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Geomorphology shapes relationships between animal communities and ecosystem function in large rivers

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Understanding how the Earth's surface (i.e. 'nature's stage') influences connections between biodiversity and ecosystem function (BEF) is a central objective in ecology. Despite recent calls to examine these connections at multiple trophic levels and at more complex and realistic scales, little is known about how landscape structure shapes BEF relationships among animal communities in nature. We coupled high-resolution habitat mapping with extensive field sampling to quantify connections among the geophysical habitat templet, invertebrate assemblages and secondary production in two large North American riverscapes. Patterns of sediment size governed invertebrate assemblage structure, with particularly strong effects on composition, richness and taxonomic and functional diversity. These relationships propagated to drive positive relationships between biodiversity and secondary production that were modified by scale, context-dependencies and anthropogenic modification. Finally, leveraging spatially-explicit descriptions of geophysical and biological properties, we uncovered distinct and nested spatial scales of biodiversity and secondary production, and suggest that multiple geophysical processes simultaneously influence these patterns at different scales. Together, our findings advance our understanding of relationships between the physical templet and patterns of BEF, and help to predict how perturbations to the Earth's surface may propagate to influence biodiversity and energy flux through food webs.

Keywords: biodiversity and ecosystem function, invertebrates, large river, riverscape, secondary production

Introduction

A central tenet of ecology is that the physical habitat templet governs ecological dynamics (Southwood 1977). Classic studies in population and community ecology have shown that habitat shapes a variety of structural attributes of ecosystems, including taxonomic and functional biodiversity (Hutchinson 1957, MacArthur 1958, Townsend and Hildrew 1994). In addition, many studies have shown that these structural attributes can influence ecosystem functions (Naeem et al. 1994, Hooper et al. 2005), at least in simplified experimental conditions (Wardle 2016). Although this

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literature has built a strong mechanistic understanding of how biodiversity relates to ecosystem functioning (BEF), most studies have ignored or downplayed the influence of the physical environment, leading to considerable difficulty in extrapolating results from simplified and short-term experiments to larger and more realistic spatial and temporal scales (Snelgrove et al. 2014, Manning et al. 2019). Thus, a current challenge is to elucidate BEF relationships across diverse landscapes, and to understand how these patterns are shaped by properties of the physical templet.

Linking patterns in physical habitat to biodiversity has been catalyzed by recent advances in high-resolution mapping techniques (Kerr and Ostrovsky 2003, Power et al. 2005, Brown et al. 2011). It is now feasible to quantify physical characteristics of diverse ecosystems from ocean floors to mountaintops in ways that were unimaginable just a few decades ago. These techniques, when coupled with in situ biological information, can reveal strong connections between the environment and biodiversity driven by, for example, habitat diversity and variation in ecological niche space (Stein et al. 2014, Tukiainen et al. 2017, Zarnetske et al. 2019). In addition, such techniques have revealed that 'keystone habitats' (sensu Tews et al. 2004, Hitchman et al. 2018) can have disproportionate effects on biodiversity relative to their abundance in the environment. Although much progress has been made in linking patterns of physical habitat to biological structure and diversity, much less is known about how these connections propagate to influence ecosystem processes across natural landscapes (Premke et al. 2016, Alahuhta et al. 2018).

Animals influence a variety of ecosystem processes and associated goods and services (e.g. filtering of pollutants, production of protein, pollination; Jones et al. 1994, Duffy 2002, Schmitz et al. 2018) through their trophic interactions, movement patterns and behavior. Animal secondary production, i.e. the formation of biomass over time, is an important ecosystem process that governs energy flow and material transfer through food webs (Benke 1993, Barnes et al. 2018). Despite well-described relationships between plant diversity and primary production (Hooper et al. 2005, Liang et al. 2016), much less is known about how animal diversity relates to secondary production (but see Statzner and Lévêque 2007, Dolbeth et al. 2015, Clare et al. 2022, Rodil et al. 2022). It is likely that animal diversity enhances secondary production through similar mechanisms described for plants (i.e. niche complementarity, species selection; Loreau 2000), and that these relationships may be constrained by properties of the physical templet. To date, few, if any, studies have examined these connections in natural settings.

Large rivers are among the most physically diverse ecosystems on Earth, and are characterized by hierarchically nested habitat mosaics that change over time (Ward et al. 2002, Stanford et al. 2005, Hauer et al. 2016). This remarkable physical diversity promotes a high degree of biological diversity that sustains ecosystem processes and a variety of ecosystem goods and cultural services (Ekka et al. 2020). For example, river floodplains support high levels of aquatic and riparian biodiversity (Ward et al. 1999) that act to attenuate disturbances and retain nutrients; tributary junctions act as hotspots of biodiversity and productivity that sustain river food webs and animal production (Cross et al. 2013, Jakubínský et al. 2021). Given widespread habitat degradation of large rivers worldwide, research is needed to reveal connections among the physical templet, diversity and river ecosystem processes at realistic and meaningful scales.

We coupled high-resolution mapping of the geophysical templet (defined here as the mosaic of main-channel benthic substrate types and off-channel habitats) with spatially-explicit estimates of invertebrate biodiversity and secondary production in two large North American riverscapes. We asked: 1) how does natural variability in the geophysical templet govern invertebrate assemblages, 2) do connections among geomorphology and invertebrate structure and diversity propagate to influence secondary production and 3) what are the spatial patterns among geomorphology, biodiversity and secondary production across riverscapes? We specifically predicted that areas with high geophysical habitat diversity, keystone habitat structures or both would contain more diverse invertebrate assemblages. Further, we anticipated positive relationships between invertebrate diversity and secondary production, and that these connections would result in distinct spatial patterns among geomorphology, invertebrate structure and diversity and invertebrate production across the riverscape.

Material and methods

Study area

Our study was conducted on the Yellowstone and Missouri rivers in Montana and North Dakota, USA (Supporting information). Although these rivers originate in close geographic proximity, the Missouri has been altered by multiple large impoundments, whereas the Yellowstone remains largely unregulated throughout its entire course (see Scholl et al. 2021 for further description of the study region). Six study reaches, between 12 to 36 km in length, were selected to encompass representative variation in river geomorphology and thermal characteristics throughout the region.

Geophysical templet

Because of the large spatial extent of our study and relatively low water clarity, we used side-scan sonar and aerial photography to map benthic substrate categories (e.g. sand, cobble/gravel, boulder) and off-channel habitats. Briefly, sonar images of riverbed textures were collected from a moving boat, geo-referenced using their corresponding latitude/longitude coordinates, delineated by polygons as different habitat types based on an a priori classification scheme, and displayed on maps with dimensional accuracy in the laboratory using ArcMap ver. 10.0 (Kaeser et al. 2013). Off-channel habitats were delineated using multiple years of aerial photography in ArcMap. Off-channel habitats can range from completely isolated from the main-channel throughout much the year, to fully connected in both the upstream and downstream directions. In our study, we specifically chose off-channels that remained largely connected to the main-channel throughout the year across all flows. However, we did not stratify off-channels based on the type of connectivity, and thus included areas that were connected on the upstream end, downstream end and both directions, depending on the study reach. For each substrate category, we applied median sediment sizes (D_{50}) using the Wentworth (1922) scale as follows: hard clay: 0.0039 mm, silt/clay: 0.02 mm, main-channel sand: 0.345 mm, clay/gravel mix: 4 mm and cobble/gravel: 65 mm. Wolman pebble counts ($n = 100$, b-axis measured) were conducted at four locations to estimate the median boulder size throughout our study reaches (154 mm). Based on field observations, we applied a median substrate size of 0.0078 mm for off-channel habitats in primarily sandy reaches (i.e. 'off-channels (sand)'; M2, M3, M4 and Y2), and 30 mm in primarily cobbly reaches (i.e. 'off-channels (cobble)'; Y1). Large woody debris was not effectively quantified using sonar and was thus assumed to compose 2% of the total available habitat at each study reach (Gippel et al. 1996).

