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Key Points:

- Heterogeneity across river basins makes it difficult to generate predictive relationships for biogeochemical functions
- We used reach-scale modeled estimates to evaluate allometric scaling patterns of hyporheic respiration across two distinct river basins
- Relatively consistent relationships of scaling patterns to hydrologic exchange fluxes and elevation may generalize to other basins

Supporting Information:

Supporting Information may be found in the online version of this article.

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Allometric Scaling of Hyporheic Respiration Across Basins in the Pacific Northwest United States

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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 for understanding cumulative hyporheic biogeochemical processes. We used previously published model predictions of reach-scale hyporheic aerobic respiration to explore patterns in allometric scaling across two climatically divergent basins with differing characteristics in the Pacific Northwest, United States. In the model, hydrologic exchange fluxes (HEFs) regulate hyporheic respiration, so we examined how HEFs might influence allometric scaling of respiration. We found consistent scaling behaviors where HEFs were either very low or very high, but differences between basins when HEFs were moderate. Our findings provide initial model-generated hypotheses for factors influencing allometric scaling of hyporheic respiration. These hypotheses can be used to optimize new data generation efforts aimed at developing predictive understanding of allometries that can, in turn, be used to scale biogeochemical dynamics across watersheds.

Plain Language Summary Hyporheic zones (HZs) in rivers and streams (where surface water and groundwater meet) play important roles in processes that affect water quality. HZs are complex and vary in space and time, making it hard to predict their total impact on river basins. Recent research using allometric scaling (how function changes with size) offers a new way to understand HZ processes across watersheds. We used modeled predictions for HZ respiration (biological organic carbon consumption) to study how factors like surface/groundwater exchange impact allometric scaling of HZ respiration across two river basins. We found that HZ respiration scaling patterns were similar when surface/groundwater exchange flow was either very low or very high but differed at moderate levels between watersheds. We also explored how elevation is related to scaling patterns. Our results suggest new ideas about what affects these patterns, which can guide future data collection to better predict water quality changes in rivers.

1. 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 zone (Bernhardt et al., 2017; Gomez-Velez & Harvey, 2014; Lee-Cullin et al., 2018; McClain et al., 2003). Because the HZ regulates nutrient exchange/processing and provides habitat to diverse biological communities, it serves as a biogeochemical reactor for aquatic metabolism along river corridors (Gomez-Velez & Harvey, 2014; Sackett et al., 2019). In fact, the HZ accounts for the majority of ecosystem metabolism in some aquatic systems (e.g., Naegeli & Uehlinger, 1997). Although characterizing hyporheic metabolism is key for understanding river corridor biogeochemistry, high spatiotemporal heterogeneity and interacting environmental drivers make it difficult to develop predictive relationships for hyporheic metabolism at reach-to-basin scales (Buser-Young et al., 2023; Stegen et al., 2023; Tureţcaia et al., 2023).

Previous research suggests that local biogeochemical processes, including metabolism, may scale predictably with the watershed area (e.g., Finlay, 2011). Allometry, defined as a power-law relationship between function and size, is a central theory of metabolism in ecology (Brown et al., 2004) and one potential framework for understanding scaling of biogeochemical processes across freshwater and estuarine environments (Bassani et al., 2024; Bertuzzo et al., 2017; Nidzieko, 2018). Recently, allometric scaling was adapted to aquatic biogeochemistry via a theoretical framework for an idealized watershed (i.e., theoretical network channels) suggesting that cumulative

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metabolism of entire river networks relates predictably to the cumulative watershed area via a power law (Wollheim et al., 2022). The ability to predict how biogeochemical processes organize across a river network could provide powerful insight into how watersheds respond to disturbances, and how they can be optimized to mitigate pollution and protect water security.

However, exploring allometry of hyporheic processes like respiration via measurements across larger scales (e.g., a river basin) poses several challenges. First, it is logistically prohibitive to directly measure respiration across all reaches of any watershed, which would require deployment, maintenance, and analysis of as many sensor packages as there are reaches. Second, parsing the contribution of the hyporheic zone to respiration remains a challenge requiring either complex sensor deployments, benthic chambers, or laboratory incubations, all of which have limitations. Third, how allometric scaling approaches like Wollheim et al. (2022) who use idealized watersheds (i.e., a synthetic river network) transfer to nonidealized cases (actual river networks), or if such power-law relationships extend to the HZ, remains unknown. Finally, although we know that watershed characteristics relate to hyporheic metabolic processes (Buser-Young et al., 2023), it is unknown how differences in watershed characteristics within or between watersheds might impact allometric scaling relationships.

A fundamental yet unanswered question is what features of real river networks influence allometric scaling in the HZ. To generate initial hypotheses that can be used to answer this question, we use model-predicted hyporheic respiration rates that account for heterogeneity in watershed characteristics to evaluate variation in allometric scaling of HZ respiration across two climatically divergent basins. For modeling predicted rates, we use the recently developed river corridor model (Fang et al., 2020), which provides HZ respiration for each reach in the two study basins (Son et al., 2022). Using model predictions for more than 16,000 reaches, we calculated allometric relationships between cumulative HZ aerobic respiration and the cumulative watershed area. Because HZ respiration in the model is governed primarily by hydrologic exchange fluxes (HEFs) between the water column and the HZ (Son et al., 2022), we examined how HEFs relate to HZ respiration allometry. We also explored other environmental variables that may influence allometric scaling, with the aim of providing model-generated hypotheses for drivers of variation in HZ respiration allometry. While our analyses are limited to predictions from the river corridor model, the outcomes are nonetheless useful as they provide clear targets for future measurement efforts.

2. Materials and 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 basin, located in the Pacific Northwest United States (Figure 1). The WRB in Central Oregon covers an area of 29,636 km^2 with 9,756 individual stream reaches, while the YRB in the southern Washington state is approximately half the size (15,887 km^2) and contains 6,538 individual stream reaches (Figure 1).

