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RESEARCH ARTICLE

Scaling spatial pattern in river networks: the effects of spatial extent, grain size and thematic resolution

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Abstract

Context Understanding how spatial pattern changes with scale can provide insights into its relationship with ecological processes. In riverine landscapes, spatial pattern could scale differently from other well-studied landscapes because of their dendritic form.

Objectives The objectives of this study were (1) to assess how spatial pattern of hydrogeomorphic habitat patches (HGP) change with spatial extent, grain size, and thematic resolution, and (2) to quantify how spatial pattern in river networks varies across the contiguous United States (CONUS).

Methods We identified hydrogeomorphic patches in river networks located in different ecoclimatic domains. We then quantified spatial pattern within each river network using a suite of landscape metrics and investigated scaling relationships for each component of scale. We also assessed whether watershed area, river network length, and drainage density were related to spatial pattern among river networks and explored regional differences in the hydrologic, geomorphologic, and climatic variables that differentiate HGP types.

Results When predictable, scaling relationships within river networks followed either linear, logarithmic, or power functions. Among river networks, spatial pattern was related to total network length, catchment area and drainage density. Rarely were HGP types in different networks characterized by the same suite of hydrologic, geomorphologic and climatic variables.

Conclusions In riverine landscapes, there are a variety of relationships between spatial pattern and scale. The scaling functions we present can provide a concise description of scale dependency in these landscapes and improve our ability to synthesize information across scales.

Keywords Hydrogeomorphic patches · Scaling · Landscape pattern analysis · Riverine ecosystems · Dendritic networks · Spatial pattern

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Introduction

Spatial pattern is closely linked to ecological processes but the relationship depends on the scale of investigation (Wiens 1989; Wu et al. 2002; Jackson and Fahrig 2015). Spatial pattern changes with scale and scaling functions concisely describe these changes (Wu et al. 2002; Šímová and Gdulová 2012). Within rivers and streams, spatial pattern of aquatic habitats is an important feature governing ecological processes (Thorp et al. 2006; Thoms et al. 2018; Erős and Lowe 2019). However, riverine ecosystems are structurally different from terrestrial landscapes and require different metrics to quantify spatial pattern within them (Williams et al. 2013; Thoms et al. 2018). Investigating how these metrics change with scale can provide insights into linkages between spatial pattern and ecological processes in riverine ecosystems (Jackson and Fahrig 2015; Qiu et al. 2019).

Spatial pattern is typically quantified using landscape metrics that measure the composition (i.e. diversity) or configuration (i.e. spatial arrangement) of habitat patches (McGarigal et al. 2012). Scale can include multiple components (Wu and Li 2006; Turner and Gardner 2015), but most often it refers to spatial extent, the area under investigation, or spatial grain, the finest resolution used for analysis (e.g. pixel size or linear unit; Wiens 1989; Wu and Li 2006; Cushman et al. 2010). A third component of scale, thematic resolution, refers to the level of detail that differentiates landscape components. For example, land cover classification maps are often represented as nested hierarchies where increasing thematic resolution reveals a greater number of subordinate land cover classes (Buyantuyev and Wu 2007; Šímová and Gdulová 2012; Qiu et al. 2019).

Each component of scale can influence landscape metrics differently and, in some instances, these effects are predictable (Wu et al. 2002; Buyantuyev and Wu 2007; Xu et al. 2020). For example, landscape metrics that represent absolute values of spatial pattern, such as mean size or distance between landscape components, should increase monotonically with spatial extent and decrease with spatial grain and thematic resolution (Baldwin et al. 2004; Šímová and Gdulová 2012). Similarly, landscape metrics that quantify diversity should increase when novel landscape components are encountered at larger spatial extents or unveiled by increased thematic detail (Turner et al. 1989; Šímová and Gdulová 2012). They should also decrease with coarsening grain because small or rare landscape components disappear (Turner et al. 1989; Šímová and Gdulová 2012). Changing scale can also cause metrics to display either staircase-like or chaotic patterns, making them less predictable (Wu et al. 2002; Šímová and Gdulová 2012).

Riverine landscapes include components of the Earth's surface that are influenced by a river, including aquatic habitats in the river, and riparian corridors and floodplains that occur alongside them (Fausch et al. 2002; Ward et al. 2002; Thorp et al. 2006). These systems are characterized by "hydrogeomorphic patches" (hereafter "HGP") which can be identified as river reaches that share similar hydrologic, geomorphologic, and climatic conditions (Thoms and Parsons 2002; Thorp et al. 2006, 2008; Williams et al. 2013). The composition and configuration of HGPs can characterize the physical structure of entire river networks (Williams et al. 2013; Thoms et al. 2018), influence species diversity patterns (Maasri et al. 2019) and ecosystem processes (Hadwen et al. 2010; Thorp et al. 2010; Collins et al. 2018).

Previous efforts to characterize river networks by their HGPs have focused on a small number of river networks at different scales (Collins et al. 2014; Thoms et al. 2018; Maasri et al. 2019). Since scale dependency is common, this could mask important relationships between spatial pattern and ecological processes (Jackson and Fahrig 2015). Although scaling functions provide an accurate way to predict changes in spatial pattern of HGPs, these functions may vary geographically because river networks are embedded in biomes that vary in their climate, hydrology and geomorphology (Dodds et al. 2015, 2019). Systematic evaluations of the factors that differentiate HGP types, their spatial pattern and scaling relationships across multiple riverine landscapes could uncover potential generalities in scale dependencies (Wu et al. 2002; Shen et al. 2004; Buyantuyev and Wu 2007).

