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Controls on Steppe River Metabolism Vary by Scale and Network Location

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Abstract. We explore geographic scaling of metabolism estimates derived from dissolved oxygen measurements with data from 75 sites in three corresponding ecoregions across the temperate steppes of Mongolia and the United States. We used a nested analysis with descending spatial scales (country, ecoregion, river basin, upper or lower watershed, and wide or constrained valleys) to assess spatial heterogeneity. We then linked estimates of metabolism with reach-to-watershed-scale metrics representing geomorphology, topography, climate, and anthropogenic activity to provide possible explanations for spatial scaling dependencies. We evaluated gross primary production (GPP) and ecosystem respiration (ER) at in-situ water temperature and after standardizing them to 20 °C (GPP_{20} and ER_{20}). There was no significant effect of scaling on ER, and river basin explained only modest variation in GPP. In contrast, GPP_{20} varied significantly with ecoregion, river basin, basin position (upper vs. lower), and valley morphology (constrained vs. wide). ER_{20} had no significant spatial predictors. Best regression models for GPP included positive relationships with water velocity and median basin slope and for ER included mean basin air temperature, percentage of urban land use in the basin, and GPP. Best subset regression models for GPP_{20} included depth, water velocity, and basin slope and for ER_{20} included depth and mean basin air temperature. The proportion of the watershed in urban or cropland was explanatory of ER, but not GPP. We conclude that fundamental components of ecosystem metabolism respond to different watershed scales and to distinct environmental controls. Thus, macrosystem-scale studies require multi-scale assessment to predict and capture variation in aquatic metabolism. This suggests that universal models of river metabolism are unlikely to perform as well as models built to match the specific scale of inquiry or management.

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1 Introduction

Estimates of river metabolism are a key indicator of ecosystem state in rivers worldwide (Jankowski et al., 2021). Rates of carbon fixation (Gross Primary Production, GPP) and biological carbon oxidation (Ecosystem Respiration, ER), as well as their balance (Net Ecosystem Production, NEP), relate biotic activity and integrity to water quality and basic ecosystem structure and integrate ecosystem processes over the upstream watershed (Dodds et al., 2013; Levi and Mcintyre, 2020). GPP and ER are major controls on riverine organic carbon fluxes (Demars et al., 2011). These rates reflect river carbon transportation, transformation, and release. They reveal a notable contribution to climate regulation and the global carbon budget even though global river area is small (Cole et al., 2007). Understanding scaling of processes that control river metabolism, and how those factors vary with location, will assist our knowledge of river ecosystem functions across broad climatic gradients (Dodds et al., 2018).

Characterizing controls on river metabolism may require understanding the fundamental scale-dependent processes that govern metabolism across reach-to-watershed and broader macrosystem scales. Furthermore, mechanistic predictions of future changes in river metabolism will require understanding how metabolic processes vary across scales. Yet, existing data sets are often limited and rarely account for cross-scale interactions (Tromboni et al., 2021; Hotchkiss et al., 2018). Metabolic processes (GPP and ER) at the reach scale can be nonlinear (Feijó-Lima et al., 2018) due to upriver processes, and inferring changes to metabolic processes is difficult at larger spatial scales given the wide variety of conditions that may occur across biomes (Gücker and Pusch, 2006).

Conceptual efforts to scale ecosystem processes to the watershed, including metabolic characteristics, led to the River Continuum Concept (Vannote et al., 1980), later supported by metabolic

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chamber measurements along four river basin continua (Bott et al., 1985). The river continuum framework was expanded across biomes by (Dodds et al., 2015) although empirical support from point-based stream metabolism studies has been modest (Mulholland et al., 2001; Bernot et al., 2010; Bernhardt et al., 2018). Work has continued scaling metabolism at the watershed scale (Dodds et al., 2018; Segatto et al., 2021; Segatto et al., 2023; Ruffing et al., 2022; Koenig et al., 2019). Additionally, the concept of Functional Process Zones (FPZ) made the case for local geomorphic and ecological controls on river ecosystems (Thorp et al., 2006), raising questions on which spatial scales are most important organizers of ecosystem metabolic processes.

We compare here the metabolism of rivers in the United States and Mongolia classified as having watersheds in comparable temperate steppe ecoregions. A major challenge in comparing studies across large spatial scales is the inconsistency in measurement approaches and that the specific methodology and /or quality control/ quality assurance measures are often not well described (Schechner et al. 2021). We avoid this issue by comparing measurements across 75 river sites using the same methodology and rigorous quality control procedures as described by (Schechner et al., 2021). Our range of sites consists of dry terminal basins in the western portions of these countries, montane steppes further east, and grassland ecoregions at the most eastward set of sites (Olson et al., 2001; Dinerstein et al., 2017). We originally hypothesized the most similar rates would be found in the matching ecoregions regardless of which country they would be in. However, we also understand that other factors could control metabolic rates in addition to ecoregion. Thus, we investigated our large metabolism dataset for rivers in these three ecoregions in both countries in conjunction with a broad range of variables including climate, geomorphology, and land use. We hypothesized that these variables could be influenced by spatial scale,

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so we explicitly consider nested spatial scales in our design (Figure 1). While many metabolic measurements are available for the United States, metabolic rates for Mongolia's rivers have not, to our knowledge, been quantified prior to our work. We then use our dataset to investigate how various scales of data aggregation related to independent variables could facilitate predictions of river metabolism across broad spatial scales.

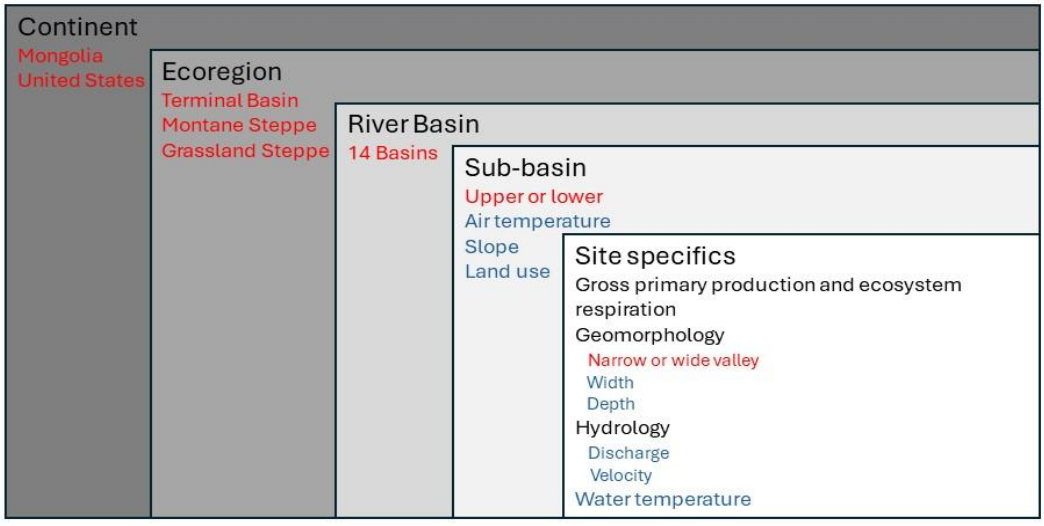

Figure 1. Scales of aggregation and variables considered in this study. Red text indicates categorical variables used to investigate scaling influences on metabolism. Blue text indicates continuous variables used in the multivariate assessment of factors influencing metabolism across all sites.

