

Allometric scaling of hyporheic respiration across basins in the Pacific Northwest USA

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Abstract: Hyporheic zones regulate biogeochemical processes in streams and rivers, but high spatiotemporal heterogeneity makes it difficult to predict how these processes scale from individual reaches to river basins. Recent work applying allometric scaling (i.e., power-law relationships between size and function) to river networks provides a new paradigm to develop a scalable understanding of hyporheic biogeochemical processes. We used reach-scale hyporheic aerobic respiration estimates to explore allometric scaling patterns across two basins, and related these patterns to watershed characteristics. We found consistent scaling behaviors at lowest and highest exchange flux (HEF) quantiles, and consistent but HEF-dependent relationships to watershed elevation, precipitation, and land-cover. Our results also suggest variability of hyporheic respiration allometry for middle exchange flux quantiles, and in relation to land-cover. Our findings provide initial evidence that allometric scaling may be useful for predicting hyporheic biogeochemical dynamics across watersheds from reach to basin scales.

Scientific Significance Statement: The hyporheic zone is a biogeochemical control point in streams and rivers, and processes like hyporheic respiration are important determinants of how watersheds move and process carbon and nutrients. However, the hyporheic zone is also characterized by high spatial heterogeneity, which makes it difficult to predict how hyporheic functions like respiration change across watersheds from reach to basin scales. This study applies allometric scaling theory, which suggests that function scales in a predictable way with size, to determine if hyporheic respiration scales with watershed area in two basins with contrasting watershed characteristics. We found some consistent patterns between basins that suggest allometric scaling of hyporheic respiration may be a tool for transferable knowledge of hyporheic function between basins, but also note some site-specific relationships may constrain the generalizability of this method to other regions and watersheds.

Introduction:

The hyporheic zone (HZ), which forms the interface between surface water and groundwater in streams and rivers, is a spatially heterogeneous and temporally dynamic biogeochemical zone (McClain et al. 2003; Gomez-Velez et al. 2014; Bernhardt et al. 2017; Lee-Cullin et al. 2018). Because the HZ regulates nutrient exchange/processing and provides habitat to diverse biological communities, it serves as a biogeochemical reactor for aquatic metabolism across river corridors (Gomez-Velez and Harvey 2014; Sackett et al. 2019). In fact, the hyporheic zone accounts for the majority of ecosystem metabolism in some aquatic systems

(e.g., Naegeli and Uehlinger 1997; Fulton et al. 2024). Although characterizing hyporheic metabolism is key for understanding river corridor biogeochemistry, high spatiotemporal heterogeneity and interacting environmental drivers in the HZ makes it difficult to develop predictive relationships for hyporheic metabolism at reach-to-basin scales (Buser-Young et al. 2023; Stegen et al. 2023; Tureçaia et al. 2023).

Allometry, or a power-law relationship between function and size, is a central theory of metabolism in ecology (e.g., Brown et al. 2004), and has been applied to understand how biogeochemical properties scale across freshwater and estuarine environments (Bertuzzo et al. 2017; Nidziko 2018). A recently introduced theoretical framework for an idealized watershed suggests ecosystem metabolism scales allometrically, meaning that cumulative metabolism of entire river networks relates predictably to cumulative watershed area via a power law (Wollheim et al. 2022). However, it remains unknown how, or even if this relationship is transferable to non-idealized cases (real watersheds), or if cumulative hyporheic metabolism exhibits equivalent allometric scaling behavior. Additionally, although we know that watershed characteristics relate to hyporheic metabolic processes, (Son et al. 2022a; Buser-Young et al. 2023), it is unknown how differences in watershed characteristics within or between watersheds might impact such scaling relationships.