We selected these two basins because they differ in terms of biophysical characteristics, including precipitation, topography, and land cover (Figure 1) and have existing estimates for hyporheic respiration (Son et al., 2022). The YRB has a higher average elevation across the watershed (822 m compared to 498 m), while the WRB is considerably wetter, with average precipitation of 1,597 mm/yr compared to 738 mm/yr in the YRB. These differences translate into generally shorter residence times in the WRB (average of 4.5 d compared to 7.7 d in the YRB), which corresponds to approximately double the average rate for hyporheic exchange across the WRB watershed (mean: 2.2e^{-4} m/s, min: 1.2e^{-10} m/s, and max: 4.7e^{-3} m/s) relative to the YRB watershed (mean: 1.2e^{-4} m/s, min: 4.0e^{-10} m/s, and max: 4.4e^{-3} m/s). The average for cumulative hyporheic respiration rates across the WRB (1.2e^{8} g CO_2/d) was approximately double the average across the YRB (5.2e^{7} g CO_2/d), though we observed a wider range of values in the WRB (min: 8.5e^{-4} g CO_2/d and max: 7.5e^{9} g CO_2/d) than the YRB (min: 2.3e^{-3} g CO_2/d and max: 1.3e^{9} g CO_2/d).

2.2. Modeling Hyporheic Respiration

Predicted aerobic respiration in the HZ at the scale of National Hydrography Dataset Plus (NHDPlus) reaches (Schwarz et al., 2018) within the two study basins was estimated by the river corridor model (RCM). These predictions were originally presented in Son et al. (2022) and a flowchart of models and outputs is shown graphically in Figure S1 of Supporting Information S1. The model computes respiration at hourly time steps,

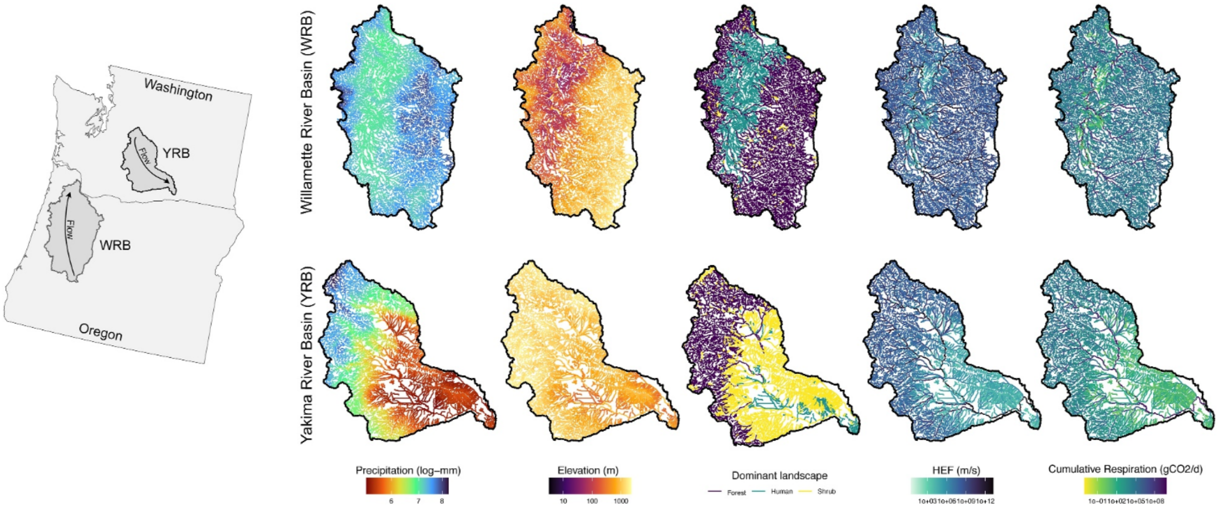

Figure 1. Basin properties for the WRB (top row) and the YRB (bottom row) for (left to right) precipitation, elevation, dominant land cover, and cumulative hydrologic exchange flux (HEF) values from the NEXSS model and long-term cumulative network scale respiration at each reach from the RCM model. Basin locations along with direction of flow within each basin are presented on the left.

using reactions, rate formulations, and kinetic rate parameters described in Fang et al. (2020). Key model inputs for each reach include hyporheic exchange fluxes (HEFs) and hyporheic residence times estimated by the Networks with Exchange and Subsurface Storage (NEXSS) model (Gomez-Velez & Harvey, 2014), and long-term (∼10 years) average stream solute concentrations (dissolved organic carbon, dissolved oxygen, and nitrate) estimated from available observations. The model was trained using USGS sites from across the Columbia River basin, including 38 sites for dissolved oxygen (using 4,470 measurements), 50 sites for dissolved organic carbon (4,842 measurements), and 64 sites for nitrate (3,070 measurements). Dissolved organic carbon is the only carbon source for HZ respiration represented in the model.

Stream dissolved organic carbon and dissolved oxygen concentrations were estimated by an empirical regression model trained on available concentrations for the study area using watershed variables such as fraction of land use, soil properties, and watershed topography variables (Schwarz et al., 2018; Son et al., 2022). Stream nitrate concentrations were derived from the SPAtially Referenced Regressions on Watershed (SPARROW) attributes model output (Wise, 2019). A detailed description of how the substrate concentrations were estimated can be found in Son et al. (2022). The key input data of the model are constant over time and represent long-term averaged values. As a result, the findings in this study present long-term annual average estimates for each NHDPlus reach, when the reactions reach dynamic equilibrium. The aerobic respiration in lateral and vertical HZs are computed independently, and respiration in each reach is the sum of the respiration from these two HZs.

We gap-filled missing vertical/lateral water exchange flux and residence time values for ∼13% of reaches using an eXtreme Gradient Boosting (XGBoost, v1.5.0.2) machine learning model (Chen & Guestrin, 2016). The XGBoost model ingested topography variables (watershed/catchment area and maximum/mean/minimum elevation), hydrology (mean annual streamflow, runoff, velocity, and precipitation), and stream geometry (slope, width, length, sinuosity, bankfull depth, median particle size, roughness, and total stream length). Here, the watershed area refers to the cumulative area draining into the considered reach and all tributaries while catchment area refers to the drainage area associated with the individual reach. We used 80% of data to train the XGBoost model, and 20% of data were used to test the model predictions. Overall, all models showed high accuracy ($R^2 > 0.94$). Important variables were included for vertical exchange flux (median grain size (D50), mean annual flow velocity, stream roughness, and stream slope), lateral exchange flux (D50, stream slope and sinuosity, and mean annual flow velocity), vertical residence time (D50, stream slope and length, and mean annual precipitation), and lateral residence time (D50, stream slope and length, and mean annual runoff).

