

Baseflow physical characteristics differ at multiple spatial scales in stream networks across diverse biomes

Janine Rüegg · Walter K. Dodds · Melinda D. Daniels · Ken R. Sheehan ·
Christina L. Baker · William B. Bowden · Kaitlin J. Farrell ·
Michael B. Flinn · Tamara K. Harms · Jeremy B. Jones ·
Lauren E. Koenig · John S. Kominoski · William H. McDowell ·
Samuel P. Parker · Amy D. Rosemond · Matt T. Trentman ·
Matt Whiles · Wilfred M. Wollheim

Received: 10 April 2015 / Accepted: 28 September 2015 / Published online: 13 October 2015
© Springer Science+Business Media Dordrecht 2015

Abstract

Context Spatial scaling of ecological processes is facilitated by quantifying underlying habitat attributes. Physical and ecological patterns are often measured at disparate spatial scales limiting our ability to quantify ecological processes at broader spatial scales using physical attributes.

Objective We characterized variation of physical stream attributes during periods of high biological activity (i.e., baseflow) to match physical and

ecological measurements and to identify the spatial scales exhibiting and predicting heterogeneity.

Methods We measured canopy cover, wetted width, water depth, and sediment size along transects of 1st–5th order reaches in five stream networks located in biomes from tropical forest to arctic tundra. We used hierarchical analysis of variance with three nested scales (watersheds, stream orders, reaches) to identify scales exhibiting significant heterogeneity in attributes and regression analyses to characterize gradients within and across stream networks.

Results Heterogeneity was evident at one or multiple spatial scales: canopy cover and water depth varied significantly at all three spatial scales while wetted width varied at two scales (stream order and reach) and sediment size remained largely unexplained. Similarly, prediction by drainage area depended on the attribute considered: depending on the watershed, increases in wetted width and water depth with

Special issue: Macrosystems ecology: Novel methods and new understanding of multi-scale patterns and processes.

Guest Editors: S. Fei, Q. Guo, and K. Potter.

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-015-0289-y](https://doi.org/10.1007/s10980-015-0289-y)) contains supplementary material, which is available to authorized users.

J. Rüegg (✉) · W. K. Dodds · M. T. Trentman
Division of Biology, Kansas State University, Manhattan,
KS 66506, USA
e-mail: jrueegg@gmail.com

M. D. Daniels
Stroud Water Resources Center, Avondale, PA 19311,
USA

K. R. Sheehan · L. E. Koenig · W. H. McDowell ·
W. M. Wollheim
Department of Natural Resources and the Environment,
University of New Hampshire, Durham, NH 03824, USA

C. L. Baker · T. K. Harms · J. B. Jones
Department of Biology and Wildlife and Institute of
Arctic Biology, University of Alaska Fairbanks,
Fairbanks, AK 99775, USA

W. B. Bowden · S. P. Parker
Rubenstein School of Environment and Natural
Resources, University of Vermont, Burlington, VT 05401,
USA

K. J. Farrell · A. D. Rosemond
Odum School of Ecology, University of Georgia, Athens,
GA 30602, USA

drainage area were best fit with a linear, logarithmic, or power function. Variation in sediment size was independent of drainage area.

Conclusions The scaling of ecologically relevant baseflow physical characteristics will require study beyond the traditional bankfull geomorphology since predictions of baseflow physical attributes by drainage area were not always best explained by geomorphic power laws.

Keywords Geomorphology · Nested ANOVA · Scaling · Grasslands · Temperate forest · Boreal forest

Introduction

Understanding how structural and functional heterogeneity change across spatial scale is essential to extrapolate ecological processes beyond measurement points (Levin 1992). Melbourne and Chesson (2006) suggested a systematic approach for scaling up ecological experiments that combines measures of nonlinear processes with measures of spatial variation to determine how experimental results transition with scale. However, most ecological measurements are spatially constrained both in terms of the area covered by a measurement and study, and extrapolating measurements from smaller (cm^2 – m^2) to larger spatial scales (m^2 – km^2) can be prone to error given that complexity and variability of ecosystems increase with spatial scale (Thrush et al. 1997; Hewitt et al. 2007). A basic understanding of how underlying physical attributes (e.g., substrate size, light) that can control ecological

processes vary within and among spatial scales could improve efforts to scale ecological processes.

Both the study area and the area of measurement are critical to understanding variation in ecological structure and function (Wiens 1989) as larger study areas (i.e., spatial extent) likely incorporate larger heterogeneity in the landscape while larger measurement areas (i.e., unit size) may average smaller scale heterogeneity. When testing the ability to scale ecological processes, knowledge of heterogeneity among regions, such as biomes, is essential because the underlying physical template for ecological processes may vary across broad spatial gradients (Dodds et al. 2015). Additionally, scaling relationships such as power laws will allow for application of research findings beyond the spatial scale studied (West et al. 1999; Brown et al. 2004). However, most studies do not explicitly include scale as a factor in their experimental design, limiting the potential to test for scale transitions and relationships (e.g., Lowe et al. 2006; Sandel and Smith 2009). The hierarchical structure of streams (Lowe et al. 2006) and their network properties, such as unidirectional flow and clear two-dimensional architecture (Campbell-Grant et al. 2007), provide specific constraints and unique patterns of connectivity important to scaling.

Stream ecosystem paradigms describing ecological patterns such as the River Continuum Concept (RCC; Vannote et al. 1980) often use stream geomorphology to help explain ecological patterns in space and time and extrapolate findings to the network scale and beyond. The RCC builds upon the Downstream Hydraulic Geometry concept (DHG; Leopold and Maddock 1953), where channel morphology changes predictably as a power function of increasing stream discharge in the downstream direction. The RCC postulates that longitudinal patterns in supply of energy, organic matter, and habitat size parallel the downstream changes in a river's geomorphology, and patterns in ecological processes thus coincide with stream order. Since the RCC's publication, numerous modifications and advances have been proposed. For example, the Serial Discontinuity Concept (Ward and Stanford 1983) accounts for lakes and reservoirs as heterogeneity in the continuum, and the Flood Pulse Concept (Junk et al. 1986) includes connections with floodplains. However, these early modifications of the RCC still suggest a downstream continuum based on geomorphology that mainly focuses on the bankfull

M. B. Flinn
Department of Biological Sciences, Murray State
University, Murray, KY 42071, USA

J. S. Kominoski
Department of Biological Sciences, Florida International
University, Miami, FL 33199, USA

Present Address:
M. T. Trentman
Department of Biological Sciences, University of Notre
Dame, Notre Dame, IN 46617, USA

M. Whiles
Department of Zoology and Center for Ecology, Southern
Illinois University, Carbondale, IL 62901, USA

assessments that are used in studies of stream channel geometry.

More recent stream eco-geomorphological concepts have moved beyond the longitudinal river approach and view the stream network as patterns of patches of similar functions (Wiens 2002). These patch dynamic concepts focus on different aspects of patch definition and distribution as a function of study scale (Poole 2002), based on stream network structure (Benda et al. 2004), or defined as functional processing zones of similar ecological processes (Thorp et al. 2006). These approaches are based on the increasing recognition that confluences, surficial geology, and biogeomorphic landscape agents (e.g., vegetation) lead to differences in things such as substrate grain sizes (Rice 1998), channel morphology (Burchsted et al. 2010) and sediment sorting processes (Montgomery and Buffington 1997; Fonstad and Andrew 2003) as controlled by bankfull geomorphology.

Stream ecologists and geomorphologists have proposed that landscape patterns and spatial hierarchies vary within as well as across stream networks and biomes (e.g., Stream Biome Gradient Concept, Dodds et al. 2015). However, ecologists typically view the biologically active area as the wetted channel, whereas geomorphologists focus on the bankfull or active channel. Bankfull or greater flows are of most interest to geomorphologists as these affect the most geomorphic change (i.e., geomorphically effective discharge) and shape the channel for subsequent lower flows. Stream ecologists, in contrast, tend to focus on baseflows when studying ecological processes because these flows describe conditions experienced for the majority of time by stream organisms (Doyle et al. 2005). To quantify ecological processes at broader spatial scales, patterns and interactions of physical and biological metrics need to be understood at lower baseflow conditions because the physical processes during high-flow conditions overwhelm biological processes (e.g., Flecker et al. 2002). In addition, physical and biological metrics are rarely studied together at similar scales or across multiple scales, which is likely limited by sampling logistics and methods. In this study, we applied a stream ecologist's view to physical stream measurements by focusing on conditions during the biologically active periods of stable flow and for the baseflow wetted channel only. Our goal was to identify spatial scales of heterogeneity in physical stream attributes as well as

how attributes change with watershed size within and across stream networks located in different biomes in order to provide a template for scaling ecological processes.