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2 Materials and Methods

2.1 Study Sites, Reach Definition, and Watershed Delineation

We obtained GIS data to indicate local geomorphology and watershed-scale values for land use, climate, slope, and elevation for each sampling site. We selected our sites using the GIS-based program RESonate (Williams et al., 2013) to represent replicates in multiple watersheds of different geomorphic patches or Functional Process Zones (FPZs). The FPZs are reoccurring longitudinal geomorphic patches that are hypothesized to control biocomplexity, including community composition and system productivity (Thorp et al., 2006). A detailed description of the FPZ delineation methodology we employed has been provided previously (Maasri et al., 2019a; Erdenee et al., 2021). We classified each study site hierarchically by country, ecoregion, river basin, upper (streams higher in the watershed) or lower (low slope rivers of lower elevations), and relatively constrained valley or wide valley. This approach allowed us to assess reach-scale properties that could directly influence the physiological controls most often collected alongside metabolism data. This provided a framework to evaluate how we may understand the determinants of metabolism at multiple scales.

We studied three large-scale temperate steppe ecoregions (Terminal Basin, TB; Montane Steppe, MS; and Grassland Steppe, GS) as characterized by Olson et al. (2001) and updated by Dinerstein et al. (2017) in two countries (Mongolia and the United States, Fig. 2). We aggregated our large-scale ecoregions for the US as follows: TB = Great Basin shrub steppe and Sierra Nevada forest, MS = South Central Rockies forest and Wyoming Basin shrub steppe, GS = Nebraska Sand Hills mixed grasslands and Northern Shortgrass prairie. We aggregated our large-scale ecoregions for Mongolia as follows: TB = Altai mountains forest and forest steppe, Gobi Lakes Valley desert steppe, Great Lakes Basin desert

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steppe, and Khangai Mountains alpine meadows, MS = Selenge-Orkhon forest steppe and Syan Mountains conifer forests, GS = Daurian Forest steppe and Mongolian-Manchurian grassland. We downloaded ecoregion data from https://www.geographyrealm.com/terrestrial-ecoregions-gis-data/ on 19 November 2025. Specific site data can be found in (Schechner et al., 2026). We note that our large-scale ecoregions also included montane areas where some of the streams that fed the steppe rivers originated.

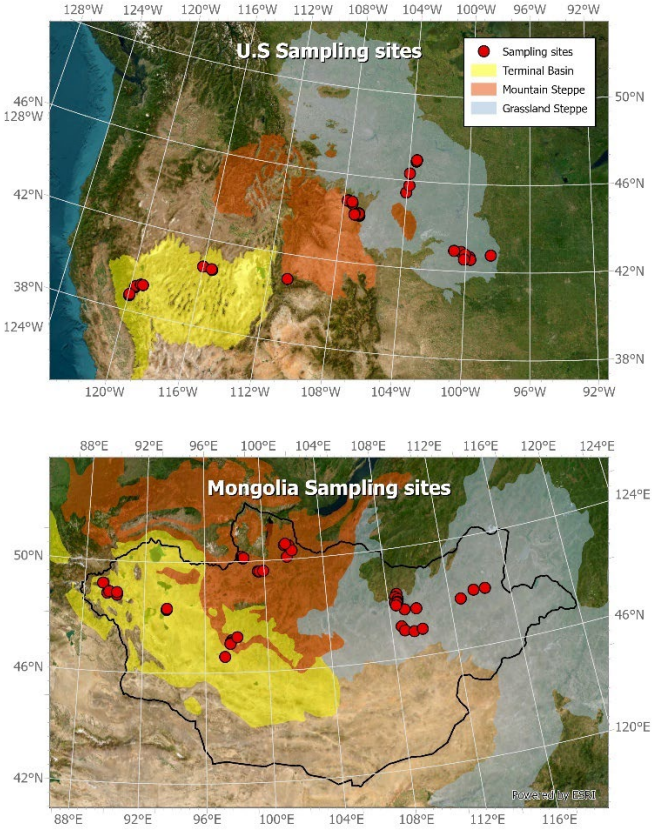

Figure 2. Large-scale steppe ecoregions in the United States and Mongolia and sample sites used in this study. Ecoregion layer under creative commons license from Dinerstein et al. (2017). Outline of Mongolia from Natural Earth Data.

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We chose sites within distinct FPZs to capture a range of conditions across river networks of each ecoregion (Williams et al., 2013; Maasri et al., 2019b; Maasri et al., 2021). We selected sites 1) with a reach of at least two riffle-pool-riffle sequences, 2) with primarily in-channel flow allowing us to account for hydrologic measurements, 3) without highly braided areas (5+ parallel channels) or areas where large portions of the reach would have fully saturated riparian areas (e.g., extensive riparian wetland), and 4) avoiding nearby upstream urban areas, bridges, or other significant anthropogenic features. We concentrated our hydrologic and geomorphic measurements based on a minimum fifteen-minute travel time, with a maximum of two kilometers. Sites were sampled during times of low flow, to increase comparability and ensure safety of the field teams (Levi and Mcintyre, 2020).

Watersheds were delineated using ArcGIS Pro hydrological geoprocessing tools and two different DEM datasets. Mongolia's watersheds were computed using the SRTM Global dataset (3 arc second- or 90-meters spatial resolution, https://lpdaac.usgs.gov/products/srtmgl3v003/), and U.S watersheds were computed using higher resolution SRTM data (spatial resolution 1 arc second- 30 meters- spatial resolution Earth Explorer https://earthexplorer.usgs.gov/). These datasets were also used to calculate slope and elevation using zonal statistics tools. Long-term (1977 – 2000) climate data across each watershed were extracted from WorldClim Data (https://www.worldclim.org/data/worldclim21.html). Land use land cover data came from the Copernicus Land Monitoring Service Land Cover 2019 (raster 100 m), global, yearly – version 3 https://land.copernicus.eu/en/products/global-dynamic-land-cover/copernicus-global-land-service-land-cover-100m-collection-3-epoch-2019-globe), which provides a global dataset at 100 meters spatial resolution.