Longitudinal patterns in sediment size and habitat diversity were quantified at each reach by manually dividing habitat maps created in ArcMap into contiguous 100 m rectangular cross sections ($n = 128$–360 per reach) centered on the thalweg and widened to include the entire channel width and adjacent off-channel habitats. This process transformed the sinuous maps into a channel-fitted longitudinal coordinate system, where $x = 100$ m longitudinal intervals and $y = 1$ at all locations. These cross-sectional data were then used for geospatial visualization and other analyses, as traditional Euclidean distances are not appropriate (Legleiter and Kyriakidis 2006) for sinuous river channels. At each 100 m section, habitat proportions were extracted to estimate habitat diversity (Shannon 1948). Habitat-weighted median sediment size was estimated as the product of habitat-specific values and habitat proportions and summed across all habitats.

Invertebrate assemblage structure, diversity and secondary production

Invertebrates were sampled from habitats at each reach during five occasions in 2014 and 2015 using methods appropriate to each habitat type (Supporting information). On each sampling occasion, we used a stratified sampling design based on areal proportions of habitats derived from side-scan sonar and aerial photographs to allocate between 25 and 30 samples per reach. A variety of methods were used to quantitatively sample invertebrates; main-channel sand habitat: a Ponar dredge sampler (0.052 m^2) attached to a sounding reel on a boat; cobble/gravel: a Hess sampler (0.086 m^2); wood: 250 µm mesh bags and scrubbed; depositional off-channels: a stovepipe core (0.031 m^2); and large boulders: scrubbed in buckets while a D-frame dip net was held downstream. Samples were preserved with buffered formalin and rinsed onto nested sieves (1 mm and 250 µm) in the laboratory. Invertebrates in both size fractions were then separated from organic material using dissecting microscopes, identified and measured (nearest mm) to estimate habitat-specific abundance and biomass following standardized protocols (Supporting information). Invertebrate taxa were assigned to functional feeding groups using the U.S. Geological Survey (USGS) Database of Lotic Invertebrate Traits for North America (Vieira et al. 2006, Merritt et al. 2019).

Invertebrate assemblage richness was calculated as the total number of unique taxa (in most cases genus) for each sample, and mean invertebrate richness, hereafter 'richness', was estimated as the mean monthly assemblage richness for each habitat type at each reach. Invertebrate assemblage diversity, hereafter 'taxonomic diversity', was estimated similarly for each habitat type using the Shannon diversity index (Eq. 1; Shannon 1948):

$$H = -\sum_{i=1}^{s} p_i \ln p_i \tag{1}$$

where assemblage diversity (H) is a function of the proportion of mean monthly invertebrate biomass attributed to a given taxon i (p_i) and the natural logarithm of this proportion ($\ln p_i$), summed across all taxa (s). Evenness of invertebrate functional feeding groups (FFG), hereafter 'functional diversity' (sensu Zhang et al. 2020), was estimated for habitat types among reaches using the Eq. 2:

$$J_{FD} = \left[-\sum_{i=1}^{S} \left(\frac{n_i}{N} \log_2 \frac{n_i}{N} \right) \right] \div \log_2 S \tag{2}$$

where n_i is the mean monthly biomass of the ith FFG, N is the total mean monthly biomass of the invertebrate assemblage for a given habitat type, and S is the total number of FFGs observed at that habitat. Values of J_{FD} range between 0 and 1, with estimates close to 0 representing an assemblage where only one or a few FFGs dominate monthly biomass and estimates close to 1 representing an assemblage where biomass is distributed evenly among all FFGs (Gamito and Furtado 2009, Zhang et al. 2020).

Invertebrate secondary production (g ash-free dry mass, [AFDM] m^{-2} year^{-1}), hereafter 'secondary production,' was estimated for each taxon by habitat type and reach using the size-frequency method, instantaneous growth rate method or by multiplying bootstrapped annual biomass estimates by published production/biomass ratios (Benke and Huryn 2017). For estimates produced using the size-frequency method, we used Q_{10} temperature-corrected CPIs (cohort production interval) to account for differences in development time due to the strong influence of Fort Peck Dam on water temperature regimes in the Missouri River (Cross et al. 2011). For all methods, we used bootstrapping to estimate medians and 2.5% and 97.5% quantiles of annual secondary production (Benke and Huryn 2017). To estimate secondary production for entire study reaches, we produced habitat-weighted vectors by multiplying bootstrapped production estimates in each habitat by the relative proportion of that habitat type per average square meter and summed among habitat types. Statistical differences in mean annual assemblage secondary production were assessed by overlap of bootstrapped 95% confidence intervals (Effron and Tibshirani 1993, Benke and Huryn 2017). All secondary production computation was conducted in R (<www.r-project.org>; code developed by Benjamin J. Koch and James R. Junker).

Invertebrate assemblages and geomorphology

Invertebrate assemblage structure was compared among habitats (i.e. substrate categories and off-channel habitats; hereafter 'habitat types') using non-metric multidimensional scaling (NMDS) ordinations in the statistical package 'Primer' ver. 6.2 (Clarke and Gorley 2006). Mean monthly invertebrate biomass values were square-root transformed to balance the contributions of rare and common taxa (Zar 1996). Analysis of similarity (ANOSIM) was used to test for statistical differences in assemblage composition among habitat types (McCune et al. 2002). In addition, a similarity percentage (SIMPER) analysis was used to identify taxa responsible for significant differences in assemblage composition among habitat types.

We compared invertebrate richness, taxonomic diversity and functional diversity among habitat types using linear mixed effect models in 'lme4' package in R (Bates et al. 2015). Our models included the fixed effect of habitat type, and a random effect of study reach and month to account for random differences within reaches and repeated sampling of habitats throughout the year. Pairwise comparisons among habitat types were estimated using the 'emmeans' package in R with a Tukey p-value adjustment for comparing multiple habitat types (Lenth 2018).

To examine how larger-scale geophysical attributes (i.e. mosaics comprised of multiple habitat types) influence biological diversity, we quantified habitat-weighted sediment size and habitat diversity at 100 m extents across the riverscape. These two metrics were used because they integrate attributes of multiple habitat types into single predictor variables that have been shown to strongly influence invertebrate assemblages (Death and Winterbourn 1995, Rice et al. 2001, Brosse et al. 2003, Béjar et al. 2020). We first calculated habitat-weighted sediment size and habitat diversity for contiguous 100 m rectangular cross sections. Within these sections we quantified habitat-weighted estimates of invertebrate richness, taxonomic diversity and functional diversity by simulating normal distributions of each metric using empirically derived annual mean and standard deviation estimates of habitat-specific diversity. We then randomly selected 100 estimates from these distributions, multiplied these values by the 100 m habitat proportions, summed across habitat types, and calculated the mean. This process was repeated across all 100 m sections at a given reach. To account for differences in reach length, we randomly selected 100 cross sections at each reach, amounting to 600 estimates of habitat diversity, habitat-weighted sediment size and habitat-weighted invertebrate richness, taxonomic diversity and functional diversity. Linear mixed effect models were used to analyze relationships between invertebrate richness, taxonomic diversity, and functional diversity, and sediment size or habitat diversity in R, accounting for random effects of reach using the package 'lme4.'