Here, we investigate scale dependency of spatial pattern using 18 river networks in the contiguous United States (hereafter "CONUS"). We identified HGPs by similarities in climate, hydrologic, and geomorphic variables and adapted several landscape metrics to quantify their configuration and composition. Within each river network we evaluated scaling functions that best describe the relationship between the landscape metrics and three components of scale. Then, among networks, we investigated the role of river network size and topology in driving variation in spatial pattern and determined if the suite of hydrologic, geomorphic and climatic variables used to differentiate HGP remains consistent across biomes.

Methods

Study sites

We chose a single river network in each of the National Ecological Observation Network (NEON; https://www.neonscience.org/) ecoclimatic domains in the CONUS (Fig. 1; Hargrove and Hoffman 2004). Ecoclimatic domains were delineated using multivariate geographic clustering of nine climate variables (Hargrove and Hoffman 2004). Where possible, we used a NEON aquatic or terrestrial site to locate a suitable river network within each ecoclimate domain. We handpicked sites in the Southern Pacific domain (17) to represent a Mediterranean climate (NEON stream sites in the domain 17 are in the Sierra Nevada mountains, with similar climate to other NEON sites), and in the Prairie Peninsula domain (06) due to restrictions in the availability of High Resolution National Hydrography Dataset (NHDHR) at the time of the study (Viger et al. 2016; Moore et al. 2019). We also selected two sites in the Ozarks complex (08) and omitted the Atlantic Neotropical domain (04) because of its relatively small spatial coverage in the CONUS (Fig. 1).

We delineated river networks by associating each site to a digital flowline in the NHDHR and navigating downstream to until reaching a catchment area closest 5,000 km^2 (range = 364.12 and 5,733.06 km^2; Strahler Stream Order > 5). We extracted all flowlines draining the catchment from the NHDHR and reconditioned them into valley and reach segments. We define a valley segment as a section of the river between a headwater and confluence, or two confluences. Valley segments < 1 km were classified as a single reach while valley segments > 1 km were split into reaches of equal length. River reaches typically ranged between 0.5 and 1 km and served as our spatial unit of replication for each river network ($1,154 \leq n \leq 13,222$; Table 1).

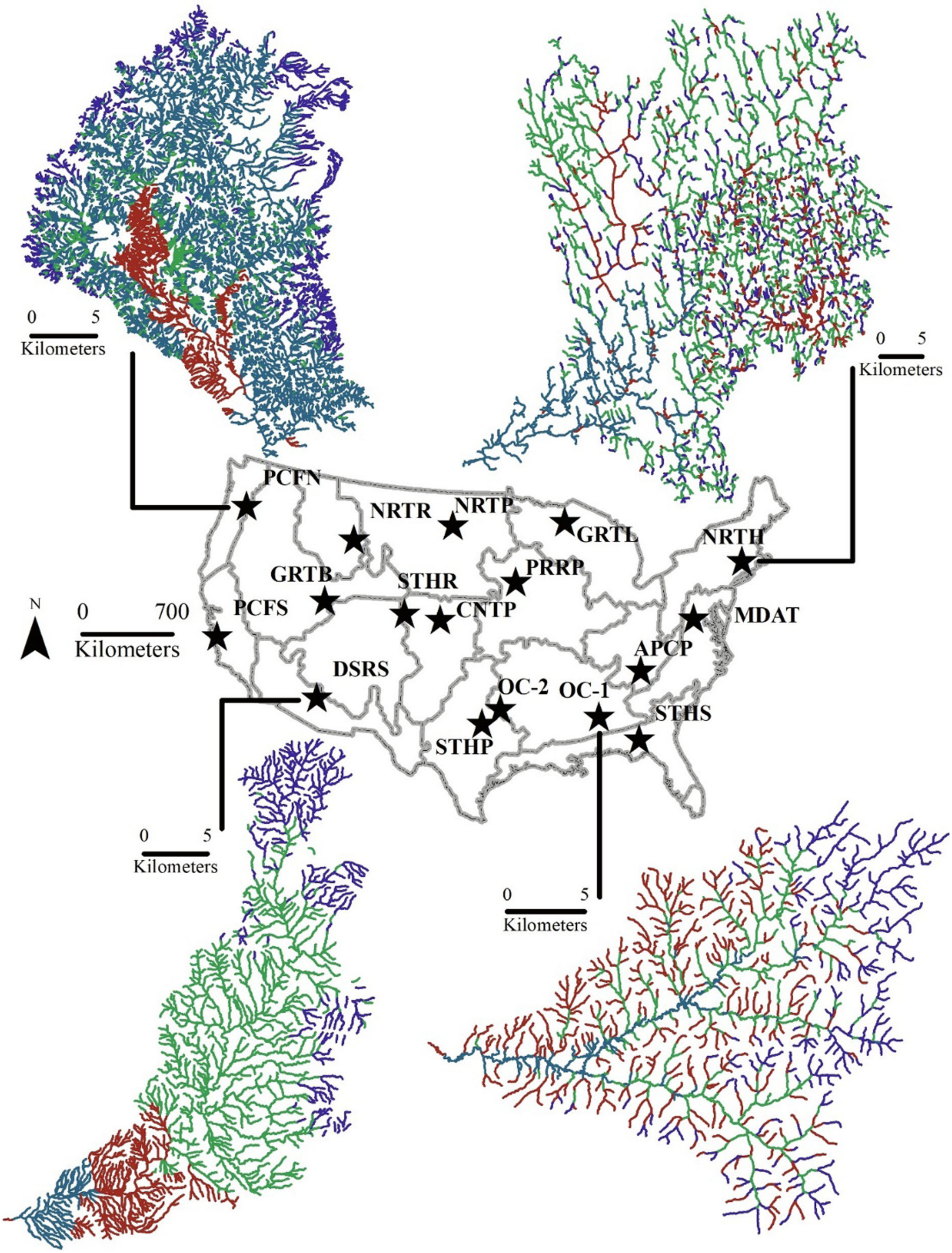
Hydrologic, geomorphologic and climatic variables