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2.2 Site Specific Field Geomorphic Characterization

We sampled each site using Physical Habitat Protocols from Environmental Monitoring and Assessment Program Section 7 (Lazorchak et al., 1998). We used recorded measurements to calculate metrics representing habitat and dominant reach geomorphic processes (Kaufmann et al., 1999). We sampled a geomorphic reach length of 40 times the average wetted width, except where total reaches would have exceeded 5 km, in which case we halved the length, following Kaufmann et al. (1999). We spaced transects at 0.1 of the total reach length, with half transects at 0.05 of the total reach length. Channel geometry data included at least five depth measurements across each transect, and wetted width at each transect and half transect. We recorded at least 100 thalweg depths along the reach length either manually or with a Sontek Acoustic Doppler Velocimeter (Sontek, San Diego, CA) in the largest rivers.

2.3 Metabolism Field Methods, Sensor Specifics, and Estimation

We quantified metabolism in rivers of the United States and Mongolian Steppe using the same equipment, methodology, and appropriated quality control/ quality assurance to control for factors that can bias metabolism estimates (Schechner et al., 2021). We used the single station open channel diel O_2 method (Demars et al., 2015) and deployed O_2 and temperature-logging miniDOT probes (PME, Vista, CA) at a minimum of two locations per site, separated by a 15-minute travel time estimating from initial velocity measurements made with either a Sontek Acoustic Doppler Velocimeter (Sontek, San Diego, CA) or a topset rod and Marsh-Mcbirney Flo-Mate (McCrometer, Hemet, CA). Deployments ranged from 24 hours to one week. MiniDOT sensors were calibrated and adjusted for drift by calibration before and

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after deployment, and multiple sensors placed in representative flow were averaged to give an overall site estimate (Schechner et al., 2021). Photosynthetically active radiation sensors (PAR, Odyssey, Christchurch, NZ) were deployed as closely as possible to each site but as several were lost to theft or animal disturbance, some additional sensors were deployed at a nearby basecamp when river reaches had high human presence. Light sensors were placed in areas without canopy or shading topography, as few of our studied rivers had substantial canopy cover. The Odyssey sensors were calibrated seasonally against a calibrated Li-COR Photometer (Li-COR, Lincoln, NE) and exhibited minimal drift.

We estimated GPP, ER, and aeration (k) using the BASE (BAyesian Single Station Estimation, V2.3, Grace et al., 2015) model with ten-minute O_2, temperature, and light data, in conjunction with average site barometric pressure. We discarded sites where we were unable to successfully model the data evaluated by the metrics of fit associated with the model, as well as a visual evaluation of modelled versus observed data. We re-ran sites where we were unable to get a good model fit using the BASE model with the (Riley and Dodds, 2012) model. These sites were mainly those with high gradient/aeration. Data from the site were discarded if this approach still gave poor fit based on visual observation. We plotted ER against aeration and observed a positive correlation suggesting models could not converge on unique solutions (equifinality). This led us to examine sites with very high aeration and remove eight of these sites. Finally, we re-checked that site names and locations matched. This led to a few sites where geomorphology data and metabolism data could not be reliably co-located. This left us with 75 sites out of 89 where we were able to model metabolism successfully, GPP/ER was realistic (<3), aeration rates were not unreasonably high and not correlated with ER, and geomorphic and watershed data were also collected successfully.

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We compared metabolism estimates at in-situ water temperature with rates standardized to a common temperature. We used this approach to make estimates more comparable across sites with different diel thermal regimes, as previous work had not found a relationship between daily metabolism and water temperature during short-term measurements (Song et al., 2018). Estimates of GPP and ER were standardized to 20ºC (GPP_{20} and ER_{20}) following Riley and Dodds (2012):

$$GPP_{20} = GPP * 1.036^{(20-t1)} \quad (1)$$

and

$$ER_{20} = ER * 1.045^{(20-t1)} \quad (2)$$

where t_1 is average stream temperature across the entire period of data logging.

2.4 Data Preparation, Variable Reduction, and Evaluation

Rates of metabolism were significantly non-normal, as were common transformations (square root, log, rate/standard deviation, 1/rate, log(max(rate)+1-rate), (rate - min(rate))/(max(rate)-min(rate)), Shapiro-Wilkes all $p < 0.00002$). Thus, we elected to use the non-transformed data. All analyses were conducted in R (v. 4.0.2, R Development Core Team, 2017) or Statistica 13 Dell Software, 2015.

We analyzed the data in two steps. First, we used hierarchical (nested) ANOVA to assess spatial effects on GPP, ER, GPP/ER, GPP_{20}, ER_{20}, and GPP_{20}/ER_{20}. For the top scale we used country (Mongolia or United States). The next scale was ecoregion (Terminal Basin, TB; Mountain Steppe, MS; and Grassland Steppe, GS). The next finer scale was the river basin (i.e., basin that included all sites derived from one distinct river network). The river basin scale was separated by upstream and downstream sites followed by a finer FPZ scale (Williams et al., 2013; Maasri et al., 2019a; Maasri et al., 2021). For the

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finest scale we separated sites classified as geologically relatively wide or constrained, and statistical thresholds were evaluated at $p < 0.05$ in each test. While we realize using this scale over multiple tests would require adjustment for repeated tests, our goal was to identify the scales of influence that were likely the most important relative to other scales.

For the next set of analyses, we picked continuous variables that we considered most likely to influence the differences revealed in the spatial analysis and built best subset linear regression models using Akaike Information Criteria (AIC). AIC is a statistical tool used for model selection to help choose the best model among a set of candidates. It balances two key aspects: the goodness of fit (how well the model explains the data) and its complexity (the number of variables in the model, to avoid overfitting). Lower AIC values indicate a better model. The variables we selected as independent drivers of metabolism were mean water temperature during metabolism measurement, average river depth, river wetted width, water velocity, discharge, long-term median air temperature in the watershed, median slope in the watershed, percentage cropland in the watershed, and percentage agriculture in the watershed.

3 Results

3.1 Scaling Rates of Metabolism

GPP ranged from 0.03 to 10.64 g O_2 m^{-2} day^{-1}, while ER ranged from 0.89 to 26.48 g O_2 m^{-2} day^{-1} (Table 1). Overall systems were net heterotrophic (Figure 3) with ER rates about twice GPP rates. Most measurements were made in rivers at <20ºC, so overall rates of GPP_{20} and ER_{20} were greater than the uncorrected rates. Hierarchical ANOVA indicated that GPP varied marginally significantly, only by river basin (Figure 4, Table S1) and GPP_{20} again was marginally significant by river basin (Table S3). The

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same analysis found no clustering scale significant for ER or ER_{20} (Table S2, S4). Data distributions by each level of hierarchy can be found in Figure S1.