The RCM used by Son et al. (2022) to produce the hyporheic respiration estimates used in our analysis does have some limitations, which are important to keep in mind when interpreting our results. First, the primary inputs to the model (exchange fluxes, residence times, and solute concentrations) are input as annual means, meaning that variance through time (seasonality, hot moments, etc.) are not represented in model outputs. Second, reaches are treated as batch reactors within the model, meaning there is no interaction between upstream and downstream reaches. Therefore, while we can estimate allometric scaling by summing reaches along a flow path (Figure S2 in Supporting Information S1), our estimates do not directly account for autochthonous processes including organic matter decomposition in upstream reaches prior to entering a given reach. Additionally, there is uncertainty associated with any modeling effort, which was explored for solutes (DO, DOC, and NO3) via sensitivity analyses for seasonal impacts—see Table 3 in Son et al. (2022)—and changes in concentrations—see Figure 10 in Son et al. (2022). Briefly, seasonal changes in the WRB and the YRB were on the order of 10%, while changes in solute concentrations were on the order of 5% or less. Finally, we note that heterogeneity in characteristics and processes across river basins makes it impossible to fully capture all relevant dynamics. Instead, this modeling approach prioritizes incorporating heterogeneity of model inputs at reach-scale resolution whenever either data or estimates are available to incorporate as much heterogeneity as possible into our modeled estimates.

Additionally, there are some assumptions made in our modeling approach that are important to keep in mind. First, this is a modeling study, and we are not ground truthing modeled estimates of cumulative hyporheic respiration with in situ data. Instead, we intend that this modeling approach will be a useful first step for generating hypotheses about allometric behavior and controls across watersheds, which can be tested using sensors and sampling to collect information on respiration in the HZ (e.g., Kaufman et al., 2024). Second, hydrology and biogeochemistry are model inputs, and therefore may be spuriously correlated to patterns in respiration. We therefore limit our interpretation of relationships between allometric scaling patterns and watershed characteristics to guide future work rather than inferring any causality or mechanism. Specifically, we explored the relationship to elevation, which is an input to modeling reach-scale HZ respiration, and we interpret this relationship as a potential common metric for relating scaling patterns across basins.

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 (including the reach itself), as visualized for a reference watershed in Figure S2 of Supporting Information S1. We calculated allometric scaling relationships as cumulative hyporheic aerobic respiration (g CO_2 d^{-1}) against the watershed area (km^2) following Wollheim et al. (2022). We used HEFs to group reaches in each basin into 10 equally sized quantiles based on cumulative HEF. We grouped reaches by cumulative HEFs because HEFs were previously shown to relate to spatial variation in hyporheic respiration (Son et al., 2022), and grouping provides a convenient way to assess allometric relationships for hydrologically similar portions of the two study basins.

We categorized the scaling behavior of relationships between cumulative hyporheic respiration and the watershed area for each combination of an HEF bin and a basin ($n = 20$) into four allometry classes: Uncertain, Sublinear, Linear, and Super-linear. We used these classes for two primary reasons. First, weak relationships lead to uncertain slope estimates that could lead to spurious inferences and indicate where in the basin allometric scaling patterns might not work (which also provides a target for future work to understand why scaling behavior is not consistently occurring). Second, Wollheim et al. (2022) predict that allometric slopes are the outcome of down-network gradients in physical dimensions and reach-scale per area respiration rates. We envision that spatial organization of physical and biological properties and processes across watersheds results in different typologies, and that these typologies may organize variation in HZ respiration allometry across the Sublinear to the Super-linear continuum. By binning allometry into categories, we can more easily evaluate how allometric behaviors are arranged across watersheds, and how they may relate to watershed characteristics.

We defined the allometry categories based on visual identification of an R^2 threshold of 0.8 where values exhibit a "knee" (Figure 3a). Relationships with mean R^2 values < 0.8 were classified as "Uncertain." This threshold is somewhat subjective, but we would not recommend using a lower threshold as there is too much uncertainty in the slope. 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 3a). We capitalize these terms throughout the rest of this study to clarify when we are referring to these definitions.

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 the watershed area. This process was then iterated 1,000 times for each combination of a bin and a basin to calculate average values and confidence intervals for slope, intercept, and R^2 values.

2.4. Statistics

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, and then calculated mutual information was normalized to the maximum information within each basin. All analyses were performed in *R* (R Core Team, 2023) or Python 3. For statistical tests with significance values, we used a p-threshold of 0.05.

3. Results

3.1. Allometric Scaling of Aerobic Respiration at the Basin Scale

To provide basin-scale context for patterns in allometric scaling of hyporheic respiration, we fit single regression lines to all values for each basin, independent of HEF (Figure S3 in Supporting Information S1). Goodness of fit was stronger in the WRB and closer to the R^2 threshold ($R^2 = 0.74$), while goodness of fit for the YRB was weaker ($R^2 = 0.60$). Based on our R^2 threshold of 0.8, scaling in both basins is classified as Uncertain. Slopes for both basins were well above 1 (1.6 and 1.8 for WRB and YRB, respectively). We note that these slopes are relatively similar, which initially suggests that there may be similar scaling patterns between basins, and these relationships would be classified as Super-linear if R^2 values were greater than 0.8. Y-intercepts were 3.2 and 1.9 for WRB and YRB, respectively. Two relatively distinct clusters can be seen in the YRB, which appear to have similar slopes, but different intercepts, which is discussed in the next section.

3.2. Allometric Scaling of Aerobic Respiration by Hyporheic Exchange Flux Quantiles

To understand how scaling relationships vary within basins, we divided reaches by their cumulative HEF as described in the methods and examined patterns across basins at finer spatial resolution (Figure 2). We also present the statistics relevant to the allometric scaling category (slope) and strength (R^2) as well as the *y*-intercept of the linear fit in Figure 3. We observed allometric scaling in both basins when divided by HEF, particularly for higher cumulative HEF quantiles (Figures 2 and 3). 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 (Figures 2 and 3). Conversely, mean R^2 values for Q40–100 were consistently higher than the 0.80 threshold across both basins, indicating stronger, interpretable allometric scaling relationships (Figures 2 and 3). 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 3).