We addressed this knowledge gap by asking two questions: 1) Does hyporheic respiration follow an allometric relationship to watershed area across reach-to-basin scales?, and 2) What ecosystem properties relate to any observed differences in allometry? We used previously modeled reach-scale hyporheic respiration for more than 16,000 individual reaches in two river basins to calculate allometric relationships between cumulative hyporheic aerobic respiration and cumulative watershed area. We then explored allometric relationships in the context of watershed characteristics to understand common patterns between our study basins. Finally, we identified next steps for developing a more generalizable understanding of the controls on hyporheic respiration allometry across basins.

2. Methods

2.1 Basin descriptions

We focused on the Willamette river basin (WRB) and the Yakima river basin (YRB), which are both part of the Columbia River watershed, located in the Pacific Northwest United States (Figure 1). The WRB in central Oregon covers an area of 29,636 km² with 9756 individual stream reaches, while the YRB in southeastern Washington state is approximately half the size (15,887 km²) and contains 6538 individual stream reaches (Figure 1). We selected these two basins because they differ in terms of biophysical characteristics (Fulton et al. 2024), including precipitation, topography, and land cover (Figure S1).

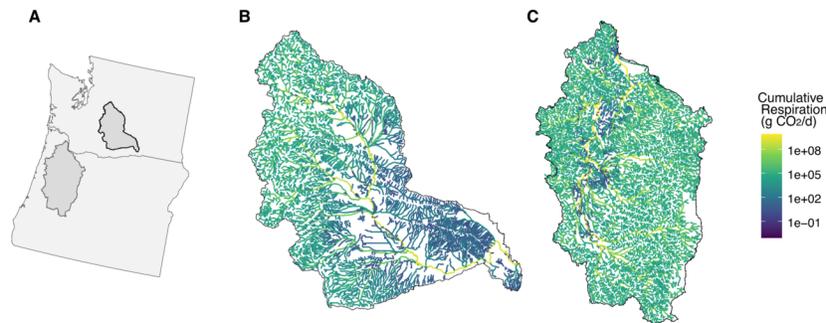


Figure 1 : A) Locations of the Yakima and Willamette river basins within the Pacific Northwest United States, and long-term cumulative network scale respiration at each reach across B) the YRB and C) the WRB.

2.2 Modeling hyporheic respiration

We used previously published modeled estimates for aerobic respiration in the hyporheic zone at the scale of NHDPLUS reaches within the two study basins using the River Corridor Model (RCM) presented in (Son et al. 2022b). The model computes at hourly timesteps, using reactions, rate formulations and kinetic rate parameters described in (Fang et al. 2020). Key model inputs for each reach include hyporheic exchange fluxes (HEF) and hyporheic residence times estimated by the Networks with Exchange and Subsurface Storage (NEXSS) model (Gomez-Velez and Harvey 2014), and long-term (~ 10 year) average stream solute concentrations (dissolved organic carbon, dissolved oxygen, and nitrate) estimated from available observations. We gap-filled missing HEF and residence time values for $\sim 13\%$ of reaches, using a eXtreme Gradient Boosting (XGBoost, v1.5.0.2) machine learning model (Chen and He 2023) ingesting topography variables (watershed/catchment area, maximum/mean/minimum elevation), hydrology (mean annual streamflow/runoff/velocity and mean annual precipitation), and stream geometry (slope, width and length, sinuosity, bankfull depth, median particle size, roughness, total stream length) with high accuracy ($R^2 > 0.94$). Detailed descriptions of the stream solute input data and our XGBoost approach are included in Supplemental Information.

2.3 Allometric scaling relationships

Prior to calculating allometric scaling relationships, we calculated cumulative values for respiration and HEFs as the sum of all reaches upstream of a given reach (and inclusive of the reach), as visualized for a watershed in Figure S2. We calculated allometric scaling relationships as cumulative hyporheic aerobic respiration ($\text{g CO}_2 \text{ d}^{-1}$) against watershed area (km^2) following Wollheim et al. (2022). First, we grouped reaches in each basin into 10 equally sized quantiles based on cumulative HEF, which is an important control of hyporheic respiration (Son et al. 2022). Within each quantile, a random subset of 50 reaches representing the range of stream orders was selected via bootstrapping and used to calculate slope, intercept, and R^2 values for the relationship between cumulative respiration and watershed area. This process was then iterated 1000 times for each combination of bin and basin to calculate average values and confidence intervals for slope, intercept, and R^2 values.