Hydrologic, geomorphologic and climatic variables were extracted or derived for each river reach from several GIS datasets and used to identify HGPs within the river networks (Table 2; Williams et al. 2013; Thoms et al. 2018; Maasri et al. 2019). Mean annual air temperature (°C) and precipitation (mm) were obtained from the PRISM Climate Group (1981–2010; https://prism.oregonstate.edu/normals/). Whole soil erodibility factor (kw) and pH values we obtained from the Digital General Soil Map of U.S. which supersedes the State Soil Geographic (STATSGO) dataset (1:250,000-scale, https://websoilsurvey.nrcs.usda.gov/) and classified as low (kw < 0.25, pH < 6.5), medium ($0.25 \leq$ kw < 0.4, $6.5 \leq$ pH < 8.5) and high (kw $\geq$ 0.4, pH $\geq$ 8.5). Depth to bedrock (cm) was obtained from Shangguan et al. (2017). Values for each variable were extracted from the appropriate raster dataset at the midpoint of each reach.

We also used the digital elevation model provided with the NHDHR to determine the elevation (cm) of a reach and to quantify a suite of geomorphologic attributes (Table 2, Figure S1). In brief, we established digital transects extending perpendicular from each river reaches' midpoint to measure valley-side slope, valley width, and valley floor width, used points at the inlet and outlet of the valley segment to measure valley slope, and the endpoints of a reach to measure channel sinuosity and mean meander length.

Hydrogeomorphic patch identification

Hydrogeomorphic patches (HGP) were identified using agglomerative hierarchical clustering on hydrologic, geomorphic and climatic variables (Table 2, Borcard et al. 2018). This approach successively groups individual river reaches into larger classes based on their similarity (Thoms et al. 2018; Maasri et al. 2019). At the lowest level of the hierarchy, each river reach is an individual class while at the highest level, all reaches are combined into a single class. We used Gower's dissimilarity index to measure pairwise associations and Ward's minimum variance to create hierarchically nested groupings (Borcard et al. 2018; Maasri et al. 2019). We objectively identified the optimal number of HGP types for each network using



0 5
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◀**Fig. 1** Representative spatial patterns of hydrogeomorphic patches within 4 river networks. Different colors correspond to distinct hydrogeomorphic patch types. Center shows river network locations used in the analysis. Boundaries demarcate NEON ecoclimate domains: *NRTH* = Northeast; *MDAT* = Mid-Atlantic; *STHS* = Southeast; *GRTL* = Great Lakes; *PRRP* = Prairie Peninsula; *APCP* = Appalachian Cumberland Plateau; *OC-2* = Ozarks Complex-2; *OC-1* = Ozarks Complex-1; *NRTP* = Northern Plains; *CNTP* = Central Plains; *STHP* = Southern Plains; *NRTR* = Northern Rockies; *STHR* = Southern Rockies; *DSRS* = Desert Southwest; *GRTB* = Great Basin; *PCFN* = Pacific Northwest; *PCFS* = Pacific Southwest

the maximum average silhouette width (Borcard et al. 2018). Silhouette width is a metric of group similarity at each partition of the dendrogram and the maximum average width corresponds to the partition with the greatest degree of separation among subordinate groups. We used the "daisy" function to generate distance matrices, the "agnes" function for agglomerative hierarchical clustering and the "silhouette" function to conduct the silhouette analysis (Maechler et al. 2019.

Spatial pattern analysis

We quantified the spatial pattern using four landscape metrics that measure the composition or configuration of HGP (McGarigal et al. 2012). To measure composition, we combined adjacent stream reaches of the same HGP type and counted the uninterrupted segments as total number of patches (TP). In addition, we calculated the Shannon Diversity index (SHDI) for each network. The SHDI is commonly used to measure landscape heterogeneity and has recently been applied to riverine landscapes (O'Neill et al. 1988; Turner et al. 1989; Thoms et al. 2018). Following Thoms et al (2018), we calculated SHDI as:

$$SHDI = -\sum p_i \ln p_i$$

where p_i is the proportional length of the ith hydrogeomorphic patch relative to the total length of the river network.

To measure the configuration of HGP within each network we calculated the mean distance separating HGP types (mean patch distance, MPD) and used the dendritic connectivity index (DCI) to measure the

Table 1 Characteristics of the river networks used in this study

Site	NEON domain name	Degrees latitude	Degrees longitude	Stream order	Catchment area (km^2)	Total length (km)	Reaches (#)
NRTH	Northeast	42.1491	− 72.6214	6	1764.45	2375.43	3747
MDAT	Mid-Atlantic	38.94293	− 78.1905	7	4153.86	6522.36	10,313
STHS	Southeast	31.1785	− 84.4741	6	2741.97	2299.17	3293
GRTL	Great Lakes	46.87233	− 89.3254	8	3480.89	5332.66	12,018
PRRP	Prairie Peninsula	42.81041	− 94.4454	6	5080.37	4058.4	5183
APCP	Appalachian Cumberland Plateau	35.92358	− 83.5851	7	976.07	2747.48	6817
OC-1	Ozarks Complex-1	33.03368	− 87.6057	5	459.18	777.57	1222
OC-2	Ozarks Complex-2	33.88835	− 95.9396	6	1753.77	3002.11	4510
NRTP	Northern Plains	46.68421	− 100.788	5	558.5	845.8	1154
CNTP	Central Plains	40.03608	− 101.53	5	4419.07	3877.19	5406
STHP	Southern Plains	32.86007	− 97.5002	6	4989.64	8845.51	13,223
NRTR	Northern Rockies	44.99472	− 110.576	7	5733.06	7352.96	10,921
STHR	Southern Rockies	40.26525	− 104.877	7	2345.82	4610.43	10,562
DSRS	Desert Southwest	33.63354	− 111.659	6	497.81	1113.26	1718
GRTB	Great Basin	40.43697	− 112.385	6	1851.59	2959.47	3937
PCFN	Pacific Northwest	45.71767	− 121.79	7	582.89	2276.95	7897
PCFS	Pacific Southwest	36.35155	− 121.209	6	364.12	1304.21	2554