Biodiversity–secondary production relationships

Relationships between invertebrate biodiversity and secondary production were examined using linear mixed effects models with habitat-specific secondary production as the dependent variable, habitat-specific richness, taxonomic diversity or functional diversity as the independent variable, and reach as a random effect in three separate models. Due to anomalously high estimates of secondary production in the tailwaters of Fort Peck Dam (reach M1 excluding sand habitat below a tributary), we first analyzed relationships omitting these habitats. In separate models we included the presence of tailwaters as a categorical fixed effect to quantify whether relationships between biodiversity and secondary production change in this highly modified environment.

We quantified spatially explicit relationships between invertebrate biodiversity and secondary production across the riverscape using two approaches. The first approach, based on heat maps of invertebrate secondary production at each study reach (12–38 km), assessed relationships between invertebrate diversity and quantiles of secondary production. For this analysis, we constructed fine-grained (20 m^2 resolution) maps of secondary production by combining in situ estimates of habitat-specific invertebrate production with the previously described characterization of benthic and off-channel habitats. The scale used for this analysis was smaller than many of our other approaches (i.e. 100 m) because we sought to explicitly locate 'hotpots' of secondary production that may be underestimated when averaging over larger spatial scales (see the Supporting information for a graphical description of these methods).

For the second analytical approach, we examined longitudinal patterns of invertebrate biodiversity and secondary production at each reach by summarizing habitat-weighted biodiversity and secondary production estimates for each of the 100 m contiguous rectangular cross sections described above. Spatial patterns in biodiversity and secondary production were then overlaid on the habitat template maps to examine longitudinal relationships between biodiversity, secondary production and geophysical habitat attributes

We used semivariogram analysis to quantify the spatial structure of biodiversity and secondary production at each reach using the mean value of habitat-weighted biodiversity metrics and secondary production for each river cross-section. Semivariogram analysis is a common geostatistical technique used to calculate the average variation between measurement values separated by some intervening distance, for a range of distance lags using the Eq. 3:

$$\gamma\left(h\right)=\frac{1}{2N\left(h\right)}\sum\left[u\left(a\right)-u\left(a+h\right)\right]^{2} \tag{3}$$

where semivariance, $\gamma(h)$, is a function of the number of data pairs separated by distance, h, ($N(h)$), $u(a)$ and $u(a+h)$ are parameter values at locations (a) and some lag distance ($a+h$) away (Curran 1988, Ettema and Wardle 2002). Empirical semivariograms were fitted using spherical models to obtain parameter estimates using the 'gstat' package in R (Pebesma 2004). We also examined qualitative patterns in empirical semivariogram shapes that are closely associated with known theoretical expectations (Ettema and Wardle 2002, Gresswell et al. 2006, McGuire et al. 2014, King et al. 2019). For example, some semivariogram shapes indicate patchiness at small spatial scales, whereas other shapes reflect no spatial structure, larger scale gradients or patchiness at both small and larger scales. Examining the shapes of semivariograms can thus provide important information about the spatial structure of biodiversity and secondary production across the riverscape, and can be useful for inferring underlying processes responsible for generating such patterns (McGuire et al. 2014).

Results

Geophysical templet

We found large spatial variability in the geophysical templet, with abrupt longitudinal shifts in habitat composition, diversity and median sediment size (Fig. 1). Sharp increases in sediment size were driven by patches of cobble/gravel, boulders (often colluvial talus) and riprap, particularly when these habitat types were embedded in main-channel sand (Fig. 1B). Longitudinal changes in habitat diversity often paralleled changes in sediment size within reaches; however, these metrics were decoupled in sandy areas with off-channels, because off-channels contributed to large changes in habitat diversity (by adding a unique habitat type) with relatively little change in sediment size (Fig. 1B; M2: km 10–15). Overall, reaches grouped into three broad categories based on the dominant benthic substrates: mixed substrate (M1), predominantly sand (M2, M3, M4, Y2) and predominantly cobble/gravel (Y1; Fig. 1C).

Connections between geophysical habitat and invertebrate assemblage structure

Scaling from the geophysical templet to BEF relationships first requires a detailed investigation of how assemblages

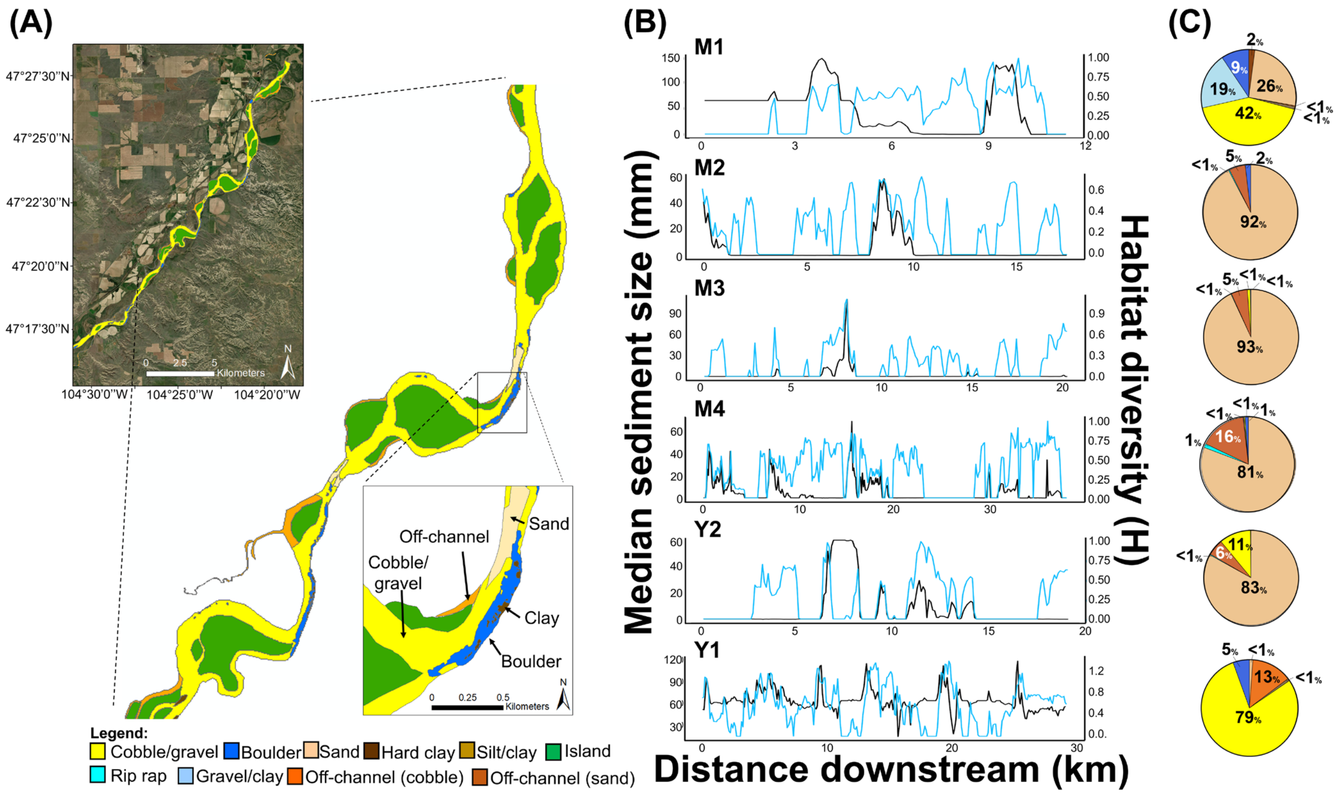

Figure 1. (A) Side-scan sonar was used to map benthic habitats with fine-scale resolution across broad (10s of km) spatial extents, revealing a complex mosaic of different habitat types (see inset; example from Y1 on the Yellowstone River). (B) Longitudinal analysis of habitat maps illustrates abrupt changes in median sediment size (black line) and Shannon habitat diversity (blue line). (C) Benthic substrate and off-channel contributions (same colors in legend of panel A) among study reaches.