2.4 Statistics

We categorized the scaling behavior of relationships between cumulative hyporheic respiration and watershed area for each combination of HEF bin and basin ($n = 20$) into four allometric classes: Uncertain, Sublinear, Linear, and Super-linear. We visually identified an R^2 threshold of 0.8 where values exhibit a “knee” (Figure S3A), which we interpret as weak or no allometric scaling. Relationships with mean R^2 values < 0.8 were classified as “Uncertain”. To classify allometric behavior for relationships with R^2 values ≥ 0.8 , we used 2.5% and 97.5% confidence intervals ($CI_{2.5}$ and $CI_{97.5}$) of slope values as follows: “Linear” for $CI_{2.5} < 1$ and $CI_{97.5} > 1$, “Sublinear” for $CI_{2.5} < 1$ and $CI_{97.5} < 1$, and “Super-linear” for $CI_{2.5} > 1$ and $CI_{97.5} > 1$ (Figure S3C). We capitalize these terms throughout the rest of this study to clarify when we are referring to these definitions.

To reveal watershed features explaining variation in the spatial distributions of hyporheic respiration across each basin, we used mutual information analysis, which calculates the dependency between two variables based on Shannon’s entropy. Mutual information analysis was conducted with the *infotheo* R package (Meyer 2022), where each variable was first discretized, then calculated mutual information was normalized to the maximum information within each analysis. For statistical tests with significance values, we used a p-threshold of 0.05. All analyses were performed in R (R Core Team 2023) or Python 3.

3. Results

3.1 Allometric scaling of aerobic respiration by hyporheic exchange flux quantiles

We observed allometric scaling in both basins, particularly for higher HEF quantiles (Figure 2, Figure S3). However, we also observed a range of behaviors in the strength (R^2 values) and slopes of cumulative allometric scaling patterns across the study basins. For lowest HEF quantiles (Q10-Q30) we observed lower mean R^2 values ($R^2 < 0.80$) consistently across basins, indicating weaker (“Uncertain”) allometric scaling

behavior (Figure 2, Figure S3). Conversely, mean R^2 values for Q40-100 were consistently higher than the 0.80 threshold across both basins, indicating stronger allometric scaling relationships (Figure 2, Figure S3). For Q40-100, we observed increasing trends in slopes, with consistent Super-linear scaling at highest quantiles (Q80-100) in both basins. For the WRB, scaling shifted from Linear (Q40-Q50) to Super-linear (Q60-Q100), while in the YRB, scaling shifted from Sublinear (Q40-Q60) to Linear (Q70) to Super-linear (Q80-100) (Figure S3). We also fitted single regression lines to each basin as a whole, independent of HEF (Figure S4). Based on our R^2 threshold of 0.8, both basins exhibited Uncertain scaling behavior, though we note that both slopes are well above 1 (3.2 and 1.9 for WRB and YRB, respectively).