As part of the MacroSystems Biology (MSB) project *Scale, Consumers, And Lotic Ecosystem Rates* (SCALER), we examined how physical characteristics during baseflow conditions varied in stream networks of five biomes across multiple measurement scales often used in stream ecological studies. We tested for heterogeneity (i.e., patchiness) at multiple spatial scales relevant to ecological patterns in streams: continental (across stream networks), stream order (stream size), reaches within a stream order, and transects (sub reach-scale variability). We hypothesized that the spatial scale at which significant heterogeneity is evident depends on the variable tested. Measuring physical attributes at baseflow conditions across spatial scales allowed us to not only quantify heterogeneity relevant to scaling ecological processes but also to determine the likely spatial extent a specific extrapolation is applicable for. We tested our ability to predict geomorphic heterogeneity using a specific metric, drainage area, and thus fit a longitudinal pattern to enable scaling to stream networks and beyond. We hypothesized that variables exhibiting heterogeneity at multiple spatial scales would be more difficult to predict using this single predictor. Our results provide insight into possible scaling approaches for ecological processes based on the scaling of the physical template which they build upon.

Methods

Study and site description

We selected five watersheds, each representing a distinct biome, with minimal anthropogenic influences. Within each watershed, our study streams encompassed a range of stream sizes that ensured that the study captured the major physical gradients within the watersheds. Biomes included arctic tundra, boreal forest, temperate grassland, temperate forest, and tropical forest (Fig. 1) and all stream networks were associated with Long-Term Ecological Research (LTER) sites. We defined watersheds by the most downstream sampling location when calculating drainage area and the given stream orders described below.

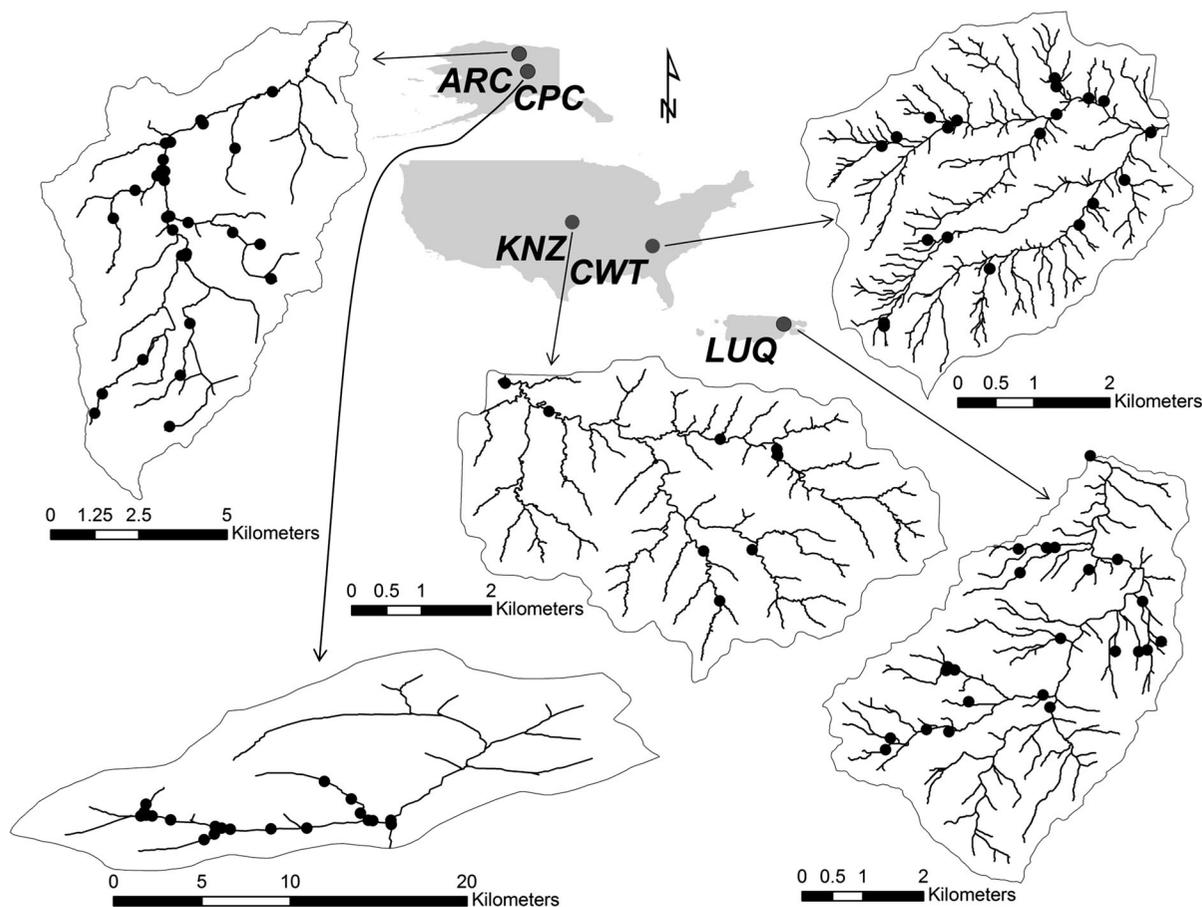


Fig. 1 Study sites embedded throughout stream networks across five distinct biomes (arctic tundra [ARC], boreal forest [CPC], temperate grassland [KNZ], temperate forest [CWT], tropical forest [LUQ]). Reaches are marked by dots

Oksrukuyik Creek (ARC) is a third-order stream draining 57.8 km² of *arctic tundra* underlain by continuous permafrost. Land cover is predominantly moist and non-acidic tundra vegetation complexes with dwarf birch (*Betula nana*) and willow (*Salix* spp.) shrubs more common in riparian areas with saturated soil conditions (Walker et al. 1994; Harvey et al. 1998). Caribou Creek (CPC) is a third-order stream draining 60.8 km² of *boreal forest* underlain by discontinuous permafrost. North-facing slopes are characterized by poorly drained soils and black spruce (*Picea mariana*) with feathermoss understory, while south-facing slopes have well-drained soils with mixed-hardwood forest. Valley bottoms have saturated soils with mosses and dwarf shrubs (Haugen et al. 1982). Kings Creek (KNZ) is a fourth-order intermittent stream that drains 13.1 km² of *native*

tallgrass prairie (grassland) and is subject to frequent and severe floods and drought (Dodds et al. 2004). Most of the watershed area is characterized by grassland vegetation maintained by prescribed burning and grazing by American bison (*Bison bison*). Many stream reaches are bordered by gallery forests that increase in continuity and width with increasing stream order and decreasing fire frequency (Whiting et al. 2011; Veach et al. 2014). Coweeta Creek (CWT) is a fifth-order stream that drains 14.4 km² of *temperate deciduous forest*, dominated by mixed hardwood over-story with an understory of *great laurel (Rhododendron maximum)* (Swank and Crosley 1988). The Río Mameyes (LUQ) is a fifth-order stream that drains 23.5 km² of *tropical forest* dominated by *tabonuco (Dacryodes excelsa)*, *ausubo (Manilkara bidentata)* and *motillo (Sloanea berteriana)* (Johnston 1992).

Field sampling

Sampling took place during seasons of high biological activity for streams in each watershed (Jan–Mar in the tropical forest, Mar–Apr in the temperate forest, May–Jun in the grassland, Jun–Aug in the boreal forest and arctic tundra). All data collection occurred during relative baseflow, defined herein as a period of stable low discharge typical of the season without any major droughts or spates (see Supplemental Fig. 1 for hydrographs for the study periods). We conducted surveys on 9–29 reaches per study watershed (Fig. 1), where a reach was defined as a length of 35–250 m depending on stream order. Where possible, sampling reaches were stratified by stream order such that more headwater sites (i.e., lower stream orders) were selected relative to higher order reaches and sampling was weighted proportionally to the relative stream length in each order. A single sampling site was situated at the mouth of each basin. When possible, sites were at least 10 stream widths downstream from tributaries or lakes to avoid effects of confluences such as mixing of sediments, as the focus of the study was to look at heterogeneity of the majority of stream length. Sampled reaches were geo-referenced using a GPS or paper maps when GPS reception was limited.

Stream order and drainage area were calculated using the coordinates of the most downstream point of each reach and a flow accumulation grid. We used LiDAR or highest available resolution DEM (1 m resolution; ARC: manual catchment delineation of 1 m contours based on 5 m resolution DEM) to create the hydrologic networks for each study watershed using the standard flow accumulation in ArcHydro. The drainage area required to initiate surface stream flow (and to define the smallest streams of our networks) was based on field observations.

A minimum of 10 evenly spaced transects oriented perpendicular to the flow direction of the thalweg were established in each reach. Transects were surveyed for canopy cover, wetted width, water depth, and substrate particle sizes. Canopy cover was measured in the middle of the stream channel at each transect using a spherical densiometer to obtain percent cover (Stumpf 1993). All sites in the arctic tundra were devoid of canopy cover. Wetted width was measured for each transect using an electronic distance measure (Sonin 10300 Multi-Measure Combo Pro), or a measuring tape, to 1-cm accuracy. Water depth was measured

relative to the water surface and based on the average of a minimum of 10 evenly spaced locations along each transect using a meter stick to 0.5-cm accuracy. A minimum of 20 substrate particles were surveyed along each transect using a gravelometer or a ruler (median axis) (Bunte and Abt 2001). We used the frequency distribution of particle sizes at each transect to determine the median particle size (D_{50}) as well as the 16th (D_{16}) and 84th (D_{84}) percentile particle size as a measure of standard deviations (Bunte and Abt 2001). Depth measurements and sediment surveys were only conducted in a subset of sites in the ARC and CPC watersheds due to logistical constraints, but the selected sites still represented the major stream orders.