relate to individual habitats across the landscape. Overall, we found that invertebrate assemblage composition, richness, taxonomic diversity and functional diversity were strongly influenced by habitat characteristics (Fig. 2, Supporting information). Assemblages were relatively unique among larger substrata, main-channel sand and off-channel habitats (NMDS: 2D stress $=0.16$, analysis of similarity: Global $R=0.57$, $p < 0.05$), and these differences were most pronounced within reaches (Supporting information). As such, invertebrate assemblages were often found to be more similar among habitats of the same type regardless of the reach (e.g. sand at M2 and sand at M3) compared to assemblages on different habitats within the same reach (e.g. sand at M2 versus boulder at M2). Invertebrate assemblages in main-channel sand habitat and off-channels generally had low to intermediate biodiversity and were dominated by collector–gatherer midges and oligochaete worms. In contrast, habitat types with larger and more stable substrata had higher richness, taxonomic diversity and functional diversity, and these habitats included a variety of unique taxa and functional feeding groups (Fig. 2, Supporting information); assemblages on large woody debris were occasionally dominated by hydropsychid caddisflies.

At larger spatial scales (i.e. 100 m), sediment size (habitat-weighted) was positively related to invertebrate richness ($F=7.52$, $p < 0.05$), taxonomic diversity ($F=7.41$, $p < 0.05$) and functional diversity ($F=7.03$, $p < 0.05$; Fig. 3). However, the strength of these relationships related to the character of individual study reaches (colored lines in Fig. 3). For instance, at Y1 there was a relatively weak relationship between larger sediments (i.e. boulder) and invertebrate richness, taxonomic diversity and functional diversity, which was the only study reach dominated by larger sediment sizes. In contrast, at Y2, particularly steep positive relationships reflected the strong influence of large sediments on invertebrate diversity in this primarily sandy reach. Despite these relationships between sediment size and invertebrate biodiversity, we found no relationships between habitat diversity and invertebrate richness, taxonomic diversity or functional diversity.

Connections between geophysical habitat and secondary production

Secondary production was strongly linked to the geophysical templet, with low and less variable production in main-channel sand habitat and much higher (often by orders of magnitude) and more variable production in off-channels and on large and stable substrates (Table 1). The contribution of each habitat to total secondary production often differed greatly from the contribution of habitats to total river area, particularly at reaches dominated by main-channel sand habitat. For example, boulders, cobble/gravel and off-channel habitats comprised < 20% of all available habitat at four of the reaches, yet these habitats supported the bulk of total secondary production (Supporting information). In contrast, the contribution of different habitats to total secondary production was roughly proportion to their areal extent at the two uppermost reaches where larger and more stable substrate were more prevalent (i.e. Y1 and M1).

Biodiversity–secondary production relationships

Invertebrate biodiversity was positively related to secondary production at all sites when reaches were pooled and excluding the tailwaters at Fort Peck Dam, with significant trends for invertebrate richness ($F=29.61$, $p < 0.001$), taxonomic diversity ($F=18.10$, $p < 0.001$) and functional diversity ($F=17.25$, $p < 0.001$; Fig. 4). For every unit increase in invertebrate richness, taxonomic diversity and functional diversity, we found a corresponding increase of 1.05, 8.40 and 16.33 g AFDM m^{-2} $year^{-1}$ in secondary production, respectively. When tailwaters were included in the models, we still observed significant effects of all diversity metrics on secondary production; however, the tailwater environment modified these relationships. For example, despite low functional diversity, the tailwater assemblages were significantly more productive (~25 g AFDM m^{-2} $year^{-1}$; $t=2.52$, $p < 0.001$) than assemblages at other sites with similarly low functional diversity. Similar patterns were observed for

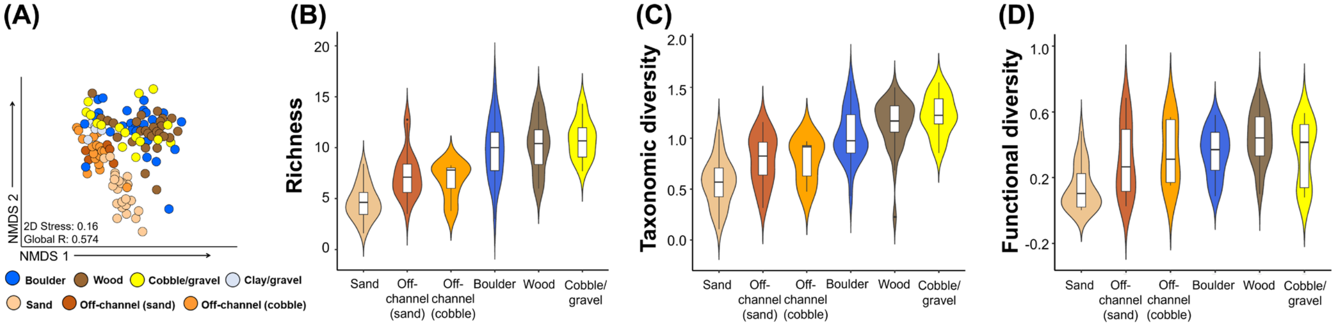

Figure 2. (A) Non-metric multidimensional scaling (NMDS) ordination of invertebrate assemblages revealed differences in assemblage composition among habitat types (benthic substrate and off-channels). Each point represents mean monthly assemblage biomass on a given habitat at each reach. (B) Invertebrate richness, (C) taxonomic diversity (Shannon *H*) and (D) functional diversity (FFG evenness J_{FD}) illustrated an overall pattern of low to intermediate diversity in main-channel sand and off-channels, and higher diversity in larger and more stable substrates. Lines in boxes are medians, box ends are quartiles and whiskers extend to the lowest or highest data point ≤ 1.5 the interquartile range. Statistically significant pairwise differences in diversity estimates among habitats can be found in the Supporting information.