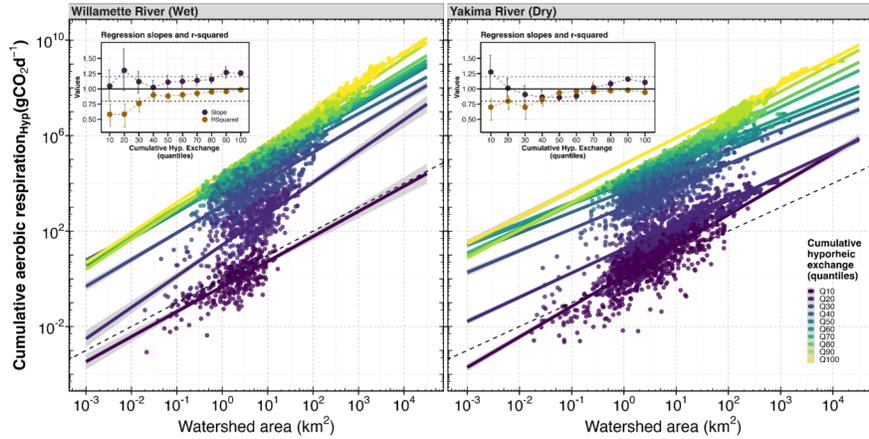


Figure 2 : Allometric scaling of log-transformed cumulative aerobic respiration with log-transformed cumulative watershed area for all reaches in A) the Willamette river basin (WRB) and B) the Yakima river basin (YRB). Colored lines show least-squares regression lines for each HEF quantile. Dashed lines represent a 1:1 relationship corresponding with linear scaling. Inset plots show mean (points) and ranges (whiskers) for best-fit line slopes and R^2 values by HEF quantile.

3.2 Spatial patterns of scaling across basins

In contrast to relatively similar scaling relationships by HEF quantile observed in Figure 2, spatial arrangement of scaling behaviors differed notably between the two study basins (Figure 3). Uncertain relationships predominantly occurred for smaller stream reaches (with less cumulative HEF) in the lower-elevation portions of each catchment (Figure 3, Figure S1), and was more widespread across the majority of the YRB, but largely present near the main stem in the WRB (Figure 3). No Sublinear scaling was observed in WRB, while reaches with Sublinear scaling in the YRB were primarily located in the higher-elevation headwaters (Figure S1). Linear scaling in the YRB was limited to higher-elevation reaches, but distributed fairly widely across the WRB (Figure 3). Super-linear scaling occurred primarily along the main stem in YRB, but largely in the forested headwaters in WRB (Figure 3). Across each basin, the WRB transitioned from Super-linear in headwaters through Linear into Uncertain for tributaries near the main-stem, while the YRB transitioned from a mix of Super-linear, Linear, and Sublinear to Uncertain, and both main-stems were consistently Super-linear.

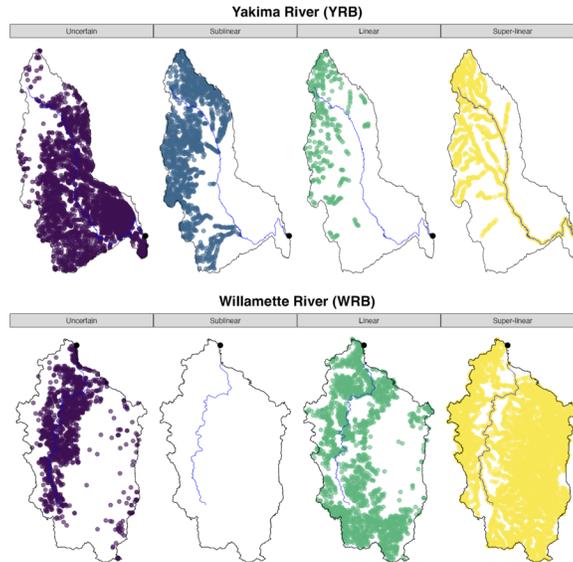


Figure 3 Spatial distributions of relationships in Figure 2 across the two study basins. The main stems of the Yakima and Willamette rivers are shown as blue lines, and the outlet of each basin is marked with a black point.

3.3 Relating allometric behavior to watershed characteristics

We calculated mutual information to understand which watershed characteristics in Figure S1 (elevation, precipitation, and land-cover) share the most information with cumulative respiration (Figure 4). We selected HEF quantile groupings with consistent scaling behavior between basins (Q10-30: Uncertain, and Q80-100: Super-linear) to assess whether basin or scaling had more consistent relationships to respiration. Maximum elevation consistently shared the most information with cumulative respiration (i.e., shared the strongest spatial relationship with respiration as quantified by mutual information) for Uncertain (Q10-Q30) quantiles in both basins, followed by forested land-cover (Figure 4). Precipitation shared the most information with cumulative respiration for Super-linear Q80-100) quantiles in both basins, followed by maximum elevation in the WRB, and human-influenced land-cover in the YRB. The consistency in highest mutual information between HEF quantiles (maximum elevation for Q10-30 and precipitation for Q80-100) indicates these factors may share similar relationships to allometric scaling patterns in the two study basins, which suggests the potential to generalize these relationships to other basins.