Table 1. Summary statistics of gross primary production (GPP), ecosystem respiration (ER) rates at ambient temperature and gross primary production (GPP_{20}), ecosystem respiration (ER_{20}) rates corrected to 20 ºC and the GPP/ER ratios over the entire dataset. All rates are in g m^{-2} day^{-1}

Rate	*N*	*Mean*	*Median*	*Minimum*	*Maximum*	*Lower Quartile*	*Upper Quartile*	*Std. Dev.*
GPP	75	3.22	2.84	0.03	10.64	1.15	4.65	2.63
ER	75	7.45	6.41	0.89	26.48	4.10	9.51	4.39
GPP/ER	75	0.52	0.42	0.00	3.56	0.17	0.69	0.56
GPP_{20}	75	3.71	3.19	0.04	17.52	1.47	4.91	3.27
ER_{20}	75	9.27	8.08	1.25	37.06	4.89	10.93	5.91
GPP_{20}/ER_{20}	75	0.51	0.39	0.00	3.67	0.16	0.69	0.56

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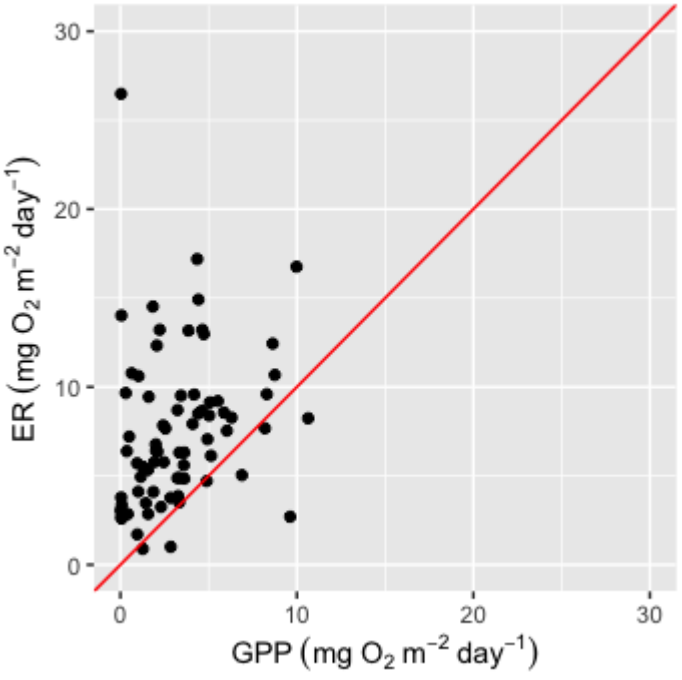

Figure 3. Relationships of gross primary production (GPP) to ecosystem respiration (ER) across all sites. Points above the 1:1 line are net heterotrophic. There was a positive linear relationship between GPP and ER ($p < 0.04$).

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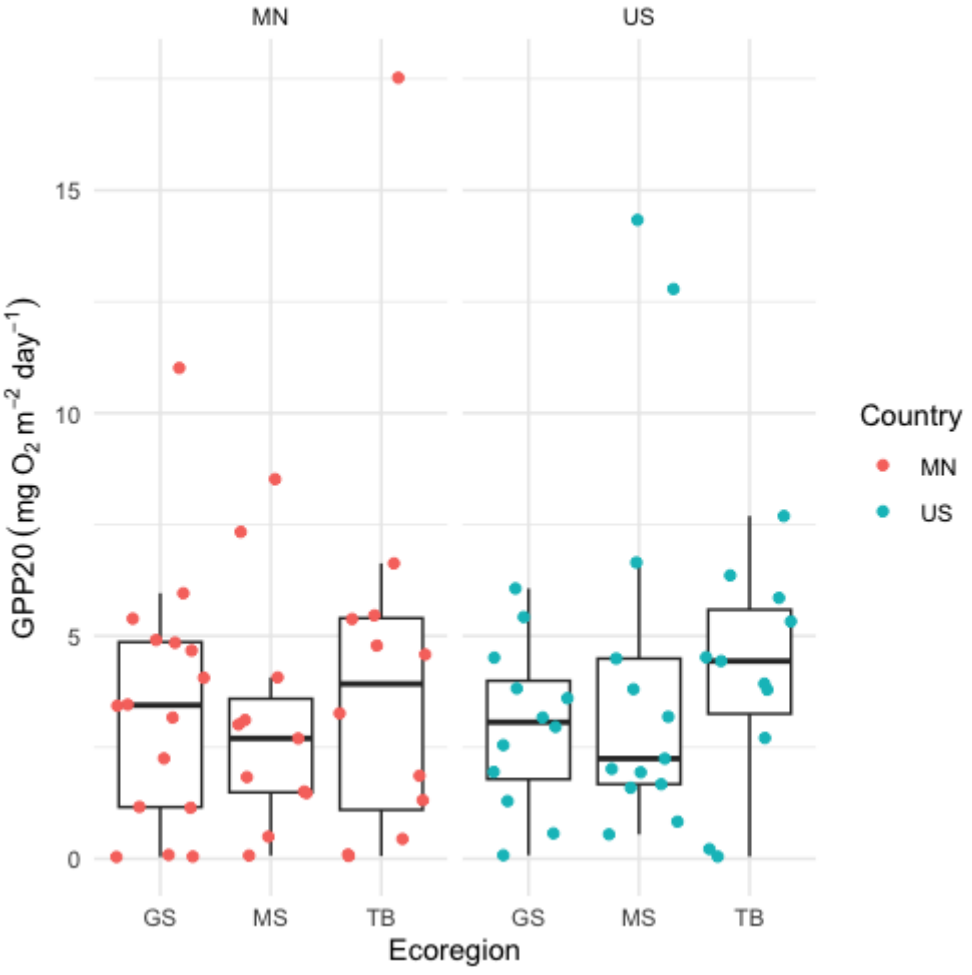

Figure 4. Temperature-corrected gross primary production (GPP) as a function of country (MN – Mongolia red dots to left, and US – United States turquoise dots to right) and ecoregion. Box plots indicate the median (middle line), the upper and lower quartiles (top and bottom of boxes). Bars indicate the upper and lower 95%. GS = Grassland Steppe, MS = Mountain Steppe, and TB = Terminal Basin.

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3.2 Continuous variables driving metabolism

We assessed best models using AIC regression models to predict GPP, ER, GPP/ER, GPP_{20}, ER_{20}, and GPP_{20}/ER_{20}. We used independent variables: mean water temperature during metabolism measurement, average river depth, river wetted width, water velocity, discharge, long-term median air temperature in the watershed, median slope in the watershed, proportion of cropland in the watershed, and proportion of agriculture in the watershed (see Supplement 1 for detailed results). The top 20 models for GPP (Table S8) all had water temperature included, and median watershed slope was in most of the models as well as the top model. In contrast, the top 20 models for ER had average basin air temperature with percentage urban also included in the top model (Table S9). The factors that appeared to control GPP/ER included depth, water temperature, and average watershed air temperature which were in the top model and most of the top ten models (Table S10). In addition, percentage urban land use and slope appeared in some of the top ten models.