Statistical analyses

We used nested hierarchical analysis of variance (ANOVA) to test for the influence of three spatial scales (watershed, stream order nested within watershed, and reach nested within each watershed's stream orders) (Table 1) on the physical metrics (canopy cover, width, depth, and sediment size as D_{16} , D_{50} and D_{84}). Within this nested design, stream orders were treated as replicates within watersheds, reaches were treated as replicates within stream orders of watersheds and individual transects served as replicates within reaches of a stream order and watershed. This statistical framework allowed for simultaneous estimation of the heterogeneity evident at different spatial scales based on the measurement unit size (i.e., the scale of the replicates) and spatial extent (i.e., the scale of the factor) of the physical attributes (Table 1). Significant ANOVA effects were interpreted as follows: (1) a significant effect at the watershed scale is due to variation among watersheds based on the stream orders within a watershed; (2) a significant effect of stream order indicates heterogeneity among stream orders within a watershed, and (3) a significant effect of reach indicates significant differences among reaches of a specific watershed's stream order. We conducted post hoc tests following significant omnibus tests for the effect of watershed or stream order scale. If watershed was significant, we calculated the means of each stream order, in each watershed, to reflect the variance partitioning of the nested ANOVA and ran a Tukey's HSD test. If stream order nested within watershed was significant, we calculated a

Table 1 Definition of the spatial scales referred to in the text, including the unit measurements (i.e., replicates), the unit sizes in space, the spatial extent of analyses, and an interpretation of significant effects

| Spatial scales—resolution and extent for analyses |
|--|
| Nested spatial scales (study extent = continent) |
| Watershed scale |
| Measurement unit = stream orders |
| Unit size = 100 s of meters to kilometers |
| Significant = watersheds differ = watershed effect |
| Stream order scale |
| Measurement unit = reaches |
| Unit size = 10 s to 100 s of meters |
| Significant = stream orders of a watershed differ = stream size effect |
| Reach scale |
| Measurement unit = transects |
| Unit size = meters to 10 s of meters |
| Significant = reaches of a watershed's stream orders differ = reach effect |
| Sub-reach scale |
| Error of nested analysis |
| Regression analyses |
| Continental scale (across watersheds) |
| Measurement unit = reaches |
| Unit size = meters to 10 s of meters |
| Study extent = 1000 s of kilometers (all watersheds) |
| Network scale (within watersheds) |
| Measurement unit = reaches |
| Unit size = meters to 10 s of meters |
| Study extent = kilometers (one watershed) |

mean for each measured reach and ran a one-way ANOVA followed by a Tukey's HSD test for each watershed individually. We did not conduct pair-wise comparisons on the nested reaches, as reaches within a specific stream order were not selected to represent any stream categories and pair-wise comparisons could thus not be attributed to spatial scales common to either stream ecology or geomorphology. In addition to tests of significance, we compared the percentage of total variance in each physical attribute explained by each of the three scales (watershed, stream order, reach).

We used regression analyses to quantify relationships between drainage area and physical attributes. We regressed reach-scale means and coefficient of

variations (CVs) for each physical variable against drainage area, selecting from linear, logarithmic, or power functions to maximize R^2 values for reaches within specific watersheds. Additionally, we regressed all reaches across watershed (continental scale) against drainage area (fixed effect) while accounting for individual watershed by using a random intercept (Table 1) and calculated the conditional (random intercept and fixed effects) and marginal R^2 (fixed effect only). All statistical analyses were performed using R 2.10.0 (R Core Development Team 2008) and the *nlme* and *MuMIn* packages for the linear mixed effects regression models.

Results

Spatial scales of heterogeneity in physical stream metrics

All variables showed significant heterogeneity among measurement units for at least one spatial scale, but the specific scale(s) depended on the variable. Canopy cover, water depth, and size of the largest substrate particles (D_{84}) differed at all three nested spatial scales, whereas wetted width only showed significant heterogeneity at the stream order and reach scales (Table 1, 2). The small (D_{16}) and median (D_{50}) sediment particle size fractions only showed significant heterogeneity at the reach scale, the finest spatial scale considered in this study (Table 2).

The watershed scale explained the majority of the variation in canopy cover, although significant heterogeneity also occurred among the watersheds' stream orders and the reaches within those stream orders (Table 2). Comparing the canopy cover among the watersheds revealed that the boreal forest watershed had significantly lower cover (mean: 26 %) compared to all other watershed (excluding the arctic tundra where canopy was open and not included in the analysis), whereas intermediate cover in grassland (mean: 62 %, due to riparian galleries) and tropical forest watersheds (mean: 82 %) could not be distinguished statistically from the canopy cover in the temperate forest watershed (mean: 91 %) (post hoc tests Table 2; Fig. 2). The significant effect of stream order was driven by the tropical forest watershed, where canopy cover was significantly more open in larger compared to

Table 2 Results of nested analysis of variance with the nested spatial scales following the details of Table 1

| Metric | Nested spatial scales | | | |
|------------------------|------------------------|---|-------------------|-----------|
| | Watershed | Stream order | Reach | Sub-reach |
| Canopy cover* | | | | |
| Degrees of freedom | 3, 12 | 12, 54 | 54, 920 | |
| <i>p</i> | <0.0001 | 0.0016 | <0.0001 | |
| Variance explained (%) | 60.64 | 9.70 | 13.59 | 10.07 |
| Post hoc tests | Watershed | Stream order | | |
| | CPC^a | CPC: n.s. | | |
| | CWT^b | CWT: n.s. | | |
| | KNZ^b | KNZ: n.s. | | |
| | LUQ^b | LUQ: 1^a 2^{ab} 3^{abc} 4^{cd} 5^e | | |
| Wetted width | | | | |
| Degrees of freedom | 4, 14 | 14, 83 | 83, 1399 | |
| <i>p</i> | 0.6491 | <0.0001 | <0.0001 | |
| Variance explained (%) | 10.24 | 56.07 | 9.71 | 23.98 |
| Post hoc tests | | Stream order | | |
| | | ARC: 1^a 2^b 3^c | | |
| | | CPC: 1^a 2^b 3^c | | |
| | | CWT: 1^a 2^{ab} 3^{bc} 4^{cd} 5^d | | |
| | | KNZ: 2^a 3^{ab} 4^b | | |
| | | LUQ: 1^a 2^b 3^b 4^{bc} 5^c | | |
| Water depth | | | | |
| Degrees of freedom | 4, 13 | 13, 54 | 54, 1000 | |
| <i>p</i> | 0.0371 | <0.0001 | <0.0001 | |
| Variance explained (%) | 28.25 | 26.08 | 4.35 | 41.32 |
| Post hoc tests | Watershed | Stream order | | |
| | n.s. | ARC: n.s. | | |
| | | CPC: 1^a 2^b 3^b | | |
| | | CWT: 1^a 2^b 3^c 4^d 5^e | | |
| | | KNZ: 2^a 3^b 4^c | | |
| | | LUQ: 1^a 2^b 3^{bc} 4^c 5^c | | |
| D₁₆ | | | | |
| Degrees of freedom | 4, 13 | 13, 54 | 57, 1025 | |
| <i>p</i> | 0.1777 | 0.8274 | <0.0001 | |
| Variance explained (%) | 2.65 | 4.62 | 32.48 | 60.25 |
| D₅₀ | | | | |
| Degrees of freedom | 4, 13 | 13, 57 | 57, 1025 | |
| <i>p</i> | 0.2098 | 0.2459 | <0.0001 | |
| Variance explained (%) | 4.76 | 9.10 | 30.84 | 55.30 |
| D₈₄ | | | | |
| Degrees of freedom | 4, 13 | 13, 57 | 57, 1025 | |
| <i>p</i> | 0.0423 | 0.0042 | <0.0001 | |
| Variance explained (%) | 15.01 | 14.47 | 22.93 | 47.59 |
| Post hoc tests | Watershed | Stream order | | |
| | n.s. | n.s. | | |

Data presented are degrees of freedom (numerator, denominator), significance level (shown as bolditalic if significant at $\alpha < 0.05$), and the percent of model variance explained by each scale. The sub-reach scale indicated the error term and thus the amount of variance (%) not explained by any of the nested scales. For significant watershed and stream order scales, we conducted one-way ANOVAs followed by Tukey’s HSD of pair-wise differences which are presented in bold with different letters to denote significant differences (see methods for details on the analyses). Abbreviations represent the different watershed (see Fig. 1) and numbers represent the different stream orders

* Canopy cover only included the four watersheds CPC, CWT, KNZ and LUQ as the arctic tundra watershed (ARC) had totally open canopy (i.e., no variance)

smaller order streams (Table 2; Fig. 2). Thus, the significant patterns in canopy cover among watersheds were driven by the boreal forest watershed, whereas significant patterns in canopy cover within watersheds were due to the tropical forest watershed.