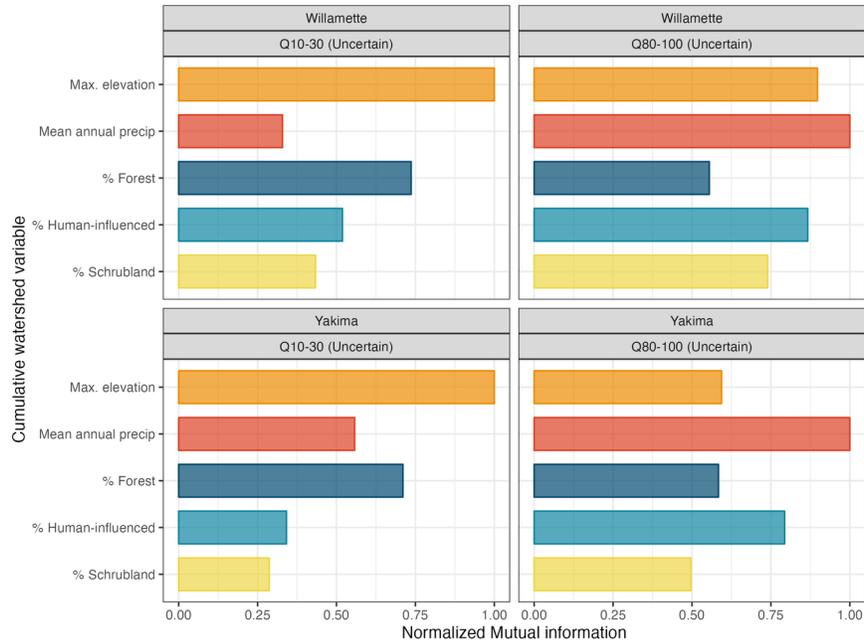


Figure 4: Mutual information between cumulative hyporheic respiration and watershed characteristics. We include Q10-30 as HEF quantiles that were consistently Uncertain in both basins and Q80-100 as quantiles that were consistently Super-linear in both basins. Mutual information values were normalized to the maximum value for each analysis.

As a first step towards generalizing scaling behavior, we plotted the relationship between maximum elevation, precipitation, and cumulative respiration within the context of scaling (Figure 5). Both basins showed significant ($p < 0.0001$) positive relationships between maximum elevation and cumulative respiration ($R^2 = 0.48$ for WRB and 0.68 for YRB, with a relatively consistent transition from Uncertain scaling behavior at lower respiration and maximum elevation values to Linear then Super-linear with increasing respiration and maximum elevation (Figure 5). This is expected, as maximum elevation positively correlates to watershed area (R^2 values of 0.19 and 0.20 for WRB and YRB respectively, Figure S5). We did observe some non-linear behavior in WRB, where reaches with the lowest maximum elevation had a much steeper relationship (higher slope) compared to reaches with higher maximum elevations (Figure 5). In contrast, the YRB showed remarkably consistent linear behavior across the full elevation range with no apparent breakpoint in the relationship. For both basins, we observed a divide along the elevation axis for Uncertain reaches between lower-precipitation and higher-precipitation values. In the YRB in particular, drier reaches generally fall close to the best-fit line, while wetter reaches consistently diverge from the dominant linear pattern.

