assemblages that "disassemble" in an upstream direction, from the main stem to the tributaries.

5 | CONCLUSION

Main stems with a larger catchment area, larger habitat area, and generally more stable conditions support a higher fish diversity than tributaries and smaller catchment areas, which have smaller habitat areas and less stable environmental conditions (Jackson et al., 2001; Miranda et al., 2018). The environmental variation is, however, much larger in the tributaries than in the main stem, and with ongoing global warming some of these tributaries could potentially be important coldwater refugia for cold stenothermic species (Brown et al., 2020; Davis et al., 2013; Dzara et al., 2019; Fullerton et al., 2018; Isaak et al., 2015; Penk et al., 2015). As water chemistry also differed between tributaries because of differences in land use, tributaries in areas with low anthropogenic impact may become very important for maintaining high species richness and abundance in the catchment. The spatial variation in water chemistry indicates that stream

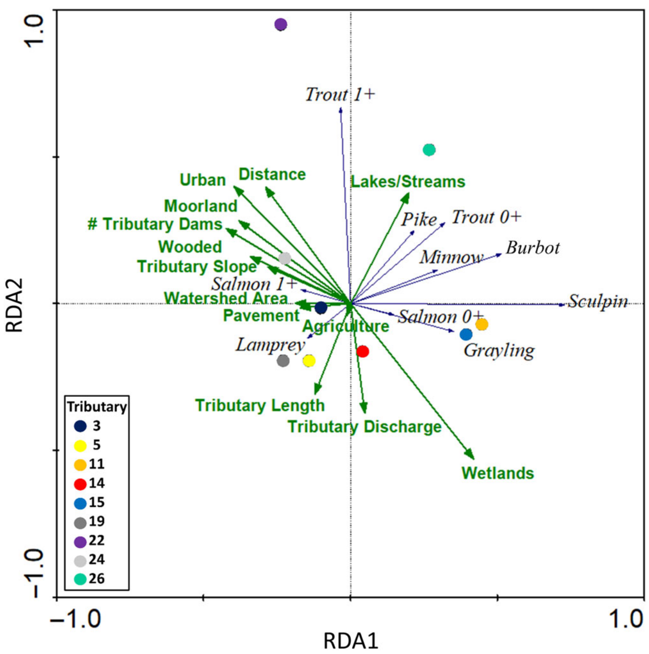

FIGURE 5 Tributary fish species abundance and landscape variables redundancy analyses (RDA) triplot. Circles indicate individual tributary samples, bolded green arrows correspond to the significant environmental variables (13), and nonbolded blue arrows correspond to the fish species abundance in the tributaries. Eigenvalues: axis 1 = 0.325, axis 2 = 0.127; *p*-value 0.0320 (*F*-ratio = 3.03; number of permutations = 499). [Color figure can be viewed at wileyonlinelibrary.com]

monitoring needs to be scale sensitive. Our results highlight the impact of different types of land use and the importance of small tributaries for a functioning network.

To understand consequences of habitat loss and fragmentation we need to understand the organization and spatial scales of river networks for maintaining biodiversity and ecosystem functioning. Integrating regional processes for assessing the needs of conservation, restoration and biomonitoring thereby become an important part in river management (Cid et al., 2022). The large differences that we show between the tributaries in this study, further emphasizes the need to evaluate at regional scales to identify refugias and ensuring connectivity, so that these refugias can be protected. Protection of, for example, forested tributaries that today function as thermal refugia for cold water fish, may become even more important in a warming world.

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DATA AVAILABILITY STATEMENT

Data are provided as private-for-peer review at the following link-25 https://doi.org/10.6084/m9.figshare.20211005.v2

ORCID

Rachel E. Bowes https://orcid.org/0000-0002-5614-069X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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