Wetted width increased with stream order in all watersheds (Fig. 3) and variation at the stream order scale accounted for over half of the variation in width (56 %). For the arctic tundra and boreal forest watersheds, each stream order was significantly different from all others (post hoc tests, Table 2). The stream orders in the other watersheds showed some overlap among adjacent stream orders such that 1st and 2nd order streams could not be distinguished in the temperate forest and 3rd and 4th order were indistinguishable by wetted width in the grassland watershed. Variation attributed to reaches of the same stream order was much smaller (10 %, Table 2). Thus, wetted width showed no significant patterns across watersheds and the strength of stream order patterns depended on the watershed.

Water depth differed significantly among watersheds, and depth increased systematically with stream order in all but the arctic tundra watershed (Table 2;

Fig. 4). Watershed and stream order scales explained approximately equal proportions of the observed variation in depth (28 and 26 %, respectively, Table 2). However, we were not able to determine which watersheds were driving differences at the watershed scale (post hoc tests, Table 2). Within a watershed, each stream order had significantly different water depths except for overlaps of 3rd, 4th, and 5th order in the tropical forest watershed with larger order streams being deeper. Depth also exhibited relatively high within-reach variability (Fig. 4), as 41 % of overall variability was unexplained and may have occurred at a sub-reach scale and thus between transects (Table 2). Patterns in water depth were similar to canopy cover in that watersheds differed significantly, though we could not identify which watersheds might drive patterns, as well as similar to wetted width in that the strength of stream order patterns depended on the watershed.

Sediment size fractions differed significantly at the reach scale explaining 23–32 % of observed variation for all three sediment size fractions (Table 2). The largest size fraction (D_{84}) also differed significantly at the watershed and stream order scales, which

Fig. 2 Canopy cover across reaches studied in the different watersheds (see Fig. 1 for details). Reaches are plotted and sorted based on increasing upstream area (note: log transformed x-axis for better visibility). Stream orders are shown as different *symbols*. Data presented are mean and standard deviation of all transects within a reach. All ARC reaches have open canopy (arctic tundra) and were not included in the figure or analyses

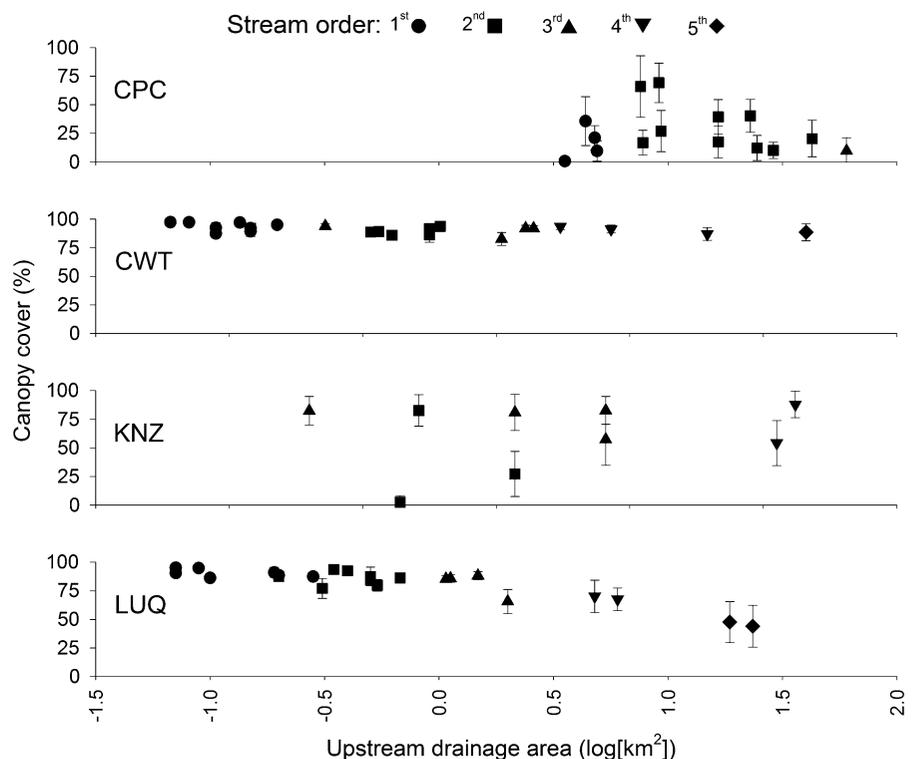
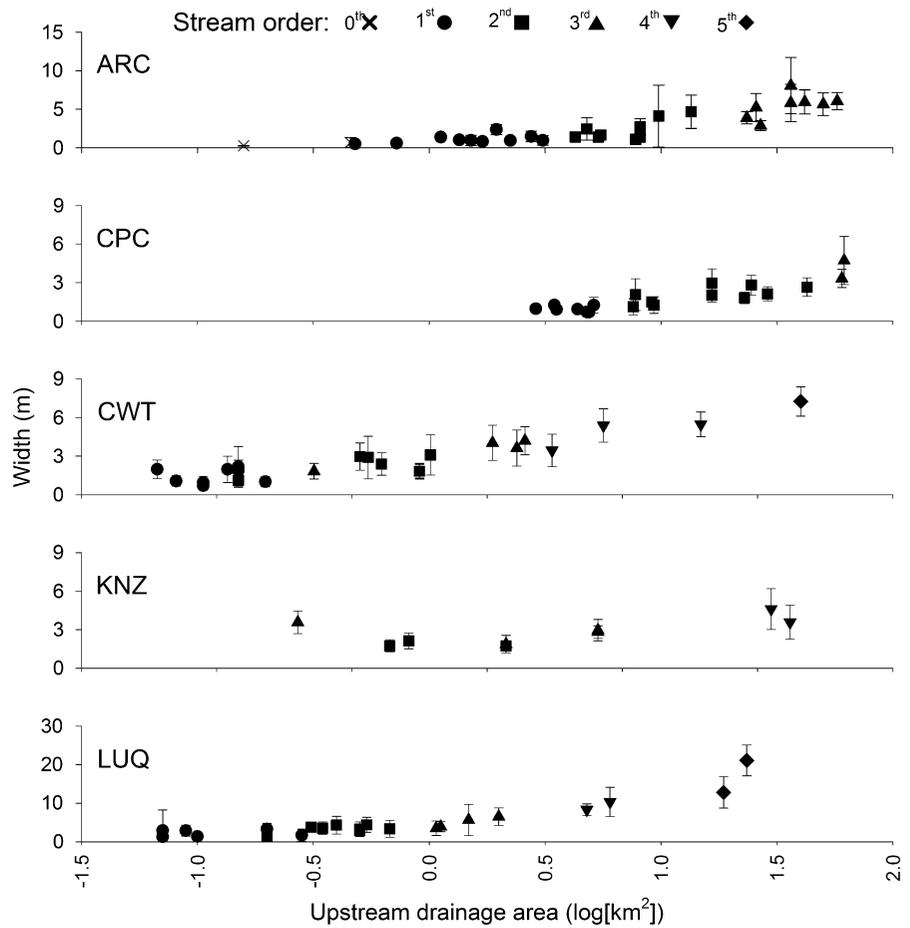


Fig. 3 Wetted widths across reaches studied in the different watersheds (see Fig. 1 for details). Reaches are plotted and sorted based on increasing upstream area (note: log transformed x-axis for better visibility). Stream orders are shown as different *symbols*. Data presented are mean and standard deviation of all transects within a reach. *Note* y-axes differ across watersheds for better visibility of variation within a stream network



explained 14 and 15 % of overall variation, respectively (Fig. 5). However, post hoc tests could not identify specific contrasts among watersheds or stream orders (Table 2). Additionally, a large portion of the overall variance in all sediment size fractions occurred at the sub-reach scale between transects (48–60 %, Table 2). Thus, the selected spatial scales did not identify patterns of heterogeneity in substrate size fractions and in fact a large portion of the variance remained unexplained as seen with water depth.