Interestingly, and in contrast to both slopes and R^2 values, we observed remarkably similar patterns in y-intercepts between the two study basins (Figure 3c). Intercepts for Q10–Q30 (Uncertain) quantiles increased rapidly from less than 1 to close to 8, but increased much slower from Q40 to Q100. We note that intercepts represent constants because they are derived in log-log space and can be conceptualized as representing the magnitude of respiration in headwater catchments (i.e., in a 1-km^2 catchment, the *y*-intercept predicts respiration rates). Therefore, the larger change in values (more than an order of magnitude) than slopes (which represent that rate at which cumulative respiration increased with area) may represent a potential break point in the scaling behavior in both catchments. Under this interpretation, the predicted respiration of headwater reaches changes most rapidly from Q10 to Q30, but more slowly for higher HEF quantiles (Q40 and above).

Dividing basins by HEF quantiles also provides insight into the two distinct clusters visually identified in the YRB in Figure S3 of Supporting Information S1. Figure 2 shows that the lower intercept cluster is primarily

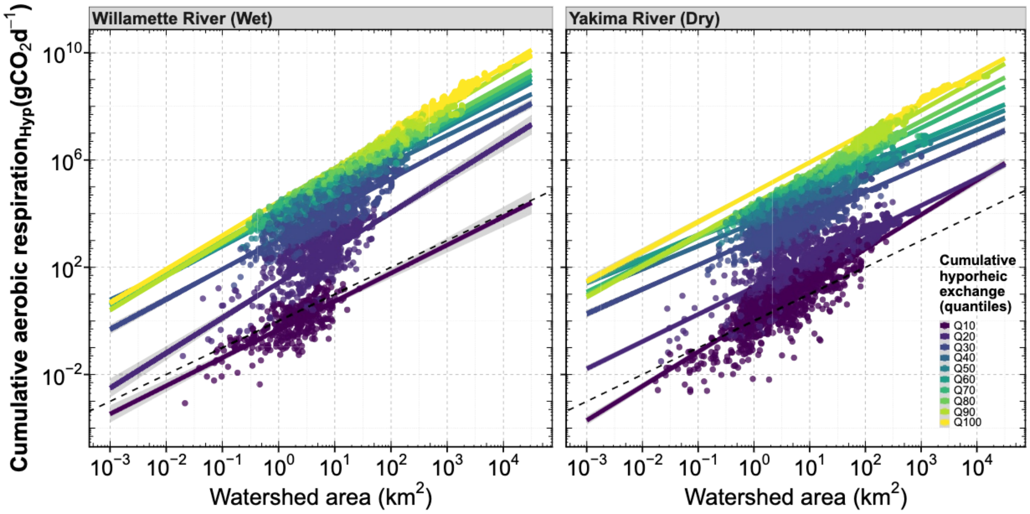

Figure 2. Allometric scaling of log-transformed cumulative aerobic respiration with log-transformed cumulative watershed area for all reaches in (a) the Willamette River basin (WRB) and (b) the Yakima River basin (YRB). Colored lines show least-squares regression lines for each HEF quantile. Dashed lines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

composed of the lowest HEF quantiles (Q10 and Q20), which likely contributes to the weaker basin-scale R^2 value for the YRB. We note that both Q10 and Q20 have considerably smaller y-intercepts (Figure 3b).

3.3. Spatial Patterns of Scaling Across Basins

In contrast to similar whole-basin allometric patterns (Figure S3 in Supporting Information S1) and relatively similar scaling relationships by HEF quantile observed in Figure 2, spatial arrangement of allometry classes differed notably between the two study basins (Figure 4). In the WRB, 1,556 reaches (16%) were Uncertain, 0 were Sublinear, 2,088 (21%) were Linear, and 6,112 (63%) were Super-linear. In the YRB, 3,333 reaches (51%) were Uncertain, 1,599 (24%) were Sublinear, 335 (5%) were Linear, and 1,271 (19%) were Super-linear. Uncertain relationships predominantly occurred for smaller stream reaches (with less cumulative HEF) in the lower

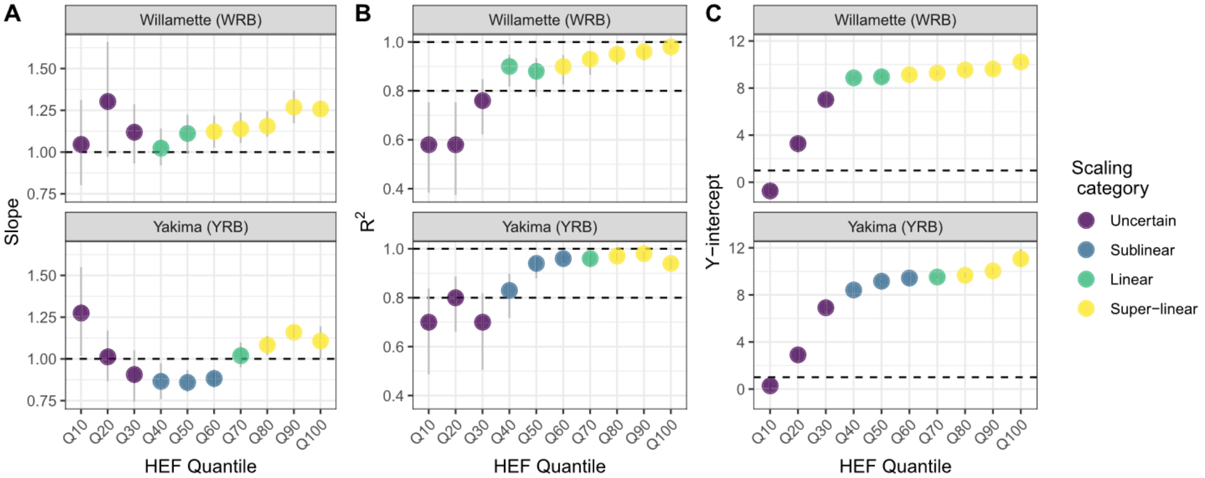

Figure 3. Scaling linear regression properties by the HEF quantile—(a) slope, (b) R^2, and (c) y-intercepts. Points represent mean values, and vertical bars represent 2.5% and 97.5% confidence intervals. Vertical bars for y-intercepts are present but in panel C, but are considerably smaller and therefore harder to see.