Once the GPP and ER rates were corrected from river water temperature to 20 ºC, the results varied from the uncorrected rates. We used all the same factors to predict GPP_{20}, ER_{20}, and GPP_{20}/ER_{20} as GPP, ER, GPP/ER except water temperature, as that was used to make the correction. Water velocity and median watershed slope played strong roles in explaining GPP_{20} and appeared in most of the top 10 models (Table S11). Depth, percentage urban, and percentage cropland also appeared in some of these models. Depth, wetted width, and average air temperature in the watershed all played potentially stronger roles in predicting ER_{20} than the other variables (Table S12).

We explored the top explanatory variables related to our hierarchical design using ANOVAS as driven by hierarchical level (Figure 5). Percentage urban only mapped significantly to the finest spatial

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category, constrained versus wide (Table S15). Percentage cropland mapped to ecoregions, driven by greater amounts of cropland in the grassland steppe regions of both countries (Table S14). Water temperature was independent of spatial scale. River depth had $p < 0.05$ at every scale of the hierarchy except country, consistent with patterns observed for spatial structure in GPP/ER and GPP_{20}/ER_{20}. Mean air temperature and median slope were also significant with every scale of hierarchy. Water velocity was only significant with the upper versus lower watershed scale. Since GPP mapped to the basin scale, this leaves depth, slope, and air temperature as probable causes of this scaling pattern. GPP/ER and GPP_{20}/ER_{20} patterns were potentially primarily driven by depth, slope, and air temp, but water velocity and percentage cropland also matched at the upper-lower and the percentage cropland scales as well.

Figure 5. Stronger drivers within individual hierarchical ANOVAS for Gross Primary Production (GPP), Ecosystem Respiration (ER), temperature corrected GPP (GPP20) and ER (ER20) and the ratio of GPP/ER as a function of potential driver variables (T = river temperature, D = mean depth, V= water velocity) for these metabolism indicators. Red shading indicates strong relationships between continuous and categorical scale variables. Detailed statistical results on Tables S1, 2,3,4,5, and 6.

Scale	GPP	ER	GPP/ ER	GPP_{20}	ER_{20}	GPP_{20}/ER_{20}	T	D	V	Slope	Air temp	% Urb	% crop
Country													
Ecoregion													
Basin													
Upper-lower													
Constrained – wide													

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4 Discussion

Our metabolism estimates fall within the range of values of GPP and ER published by Song et al. (2018) across the United States (Figure S1). They also fell within the range for rivers in the Western United States (Hall et al., 2016), which also occurred in the US terminal basin. We also found similar levels of autotrophy as Hall et al. (2016); they noted that two of their fourteen rivers had GPP exceeding ER and we found the same for three out of eleven rivers we studied in the US terminal basin. Across our entire dataset, only five of 76 river sites had GPP exceeding ER. Carter et al. (2024) documented autotrophy in approximately 6% of 236 rivers across the United States, although rivers in the Western United States (where many of our sites were located) were more likely to have GPP/ER values around 1. They also found that higher GPP/ER was more common at sites at higher elevations and lower air temperatures. Our results also suggested that lower air temperatures were positively correlated with greater GPP/ER. However, our results suggest that GPP, ER, and the ratio GPP/ER respond differently to spatial scale and environmental controls of metabolism. Identifying how these controls vary across multiple sites could clarify the scale at which metabolic processes are organized and improve our ability to predict metabolism under baseline conditions and in response to anthropogenic change. We analyzed hierarchical scaling factors and continuous predictors separately because our sample size did not permit a single integrated model including all independent variables.

4.1 Approaches to Scaling Metabolism

Several general approaches have been used previously to consider the drivers of stream and river metabolism based on known physiological variables that constrain metabolism of individual organisms. These include light, temperature, and nutrients for primary producers and temperature and carbon quantity

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and quality, temperature, and other nutrients for heterotrophs. These relationships were based on small scale physiological experiments on single organisms or small-scale incubations of multi-species collections from the natural environment. However, Likens (1985) argued that whole ecosystem measurements and experiments may be necessary to understand ecosystem properties. The pioneering metabolism work (Odum, 1956) allowed the estimation of stream metabolism at a reach-scale. This has allowed integration of a larger portion of the ecosystem than smaller scale instream or laboratory incubations. Comparing results from ecosystem rate mesurements at widely different scales has led some to express concerns about upscaling from smaller to larger experiments (Schindler, 1998) and to the problem mentioned in the introduction: reality must be sacrificed for generality (Levins, 1966). Here, we take the scaling exercise a step further and ask how whole ecosystem measures of stream-reach metabolism vary predictably with scale within and among watersheds across broad geographic scales.

As large datasets of metabolism have become available, lotic system ecologists (e.g., Bernot et al., 2010; Hall et al., 2016; Song et al., 2016; Bernhardt et al., 2018; Dodds et al., 2018; Song et al., 2018; Carter et al., 2024; Guan et al., 2025) attempted to generalize patterns by aggregating as much data as possible. They then fit the data to a representative model to evaluate the relative importance of different drivers, and these models are used to predict metabolism under local conditions. However, our ability to scale metabolic rates to understudied areas (e.g. Mongolia) remains limited. Beyond fundamental principles: that high nutrients, high light, and low disturbance allow greater GPP, and that more labile organic carbon inputs stimulate ER, we still lack robust guidance on how to generalize metabolic patterns across broader spatial scale.

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Physiological parameters that influence GPP (e.g., light, nutrients, losses of photosynthetic matter from grazing or flow, temperature) and ER (e.g., biomass of organisms, available carbon, temperature, and hydrology) and the importance of these factors and their interactions could vary predictably depending upon the scale of agglomeration. Our analysis revealed that ER, GPP, and GPP/ER varied depending on the scale of analysis as well as the range of physiological drivers across all the studied sites.

4.2 Consistency of our results with other large-scale syntheses

Broad-scale syntheses have evaluated potential controls and drivers on metabolism, with varying scale, scope, and data context. Our result that ER was driven in part by GPP makes logical sense as primary producers respire as well as producing carbon that heterotrophs can respire. This statistical result was consistent with work by Rodríguez-Castillo et al. (2019) evaluating scaling of metabolism across multiple watersheds, who also found that GPP was best explained by catchment size, while ER was best predicted by cross-sectional area in addition to GPP, supporting the River Continuum concept.

Other researchers have identified several factors for predicting metabolism. Savoy et al. (2019) found that larger watershed areas better explained productivity, along with temperature and discharge. Bernot et al. (2010) compared metabolism as a function of land use across biomes and found GPP and ER were both explained by land use (native reference, urban, or agricultural) and by important interactions: anthropogenic nutrient loading mattered more when nutrients were limiting in reference sites, and the response of ER to land use varied regionally. In contrast to our sites, Bernot et al. (2010) found that ER models involved more variables than did their GPP models for comparable fit and parsimony, and that GPP wasn't explained by photosynthetically available radiation in impacted sites but was in native sites.