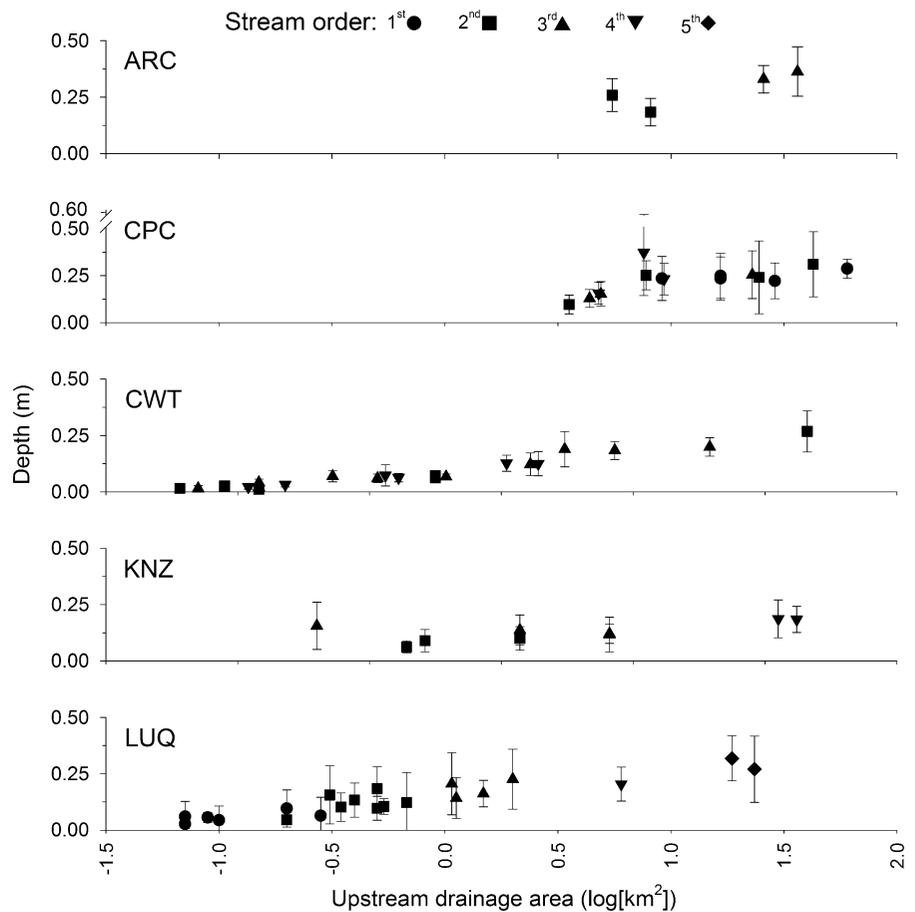
Spatial patterns in physical variables

Drainage area was generally a good predictor of physical patterns within each stream network (i.e., the network scale), and certain metrics revealed a relationship across stream networks (i.e., the continental scale) (Table 3). Canopy cover was logarithmically related with drainage area across networks

($p < 0.0001$, $R^2_{\text{cond}} = 0.70$, Table 3), but the relationship was driven by differences in the intercepts across watersheds and drainage area explained only a small fraction ($R^2_{\text{marginal}} = 0.06$). Only the tropical stream network decreased significantly in canopy cover with increasing drainage area within the stream network (Table 3), which confirmed the significant differences among stream orders found in the nested analyses. Within-reach variability in canopy cover (as the coefficient of variation [CV] among transects) increased linearly downstream in the tropical and temperate forested stream networks, meaning that canopy cover was more variable within reaches downstream (linear function) (Canopy CV, Table 3).

Wetted width increased significantly with drainage area in each individual watershed as well as across watersheds. Arctic tundra and boreal forest reaches scaled based on a power function, whereas the best model fits were logarithmic for the temperate forest

Fig. 4 Water depths across reaches studied in the different watersheds (see Fig. 1 for details). Reaches are plotted and sorted based on increasing upstream area (note: log transformed x-axis for better visibility). Stream orders are shown as different *symbols*. Data presented are mean and standard deviation of transect means (min. 10 measurements) within a reach



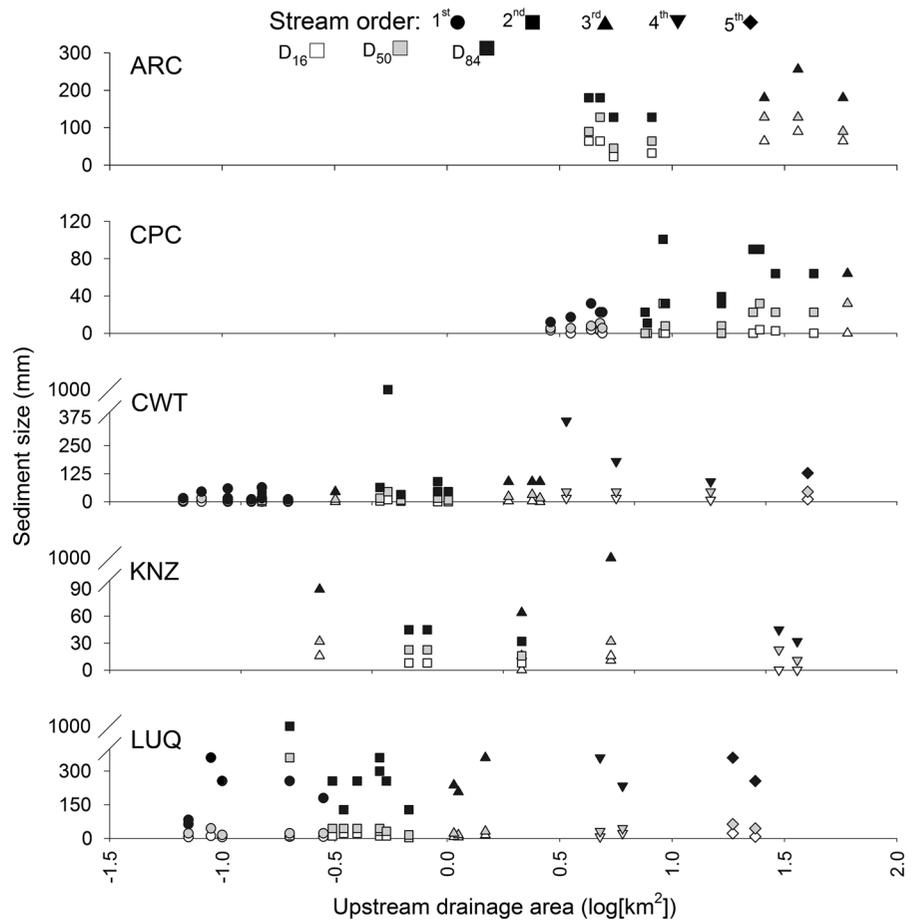
reaches and linearly for the grassland and tropical forest reaches (Width Mean, Table 3; Fig. 6b). Power functions, though not the best model, were significant with high explanatory power for all watersheds except for the grassland. The exponents suggested that the arctic and boreal forest networks, with power function being the best model fit, increased more in wetted width (exponent 0.522 and 0.487, respectively) than the temperate and tropical forest networks (exponent 0.359 and 0.387, respectively) with drainage area. Variability in wetted width (CV) decreased with increasing upstream area only in tropical and temperate forested stream networks meaning that the reach width became more uniform with distance downstream. Though wetted width increased with drainage area across all reaches of all networks, the predictive power of the continental scale relationship was low.

Water depth increased logarithmically at the continental scale (i.e., across networks, Table 1)

($p < 0.0001$, $R^2_{\text{cond}} = 0.82$; Fig. 6c). All but the arctic stream network also increased significantly at the network scale (i.e., within networks, Table 1), although the predictive power was generally similar to the continental scale relationship (except for temperate and tropical forest stream networks, logarithmic relationships, Depth Mean, Table 3). The power functions were significant for all but the arctic and grassland watersheds and the exponents suggest that the temperate forest watershed increases more in water depth with increasing drainage area (exponent 0.586) than the tropical (exponent: 0.349) and the boreal forest watershed (exponent: 0.272). In contrast, variability in water depth was not explained by drainage area.

Sediment size fractions were poorly predicted by drainage area, with the exception of the temperate forest stream network and for some size fractions in the boreal (D_{50} , D_{84}) and grassland stream networks (D_{16}) (Table 3). Relationships between the reach

Fig. 5 Sediment size fractions across reaches studied in the different watersheds (see Fig. 1 for details). Reaches are plotted and sorted based on increasing upstream area (note: log transformed x-axis for better visibility). Stream orders are shown as different *symbols*. Sediment sizes are shown as median (D_{50} , grey) as well as 16th (D_{16} , white) and 84th (D_{84} , black) percentile of all sediment particles surveyed within a reach while data used for analyses reflect D_{16} , D_{50} and D_{84} of individual transects. *Note* y-axes differ across watersheds for better visibility of variation within a stream network



means of individual physical metrics and drainage area were applicable at the continental scale for some variables (canopy cover, water depth) and at the watershed scale for others (wetted width), while some were not well predicted at all (sediment size).

Discussion

The Stream Biome Gradient Concept postulates that rivers and streams are embedded in and partially defined by the terrestrial biomes they drain (Dodds et al. 2015). However, although biome gradients allow for a degree of prediction in physical habitat attributes, variability in specific conditions is large and predictions based on the current knowledge of a small sample of streams in a particular region may be difficult. Our study provides an initial proof-of-concept for describing and predicting variability in

the physical variability of the wetted stream channel across multiple spatial scales.

The hierarchy of river networks is useful for understanding scaling of ecological processes. We undertook hierarchical analyses of physical attributes of stream networks spanning different biomes and identified heterogeneity in these attributes at various spatial scales. These patterns of heterogeneity may be used to quantify and scale ecological processes. Ecological processes are likely to exhibit variation related to the physical habitat characteristics of canopy cover, stream width and depth, and substrate sizes which we found to vary in the spatial scales exhibiting heterogeneous patterns.