Table 2 Hydrologic, geomorphic and climatic variables and data sources used to identify hydrogeomorphic patches

Variable	Description	Source
Elev	Elevation at reach midpoint	NHDPlusHR: https://www.usgs.gov/core-science-systems/ngp/national-hydrography/nhdplus-high-resolution
Ann. Precip	Mean annual precipitation (1981–2010)	PRISM Climate Group: https://prism.oregonstate.edu/
Ann. Temp	Mean annual temperature (1981–2010)	
Erosion Factor	Whole Soil Erosion factor (kw) measures susceptibility of soil to erosion	SSURGO: https://websoilsurvey.nrcs.usda.gov/
Soil pH	Soil pH	
Bedrock Depth	Depth of soil or regolith covering bedrock	Soil Grids http://globalchange.bnu.edu.cn/
Valley Width	Width of the catchment perpendicular to the river channel	Derived for this study from NHDPlusHR: https://www.usgs.gov/core-science-systems/ngp/national-hydrography/nhdplus-high-resolution
Valley Floor Width	The lateral extent of a flood reaching a depth 4 times bankfull depth*	
Valley Floor Ratio	Ratio between valley floor width and valley width	
Valley Slope	Slope between upstream and downstream points of a valley	
Valley Side Slope	Mean of the slope between the river and ridgeline on either side of the channel	
Channel Sinuosity	Ratio of the channel distance to straight line distance of a reach	
Channel Slope	Slope between upstream and downstream points of a reach	
Mean Meander Length	Mean channel distance separating two sequential meanders	

*Bankfull depth estimated from upstream catchment area (Bieger et al. 2015)

connectivity between HGP types (Cote et al. 2009). DCI is based on the probability that an organism can cross a boundary separating one patch from another:

$$DCI = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{ij}\frac{l_i}{L}\frac{l_j}{L} * 100$$

where c_{ij} is probability that an organism can traverse a boundary separating patch i and j, l is the length of patch and L is the total length of the network. The index is multiplied by 100 to scale the value between 1 and 100. This index assumes boundaries do not occupy space in the network such that when $c_{ij} = 1$ (i.e. complete boundary permeability), $DCI = 1$ (Cote et al. 2009). Because we expected the connectivity between two HGPs depends on the distance separating them, we modified DCI as:

$$DCI_k = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{k_ik_j}\frac{l_{k_i}}{L_k}\frac{l_{k_j}}{L_k} * 100$$

where k indexes HGP type. We consider $c_{k_ik_j}$ equivalent to the probability that an organism can travel the distance separating patch i and j of type k. Here, dispersal distance of an organism, X, is a random variable with a probability distribution,$X \sim \exp(\lambda)$. We parameterize the probability density function using the median maximum parent–offspring dispersal distance for riverine fishes (i.e.λ = 1/12 km, Comte and Olden 2018). Thus, for a parent fish living in patch i of type k, $c_{k_ik_j}$ reflects the probability that the offspring of that fish can travel distance,X, to patch j. Accordingly, DCI_k generally increases when larger HGP types are separated by smaller watercourse distances. We used mean DCI_k to aggregate patch-scale connectivity values to the entire river network.

R-code

We provide example R-code to identify HGPs and calculate landscape metrics at https://github.com/dkopp3/HydrogeomorphicPatches. We reconditioned NHDHR flowlines, identified reaches, sampling points, and transects using the "create module". We assigned hydrogeomorphic variables to each reach using the "attribute module" and preformed the cluster analysis using the "cluster module". Finally, landscape metrics were calculated using the "landscape metrics" module.

Statistical analysis

Within each river network we evaluated how HGP spatial patterns change with spatial extent, spatial grain, and thematic resolution. In rivers, spatial extent is represented by watershed area, or the surface area contributing runoff to a river channel during precipitation events. We changed spatial extent by randomly identifying sub-networks at 10 km^2 increments of increasing catchment area (Fig. 2). We assessed between 25 and 234 values of spatial extent depending on the size of the network. We manipulated the spatial grain of a stream network by increasing the minimum channel length represented in the network (Fig. 2). Each interval coarsened or "pruned" the river network, to provide a range of 24 to 94 values of spatial grain in our analysis. Finally, we manipulated the thematic resolution by decreasing the level of dissimilarity among HGP types beginning at the level specified by the silhouette analysis (i.e. 4–8 HGP types) up to 30 HGP types for each network (Fig. 2).

We visually inspected the scaleograms for each river network prior to fitting linear, power, and logarithmic functions. This allowed us to classify a relationship as "predictable", if the functions could provide a reasonable approximation for the data, or "unpredictable" if the relationship was better characterized by staircase-like patterns or behaved erratically (Wu et al. 2002). For predictable relationships, we fit each function to the data and used the coefficient of determination (i.e. R^2) to identify the strongest relationship (Rüegg et al. 2016).

We used a regression analysis to test whether river network length, total catchment area or drainage density explained variation in spatial pattern among river networks in different ecoclimatic regions. Network length is the total length of streams in a network; catchment area is the surface area that contributes overland runoff to a river network; and drainage density is the network length divided by the catchment area. Similar to above, we fit linear, power, and logarithmic models to each pairwise combination of spatial pattern and river network characteristic and evaluated the best fit model using the coefficient of determination.