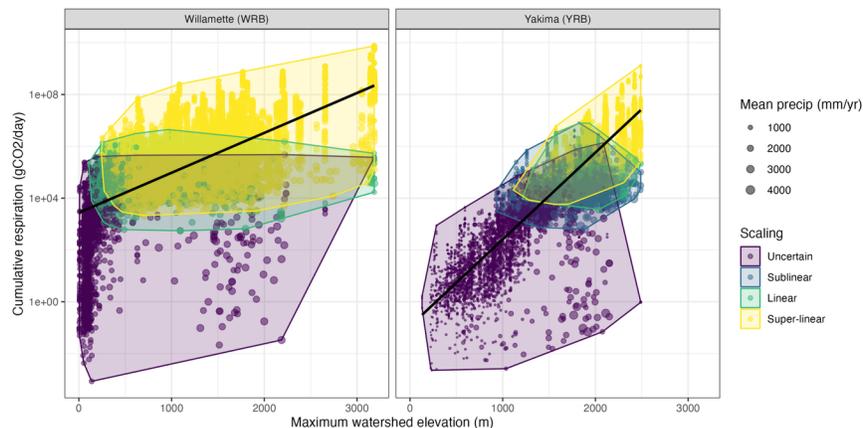


Figure 5 : Relationships between cumulative respiration and maximum watershed elevation for the A) WRB and B) YRB. Each reach is color-coded based on scaling as described above, and the size of each point corresponds to mean annual precipitation.

4. Discussion

To the authors' knowledge, this study presents the first basin-scale analysis of allometric scaling of hyporheic respiration. Our analysis demonstrates considerable variability in scaling relationships, both within and across the study basins, but also suggests some common responses, which provides initial evidence that some aspects of hyporheic respiration allometry may generalize across basins. Below, we discuss where we found consistent relationships, where we did not, potential connections to watershed characteristics, limitations of our approach, and future research directions.

4.1 Hydrologic exchange fluxes organize hyporheic respiration allometry

We found two consistent patterns in allometric relationships across the study basins where 1) scaling was consistently weakest (Uncertain) for lowest HEF quantiles, and 2) scaling was consistently strong (high R^2) and Super-linear at highest HEF quantiles (Figure 2). Because HEFs regulate carbon and nutrient delivery to the hyporheic zone and residence times, which in turn influence respiration (Krause et al. 2022), consistency in the relationship between cumulative respiration and cumulative HEF is expected. Reaches with Uncertain scaling relationships were largely clustered in the lower elevation headwater portions of each watershed (Figure 3, Figure S1), which is likely linked to weaker vertical hydrologic connectivity between surface water and the hyporheic zone. Lower water velocities may result in higher heterogeneity in subsurface biogeochemistry, including redox (Briggs et al. 2013), resulting in more variable (and therefore weaker) allometric behavior. Conversely, strong, Super-linear scaling at highest cumulative HEFs is consistent with previous observations that HEFs control biogeochemical processes in the hyporheic zone, including denitrification (Son et al. 2022a).

We observed differences in scaling patterns between the YRB and WRB for middle HEF quantiles, which may indicate that basin-specific characteristics limit our ability to effectively predict respiration scaling behavior for these portions of the basin. Specifically, we suggest that, at lower HEF quantiles, hyporheic respiration is transport-limited where movement of carbon, nutrients, and oxygen between surface and subsurface is the limiting factor, but also highly variable. In contrast, at highest HEF quantiles, hyporheic respiration is reaction-limited because of high exchange fluxes between the surface and subsurface. This is consistent with observations from surface water biogeochemistry that watersheds are generally transport-limited for smaller watershed areas and transition to reaction-limited as watershed area grows (Liu et al. 2022), and likely also varies in time, where baseflow conditions are more transport-limited while quickflow conditions are more reaction-limited (Raymond et al. 2016; Wollheim et al. 2022).