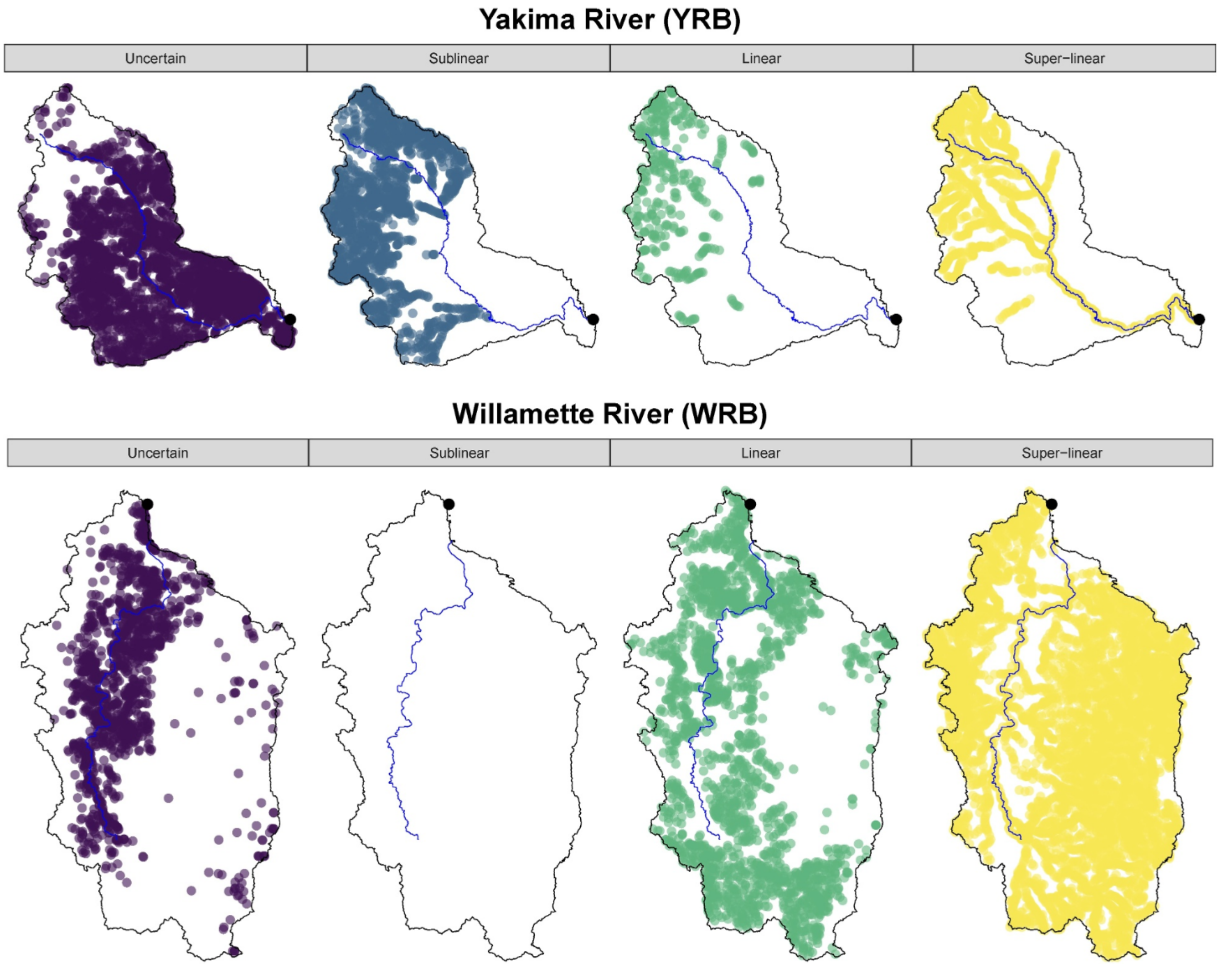

Figure 4. Spatial distributions of relationships in Figure 2 across the two study basins. The main stems of Yakima and Willamette rivers are shown as blue lines, and the outlet of each basin is marked with a black point.

elevation portions of each catchment (Figures 1 and 4, Figure S4 in Supporting Information S1), and was more widespread across the majority of the YRB, but largely present near the main stem in the WRB (Figure 4). No Sublinear scaling was observed in the WRB, while reaches with Sublinear scaling in the YRB were primarily located in the higher elevation headwaters (Figure 1). Linear scaling in the YRB was limited to higher elevation reaches, but distributed widely across the WRB (Figures 1 and 4). Super-linear scaling occurred primarily along the main stem in the YRB, but largely in the forested headwaters in the WRB (Figure 4). At the basin scale, 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.

As a first step toward exploring how scaling behavior might generalize across biophysical gradients in the study basins, we plotted the relationship between maximum elevation and cumulative respiration within the context of scaling (Figure 5). We selected maximum elevation as a parameter that is readily available for most watersheds (including ungauged watersheds), likely organizes key watershed characteristics like HEFs, appears to covary spatially with cumulative respiration (Figure 1), and, based on initial mutual information analysis, shares more information with respiration than land cover or precipitation in both basins (Figure S5 in Supporting Information S1). Both basins showed significant ($p < 0.0001$) positive relationships between maximum elevation and cumulative HZ respiration ($R^2 = 0.48$ for the WRB and 0.68 for the YRB), with a relatively consistent transition from Uncertain scaling behavior at lower HZ respiration/maximum elevation values to Linear and then Super-