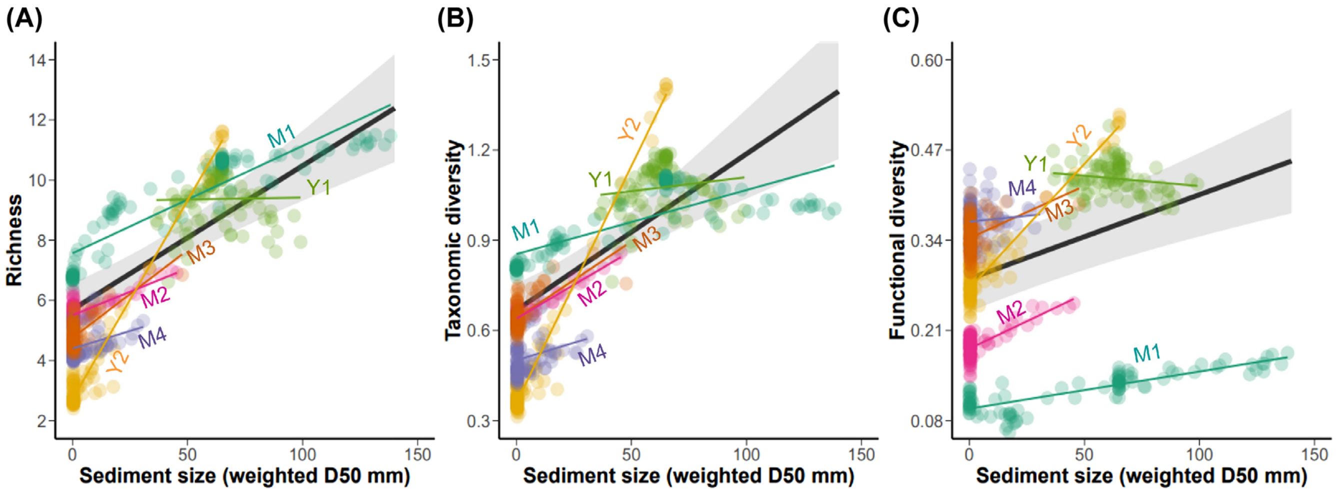

Figure 3. Relationships among habitat-weighted median sediment size and similarly weighted estimates of invertebrate (A) richness, (B) taxonomic diversity (Shannon *H*) and (C) functional diversity (FFG evenness J_{FD}) at 100 m scales. Random slopes and intercepts were fitted for individual reaches and are depicted by the different colored circles and lines. The black bolded line represents the predictions of the linear mixed effects models with standard error of the slope displayed as grey.

both richness and taxonomic diversity (Fig. 4); however, the tailwater effect was not statistically significant, likely due to small sample sizes.

Although relationships between invertebrate diversity and secondary production were generally positive among (Fig. 4) and within (Supporting information) reaches, we found more variability in the direction of these relationships on individual habitat types (Fig. 4 colored circles and lines). For example, assemblages in both sand and large woody debris habitats showed little, or even negative, relationships among diversity and secondary production, suggesting that patterns between invertebrate diversity and secondary production may depend on spatial scale and arise most readily at scales that aggregate multiple diverse habitat types.

Across the riverscape, invertebrate assemblages were consistently the most productive in locations with the highest

Table 1. Major habitat types (aerial proportions), median annual invertebrate secondary production (g AFDM m^{-2} year^{-1} (95% confidence intervals)), mean annual invertebrate richness (± 1 SD), mean annual taxonomic (*H*) diversity (± 1 SD) and mean annual functional (J_{FD}) diversity (± 1 SD). CG = cobble/gravel, GC = gravel clay, S = sand, B = boulder, W = large woody debris and OC = off-channels.

Reach	Habitat	Secondary production	Richness	Taxonomic diversity	Functional diversity
M1	CG (0.42)	23.14 (19.73–26.84)	10.63 (1.20)	1.10 (0.39)	0.11 (0.10)
	GC (0.19)	16.96 (13.55–20.92)	8.60 (1.74)	0.85 (0.31)	0.07 (0.11)
	S (0.26)	1.89 (1.22–2.80)	6.79 (1.37)	0.80 (0.31)	0.04 (0.13)
	B (0.09)	28.39 (22.99–34.37)	11.42 (1.74)	0.99 (0.34)	0.15 (0.12)
	W (NA)	14.27 (9.36–19.25)	11.86 (1.95)	1.11 (0.39)	0.25 (0.17)
M2	OC (0.05)	6.89 (5.38–8.59)	8.37 (2.74)	0.80 (0.40)	0.19 (0.23)
	S (0.92)	0.64 (0.45–0.96)	5.29 (0.91)	0.63 (0.38)	0.08 (0.18)
	B (0.02)	12.50 (10.58–14.91)	11.44 (1.89)	1.37 (0.43)	0.45 (0.17)
	W (NA)	6.57 (5.15–8.13)	12.72 (1.22)	1.27 (0.38)	0.55 (0.17)
M3	OC (0.05)	7.80 (5.90–10.37)	9.00 (2.21)	1.06 (0.40)	0.47 (0.28)
	S (0.93)	0.29 (0.19–0.43)	4.46 (1.42)	0.62 (0.36)	0.19 (0.31)
	B (0.002)	5.91 (4.12–8.21)	10.40 (3.38)	0.92 (0.49)	0.38 (0.25)
	W (NA)	11.49 (6.15–17.24)	9.44 (2.01)	1.00 (0.43)	0.44 (0.21)
M4	OC (0.16)	7.46 (4.07–11.52)	6.31 (0.93)	0.71 (0.41)	0.33 (0.34)
	S (0.81)	0.40 (0.30–0.54)	4.06 (0.63)	0.46 (0.42)	0.22 (0.32)
	B (0.01)	8.96 (5.37–14.16)	8.97 (2.18)	1.02 (0.46)	0.47 (0.19)
	W (NA)	8.56 (4.65–13.49)	10.13 (3.44)	1.02 (0.46)	0.46 (0.25)
Y1	CG (0.79)	6.00 (4.49–8.17)	10.31 (2.60)	1.17 (0.39)	0.44 (0.19)
	OC (0.13)	4.53 (2.67–6.76)	6.65 (1.91)	0.77 (0.49)	0.35 (0.28)
	B (0.05)	3.03 (2.01–4.25)	6.24 (2.00)	0.85 (0.53)	0.31 (0.25)
	W (NA)	4.33 (3.30–5.55)	9.36 (1.82)	1.29 (0.45)	0.52 (0.19)
Y2	CG (0.11)	10.76 (8.28–13.41)	11.49 (1.84)	1.44 (0.30)	0.51 (0.15)
	OC (0.06)	4.59 (3.54–5.63)	5.37 (1.38)	0.58 (0.33)	0.23 (0.29)
	S (0.83)	0.72 (0.54–0.92)	2.65 (0.79)	0.33 (0.33)	0.14 (0.26)
	W (NA)	2.25 (1.66–3.02)	8.08 (2.12)	1.19 (0.43)	0.46 (0.25)