The systematic variation in physical attributes that we found with the categorical approach of stream order or the continuous approach of drainage area provides a promising avenue for scaling ecological processes. In order to scale aquatic ecosystem

Table 3 Results of regression model fits predicting physical stream variables from upstream drainage area (km²)

| Variable | Best model | P value | R ² | Parameters | | Power function a, b, R ² , p |
|-------------|-----------------------|---------|----------------|------------|--------|--|
| | | | | a | b | |
| Canopy | | | | | | |
| MEAN | | | | | | |
| Continental | Logarithmic | <0.0001 | 0.70(0.06) | 66.875 | −3.796 | |
| Network | | | | | | |
| CPC | n.s. | – | – | – | – | |
| CWT | R ² < 0.30 | – | – | – | – | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | Linear | <0.0001 | 0.80 | 87.319 | −2.078 | |
| CV | | | | | | |
| Network | | | | | | |
| CPC | n.s. | – | – | – | – | |
| CWT | Linear | 0.0026 | 0.36 | 2.998 | 0.407 | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | Linear | <0.0001 | 0.90 | 4.288 | 1.718 | |
| Width | | | | | | |
| MEAN | | | | | | |
| Continental | Power | <0.0001 | 0.92 (0.43) | 1.801 | 0.411 | <i>1.801, 0.411, 0.92 (0.43), <0.0001</i> |
| Network | | | | | | |
| ARC | Power | <0.0001 | 0.86 | 0.790 | 0.522 | <i>0.790, 0.522, 0.86, <0.0001</i> |
| CPC | Power | <0.0001 | 0.70 | 0.499 | 0.487 | <i>0.499, 0.487, 0.70, <0.0001</i> |
| CWT | Logarithmic | <0.0001 | 0.85 | 3.647 | 1.030 | <i>3.158, 0.359, 0.76, <0.0001</i> |
| KNZ | Linear | 0.0277 | 0.52 | 2.246 | 0.148 | n.s. |
| LUQ | Linear | <0.0001 | 0.89 | 3.094 | 0.711 | <i>4.620, 0.387, 0.83, <0.0001</i> |
| CV | | | | | | |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | |
| CPC | n.s. | – | – | – | – | |
| CWT | Power | 0.0001 | 0.54 | 1.492 | −0.172 | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | Power | 0.0011 | 0.42 | 43.926 | −0.197 | |
| Depth | | | | | | |
| MEAN | | | | | | |
| Continental | Logarithmic | <0.0001 | 0.82 (0.78) | 12.794 | 4.144 | <i>9.849, 0.401, 0.81 (0.73), <0.0001</i> |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | n.s. |
| CPC | Power | 0.0086 | 0.42 | 11.228 | 0.272 | <i>11.228, 0.272, 0.42, 0.0086</i> |
| CWT | Logarithmic | <0.0001 | 0.93 | 12.222 | 4.557 | <i>9.453, 0.586, 0.86, < 0.0001</i> |
| KNZ | Linear | 0.0153 | 0.59 | 10.403 | 0.664 | n.s. |
| LUQ | Logarithmic | <0.0001 | 0.84 | 15.722 | 4.415 | <i>13.377, 0.349, 0.72, < 0.0001</i> |
| CV | | | | | | |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | |
| CPC | n.s. | – | – | – | – | |

Table 3 continued

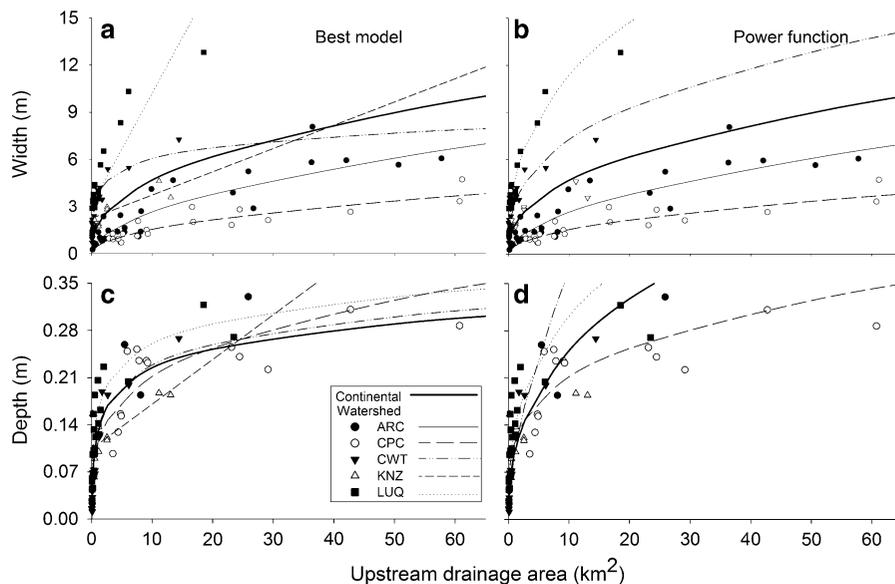
| Variable | Best model | P value | R ² | Parameters | | Power function a, b, R ² , p |
|-----------------|-----------------------|---------|----------------|------------|--------|--|
| | | | | a | b | |
| CWT | n.s. | – | – | – | – | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | R ² < 0.30 | – | – | – | – | |
| Sediment size | | | | | | |
| D ₁₆ | | | | | | |
| Continental | R ² < 0.30 | – | – | – | – | |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | |
| CPC | n.s. | – | – | – | – | |
| CWT | Logarithmic | 0.0006 | 0.43 | 5.619 | 2.224 | |
| KNZ | Power | 0.0391 | 0.48 | 3.993 | –1.074 | |
| LUQ | n.s. | – | – | – | – | |
| D ₅₀ | | | | | | |
| Continental | n.s. | – | – | – | – | |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | |
| CPC | Linear | 0.0049 | 0.44 | 5.413 | 0.484 | |
| CWT | Logarithmic | <0.0001 | 0.63 | 26.353 | 8.131 | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | n.s. | – | – | – | – | |
| D ₈₄ | | | | | | |
| Continental | n.s. | – | – | – | – | |
| Network | | | | | | |
| ARC | n.s. | – | – | – | – | |
| CPC | Power | 0.0016 | 0.52 | 0.966 | 0.569 | |
| CWT | Power | 0.0025 | 0.36 | 1.941 | 0.462 | |
| KNZ | n.s. | – | – | – | – | |
| LUQ | n.s. | – | – | – | – | |

For all variables, we fit regression models within each individual stream network (i.e., network scale) as well as across all watersheds (i.e., continental scale). For continuous variables (canopy cover, width, and depth) we tested for changes in mean as well as changes in variability (expressed by the coefficient of variation (CV)). Best model indicates the type of regression explaining the most variation (i.e., highest R²): linear: variable = a + b* upstream area; logarithmic: variable = a + b* ln (upstream area); power: variable = a* (upstream area)^b. If none of the models were significant (n.s.) or significant models explained less than 30 % of the variation, no model results are shown. At the continental scale, we detail both the conditional (whole model) and marginal R² (fixed effect only; in parentheses). For mean wetted width and water depth, we also present the results for the power function suggested by the literature for bankfull flow if significant and R² > 30 % (if best fit was a power function, it is in italics)

processes from the reach scale to the river network scale, we need to know at which spatial scales we find heterogeneity of the underlying physical variables (e.g., water depth heterogeneous within stream orders vs. across stream orders) and how we might extrapolate between scales (e.g., using stream reach means to scale within vs. across watersheds). However, significant variation for all measured attributes at the reach

scale (our finest spatial scale), as well as substantial variation occurring at sub-reach scales (i.e., error in our model), underscores the importance of replication and the measurement unit size necessary to generate the appropriate and representative estimates from which to scale. The role of sub-reach scale variation in defining reach-scale processes must also be determined.

Fig. 6 Upstream drainage area as a predictor of wetted width (a, b) and water depth (c, d) across one watershed each of five North American biomes (indicated by different symbols, see Fig. 1 for details). The left panels (a, c) show the best fit models (linear, logarithmic, power) while the right panels (b, d) are power functions only based on fluvial geomorphology. See Table 3 for details on regression analyses



Spatial scales of variation in physical variables

We found that the watershed scale encompassed significant heterogeneity in about half of the studied variables (canopy cover, water depth, and largest sediment size fraction) but the smaller reach scale showed significant heterogeneity in all variables. Sediment size was least explained by our statistical model (Table 2) suggesting even finer scale heterogeneity could dominate. The approach of using reach means (i.e., averaging out small scale variation) allowed canopy cover, wetted width and water depth to be predicted within and, for some, across watershed by the size of the basins studied. However, our study watersheds were also relatively small. As a result, drainage area was not as good a predictor as we expected, especially for canopy cover (a function of tree height and canopy width) that remained sufficiently high in certain watersheds, relative to channel width, that canopy cover did not decline with river size.