To investigate which variables were most important in differentiating HGP types within river networks we used an Analysis of Similarity (ANOSIM) followed by Similarity Percentage Analysis (SIMPER) (Harris et al. 2009; Thoms et al. 2018; Oksanen et al. 2019). ANOSIM confirmed a statistical difference among HGP types within each river network and SIMPER identified the single variable that was most dissimilar for each pairwise combination. We used the aggregated list of variables for each river network to describe the suite of climatic, hydrologic, and geomorphic variables that contribute most to the differentiation of HGP types for each river network.

Results

Effects of scale on spatial pattern of HGP depended on the component of scale and the landscape metric (Fig. 3). For composition metrics, we found a logarithmic function consistently explained the relationship between Shannon diversity index (SHDI) and spatial extent in five river networks (R^2 range: 0.61—0.77, Table S1). The relationship between SHDI and spatial grain on the other hand, often followed a staircase-like pattern and was not reasonably represented by simple functions we considered in our analysis (Figure S2). Total patches (TP) had a consistently strong linear relationship with spatial extent in 12 stream networks ($R^2 > 0.93$) and followed a power relationship with spatial grain in three networks ($R^2 > 0.93$, Table S1). Finally, thematic resolution was almost perfectly related to both SHDI ($R^2 > 0.98$) and TP ($R^2 > 0.96$) by either, logarithmic or power functions (Fig. 3).

In general, scaling relationships for configuration metrics were different from composition metrics (Fig. 3). For example, scaling the modified dendritic connectivity index ($\overline{DCI_k}$) with spatial extent followed

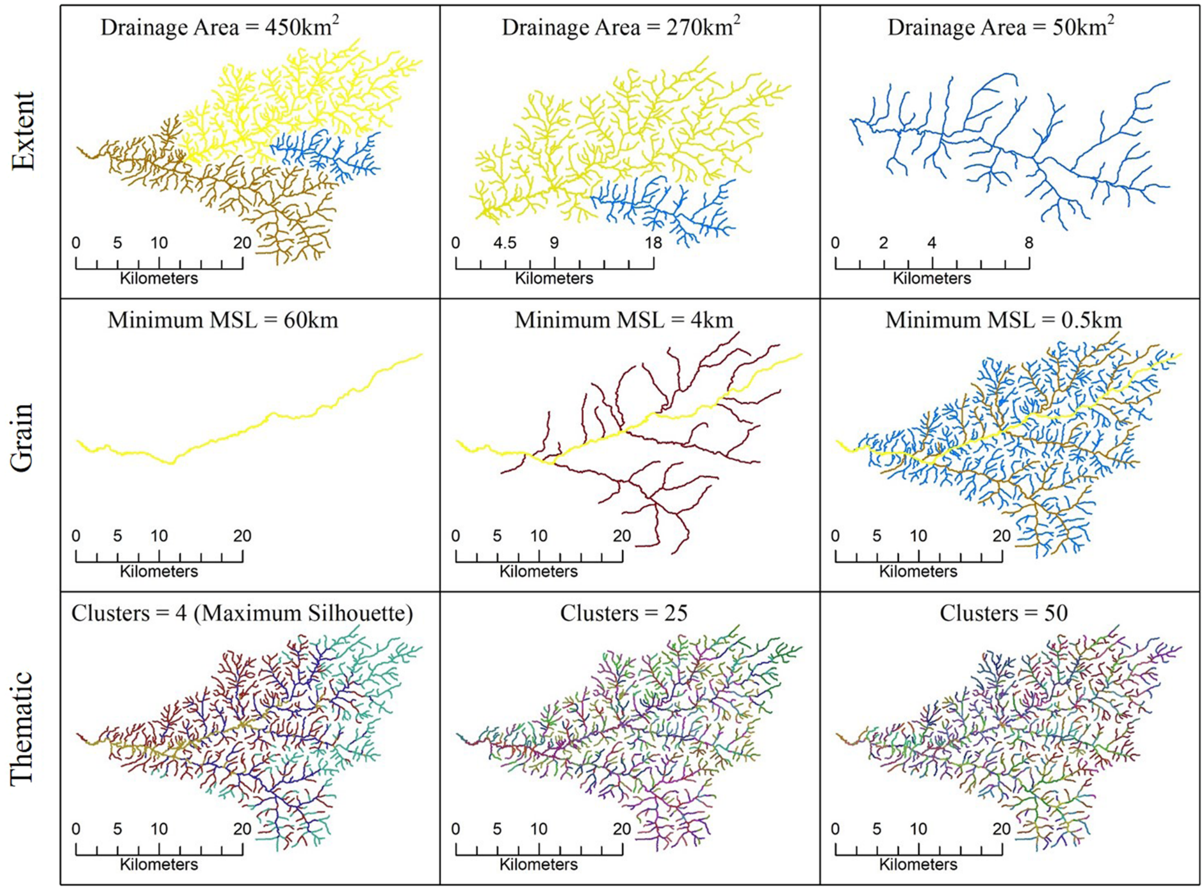

Fig. 2 Schematic demonstrating the changing the scale of spatial extent (top), spatial grain (middle) and thematic resolution (bottom) in river networks. Colors are a visual indication of changing scale from left to right. *MSL* = minimum stream length