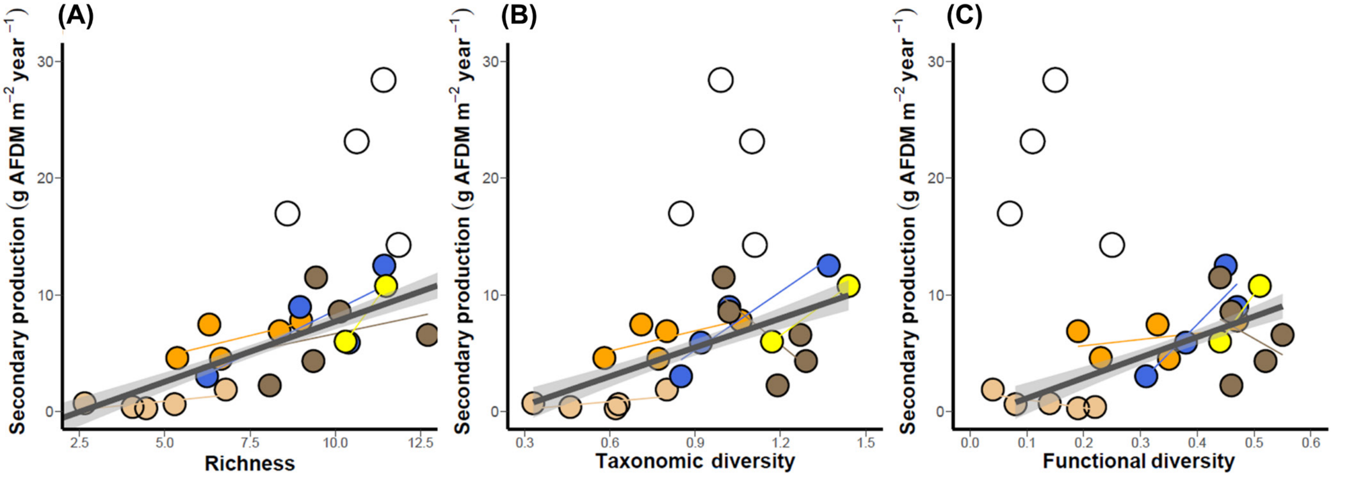

Figure 4. Relationships between invertebrate (A) richness, (B) taxonomic diversity (Shannon H) and (C) functional diversity (FFG evenness J_{FD}) and secondary production (g AFDM m^{-2} year^{-1}). Black bolded lines represent predictions of linear mixed effects models for reaches excluding tailwaters with the standard error of the slope displayed as grey. Each circle represents estimates of habitat-specific secondary production and diversity. Orange circles = backwaters, beige = sand, blue = boulder, brown = wood, and yellow = cobble-gravel. Open circles highlight tailwater habitats on the Missouri River.

diversity (richness, F = 32.82, $p < 0.001$; taxonomic diversity, F = 15.10, $p < 0.001$; functional diversity, F = 18.69, $p < 0.001$; Fig. 5). Pairwise comparisons among secondary production quantiles indicated that these trends were most pronounced when comparing richness (t = 10.41, $p < 0.001$), taxonomic diversity (t = 6.94, $p < 0.001$) and functional diversity (t = 7.81, $p < 0.001$) between secondary production coldspots (i.e. areas representing lowest 20th percentile of reach production) and hotspots (i.e. highest 20th percentile of reach production; Fig. 5).

Strong ties among habitat, invertebrate diversity and secondary production also resulted in distinct spatial patterns of BEF across the riverscape (Fig. 6). For instance, abrupt and localized increases in biodiversity and secondary production were associated with large and stable substrates, particularly in locations embedded in main-channel sand habitat (Fig. 6, arrows B and F). Interestingly, these same relationships were dampened (e.g. Fig. 6, arrow A) or even reversed (e.g. Fig. 6, arrow G) in areas dominated by larger substrates. Similar increases in secondary production were found in response to sandy off-channel habitats embedded within main-channel sand (Fig. 6, arrows C, D and E). However, in contrast to habitats with large sediment size, which often resulted in large increases in secondary production and diversity, sandy off-channels generally had much weaker effect on diversity (Fig. 6 arrow C; also see habitat comparisons between sand and off-channels in Table 1).

Semivariogram analysis revealed distinct spatial structure in invertebrate richness, taxonomic diversity, functional diversity and secondary production at all study reaches (Fig. 7). The range of longitudinal autocorrelation (lag distance where asymptote of spherical model occurs; 'range') for diversity and secondary production varied between 1 and 8 km across reaches. There were many instances of nested semivariogram structure beyond these distances revealed by inflection points (Fig. 7, Supporting information). Many of these inflection points were nearly identical for diversity and secondary production within study reaches (e.g. inflections points ~6 km for all metrics at Y1), suggesting that spatial patterns in biodiversity and ecosystem function were often tightly coupled across the riverscape despite context-dependencies mentioned above.

Discussion

Our study is among the first to uncover positive relationships between invertebrate diversity and secondary production across large riverscapes, a finding consistent with previous research on primary producers and fishes (Hooper et al. 2005, Oehri et al. 2017, Myers et al. 2021). BEF patterns revealed in our study were strongly linked to the spatial scale of observation, demonstrating that, in nature, these relationships may emerge most readily in response to mosaics of divergent habitat patches. For instance, the positive relationships between diversity and secondary production both within and among our study reaches resulted from aggregating local habitat patches that ranged from low (i.e. sand) to high (i.e. cobble/gravel, boulder) diversity and production. Consequently, BEF relationships at larger scales that incorporated diverse habitats were generally positive, whereas patterns within individual habitats were more variable, and sometimes negative. Thus, failing to consider how single habitat patches fit into landscape mosaics may influence conclusions about BEF patterns in nature, highlighting the need for additional studies that explicitly examine the scale-dependency of these relationships (Thompson et al. 2018, Gonzalez et al. 2020).

Hotspots of invertebrate diversity and production were patchily distributed in space, with abrupt spikes occurring in parallel with changes in the geophysical templet.

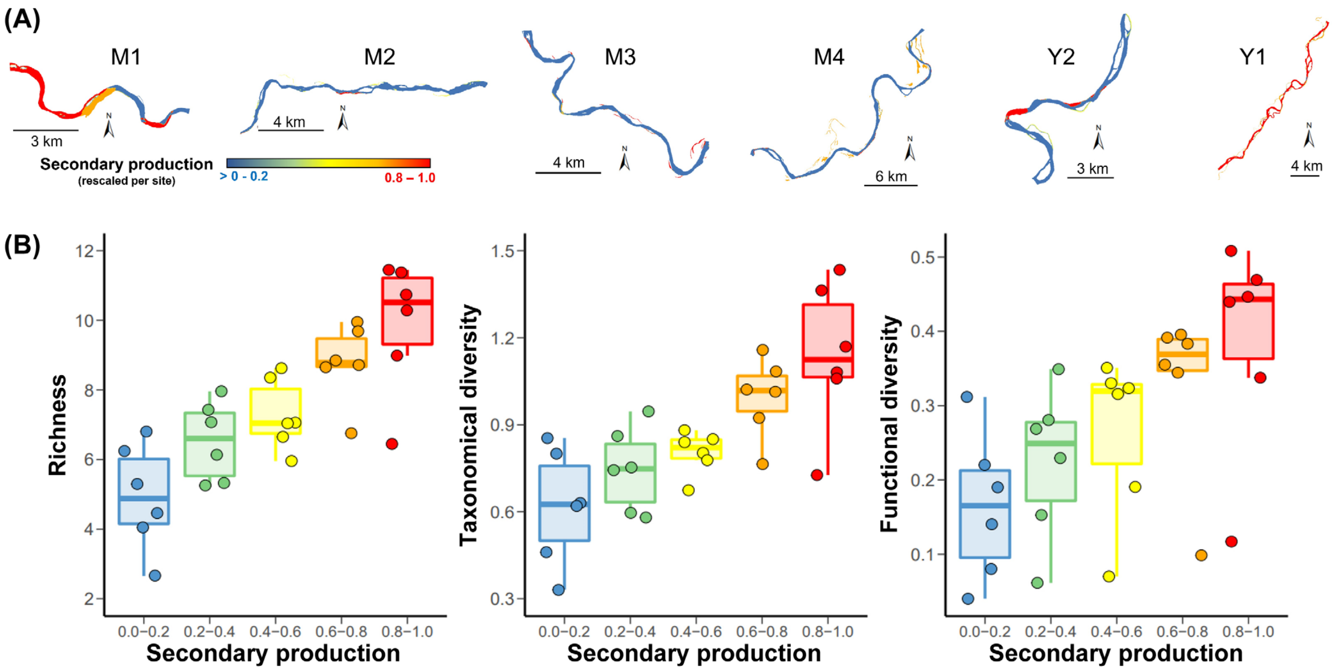

Figure 5. (A) Heat maps of invertebrate secondary production scaled between 0 and 1 for each study reach. Colors are displayed in five categories that represent quantiles of secondary production at each reach. Dark blue and red areas represent locations with the lowest and highest secondary production estimates at each reach, respectively. (B) Boxplots showing differences in invertebrate richness, taxonomic diversity (Shannon *H*) and functional diversity (FFG evenness J_{FD}) between areas ranging from low (blue; lowest 20th percentile) to high (red; highest 20th percentile) secondary production. Circles represent the mean diversity estimate of all grid cells in a given production quantile for each of the 6 study reaches (Supporting information). Bolded lines in boxes are medians, box ends are quartiles and whiskers extend to the lowest or highest data point ≤ 1.5 the interquartile range.