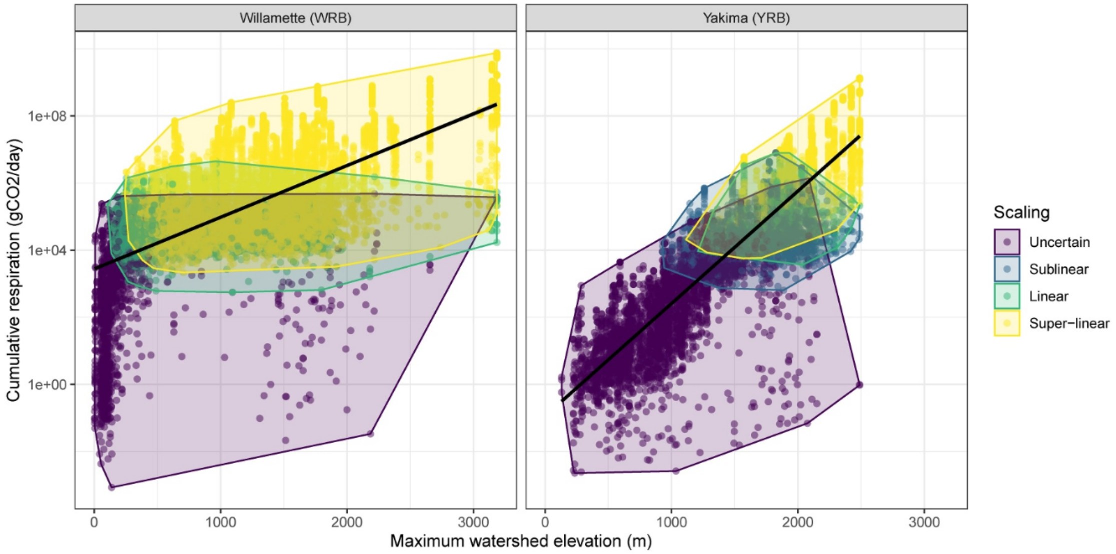

Figure 5. Relationships between cumulative respiration and maximum watershed elevation for the (a) WRB and (b) the YRB. Each reach is color-coded based on scaling as described above. The black line represents the linear best-fit line.

linear with higher HZ respiration/maximum elevation values (Figure 5). This is expected, as maximum elevation positively correlates to the watershed area (R^2 values of 0.19 and 0.20 for the WRB and the YRB respectively, Figure S6 in Supporting Information S1).

We did observe some nonlinear behavior in the WRB, where reaches with the lowest maximum elevation had a much steeper relationship (higher slope) than reaches with higher maximum elevations (Figure 5). In contrast, the YRB showed remarkably consistent linear behavior across the full elevation range with no apparent break point in the relationship.

4. Discussion

To the authors' knowledge, this study presents the first model-based analysis of fine-scale (reach-scale) allometric scaling of hyporheic respiration to entire river networks. Our results provide initial model-based evidence that some aspects of hyporheic respiration allometry may generalize across basins. We found some common patterns, including consistent Super-linear scaling at high HEFs, which matches findings by Wollheim et al. (2022) of consistent linear to superlinear relationships between whole-stream metabolism and the watershed area. However, we also observed considerable variability in scaling relationships for lower HEF portions of each basin (Figures 1–3). Together, these findings are consistent with previous observations that variability in function among smaller nested watersheds is high but increasingly averages out at the larger basin scale (e.g., Abbott et al., 2018). Below, we discuss where we found consistent relationships and a hypothesis they generate, potential connections to watershed characteristics, limitations of our approach, and future research directions.

4.1. Emergent Hypothesis: Hydrologic Exchange Fluxes Organize Hyporheic Respiration Allometry

We found two consistent patterns in allometric relationships across the study basins: (a) scaling was consistently weakest (Uncertain) for the lowest HEF quantiles, and (b) scaling was consistently strong (high R^2) and Super-linear at the highest HEF quantiles (Figure 2). At moderate HEFs, scaling patterns were variable between the YRB and the WRB (Figure 3). This indicates a continuum: low HEFs lead to a relatively unconstrained system, that is, high variability in metabolic function, that does not show strong allometry; moderate HEFs represent a transition in which allometric scaling patterns can be strong (i.e., high R^2) but remain highly variable in terms of slope; and high HEFs lead to a highly constrained system with strong allometries in which cumulative respiration increases faster than upstream area as smaller streams combine. Along with slopes, patterns in intercepts, which were remarkably consistent between the two basins (Figure 3c) suggest that high-HEF portions of the watershed have higher rates in the headwaters (larger intercepts), and rates accumulate more quickly down-network (higher slopes), potentially representing portions of the basins with more processing of organic matter into CO_2. This has significance for identifying not only potential biogeochemically significant control points (Bernhardt et al., 2017) within basins but also where CO_2 evasion to the atmosphere, an active area of research for constraining the global riverine carbon cycle (e.g., Horgby et al., 2019; Tian et al., 2023), is maximized. The suggestion of reduction in variation (i.e., increasing constraint) as smaller streams combine based on our modeling efforts is in agreement with previous empirical and theoretical studies (Abbott et al., 2018; Mallard et al., 2014; Zimmer et al., 2013). To help refine this hypothesis and guide future data generation, we explore reasons why such a continuum may arise below.

Based on our definition, Uncertain scaling is due to an R^2 value less than 0.8 between cumulative respiration and the watershed area. Thus, in portions of a given basin with Uncertain scaling, predicted respiration does not relate strongly to the size of the upstream drainage area. We suggest that the most likely cause of this is factors that lead to high levels of unstructured spatial heterogeneity in reach-scale HZ respiration rates. By "unstructured", we mean either spatial heterogeneity that does not follow a clear pattern moving down the stream network (i.e., no consistent slope or intercept down the network) or higher variability that masks any potential trend down the network. This type of heterogeneity could be related to physical position in the network. For instance, low HEF reaches with Uncertain scaling relationships were largely clustered in the lower elevation headwater portions of each watershed (Figures 1 and 4, Figure S4 in Supporting Information S1). These locations have slower water exchange between surface water and groundwater that can result in higher heterogeneity in subsurface biogeochemistry, including redox (Briggs et al., 2013), resulting in more variable (and therefore weaker) allometric behavior. We also observed that reaches draining lands that were >50% urban were primarily characterized by Uncertain scaling across both basins (Figure S7 in Supporting Information S1), which matches prior observations that the strength of the scaling relationship between ecosystem respiration and the watershed area was weaker for an urbanized system than a reference system (Finlay, 2011). We infer that HZ respiration rates in locations with low gradients, low velocities, and low HEFs can be influenced by spatially unstructured localized factors that effectively break the power-law behavior expected from an idealized watershed.