4.2 Generalizability of relationships between allometry and watershed characteristics

Consistent with findings in Figure 2, the spatial distribution of allometric scaling of hyporheic respiration (Figure 3) and its relationships to various watershed characteristics (Figure 4, Figure 5) suggest some common patterns between the study basins, which may generalize to other basins, but also identify several basin-specific behaviors. Specifically, maximum elevation shared the most mutual information with cumulative respiration for low-HEF reaches (Figure 4), with relatively strong linear relationships in both basins (Figure 5). This finding matches previous reports that elevation organizes biogeochemical processes related to metabolism in other watersheds, including greenhouse gas concentrations and ratios, and oxygen content (Chiriboga and Borges 2023). We also observed consistent relationships to precipitation for high HEF quantiles, consistent with other findings that precipitation influences hyporheic processes, including respiration (Leggieri et al. 2013; Son et al. 2022b; Coulson et al. 2022).

Although it is beyond the scope of this study, we suggest that common responses to general watershed characteristics like elevation and precipitation may also organize hyporheic respiration scaling in other river basins. However, we also note that there are distinct differences in respiration allometry between the study basins, notably in spatial patterns (Figure 3). Thus, while the relationships we observed in our two basins may be transferable to others, basin-specific patterns may limit our ability to generalize a predictive understanding of hyporheic respiration allometry to other basins.

4.3 Study limitations

Our estimates of hyporheic respiration allometry are based on a largely mechanistic model which incorporates numerous assumptions. We also note that our approach simplifies some important, yet complex, watershed characteristics that influence hyporheic respiration. First, our cumulative respiration rates are time-averaged, and likely smooth over hot moments of respiration within different portions of the basin, or potentially across the entire basin. Additionally, we did not explicitly incorporate stream intermittency, which can dramatically alter how nutrients and associated biogeochemical processes like respiration change not only across space but through time (Newcomer et al. 2018; Coulson et al. 2022). Together, integration of spatial and temporal information, and explicitly investigating the role of variable inundation on disconnecting and reconnecting portions of the watershed will lead to a more realistic representation of watershed biogeochemistry, and more accurate predictions of allometric scaling of hyporheic respiration across spatial and temporal scales under shifting climate regimes.

4.4 Future research directions

Ground-truthing model outputs by collecting samples or deploying sensors in every reach is logistically impossible even for a small sub-catchment. Our RCM approach already incorporates a model-experiment (Modex) loop (Serbin et al. 2021), where laboratory measurements of sediments collected within the Columbia River Basin were used to parameterize biogeochemical rates in the model. We suggest implementing a subsequent ModEx loop, where our allometry estimates can identify sub-catchments that may function as biogeochemical control points (*sensu* Bernhardt et al. 2017). For instance, by examining residuals in Figure 2 for each regression line fit, we could iteratively identify which reaches adhered most poorly to scaling relationships (where the largest positive residuals represent respiration hot spots) and target field sampling campaigns to confirm whether outliers are due to high respiration or heterogeneity poorly captured by the model.

Predictions of how hyporheic respiration allometrically scales across watersheds that can generalize between basins will dramatically improve our ability to model and therefore forecast how biogeochemical processes influencing, and influenced by, aquatic metabolism will respond to natural or anthropogenic changes in watershed dynamics. Our findings present an initial attempt to characterize how hyporheic respiration scales allometrically with watershed area across two environmentally distinct basins. We found that, while some commonalities exist in allometric scaling patterns and relationships to watershed characteristics, particularly precipitation and elevation, basin-specific patterns suggest that the factors driving hyporheic respiration scaling require additional study. We suggest future studies incorporate a larger number of study basins to more effectively assess generalizability of patterns and relationships to watershed characteristics.

Further, incorporation of key disturbances, including non-perenniality, wildfires, and urbanization, whose downstream impacts increasingly influence, and are influenced by, surface and hyporheic biogeochemical processes (Lawrence et al. 2013; Zhao et al. 2021; Ball et al. 2021; DelVecchia et al. 2022), will improve our ability to model the hyporheic zone and more accurately represent river corridor function in earth system models.

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