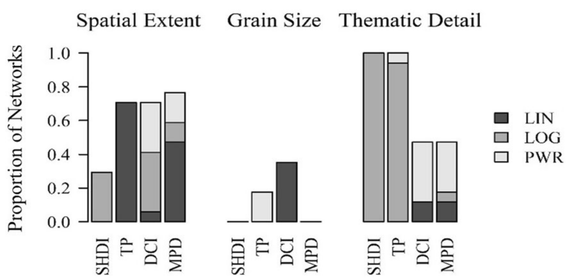

Fig. 3 Proportion of river networks where spatial pattern metrics follow simple scaling functions. *SHDI* = Shannon diversity index; *TP* = total number of patches, *DCI* = modified dendritic connectivity index (see text); *MPD* = mean patch distance; *LIN* = Linear function ($y = \alpha + \beta x$); *LOG* = Logarithmic function ($y = \alpha + \beta \log x$); and *PWR* = Power Function ($y = \alpha x^{\beta}$) where *x* is the value of extent, grain, or thematic resolution and *y* is the spatial pattern

linear, power, or logarithmic functions in 12 networks (R^2 range: 0.66–0.94) and scaling with thematic resolution followed linear or power functions in 8 networks (R^2 range: 0.69–0.92, Table S1). When mean patch distance (MPD) was predictable, it also scaled with extent and thematic resolution following linear, power, or logarithmic functions. The effect of changing grain on $\overline{DCI_k}$ were predictable in 6 networks using linear functions (R^2 range: 0.80–0.97) but was unpredictable for MPD (Figure S2).

Among river networks, spatial pattern was related to network length, catchment area and drainage density (Fig. 4). Catchment area and total length of the network were positively associated with TP ($R^2 = 0.29$, $P < 0.001$; $R^2 = 0.59$, $P < 0.001$, respectively), and MPD ($R^2 = 0.80$, $P < 0.001$; $R^2 = 0.90$, $P < 0.001$, respectively). Total network length was negatively associated with $\overline{DCI_k}$ ($R^2 = 0.32$, $P < 0.05$) and drainage density was negatively

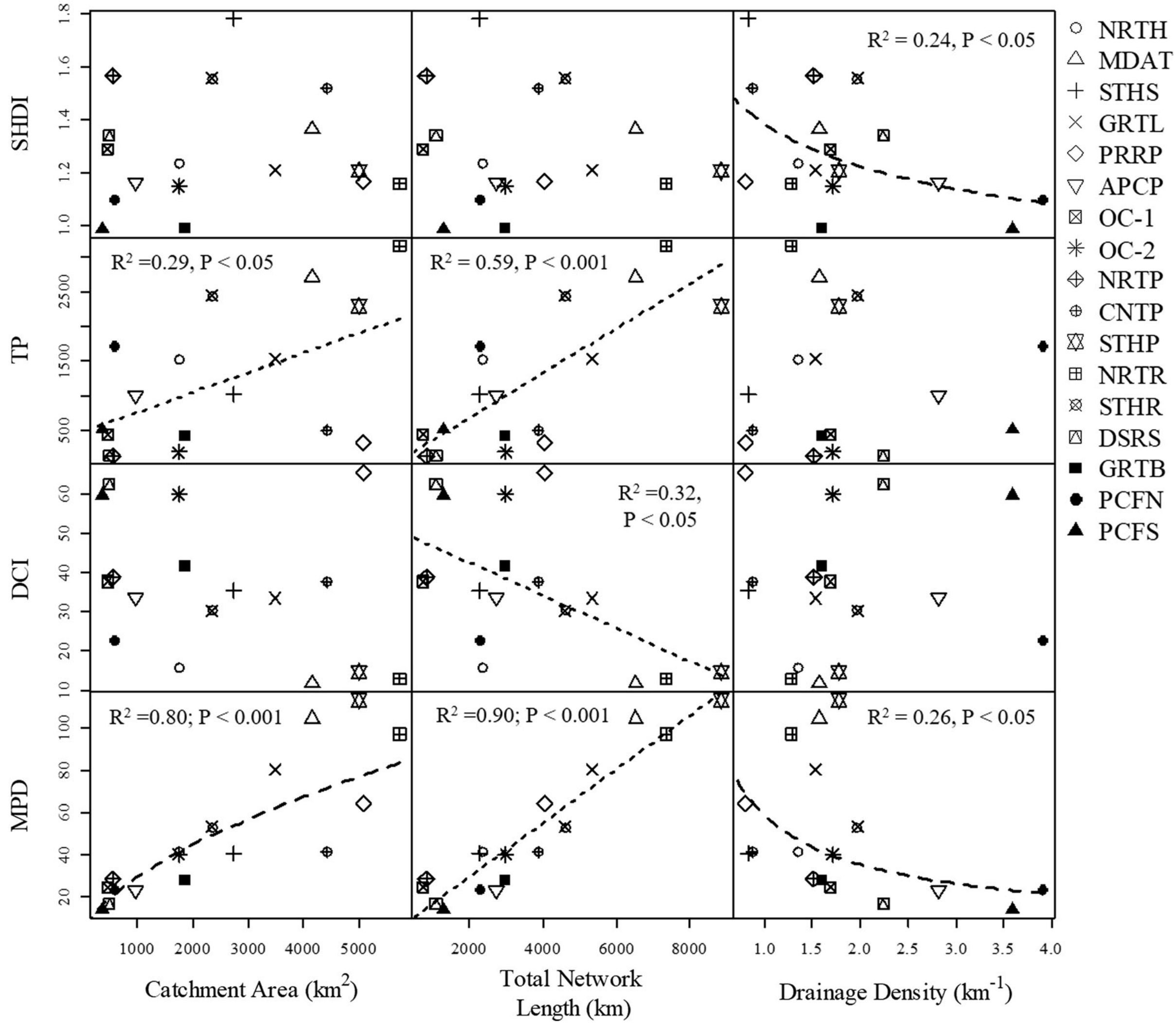

Fig. 4 Relationship between spatial pattern and catchment area, total length and drainage density among river networks. *SHDI* = Shannon diversity index; *TP* = total number of patches, *DCI* = dendritic connectivity index; *MPD* = mean distance between patches. Lines of best fit are drawn for significant relationships ($p < 0.05$). Hashed lines represent power function ($y = \alpha x^{\beta}$) and dotted lines represent linear function ($y = \alpha + \beta \log x$) where x is the value of and catchment area, total length or drainage density. *NRTH* = Northeast; *MDAT* = Mid-Atlantic; *STHS* = Southeast; *GRTL* = Great Lakes; *PRRP* = Prairie Peninsula; *APCP* = Appalachian Cumberland Plateau; *OC-2* = Ozarks Complex-2; *OC-1* = Ozarks Complex-1; *NRTP* = Northern Plains; *CNTP* = Central Plains; *STHP* = Southern Plains; *NRTR* = Northern Rockies; *STHR* = Southern Rockies; *DSRS* = Desert Southwest; *GRTB* = Great Basin; *PCFN* = Pacific Northwest; *PCFS* = Pacific Southwest