For middle HEF quantiles (Q40-Q70), high R^2 values indicated well-constrained allometric scaling behavior, but the difference in scaling patterns between the YRB (primarily Sublinear) and the WRB (Linear or Super-linear) suggests basin-specific characteristics may limit our ability to generalize scaling for moderate HEF reaches across basins (Figure 3, Figure S4 in Supporting Information S1). We suggest that, at lower HEF quantiles, hyporheic respiration is transport-limited where movement of carbon, nutrients, and oxygen between the surface and the subsurface is the limiting factor consistent with prior modeling studies (e.g., Stewart et al., 2011), but also highly variable as discussed above. We note that patterns for loads of dissolved organic carbon, the only carbon source for HZ respiration in our model, differ between basins for lowest HEF quantiles (Figure S8 in Supporting Information S1), which may help explain visual differences in whole-basin scaling relationships for lowest HEF quantiles (Figures 2 and 3). In contrast, at highest HEF quantiles, hyporheic respiration is reaction-limited because of high exchange fluxes between the surface and the 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 with surface discharge, where baseflow conditions in larger rivers are more transport-limited while storm flow conditions are more reaction-limited (Raymond et al., 2016; Wollheim et al., 2022). In this context, the middle HEF quantiles represent the portion of the watershed transitioning from reaction-limited to transport-limited under the mean annual flow conditions assumed in the model. Despite differences in scaling slopes, we note that reach-scale respiration rates at middle HEF quantiles consistently occupied a narrower range than low and high HEF quantiles in both basins (Figure S9 in Supporting Information S1). This pattern may be related to higher sediment respiration rates in middle stream orders (e.g., Buser-Young et al., 2023), transitions in resource partitioning (Vannote et al., 1980), or some other mechanism.

Strong, Super-linear scaling at highest cumulative HEFs is consistent with previous observations that HEFs influence biogeochemical processes in the HZ, including denitrification (Stewart et al., 2011). Because HEFs regulate carbon and nutrient delivery to the HZ and residence times, which in turn influence respiration (Krause et al., 2022), consistency in the relationship between cumulative respiration and cumulative hyporheic exchange for highest HEFs is expected. This pattern also aligns with theory presented by Wollheim et al. (2022) who observed consistent superlinear behavior, which was controlled by geomorphology, hydrology, and biology.

Based on our model-based analysis, we hypothesize that in areas of watersheds with low cumulative HEFs (generally smaller watersheds), spatial variation in HZ respiration is controlled primarily by variation in chemical (e.g., nutrients) and biological (e.g., microbial diversity) factors. These spatial domains are expected to exhibit inconsistent allometric scaling due to the lack of spatially structured drivers both within and among flow paths, as observed in Figure 2. For areas of watersheds with moderate HEFs, we also hypothesize more mixed control among physical, chemical, and biological factors that can lead to stronger, but basin-dependent, allometric scaling relationships. Finally, we hypothesize that in areas of watersheds with high HEFs (large watersheds), HZ respiration is controlled primarily by physical factors (i.e., hydrology), averaging out of the variability of numerous smaller nested flow paths with higher variability, similar to increasing chemostasis observed in other biogeochemical processes (Abbott et al., 2018; Creed et al., 2015). Because of strong down-network gradients in physical processes, high HEFs areas will exhibit consistently Super-linear allometric scaling relationships.

Together, these hypotheses suggest that field measurements to constrain drivers of HZ respiration may be most useful in areas with lower HEFs because spatial variation in respiration rates is less predictable from the physical watershed properties. These low-HEF areas may not exhibit clear allometry, thereby challenging our capacity to scale rates, and predict outcomes of perturbations. We propose it is these areas that need the most attention from in situ measurements and consideration of local processes that alter the chemical and biological environment. However, it is also important to note that large rivers contribute substantially to basin-scale respiration when Super-linear (Figure 2, Wollheim et al., 2022), and cannot be assumed to simply scale inputs up from smaller streams and rivers comprising their upstream watershed (Roley et al., 2023). Functionally, our allometric scaling groupings may infer where processing of carbon is occurring within the stream network. For example, in Super-linear areas of the watershed, HZ respiration may become increasingly important moving downstream where processing of carbon occurs primarily in larger-order downstream reaches. In contrast, in Sublinear areas, processing of carbon may occur primarily in the upstream reaches. Knowing where in a given stream network processing is primarily occurring could provide fundamental insights into watershed function, which is relevant across many contexts, including watershed responses to disturbance (drought, wildfire, and land use changes), and water security for the downstream users (both natural and human).

4.2. Exploring Generalizable Patterns Between Allometric Scaling and Elevation

Consistent with findings in Figure 2, the spatial distribution of allometric scaling of hyporheic respiration (Figure 4) and its relationships to various watershed characteristics (Figure 5) suggest some common patterns between the study basins, which may generalize to other basins. Specifically, maximum elevation showed stronger 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 & Borges, 2023).

Although it is beyond the scope of this study, we suggest that common responses to general watershed characteristics like precipitation and land use may also provide important information to understand allometric patterns. As an example of how watershed characteristics may relate similarly or differently to cumulative respiration between our two study basins, we conducted mutual information analysis for the three watershed characteristics presented in Figure 1: precipitation, elevation, and land cover (Figure S5 in Supporting Information S1). Mutual information was selected in preference to other parametric and nonparametric approaches because (a) it is considered somewhat robust to autocorrelation, which is prevalent in our data sets, and (b) it is generally not used to understand causality, which is an assumption we want to avoid as the watershed characteristics explored either indirectly or directly correlate to model inputs. Maximum elevation shared the most mutual information with cumulative hyporheic respiration (Figure S5 in Supporting Information S1) for both basins, supporting the suggestion that maximum elevation may therefore be a useful starting point for understanding transferable relationships between watershed characteristics and respiration.

However, we also note that there are distinct differences in respiration allometries between the study basins, notably in spatial patterns (Figure 4) and in the order of mutual information for precipitation and land cover (Figure S5 in Supporting Information S1). Thus, while the relationships we observed in our two basins maybe transferable to others, basin-specific patterns may limit our ability to generalize a predictive understanding of hyporheic respiration allometry to other basins. These results also suggest that capturing gradients in elevation and other watershed characteristics that organize drivers of HZ processes will be an important consideration for field measurements evaluating allometric scaling of HZ processes.