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Bernhardt et al. (2018) described patterns of metabolism based on annual regimes and found difficulty predicting reach scale patterns from broader models due to local controls, including local shading, which varied much more in aquatic than terrestrial systems. These findings are consistent with our models at specific scales varying in the factors that offer the most explanatory power. Bernhardt et al. (2018) subsequently proposed a river "climate" consisting of hydrology, light, and temperature. Their work and our findings both support applicability of the network dynamics hypothesis through the importance of hydrology (Benda et al., 2004) where we found both average watershed slope and wide versus constrained valleys to be important with respect to GPP/ER. Our hierarchical analysis supports the river continuum concept (Vannote et al., 1980) by highlighting the importance of watershed-scale variables and contrasting upper- and lower-basin sites for GPP/ER. We also find support for the freshwater biome gradient concept (Dodds et al., 2019) through the relationships with climatic controls and the importance of ecoregions for GPP/ER .

4.3 Continuous variables to explain components of metabolism linked to the significance of scales

We explained a modest amount of the variation in metabolism using interrelated variables across different scales and data types. We discuss most explanatory variables by scale, understanding that they are likely related to other direct factors. Many of the variables we used that were highlighted in the best models (e.g. depth, velocity, average watershed slope, constrained versus wide valleys) were related to the main shaping processes of the river (Wolman and Miller, 1960; Poff et al., 1997). However, these variables can influence more proximate variables. For example, velocity can influence scouring, and depth can influence light penetration and water replacement time.

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There was no significant difference in GPP by country, but United States streams had substantially more riparian cover than those in Mongolia. This suggests that light mediation by local factors was not an important variable in these rivers that mostly occurred in relatively dry biomes. The relative importance of canopy versus other riparian metrics has previously been linked to spiraling length rather than respiration (Reisinger et al., 2019). Hosen et al. (2019) studied metabolism in a nested network in the northeastern United States during drought and found warmer water temperatures, 10°C higher than typical summer baseflow, stimulated ER and GPP in the larger rivers and riparian control of GPP by light interception became less important in the larger rivers. Their results are consistent with ours where water temperature had stronger effects on GPP than ER (which was driven more by basin-wide average air temperature).

4.4 Anthropogenic influences

Mongolia and the United States differ in their development status, geologic histories, anthropogenic influences, latitudes, and climates. The variable "country" was not significant in any of the hierarchical scaling models for metabolism, indicating that most of these differences were not relevant to river metabolism. Our finding that ecoregions significantly influenced GPP, while country did not, suggests that for metabolism in drier temperate areas, results from one country can likely be applied to another. Climate drives ecoregion characteristics (e.g. riparian canopy) and serves as a key variable that can indicate if ecoregion scaling is appropriate.

We were surprised to find that human influence variables (e.g., hydrology, land use) were not explanatory of United States GPP, which we attribute to our experiment design which was to avoid direct anthropogenic influences when selecting sites. Among the recent increases in urbanization, mining, and

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grazing in Mongolia, we were able to assess only the (limited) effects of cropland and urbanization which was modest and influenced ER. Most population centers in Mongolia are small but do not treat sewage for nutrients and can have concentrated animal holding areas. Because Mongolia is not yet highly developed and we found few prior measurements of river metabolism the country (except for Tromboni et al., 2022), our data could provide important baseline information for assessing future anthropogenic pressures on these rivers.

5 Conclusions

This paper provides the largest metabolism dataset for Mongolian rivers that we are aware of, alongside that of comparable ecoregions in the United States. We evaluated patterns and explanatory variables using biogeochemical, geomorphic, and land use data and identified how we can best predict metabolism across this dataset with scale-specific approaches. These data help fill a major gap in the understanding of aquatic ecosystems in grasslands, the temperate steppe, and Central Asia. Filling this gap is important because Mongolian rivers are particularly vulnerable to changing climate, due to inland high elevation, low precipitation, and snowmelt driven hydrology in a rapidly warming area. Mining and urban development are also increasing rapidly in Mongolia as are plans to build reservoirs on major river systems. Although more research exists for temperate Western rivers, much of our understanding is based on forested areas of the United States and Europe.

We sought to understand the drivers of differences in river metabolism across scales. Our data suggest that synoptic studies of river metabolism should be designed to sample sites with a range of widths and orders and to consider a broader data context, including vegetation, human impacts, and substrate

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characteristics. We found that GPP/ER was dependent upon a range of scales from position in the watershed, to drainage basin, and ecoregion, whereas GPP only scaled to ecoregion and ER did not scale to anything. This suggests that GPP/ER could be a particularly sensitive indicator of ecosystem characteristics. Sampling designs should match the scale of interest as well as the response variable of interest.

Across all sites, ecosystem respiration was related to long-term (40-year) climate conditions. This suggests that ER may be more sensitive to global warming than GPP in these ecoregions, a hypothesis that bears further investigation. We set out to broaden the context for metabolism by linking to a large, interdisciplinary dataset, thereby expanding our ability to predict and explain rates of GPP and ER, to assess the relative roles of traditional ecological frameworks that account for human impact, and to anticipate changes associated with a changing climate. We placed our estimates in data contexts familiar to hydrologists, managers, and macroscale researchers, and identified approaches to scaling that can complement the limnologist's toolkit.

Author Contributions

WKD, SC, SK, and AM planned the larger project. All authors were involved in the data collection and writing of this manuscript.

Code/Data availability

Data are available at Schechner et al. 2026 https://doi.org/10.6073/pasta/955165f17b3890d1c44ae3893ec4b9cb

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Competing Interests

The authors declare no competing interests

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References

Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., and Pollock, M.: The network dynamics hypothesis: how channel networks structure riverine habitats, BioScience, 54, 413, 2004.

Bernhardt, E. S., Heffernan, J. B., Grimm, N. B., Stanley, E. H., Harvey, J., Arroita, M., Appling, A. P., Cohen, M., McDowell, W. H., and Hall Jr, R.: The metabolic regimes of flowing waters, Limnology and Oceanography, 63, S99–S118, 2018.

Bernot, M. J., Sobota, D. J., Hall, R. O., Mulholland, P. J., Dodds, W. K., Webster, J. R., Tank, J. L., Ashkenas, L. R., Cooper, L. W., and Dahm, C. N.: Inter-regional comparison of land-use effects on stream metabolism, Freshwater Biology, 55, 1874–1890, 2010.

Bott, T., Brock, J., Dunn, C., Naiman, R., Ovink, R., and Petersen, R.: Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept, Hydrobiologia, 123, 3–45, 1985.

Carter, A. M., Lowman, H. E., Blaszczak, J. R., Barbosa, C. C., DeSiervo, M., Torrens, C. L., Dunkle, M. R., Collins, S. M., Oleksy, I., Katona, L. R., and Hall, R. O.: Exceptions to the Heterotrophic Rule: Prevalence and Drivers of Autotrophy in Streams and Rivers, Ecosystems, 27, 969–985, 10.1007/s10021-024-00933-w, 2024.

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., Duartte, C. M., Kortelainen, P., Downing, J. A., Middelburg, J. J., and Melack, J.: Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget, Ecosystems, 10, 171–184, 2007.