Interestingly, these patterns related more to keystone habitat characteristics (i.e. large sediment size) than changes in habitat diversity, a finding that has received growing support from other studies (Tews et al. 2004, Hitchman et al. 2018). The magnitude of spikes in secondary production, in particular, was often so large that the bulk of the production at a given reach could be attributed to rare and patchy habitats. Although similar patterns are well known in smaller streams (within 100 m reaches; Benke et al. 1984, Huryn and Wallace 1987), our study suggests that analogous patterns emerge in large rivers, albeit at spatial extents that exceed the scope (i.e. multiple kilometers) of traditional sampling schemes (Poff and Huryn 1998, Fausch et al. 2002). Furthermore, the patchy and abrupt changes in secondary production and biodiversity resemble other longitudinal discontinuities in river habitats (Poole 2002, Carbonneau et al. 2012), such as sharp changes in sediment size near tributary confluences (Rice et al. 2001). Our study thus provides unique evidence that discontinuities in the habitat templet can propagate to shape spatial patterns in BEF across the landscape.

Despite clear relationships among diversity, production and habitat described above, we observed important exceptions related to both context and human perturbation. For example, although diversity and secondary production often increased abruptly when sand habitat transitioned to patches of large boulders, there were only weak increases, or sometimes reductions, in production when cobble/gravel transitioned to boulders. These findings suggest that boulders may act as hotspots of diversity and production in some, but not all, locations, and that relationships between geomorphology, diversity and production can depend on properties of the larger environmental context. Additionally, we found that invertebrate diversity was unrelated to production in the highly productive tailwaters of Fort Peck Dam, despite positive relationships among other reaches. Similar findings have been reported in other altered ecosystems, where habitat modification, increased primary production and species invasions can result in highly productive assemblages dominated by few specialized, tolerant or non-native species (Wotton 1988, Hall et al. 2006, Sousa et al. 2008). Although most BEF literature has focused on significant positive relationships, elucidating where and when production is decoupled from diversity will be crucial for refining predictions to include how context and habitat perturbations will modulate future changes in biodiversity and ecosystem processes.

We applied a riverscape perspective (sensu Torgersen et al. 2022) to reveal connections between habitat and BEF across spatial scales. Our geospatial analyses identified both local- and larger-scale spatial signals in biodiversity and secondary production, suggesting that multiple processes may simultaneously influence these patterns at different spatial scales (Ettema and Wardle 2002, McGuire et al. 2014). These

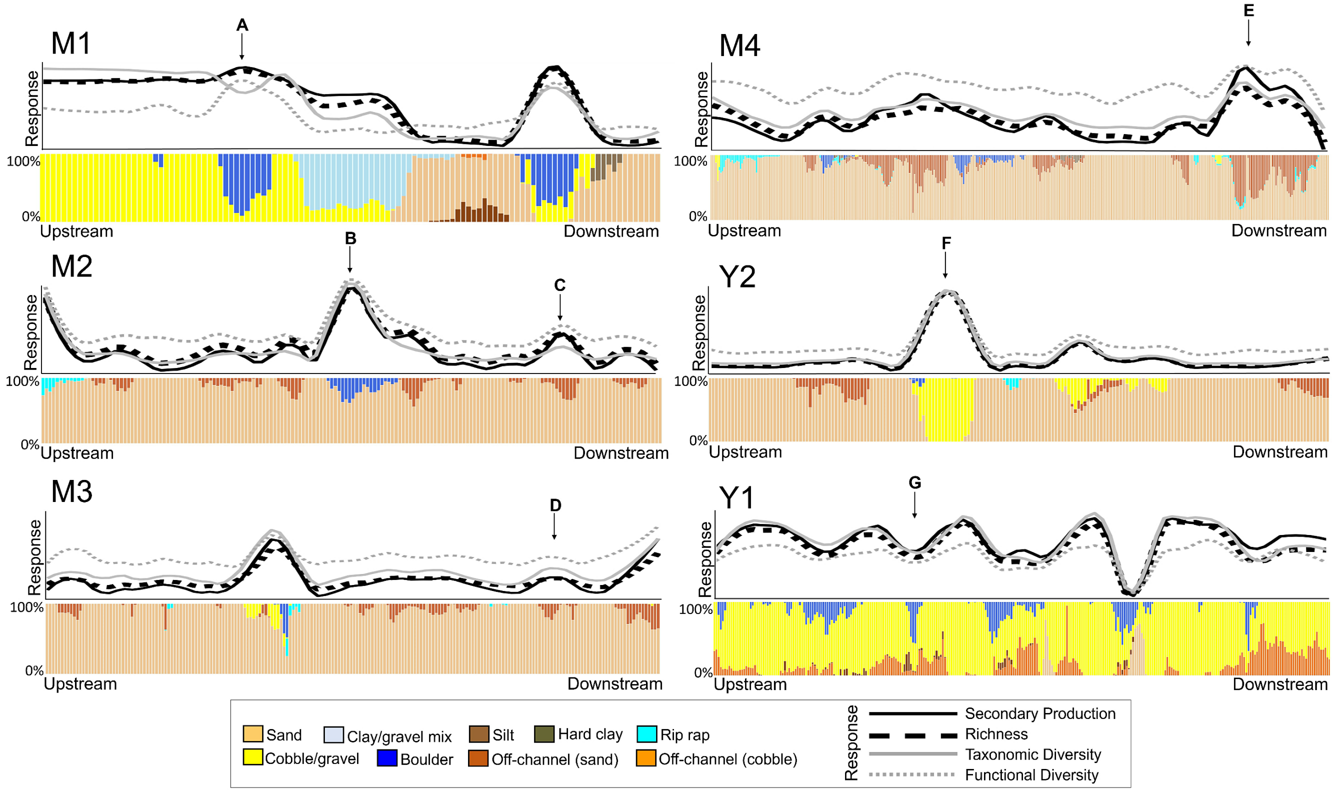

Figure 6. Longitudinal patterns of river habitat composition, invertebrate richness, taxonomic diversity (Shannon *H*), functional diversity (FFG evenness J_{FD}) and invertebrate secondary production (g AFDM m^{-2} year^{-1}) within study reaches. Each colored vertical bar represents habitat proportions summarized for a 100 m reach of river. The lines above habitat descriptions represent mean habitat-weighted invertebrate richness (black dashed), taxonomic (grey) and functional (grey dotted) diversity and secondary production (solid black). These estimates were rescaled between 0 and 1 and smoothed across 100-m increments using a loess function. Letters with arrows correspond to descriptions in the main text.

patterns are consistent with a previous study focused on habitat (Scholl et al. 2021), which observed multiple spatial inflections in semivariograms describing autocorrelation in benthic substrate, and suggested that different physical processes influence substrate size at different scales. For example, autogenic river characteristics such as water velocity and benthic sediment movement were predicted to drive small-scale patchiness in sediment size, whereas larger allogenic characteristics such as tributary junctions and erosion of colluvial talus shaped patterns at larger scales. The present study demonstrates that similar physical processes may shape patterns in biodiversity and secondary production through their strong influence on the geophysical templet. Moreover, although sediment size and stability appeared to be a first-order control on these patterns, other factors that vary across space, including temperature, flow and nutrient concentrations, may also play important roles. Disentangling how connections among habitat, biodiversity and ecosystem function change across spatial and temporal scales (O'Neill et al. 1986, Poole 2002) will be challenging, but there is reason to be optimistic. Emerging conceptual frameworks (Torgersen et al. 2022) and new technologies (drones, sensors, remote sensing, data analytics; see references in Carbonneau et al. 2005) offer exciting opportunities to advance riverscape science, and to inform the management and conservation of rivers globally.