4.3. Study Limitations

Because it is logistically impossible to measure hyporheic respiration across a basin with the size of the YRB or the WRB (which would require simultaneous measurements (via sensors, chambers, or sampling) in all reaches), we relied on a modeling approach to estimate hyporheic respiration. As a first attempt to explore validation of modeled hyporheic respiration patterns with measured data, Figure S10 in Supporting Information S1 presents a linear regression between modeled rates for hyporheic respiration and sediment-associated respiration rates collected in laboratory incubations using sediments sourced from across the YRB for matching COMIDs, which are unique flowline identifiers (Forbes et al., 2023). We note that a strong relationship between laboratory incubations and model estimates should not be expected for several reasons. First, methods are mismatched in space and time: incubations are sampled at a single point at the SW-GW interface, while model estimates integrate an entire reach and annual timescales. Second, assumptions between the methods differ: for instance, the model does not account for primary production that is occurring alongside respiration in incubations. Finally, units are not directly comparable, where modeled estimates are reported in g CO_2 associated only with aerobic respiration, while incubations report consumption of oxygen. Thus, we conducted this validation to provide initial context for how two independent methods of estimating respiration were compared. Based on all available data ($n = 40$, Figure S10a in Supporting Information S1), there was no clear relationship between these parameters. However, when excluding outlier clusters, we observed a weak but significant linear relationship ($R^2 = 0.09$, $p = 0.03$, Figure S10b in Supporting Information S1). Despite the distinct differences in methods, these results may suggest that the model is capturing patterns that agree with laboratory data. The lack of data available to validate modeled respiration highlights the importance of collecting field data that can be more directly compared to our modeled outputs.

We 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 streamflow variability or intermittency, which can dramatically alter how nutrients and associated biogeochemical processes like respiration change not only across space but through time (Coulson et al., 2022; Newcomer et al., 2018). Finally, the soil type and texture are not explicitly included in our analyses but likely play a crucial role in regulating processes that control hyporheic respiration. In the RCM, for example, a key input parameter is D50, which is influenced by precipitation, elevation, channel slope, and other landscape characteristics (Gómez-Vélez et al., 2015). Previous studies (Abimbola et al., 2020; Jha et al., 2022) have also shown that D50 is a function of local and landscape-scale soil variability. As a result, both D50 and streambed hydraulic conductivity exhibit spatial variability depending on landscape features. We expect that this variability is implicitly captured in the model's parameterization. For instance, soil texture is implicitly included in computing HZ HEFs and residence times in the NEXSS model, which therefore influence our RCM HZ respiration estimates. While incorporating soil characteristics is beyond the scope of our study, future research integrating this information into the modeling framework could enhance process representation and improve our understanding of the drivers of hyporheic respiration across watersheds. 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

Our analysis is based solely on modeling, and future work involving field measurements will be needed to evaluate hypotheses and assess transferability of modeled allometry across broader environmental and climatic gradients. To investigate allometric scaling patterns of HZ respiration in a given watershed, we suggest selecting reaches capturing a wide range of cumulative watershed area and HEFs to effectively characterize end-members. Within those criteria, we suggest focusing measurements in lower stream orders with low HEFs, where our modeling found highest variability and lowest strength of the allometric scaling relationship (Figure 2, Figure S2 in Supporting Information S1). As an example, if 10 sites are selected in a watershed with stream orders 1–7, we suggest one site in each stream order, and additional 1st, 2nd, and 3rd order sites.

Reach-scale measurements of HZ respiration will require a combination of approaches. Laboratory incubations are effective for directly measuring HZ respiration across many different sampling locations, and allow for more control or manipulation over environmental conditions (von Schiller et al., 2019; Stegen et al., 2023; Tureţcaia et al., 2023), but isolate sediments from environmental variability. Estimating ecosystem respiration using in situ oxygen sensors (Hall & Hotchkiss, 2017) provides temporally resolved information about stream respiration, but generally do not directly measure respiration in the HZ (but see Vieweg et al., 2016). HZ activity can also be inferred from reactive tracers like resazurin (González-Pinzón et al., 2012; Haggerty et al., 2008), although these approaches require significant field efforts, and are subject to nonidealities including incomplete mass recovery (Dallan et al., 2020). Benthic chambers allow for in situ measurements of HZ respiration within the natural environment (Fellows et al., 2001), but are generally more labor-intensive than incubations or in situ sensors, limiting sample size. We suggest combining some or all of these approaches to balance direct measurements with higher sample size to effectively evaluate HZ respiration allometry across watersheds. Finally, we note the rise in popularity and availability of do-it-yourself sensing and sampling platforms that may improve our ability to more rapidly, accurately, and cost-effectively measure processes like HZ respiration to evaluate hypotheses generated by model-based studies (Brandt et al., 2017; González-Pinzón et al., 2019; Khandelwal et al., 2023).

The modeling approach used here 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 modeled allometry estimates can identify candidate subcatchments that may function as biogeochemical control points (sensu Bernhardt et al., 2017) to guide measurement campaigns. 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). These outliers represent reaches with higher HZ respiration than expected based on allometric scaling patterns. We suggest that targeting outlier reaches during field campaigns would be useful to confirm whether outliers are due to high respiration or some parameter that was not well parameterized in the model. Further, we suggest incorporating key disturbances, including nonperenniality, wildfires, reservoirs, and urbanization, whose downstream impacts increasingly influence, and are influenced by, surface and hyporheic biogeochemical processes (Ball et al., 2021; DelVecchia et al., 2022; Lawrence et al., 2013; Zhao et al., 2021).

5. Conclusions

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. Based on modeled estimates, we observed that scaling patterns coalesced between basins at low and high HEFs, but scaling patterns diverged for moderate HEFs. The hypotheses we generated suggest future studies incorporate a larger number of study basins across broader environmental gradients to more effectively assess generalizability of patterns and relationships to watershed characteristics, and note the need for direct measurements of hyporheic respiration in the field to evaluate the hypotheses generated by this study, and make suggestions for measurement campaign design. Although our results are entirely based off a model, we hope our findings and emergent hypothesis will guide future work generalizing scaling relationships between hyporheic processes and watershed characteristics. This knowledge will improve our ability to model the HZ and more accurately represent river corridor function in earth system models.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data used in this study include model outputs from the River Corridor Model and watershed characteristics. All data and *R* scripts used to analyze and plot the data are publicly available in a ESS-DIVE repository, which can be found at https://data.ess-dive.lbl.gov/datasets/doi:10.15485/2527349 (Regier et al., 2025).

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