Demars, B. O., Russell Manson, J., Olafsson, J. S., Gislason, G. M., Gudmundsdottír, R., Woodward, G., Reiss, J., Pichler, D. E., Rasmussen, J. J., and Friberg, N.: Temperature and the metabolic balance of streams, Freshwater Biology, 56, 1106–1121, 2011.

https://doi.org/10.5194/egusphere-2026-555
Preprint. Discussion started: 19 February 2026

Demars, B. O. L., Thompson, J., and Manson, J. R.: Stream metabolism and the open diel oxygen method: Principles, practice, and perspectives, Limnology and Oceanography: Methods, 13, 356–374, 10.1002/lom3.10030, 2015.
Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J. E. M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J. C., Llewellyn, O. A., Miller, A. G., Patzelt, A., Ghazanfar, S. A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P. B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K. F., and Saleem, M.: An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm, BioScience, 67, 534–545, 10.1093/biosci/bix014, 2017.
Dodds, W. K., Gido, K., Whiles, M. R., Daniels, M. D., and Grudzinski, B. P.: The stream biome gradient foncept: Factors controlling lotic systems across broad biogeographic scales, Freshwater Science, 34, 1–19, 10.1086/679756, 2015.
Dodds, W. K., Veach, A. M., Ruffing, C. M., Larson, D. M., Fischer, J. L., and Costigan, K. H.: Abiotic controls and temporal variability of river metabolism: multiyear analyses of Mississippi and Chattahoochee River data, Freshwater Science, 32, 1073–1087, 2013.
Dodds, W. K., Bruckerhoff, L., Batzer, D., Schechner, A., Pennock, C., Renner, E., Tromboni, F., Bigham, K., and Grieger, S.: The freshwater biome gradient framework: Predicting macroscale properties based on latitude, altitude, and precipitation, Ecosphere, 10, e02786, 10.1002/ecs2.2786, 2019.
Dodds, W. K., Higgs, S. A., Spangler, M. J., Guinnip, J., Scott, J. D., Hedden, S. C., Frenette, B. D., Taylor, R., Schechner, A. E., Hoeinghaus, D. J., and Evans-White, M. A.: Spatial heterogeneity and controls of ecosystem metabolism in a Great Plains river network, Hydrobiologia, 1–18, 10.1007/s10750-018-3516-0, 2018.
Erdenee, B., Maasri, A., Gelhaus, J. K., Hayford, B. L., Thorp, J. H., and Kotlinski, N. E.: Comparison of streamflow patterns in drainages of two major terminal basins: the United States Great Basin and Mongolia's Central Asian Internal Drainage, Inland Waters, 11, 368–380, 10.1080/20442041.2021.1956269, 2021.
Feijó-Lima, R., Mcleay, S. M., Silva-Junior, E. F., Tromboni, F., Moulton, T. P., Zandonà, E., and Thomas, S. A.: Quantitatively describing the downstream effects of an abrupt land cover transition: buffering effects of a forest remnant on a stream impacted by cattle grazing, Inland Waters, 8, 294–311, 2018.
Grace, M. R., Giling, D. P., Hladyz, S., Caron, V., Thompson, R. M., and Mac Nally, R.: Fast processing of diel oxygen curves: Estimating stream metabolism with BASE (BAyesian Single-station Estimation), Limnology and Oceanography: Methods, 13, 103–114, 10.1002/lom3.10011, 2015.
Guan, Q., Shi, K., Woolway, R. I., Qin, B., Zhang, Y., and Ran, L.: Declining Predictions of Net Ecosystem Production in US Rivers and Streams Throughout the 21st Century, Environmental Science & Technology, 59, 27800–27810, 10.1021/acs.est.5c05623, 2025.
Gücker, B. and Pusch, M. T.: Regulation of nutrient uptake in eutrophic lowland streams, Limnology and Oceanography, 51, 1443–1453, 2006.
Hall, R. O., Tank, J. L., Baker, M. A., Rosi-Marshall, E. J., and Hotchkiss, E. R.: Metabolism, gas exchange, and carbon spiraling in rivers, Ecosystems, 19, 73–86, 2016.
Hosen, J. D., Aho, K. S., Appling, A. P., Creech, E. C., Fair, J. H., Hall Jr., R. O., Kyzivat, E. D., Lowenthal, R. S., Matt, S., Morrison, J., Saiers, J. E., Shanley, J. B., Weber, L. C., Yoon, B., and Raymond, P. A.: Enhancement of primary production during drought in a temperate watershed is greater in larger rivers than headwater streams, Limnology and Oceanography, 64, 1458–1472, https://doi.org/10.1002/lno.11127, 2019.
Hotchkiss, E., Sadro, S., and Hanson, P.: Toward a more integrative perspective on carbon metabolism across lentic and lotic inland waters, Limnology and Oceanography Letters, 3, 57–63, 2018.
Jankowski, K. J., Mejia, F. H., Blaszczak, J. R., and Holtgrieve, G. W.: Aquatic ecosystem metabolism as a tool in environmental management, Wiley Interdisciplinary Reviews: Water, 8, e1521, 2021.
Kaufmann, P. R., Levine, P., Robison, E. G., Seeliger, C., and Peck, D. V.: Quantifying physical habitat in wadeable streams: surface waters, 1999.
Koenig, L. E., Helton, A. M., Savoy, P., Bertuzzo, E., Heffernan, J. B., Hall Jr, R. O., and Bernhardt, E. S.: Emergent productivity regimes of river networks, Limnology and Oceanography Letters, 4, 173–181, doi:10.1002/lol2.10115, 2019.
Lazorchak, J. M., Klemm, D. J., and Peck, D. V.: Environmental monitoring and assessment program surface waters: field operations and methods for measuring the ecological condition of wadeable streams, 1998.

https://doi.org/10.5194/egusphere-2026-555
Preprint. Discussion started: 19 February 2026