associated with SHDI ($R^2 = 0.24$, $P < 0.05$) and MPD ($R^2 = 0.26$, $P < 0.05$).

We identified between 4 and 8 HGP types in each river network (ANOSIM global R range: 0.4, 0.95, $p < 0.001$ for all networks; Table 3). Although the suite of variables that differentiated HGPs were generally different, many networks had at least a single variable in common. For example, soil erodibility was an important factor driving dissimilarity between HGP types in 13 networks and valley-floor ratio was important for 9 networks. Further, HGP types that were characterized by similar variables were often located in different ecoclimate regions (Table 3).

Table 3 The hydrologic, geomorphologic and climate variables with the highest contribution to dissimilarity among hydrogeomorphic patch types within a river network

NEON Domain	HGP (#)	Global R*	Erosion Factor	Valley-Floor Ratio	Ann. Precip	Soil pH	Ann. Temp	Mean Meander Length	Bedrock Depth	Elev	Valley Slope
Northeast	4	0.50		X				X		X	
Mid-Atlantic	4	0.67	X					X			X
Southeast	7	0.79	X	X	X		X	X	X		
Great Lakes	4	0.85	X	X		X					
Prairie Peninsula	4	0.86	X	X			X				
Appalachian Cumberland Plateau	4	0.76	X		X				X		
Ozarks Complex-1	4	0.58		X	X			X		X	
Ozarks Complex-2	4	0.95	X			X				X	
Northern Plains	6	0.91	X		X	X			X		
Central Plains	5	0.98	X			X	X				
Southern Plains	4	0.88	X	X		X					
Northern Rockies	4	0.59		X	X						X
Southern Rockies	6	0.83	X	X	X	X	X				
Desert Southwest	5	0.95			X	X	X		X		
Great Basin	4	0.94	X			X	X				
Pacific Northwest	4	0.70	X	X			X				
Pacific Southwest	4	0.70	X	X	X						

*Bankfull depth estimated from upstream catchment area (Bieger et al. 2015)

Discussion

Understanding scale dependencies in spatial patterns can elucidate the operational scale underpinning its relationship to an ecological process (Wu et al. 2002; Jackson and Fahrig 2015). Increasingly, spatial pattern is quantified within river networks to understand the physical and ecological characteristics of the entire ecosystem (Thoms et al. 2018; Maasri et al. 2019). However, river networks under investigation can vary in their spatial extent and spatial grain (Benstead and Leigh 2012; Rüegg et al. 2016), and habitat patches can be differentiated with increasing levels of detail (Thoms et al. 2018). An explicit understanding of the effects of scale on spatial pattern could increase opportunities to synthesis information collected at different scales or unmask important ecological relationships. We extended the framework developed by Wu et al. (2002) and found scaling relationships in river networks vary across a broad geographic area. The effect of thematic resolution was most predictable for composition metrics while the effect of spatial extent was most predictable for configuration metrics. We also found that the effects of changing spatial grain are least predictable, possibly owing to the dendritic structure of river networks and the method used to manipulate grain size (i.e. minimum mapping unit). Importantly, this work demonstrates that within riverine landscapes there are a variety of scaling relationships for spatial pattern that vary in their predictably, but among river networks, spatial pattern is related to river network size or typology.

Scaling relationships within riverine landscapes

We assessed how spatial patterns of HGP are influenced by three different components of scale and, similar to other landscapes, found that some landscape metrics could change predictably (i.e. following simple scaling functions). In general, we found the effects of changing spatial extent were more predictable than the effects of changing grain size. Indeed others have found that changing grain size is more predictable (Wu et al. 2002; Wu 2004). These differences could support the notion that the method used to manipulate spatial grain influences the type of scaling relationship (Shen et al. 2004; Turner and Gardner 2015; Xu et al. 2020). For example, data stored as raster images is commonly upscaled by aggregating smaller pixels via majority rules (Wu and Li 2006; Qiu et al. 2019). River networks on the other hand, are represented as vector data because of their dendritic structure. Accordingly, we manipulated spatial grain by changing the minimum mapping unit (i.e. iteratively pruning the river networks) such that coarsening grain removed HGP types. Importantly, our results suggest that scaling functions may be more applicable to synthesizing studies that differ in their spatial extent rather than the resolution of their hydrography dataset (*cf.* Lehner et al. 2008; McKay et al. 2012; Moore et al. 2019).

Effects of thematic resolution are expected to be similar to those of spatial grain (Buyantuyev and Wu 2007). In general, we found that these effects were more predictable than those of spatial grain for composition metrics and less predictable for configuration metrics. The relationship between thematic resolution and spatial pattern for the composition metrics is unsurprising because increasing the number of HGP types simultaneously increases richness and fragmentation (i.e. larger patches are subdivided at greater thematic resolution). Configuration metrics on the other hand, were less predictable and often behaved erratically. Indeed, changing thematic resolution may combine, or separate, spatially distant patches and lead to unpredictable scaling relationships (Buyantuyev and Wu 2007).