Differences in canopy cover among watersheds, and thus biomes, were likely driven by large-scale differences in terrestrial vegetation architecture (Dodds et al. 2015). Canopy cover in our study reflected three contrasting states of vegetation in the riparian areas: closed forest (temperate deciduous and tropical evergreen), mixed canopy of shrubs and gallery forest (grassland and boreal), or open due to

low vegetation height (arctic). Because we studied relatively non-impacted sites, variation in canopy cover within reaches of the forested biomes may be due to forest gaps from tree falls (e.g., Pringle et al. 1988). We expected the importance of tree falls to canopy cover variability to decline downstream, when canopy cover decreases as stream channels widen (Vannote et al. 1980). However, our regression analyses suggested that canopy cover was more heterogeneous within reaches farther downstream (i.e., with larger drainage area). The increased patchiness may occur because headwater streams are narrower and the trees can more consistently span the channel, so this increase in heterogeneity with stream size may be an indication of transition to more open canopies predicted by the RCC. Also, biologically significant canopy cover may have been underestimated in the smallest boreal and grassland streams of our study because low shrubs and grasses were below the measuring height of the densiometer but may provide significant shading to streams. Surprisingly, we found drainage area predicted canopy cover only in the tropical forest, potentially because the tropical streams studied here flood frequently and the wide bankfull channels remain without vegetation and regulates proximity of riparian trees to the wetted width and therefore canopy cover. Although differences in canopy cover and thus light availability to stream organisms among our study watersheds are not

surprising, the variation in canopy cover across the smaller spatial scales of stream orders and reaches illustrates the need to address multiple spatial scales when scaling this parameter as a driver of ecological processes.

Riparian vegetation type can influence fluvial geomorphic traits such as width and depth but the stream networks in the different biomes followed the general scaling patterns of increasing width and depth with increasing drainage area (Leopold and Maddock 1953). However, we found the specific form (e.g., power versus logarithmic) and parameterization of the scaling relationships was related to watershed, and thus biome, at baseflow. Using the power function applied to bankfull flow showed that the influence of drainage area (i.e., exponent) varied by a factor of two among watersheds and the intercepts varied by a factor of four and ten for wetted width and water depth, respectively, suggesting watershed differences beyond drainage area are important. We found variance in width and depth was explained mostly by the stream order and reach scales, suggesting the accumulation of stream flow was explained to a high degree by drainage area. However, while the watershed scale was not an important scale for wetted width, we found no significant relationship that fit across stream networks, and while the watershed scale exhibited significant variation in water depth, we did find a relationship that was a reasonable fit across stream networks and thus biomes. The influence of watershed on the physical variable-drainage area relationship needs further consideration for scaling of these variables at baseflow.

In geomorphological studies, bankfull widths and depths are scaled based on a power function within a watershed (e.g., Fonstad and Marcus 2010). Our results confirmed these patterns for baseflow water depth and wetted width but only in the arctic tundra and boreal forest stream networks potentially due to the box-like geometry of these stream channels (increase in flow deepens rather than widens channels) keeping width fairly constant across different flows. In fact, wetted width increased less per unit drainage area in the boreal forest watershed compared to its water depth. At the continental scale (i.e., across watersheds), the differences in landscapes (i.e., slope, aspect, or precipitation, e.g., Yair and Raz-Yassif 2004) affect hydrology and thus create differences in how the power function applicable at bankfull flow

translates to baseflow patterns. For example, the wider streams and higher stream orders in the tropical stream network compared to the other stream networks may reflect a greater discharge per unit of watershed area due to higher annual precipitation and thus wider streams at the bottom of a watershed of similar size. The differences in heterogeneity of wetted width and water depth at baseflow conditions compared to the generally used bankfull measurements are critical when trying to scale physical characteristics for the ecologically important baseflow conditions.

Some of the unexplained variability for each of the variables may also be due to measurement unit size and accuracy of measurements. Wetted width is easily and accurately measured and can even be obtained from high-resolution imagery, at least for certain stream sizes or biomes (Carbonneau et al. 2012). Water depth, however, is more difficult to measure, especially in small streams or those with large sediment particles. This is a known issue in stream ecology, which is why depth is generally calculated based on discharge, water velocity, and wetted width. We decided to remove some of the variation a priori by using mean transect depth, but a large proportion of the variation still remained unexplained by watershed, stream order, or reach. Some within-reach variability in both depth and width likely originates from differences between pool, run, and riffle habitats. Thus, small scale variation is not described well by the spatial scales chosen to categorize patches in streams. In fact, such variation is often removed for scaling, similar to the use of reach means in our relationships with drainage area. Determining the importance of such small scale variation to scaling of the physical parameters and the ecological processes they support as well as the selection of the appropriate spatial scale of measurements for scaling is a key question of the SCALER project.

Inorganic sediment particle size was highly heterogeneous at very small spatial scales and fine scale patterns outweigh any potential relationships with drainage area (though our study networks were relatively small). However, drivers of sediment sizes have been proposed to act at multiple spatial scales more in line with patch dynamic concepts (e.g., Benda et al. 2004; Thorp et al. 2006). Geology differs across the continent and thus the watersheds and biomes chosen for this study, though we only observed significant watershed differences for the large size

fraction (D_{84}). These watershed differences may be due to the lack of exposed bedrock in some watersheds as well as differences in hydrologic regime and thus movement by flood. Similarly, only D_{84} exhibited differences among stream orders, potentially due to the presence of bedrock mainly in the 2nd and 3rd order streams of our study watersheds. The differences among reaches within stream orders may be due to finer scale heterogeneity in the underlying geology (e.g., Pike et al. 2010 for the tropical watershed). Finally, particle sorting by geomorphic processes and historic patterns of deposition/erosion could control reach-scale variation in sediment size in conjunction with, for example, slope and flow (cf. Carbonneau et al. 2012). Differences among habitats likely played a role in sediment heterogeneity within reaches as sample transects included pools, runs, and riffles (Palmer et al. 2000). Sediment variability is similar to the within-reach heterogeneity in depth. Sediment sizes were poorly predicted by drainage area maybe because landscape patterns influencing sediment sizes (e.g., geology) do not coincide with the watershed boundaries. Thus, the scales significant for sediment size heterogeneity were not well-represented by the scales studied here. Accordingly, scaling sediment size may fit only with a patch concept (e.g., Poole 2002), rather than the downstream continuum (e.g., Vannote et al. 1980), at least for the watersheds included in this study.

Baseflow physical template, ecological scaling and stream paradigms

Scale-specific patterns in spatial heterogeneity among physical attributes suggest that ecological processes that these attributes influence might not be encompassed by a single ecological paradigm though we found longitudinal patterns in most variables. Factors that potentially influence ecosystem rates and thus the ability to scale to entire watersheds are often dependent upon non-linear relationships with watershed size or not related to watershed size at all. The relationship between drainage area and canopy cover observed in the tropical stream network neatly matches predictions of the RCC (Vannote et al. 1980), but such patterns were not observed elsewhere, including in the temperate forest, likely because study watersheds were relatively small and thus did not encompass the full spatial scale on which the RCC is based. Stream wetted

width and water depth at, or near, baseflow did scale with drainage area even in these relatively small watersheds, indicating that the physical dynamics creating stream flow were not dependent on the size of the study watersheds. In fact, our findings were consistent with the Downstream Hydraulic Geometry (DHG) for bankfull conditions (Leopold and Maddock 1953) and thus the RCC, though not all best-fit relationships were power functions and in some cases only non-power functions were significant. Sediment size was the physical variable that was least related to longitudinal patterns of those considered in this study. To provide a framework for scaling a physical stream template, the different physical stream attributes need to be described simultaneously and allow for both longitudinal and patch patterns.

Scaling a stream ecosystem process such as gross primary production and nutrient dynamics will necessitate a function that accounts for the effect of substrate availability, stream width, depth, and canopy cover, each of which may vary differently throughout a river network, and which together influence total habitat area and light conditions that are a key control of the process. Sediment size can also interact with biofilms to alter biogeochemical cycling rates (Battin et al. 2003) and the scaling function would need to account for spatial patterns unrelated to drainage area. Given the multiple spatial scales of heterogeneity in our study, incorporating the dynamics of stream physical attributes we identified into the scaling of ecological processes will likely require spatially distributed modeling. Our findings suggest that the scaling of ecological processes will be watershed-specific, as watersheds were a significant scale of heterogeneity and the role of drainage area differed across watersheds.

The drivers of ecological patterns and processes need to be understood at increasingly broader scales for management and for understanding responses to global change (e.g., continental; Peters et al. 2008; Heffernan et al. 2014). However, measurements of ecological processes are often restricted to smaller scales due to logistical constraints and methodologies. Stream metabolism can be studied at small (0.1 m^2 , e.g., Dodds and Brock 1998; Rüegg et al. 2015) to medium ($10\text{--}100 \text{ s m}^2$, e.g., Marzolf et al. 1994; Hall et al. 2015) scales. We found a substantial amount of variation in multiple physical variables that was not explained by watershed, stream order, or reach. Higher resolution measurements (i.e., small unit size) can

document heterogeneity at the smallest scales, but reach-scale measures, where available, can integrate across the small scale heterogeneity. Understanding how fine-scale heterogeneity is averaged in coarser-scale measurements may be important, especially when considering relationships among the physical characteristics and ecological processes that are non-linear (Rastetter et al. 1992). The scale at which an ecological process is measured must be explicitly considered when applying that measurement across stream sizes and watersheds. Thus, the selection of measurement scales, the clear distinction of measurement unit sizes, the number of replicates and the spatial extent of the study need to be carefully considered in light of the research questions that require scaling physical attributes and the ecological processes they support. Our data suggest that none of the spatial scales classically used in stream ecology were singly suited to encompass heterogeneity within or across watersheds.