Levi, P. S. and McIntyre, P. B.: Ecosystem responses to channel restoration decline with stream size in urban river networks, Ecological Applications, 30, e02107, 10.1002/eap.2107, 2020.
Levins, R.: The strategy of model building in population biology, Erican Scientist, 54, 421–430, 1966.
Likens, G. E.: An experimental approach for the study of ecosystems, Journal of ecology, 73, 1985.
Maasri, A., Thorp, J. H., Gelhaus, J. K., Tromboni, F., Chandra, S., and Kenner, S. J.: Communities associated with the Functional Process Zone scale: A case study of stream macroinvertebrates in endorheic drainages, Sci. Total Environ., 677, 184–193, https://doi.org/10.1016/j.scitotenv.2019.04.394, 2019a.
Maasri, A., Thorp, J. H., Kotlinski, N., Kiesel, J., Erdenee, B., and Jähnig, S. C.: Variation in macroinvertebrate community structure of functional process zones along the river continuum: New elements for the interpretation of the river ecosystem synthesis, River Research and Applications, 37, 665–674, 2021.
Maasri, A., Schechner, A. E., Erdenee, B., Dodds, W. K., Chandra, S., Gelhaus, J. K., and Thorp, J. H.: Does diel variation in oxygen influence taxonomic and functional diversity of stream macroinvertebrates?, Freshwater Science, 38, 692–701, 10.1086/705916, 2019b.
Mulholland, P. J., Fellows, C. S., Tank, J. L., Grimm, N. B., Webster, J. R., Hamilton, S. K., Marti, E., Ashkenas, L., Bowden, W. B., Dodds, W. K., McDowell, W. H., Paul, M. J., and Peterson, B. J.: Inter-biome comparison of factors controlling stream metabolism, Freshwater Biology, 46, 1503–1517, 2001.
Odum, H. T.: Primary production in flowing waters, Limnology and Oceanography, 1, 102–117, 1956.
Olson, D. M., E. Dinerstein, E. D. W., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreaux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R.: Terrestrial ecoregions of the world: A new map of life on earth, BioScience, 51, 933–938, 2001.
Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., and Strolmberg, R. E. S. a. J. C.: The natural flow regime. A paradigm for river conservation and restoration, BioScience, 47, 769–784, 1997.
Reisinger, A. J., Doody, T. R., Groffman, P. M., Kaushal, S. S., and Rosi, E. J.: Seeing the light: urban stream restoration affects stream metabolism and nitrate uptake via changes in canopy cover, Ecological Applications, 29, e01941, 10.1002/eap.1941, 2019.
Riley, A. J. and Dodds, W. K.: Whole-stream metabolism: strategies for measuring and modeling diel trends of dissolved oxygen, Freshwater Science, 32, 56–69, 10.1899/12-058.1, 2012.
Rodríguez-Castillo, T., Estévez, E., González-Ferreras, A. M., and Barquín, J.: Estimating Ecosystem Metabolism to Entire River Networks, Ecosystems, 22, 892–911, 10.1007/s10021-018-0311-8, 2019.
Ruffing, C. M., Veach, A. M., Schechner, A., Rüegg, J., Trentman, M. T., and Dodds, W. K.: Prairie stream metabolism recovery varies based on antecedent hydrology across a stream network after a bank-full flood, Limnology and Oceanography, 67, 1986–1999, https://doi.org/10.1002/lno.12182, 2022.
Savoy, P., Appling, A. P., Heffernan, J. B., Stets, E. G., Read, J. S., Harvey, J. W., and Bernhardt, E. S.: Metabolic rhythms in flowing waters: An approach for classifying river productivity regimes, Limnology and Oceanography, 64, 1835–1851, 10.1002/lno.11154, 2019.
Schechner, A. E., Dodds, W. K., Tromboni, F., Chandra, S., and Maasri, A.: How do methodological choices influence estimation of river metabolism?, Limnology and Oceanography: Methods, 19, 659–672, https://doi.org/10.1002/lom3.10451, 2021.
Schechner, A. E., W. Dodds, A. Maasri, J. Costello, S. Chandra, B. Dashdorj, F. Tromboni, and H. Avocat: Daily river metabolism using oxygen flux at 75 sites in Mongolia or the United States in steppe ecoregions ver 1. [dataset], https://doi.org/10.6073/pasta/955165f17b3890d1c44ae3893ec4b9cb, 2026.
Schindler, D. W.: Whole-ecosystem experiments: replication versus realism: the need for ecosystem-scale experiments, Ecosystems, 1, 323–334, 1998.
Segatto, P. L., Battin, T. J., and Bertuzzo, E.: The Metabolic Regimes at the Scale of an Entire Stream Network Unveiled Through Sensor Data and Machine Learning, Ecosystems, 24, 1792–1809, 10.1007/s10021-021-00618-8, 2021.
Segatto, P. L., Battin, T. J., and Bertuzzo, E.: A Network-Scale Modeling Framework for Stream Metabolism, Ecosystem Efficiency, and Their Response to Climate Change, Water Resources Research, 59, e2022WR034062, 2023.
Song, C., Dodds, W. K., Trentman, M. T., Rüegg, J., and Ballantyne, F.: Methods of approximation influence aquatic ecosystem metabolism estimates, Limnology and Oceanography: Methods, 14, 557–569, 10.1002/lom3.10112, 2016.

https://doi.org/10.5194/egusphere-2026-555
Preprint. Discussion started: 19 February 2026

Song, C., Dodds, W. K., Rüegg, J., Argerich, A., Baker, C. L., Bowden, W. B., Douglas, M. M., Farrell, K. J., Flinn, M. B., Garcia, E. A., Helton, A. M., Harms, T. K., Jia, S., Jones, J. B., Koenig, L. E., Kominoski, J. S., McDowell, W. H., McMaster, D., Parker, S. P., Rosemond, A. D., Ruffing, C. M., Sheehan, K. R., Trentman, M. T., Whiles, M. R., Wollheim, W. M., and Ballantyne, F.: Continental-scale decrease in net primary productivity in streams due to climate warming, Nature Geoscience, 11, 415–420, 10.1038/s41561-018-0125-5, 2018.

Team, R. C.: R language definition, Vienna, Austria: R foundation for statistical computing, 3, 116, 2017.

Thorp, J. H., Thoms, M. C., and Delong, M. D.: The riverine ecosystem synthesis: Biocomplexity in river networks across space and time, River Research and Applications, 22, 123–147, 2006.

Tromboni, F., Hotchkiss, E. R., Schechner, A. E., Dodds, W. K., Poulson, S. R., and Chandra, S.: High rates of daytime river metabolism are an underestimated component of carbon cycling, Communications Earth & Environment, 3, 270, 10.1038/s43247-022-00607-2, 2022.

Tromboni, F., Liu, J., Ziaco, E., Breshears, D. D., Thompson, K. L., Dodds, W. K., Dahlin, K. M., LaRue, E. A., Thorp, J. H., Viña, A., Laguë, M. M., Maasri, A., Yang, H., Chandra, S., and Fei, S.: Macrosystems as metacoupled human and natural systems, Frontiers in Ecology and the Environment, 19, 20–29, https://doi.org/10.1002/fee.2289, 2021.

Vannote, R. L., Minshall, C. W., Cummins, K. W., Sedell, J. R., and Cushing, C. E.: The river continuum concept, Canadian Journal of Fisheries and Aquatic Sciences, 37, 130–137, 1980.

Williams, B. S., D'Amico, E., Kastens, J. H., Thorp, J. H., Flotemersch, J. E., and Thoms, M. C.: Automated riverine landscape characterization: GIS-based tools for watershed-scale research, assessment, and management, Environmental monitoring and assessment, 185, 7485–7499, 2013.

Wolman, M. G. and Miller, J. P.: Magnitude and frequency of forces in geomorphic processes, The Journal of geology, 68, 54–74, 1960.