Although our study was well-suited for quantifying BEF patterns across the riverscape, our observational approach cannot necessarily infer causation between diversity and secondary production (Platt 1964). Additionally, without experiments to examine how secondary production of diverse assemblages compares to monocultures we cannot infer specific mechanisms, such as niche complementary or species selection, that underpin these patterns. Nonetheless, such experiments would not be possible at realistic scales and contexts under which riverscapes operate. In addition, given the context-dependencies we observed, it is an open question whether generalized mechanisms should be the sole focus of such studies. Future work will benefit from a multi-faceted approach that combines large-scale observations (e.g. our study) with detailed field experiments across environmental gradients to explore how the drivers of BEF relationships may change across the landscape. Prioritizing such approaches will be critical for describing the complexity of BEF patterns at scales that are most relevant to addressing ongoing declines in biodiversity (Sagarin and Pauchard 2010, Snelgrove et al. 2014).

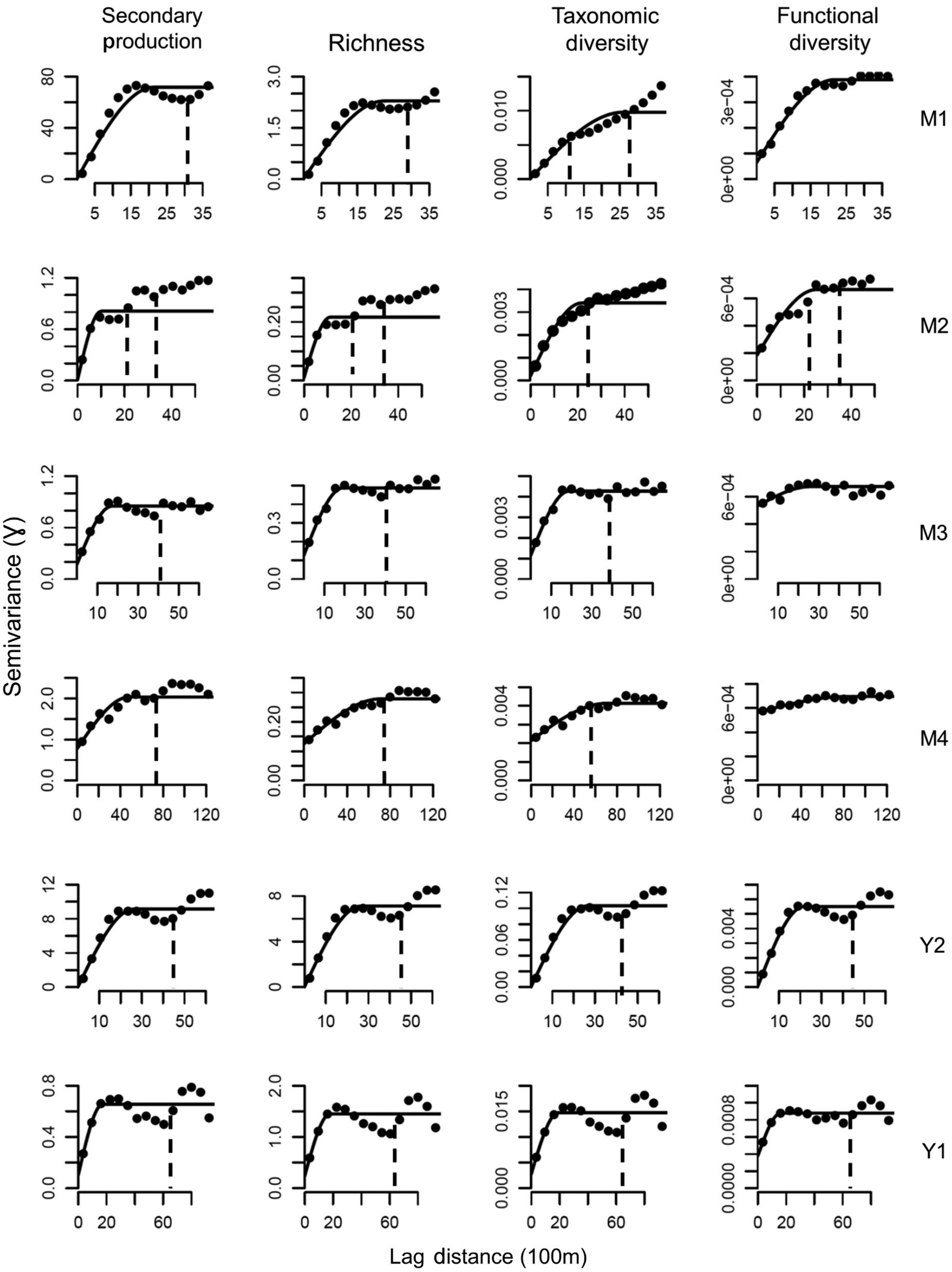

Figure 7. Empirical semivariograms of invertebrate secondary production (g AFDM m^{-2} year^{-1}), invertebrate richness, taxonomic diversity (Shannon *H*) and functional diversity (FFG evenness J_{FD}) at all study reaches are represented by the black circles. Fitted spherical semivariogram models are represented by the solid black lines. Vertical dashed lines represent visual estimates of inflection points on the empirical semivariogram. Parameter estimates from spherical models and visually estimated ranges of inflection points can be found in the Supporting information.

Conclusions

Human activities have transformed the Earth's surface to such an extent that they are now a primary geomorphic agent (Hooke 2000, Brown et al. 2017, Cooper et al. 2018). This anthropogenic signature is particularly evident in rivers and streams where impoundments, channel modifications and changes in climate and land use have altered or homogenized river habitat (Best 2019). Despite the ubiquity of these perturbations, we still know little about their influence on connections between animal communities and ecosystem functioning. Revealing these connections requires studies conducted at realistic spatial and temporal scales, embracing natural variability and the difficulty of large field campaigns that retain fine-scale data resolution. Our study is among the first to link positive relationships between animal diversity and secondary production to characteristics of the geophysical templet, and to show that acute modification of the riverscape (e.g. tailwaters) can modify these patterns at spatial scales that may subsume key food web linkages, including large mobile consumers (Scholl 2021). Given the relatively tight coupling among the geophysical templet, community structure and ecosystem function, future efforts that work across scales and ecosystem types will go far towards elucidating how 'nature's stage' shapes relationships between ecosystem structure and function.

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Author contributions

Eric A. Scholl: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Wyatt F. Cross**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Christopher S. Guy**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3ffbg79n6> (Scholl et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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