Measurements of fluvial geomorphology at or near baseflow, when biological processes are most active in streams (Doyle et al. 2005), can provide a basis for understanding spatial heterogeneity in ecological function across scales. However, linking geomorphology directly to ecological processes has proven challenging, because processes respond to multiple physical drivers that vary at different scales (Newson and Newson 2000), including drivers we did not consider in this study (e.g., chemical drivers such as nutrient concentrations). Our results suggest that to scale an ecological process such as stream metabolism requires a framework linking habitat templates and ecological processes that can accommodate both longitudinal patterns and patch dynamics as our results indicate the presence of both in just a few physical variables. The ecological processes depend on templates of many variables, which may be as heterogeneous as the range of the variables presented in this study. Furthermore, such scaling will need to consider within and among watershed variability to identify which properties of scaling functions may be applicable at the continental scale.

Acknowledgments We thank Kyle Arndt, Ford Ballantyne, John Brant, Phillip Bumpers, Jason Coombs, Cindy Fifield, Derrick Jent, Audrey Mutschlechner, Katie Norris, Claire Ruffing, Geoff Schwaner, Ryan Sleeper, Chao Song, Rachel Voight for help with field measurements. This research was funded by US NSF Macrosystems grant #EF1065255. This is

publication 16-134-J from the Kansas Agricultural Experiment Station.

References

- Battin TJ, Kaplan LA, Newbold JD, Hansen CM (2003) Contributions of microbial biofilms to ecosystem processes in stream mesocosms. *Nature* 426:439–442
- Benda L, Andras K, Miller D, Bigelow P (2004) Confluence effects in rivers: interactions of basin scale, network geometry, and disturbance regimes. *Water Resour Res* 40(4)
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Bunte K, Abt SR (2001) Sampling frame for improving pebble count accuracy in coarse gravel-bed streams. *J Am Water Resour Assoc* 37:1001–1014
- Burchsted D, Daniels MD, Thorson RM, Vokoun JC (2010) The river discontinuum: beavers (*castor canadensis*) and baseline conditions for restoration of forested headwaters. *Bioscience* 60:908–921
- Campbell-Grant EH, Lowe WH, Fagan WF (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol Lett* 10:165–175
- Carboneau P, Fonstad MA, Marcus WA, Dugdale SJ (2012) Making riverscapes real. *Geomorphology* 137:74–86
- Dodds WK, Brock J (1998) A portable flow chamber for in situ determination of benthic metabolism. *Freshw Biol* 39:49–59
- Dodds WK, Gido K, Whiles MR, Fritz KM, Matthews WJ (2004) Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54:205–216
- Dodds WK, Gido K, Whiles MR, Daniels MD, Grudzinski BP (2015) The Stream Biome Gradient Concept: factors controlling lotic systems across broad biogeographic scales. *Freshw Sci*. doi:10.1086/679756
- Doyle MW, Stanley EH, Strayer DL, Jacobson RB, Schmidt JC (2005) Effective discharge analysis of ecological processes in streams. *Water Resour Res* 41(11)
- Flecker AS, Taylor BW, Bernhardt ES, Hood JM, Cornwell WK, Cassatt SR, Vanni MJ, Altman NS (2002) Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. *Ecology* 83:1831–1844
- Fonstad M, Andrew MW (2003) Self-organized criticality in riverbank systems. *Ann Assoc Am Geogr* 93:281–296
- Fonstad MA, Marcus WA (2010) High resolution, basin extent observations and implications for understanding river form and process. *Earth Surf Proc Land* 35:680–698
- Hall RO, Yackulic CB, Kennedy TA, Yard MD, Rosi-Marshall EJ, Voichick N, Behn KE (2015) Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. *Limnol Oceanogr*. doi:10.1002/lno.10031
- Harvey CJ, Peterson BJ, Bowden WB, Hershey AE, Miller MC, Deegan LA, Finlay JC (1998) Biological responses to fertilization of Oksrukuyik Creek, a tundra stream. *J N Am Benthol Soc* 17:190–209

- Haugen RK, Slaughter CW, Howe KE, Dingman SL (1982) Hydrology and climatology of the Caribou-Poker Creeks Research Watershed, Alaska. Cold Regions Research and Engineering Laboratory Report 82-26
- Heffernan JB, Soranno PA, Angilletta MJ Jr, Buckley LB, Gruner DS, Keitt TH, Kellner JR, Kominoski JS, Rocha AV, Xiao J, Harms TK, Goring SJ, Koenig LE, McDowell WH, Powell H, Richardson AD, Stow CA, Vargas R, Weathers KC (2014) Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Front Ecol Environ* 12:5–14
- Hewitt JE, Thrush SF, Dayton PK, Bonsdorff E (2007) The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *Am Nat* 169:398–408
- Johnston MH (1992) Soil-vegetation relationships in a tabonuco forest community in the Luquillo Mountains of Puerto Rico. *J Trop Ecol* 8:253–263
- Junk W, Bayley PB, Sparks RE (1986) The flood pulse concept in river-floodplain systems. International large river symposium
- Leopold LB, Maddock T (1953) The hydraulic geometry of stream channels and some physiographic implications. United States Geological Survey Professional Paper. United States Government Printing Office, Washington, DC, p 252
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Lowe WH, Likens GE, Power ME (2006) Linking scales in stream ecology. *Bioscience* 56:591–597
- Marzolf ER, Mulholland PJ, Steinman AD (1994) Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Can J Fish Aquatic Sci* 51:1591–1599
- Melbourne BA, Chesson P (2006) The scale transition: scaling up populations dynamics with field data. *Ecology* 87:1478–1488
- Montgomery DR, Buffington JM (1997) Channel reach morphology in mountain drainage basins. *Geo Soc Am Bull* 109:596–611
- Newson M, Newson C (2000) Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Prog Phys Geog* 24:195–217
- Palmer MA, Swan CM, Nelson K, Silver P, Alvestad R (2000) Streambed landscapes: evidence that invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecol* 15:563–576
- Peters DP, Groffman PM, Nadelhoffer KJ, Grimm NB, Collins SL, Michener WK, Huston MA (2008) Living in an increasingly connected world: a framework for continental-scale environmental science. *Front Ecol Environ* 6:229–237
- Pike AS, Scatena FN, Wohl EE (2010) Lithological and fluvial controls on the geomorphology of tropical montane stream channels in Puerto Rico. *Earth Surf Proc Land* 35:1402–1417
- Poole GC (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshw Biol* 47:641–660
- Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Welcomme RL, Webster JR (1988) Patch dynamics in lotic systems: the stream as a mosaic. *J N Am Benthol Soc* 7:503–524
- Rastetter EB, King AW, Cosby BJ, Hornberger GM, O'Neill RV, Hobbie JE (1992) Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecol Appl* 2:55–70
- Rice S (1998) Which tributaries disrupt downstream fining along gravel-bed rivers? *Geomorphology* 22:39–56
- Rüegg J, Brant J, Larson D, Trentman M, WK Dodds (2015) A portable, modular, self-contained recirculating chamber to measure benthic processes under controlled water velocity. *Freshw Sci* 34:831–844
- Sandel B, Smith AB (2009) Scale as a lurking factor: incorporating scale-dependence in experimental ecology. *Oikos* 118:1284–1291
- Stumpf KA (1993) The estimation of forest vegetation cover descriptions using a vertical densitometer. Joint Inventory and Biometrics Working Groups session at the SAF National Convention, Indianapolis, IN
- Swank WT, Jr Crossley DA (1988) Forest hydrology and ecology at Coweeta. Ecological studies, vol 66. Springer, New York
- Thorp JH, Thoms MC, DeLong MD (2006) The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Res Appl* 22:123–147
- Thrush SF, Schneider DC, Legendre P, Whitlatch RB, Dayton PK, Hewitt JE, Hines AH, Cummings VJ, Lawrie SM, Grant J, Pridmore RD, Turner J, McArdle BH (1997) Scaling up from experiments to complex ecological system: where to next? *J Exp Mar Biol Ecol* 216:243–254
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. *Can J Fish Aquat Sci* 37:130–137
- Veach AM, Dodds WK, Skibbee A (2014) Fire and grazing influences on rates of riparian woody plant expansion along grassland streams. *PLoS ONE* 9:e106922
- Walker MD, Walker DA, Auerbach NA (1994) Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *J Veg Sci* 5:843–866
- Ward JV, Stanford JA (1983) The serial discontinuity concept of lotic ecosystems. *Dynam Lotic Ecosyst* 10:29–42
- West GB, Brown JH, Enquist BJ (1999) The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284:1677–1679
- Whiting DP, Whiles MR, Stone ML (2011) Patterns of macroinvertebrate production, trophic structure, and energy flow along a tallgrass prairie stream continuum. *Limnol Oceanogr* 56:887–898
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. *Freshw Biol* 47:501–515
- Yair A, Raz-Yassif N (2004) Hydrological processes in a small arid catchment: scale effects of rainfall and slope length. *Geomorphology* 61:155–169