Lotic ecosystems are known vary geographically as a result of regional differences in climate and geomorphology (Dodds et al. 2015, 2019) and we found the predictably of spatial pattern scaling relationships generally differed among river networks. However, we only included one river network for each ecoclimate domain and could not ascertained whether our scaling relationships are regionally consistent. Indeed, Rüegg et al. (2016) documented that other scaling relationships (i.e. width and depth and catchment area) are geographically variable and investigating the mechanisms driving apparent variation in scaling relationships should be an avenue for future research.

Spatial patterns among riverine landscapes

We found that variation in spatial pattern among networks was related to catchment area, network length and drainage density. Comparing the spatial pattern among river networks could provide insights into potential ecological differences. For example, Shannon diversity index is commonly used in landscape ecology to measure the variety of physical habitat types (i.e. spatial heterogeneity, O'Neill et al. 1988; Turner et al. 1989; Thoms et al. 2018). We found that drainage density was negatively related to SHDI. Given the tight coupling between HGP and ecological processes (Harris et al. 2009; Thoms et al. 2018; Maasri et al. 2019), drainage density may also explain ecological differences. Although the direction of this relationship was surprising because increasing drainage density can increase habitat complexity in river networks (Benda et al. 2004; Fullerton et al. 2017). In our study, higher drainage density likely resulted in stream reaches coming in closer proximity to one another and thereby having similar hydrologic, geomorphologic and climatic values. Interestingly, this could suggest that hydrogeomorphic variables may be more important for maintaining spatial heterogeneity in less dense networks while tributaries and confluence effects may be more important in denser networks.

Connectivity among HGPs in stream networks could have implications for species diversity patterns and meta-community dynamics (Cote et al. 2009; Campbell Grant 2011). We found the modified dendritic connectivity index varied among river networks and was negatively related to the total length of the network. Since the total length of a river network allows for longer watercourse distances separating two HGPs, this relationship is somewhat unsurprising. From an ecological perspective, this could suggest dispersal limitation may be important in large river networks (Tonkin et al. 2017; Schmera et al. 2018). Still, we used the watercourse distance as a measure of permeability and did not consider the concurrent effects of any other barriers (e.g. dams and road culverts, Cote et al. 2009). As such, the actual connectivity between HGP types is likely more complex than simple distances measures.

Finally, the total number of patches and mean distance separating them are absolute measurements of spatial pattern that reflect degree of fragmentation and isolation of HGP types, respectively. We found river networks with greater total stream length had more patches and greater distances separating them. If HGP types are associated with asynchronous dynamics, river networks with more patches could potentially have greater stability in their ecological processes (Moore et al. 2015). Alternatively, the positive association between stream length and mean patch distance suggests dispersal may be limited in larger networks. In general, quantifying spatial patterns in river networks can concisely describe their characteristics and potentially provide explanations for ecological differences (Le Pichon et al. 2007; Datry et al. 2016; Thoms et al. 2018).

Hydrogeomorphic patch characteristics

Although the river networks we studied differed in the suite of hydrologic, geomorphologic and climatic variables that differentiated HGP types, some variables were common among them. For example, soil erodibility was an important factor in all river networks. If these locations receive relatively high sediment loads from adjacent terrestrial environments (Walling 1999), they could have distinct benthic macroinvertebrate communities and by extension ecological processes (Hubler et al. 2016). Rarely, however did we find two networks share the same suite of variables and intra- and inter-patch interactions are likely important determinants of a HGP's ecological function (Wu and Loucks 1995; Thorp et al. 2006). A logical next step would be to combine our approach with biological monitoring data to investigate the degree of biological similarity and the potential for patch interactions.

Limitations and caveats

Hydrologic, geomorphologic and climatic characteristics can be readily calculated with GIS-based approaches (Williams et al. 2013; Thoms et al. 2018). For this study, we created a suite of scripts using R (https://www.r-project.org/) to eliminate dependencies on proprietary software (e.g. ArcGIS, ESRI, Redlands, CA). We also designed these scripts to depend exclusively on the High Resolution National Hydrography Dataset to facilitate large scale, comparative analyses across the CONUS (Moore et al. 2019). However, the major limitation with this approach is that it can take several weeks of processing and is potentially limited to river networks < 5,000 km^2 because of computational demands. Further, given the scale of our study it was not feasible to ground-truth the accuracy the GIS-based variables. Still, we followed a similar approach to others that found GIS-derived variables can produce similar results to empirical field-based measures (Thorp et al. 2008; Williams et al. 2013; Thoms et al. 2018).

The choice of the landscape metrics used to quantify spatial pattern should be ecologically justified (Li and Wu 2004). There are literally hundreds of landscape metrics and many respond differently to scale (McGarigal et al. 2012; Šímová and Gdulová 2012). We found scaling relationships vary among different river networks, but we only considered four metrics. There are few landscape metrics that are suitable for riverine landscapes (Le Pichon et al. 2007; Datry et al. 2016; Erős and Lowe 2019) and developing and evaluating a novel metrics will improve our ability to describe general scaling laws for spatial pattern in riverine landscapes.

Conclusions

Spatial pattern analysis can reveal complex linkages between spatial pattern and ecological processes in landscapes (Jackson and Fahrig 2015; Qiu et al. 2019). Although spatial pattern is quantified within river networks to understand ecological processes (Thorp et al. 2006; Erős and Lowe 2019), issues of scale dependence can limit opportunities to synthesize information collected at different spatial scales or potentially mask important ecological relationships. Scaling functions can provide concise descriptions of the multiscaled characteristics of spatial pattern and will improve our ability to detect the most appropriate scale underpinning a linkage between spatial pattern and ecological process in riverine ecosystems.

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Data availability The datasets generated during the current study are available at https://github.com/dkopp3/HydrogeomorphicPatches and from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declares no conflict of interest.

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