

1 **Title: Point-scale organic-matter decomposition in streambeds is weakly associated with reach-scale**  
2 **respiration**

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12

13 **Abstract**

14 Stream and river ecosystems play a central role in the movement and decomposition of particulate  
15 organic matter, serving as a conduit between terrestrial hillslopes and coastal environments. Microbe-  
16 catalyzed decomposition generates simpler organic molecules that fuel respiration, often in the  
17 sediments of these ecosystems. However, the degree of connection between sediment-associated  
18 respiration ( $ER_{sed}$ ) and organic-matter-decomposition potential remains poorly understood. It is also  
19 unclear whether organic-matter-decomposition potential is more closely associated with  $ER_{sed}$ , whole-  
20 ecosystem respiration ( $ER_{tot}$ ), or water-column respiration ( $ER_{wc}$ ). We examined the link between  
21 particulate organic-matter-decomposition potential—using cellulose-based cotton strips as a  
22 standardized substrate—and all three components of respiration across 48 sites in the environmentally  
23 diverse Yakima River Basin (Washington State, USA). We hypothesized that decomposition within  
24 sediments would be most strongly related to  $ER_{sed}$ , but decomposition rates were more closely  
25 associated with  $ER_{tot}$ , less so with  $ER_{sed}$  and not at all with  $ER_{wc}$ . This suggests that point-scale particulate  
26 organic-matter-decomposition potential within stream/river sediments is more closely associated with  
27 integrated system respiration rather than with processes confined to sediments or the water column  
28 alone though these relationships were weak overall. Further, across the basin, decomposition rates  
29 nearly spanned the previously reported global range for streams and rivers and were best explained by  
30 total dissolved nitrogen (TDN), sediment grain size, and aridity of the upstream drainage area. These  
31 results highlight the strong influence of land cover and basin-scale biophysical variation on sediment-  
32 associated decomposition processes and indicate that mechanistic models of organic-matter  
33 decomposition in streams and rivers should account for coupled sediment–water–land interactions.

34 **Key words:** Yakima River; organic-matter decomposition; sediment respiration; stream metabolism;  
35 cotton-strip assay; hyporheic zone respiration

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37

## 38 Introduction

39 Stream networks are major components of the global carbon cycle (Cole et al., 2007; Drake et al., 2018;  
40 Talluto et al., 2024). Whole-stream metabolism is often studied as an integrated outcome of processes  
41 occurring across the continuum from the air-water interface down through sediments that are below  
42 the stream itself (Battin et al., 2023; Tank et al., 2010). The sediments include the interface between the  
43 streambed and water column (i.e., the benthic zone) and the spatial domain below this interface,  
44 referred to as the hyporheic zone (Boulton et al., 1998; Krause et al., 2011; Wondzell, 2011). The benthic  
45 zone can be highly productive with significant primary producer (e.g., algae) and heterotrophic microbial  
46 biomass (Allan et al., 2021). The hyporheic zone is also highly biogeochemically active due, in part, to  
47 surface water flowing through it and mixing with groundwater to stimulate heterotrophic microbial  
48 activity (Boano et al., 2014; Lewandowski et al., 2019; Zarnetske et al., 2011). Processes occurring on  
49 and around sediments across the benthic-to-hyporheic continuum are often jointly responsible for the  
50 bulk of biogeochemical activity in stream systems (Burrows et al., 2017; Fellows et al., 2001; Garayburu-  
51 Caruso et al., 2025; Naegeli and Uehlinger, 1997), with important exceptions in large rivers (Roley et al.,  
52 2023).

53 Metabolic processes within integrated stream systems are linked to the building of and breaking down  
54 of organic matter (Hall and Hotchkiss, 2017a; Odum, 1956). Streams are commonly net heterotrophic,  
55 meaning they mineralize more organic-matter-associated carbon than they fix by in-stream primary  
56 production (Battin et al., 2023; Bernhardt et al., 2022). This emphasizes the importance of  
57 understanding organic-matter decomposition in streams and its connection to respiration rates, which  
58 are ultimately linked to rates of elemental cycling. Organic-matter decomposition is commonly  
59 measured in stream systems by quantifying the breakdown of specific substrates (Benfield et al., 2017;  
60 Woodward et al., 2012). Cellulose-based cotton strips are an increasingly common model substrate for  
61 such studies as they enable broad comparisons across streams (and other types of ecosystems) (Colas et  
62 al., 2019; Filbee-Dexter et al., 2022; Tiegs et al., 2024; Vyšná et al., 2014). Like other standardized  
63 substrates used in decomposition studies (e.g., litter bags), cotton-strips quantify organic-matter-  
64 decomposition potential, that is, the capacity of the ecosystem to decompose organic matter, rather  
65 than the actual rate of native organic-matter decomposition *in situ*. A standard approach is to place  
66 them in the field for a known amount of time, retrieve them, and measure the loss in tensile strength, as  
67 a measure of the degree of decomposition. This approach has revealed many factors that impact  
68 decomposition in streams such as temperature, land use, aqueous chemistry, sediment texture, stream  
69 flow, location within the stream network, and canopy cover, among others (Griffiths and Tiegs, 2016;  
70 Tiegs et al., 2024).

71 Studies have examined the relationship between organic-matter decomposition and whole-stream  
72 respiration (Mancuso et al., 2023; Pingram et al., 2020; Young and Collier, 2009), but have not  
73 specifically tied organic-matter decomposition within sediments to sediment-associated respiration. This  
74 leads to an open question and the focus of our study: To what degree are point-scale rates of organic-  
75 matter-decomposition potential within sediments linked to reach-scale respiration associated with the  
76 whole-stream ecosystem ( $ER_{tot}$ ), the sediments ( $ER_{sed}$ ), or the water column ( $ER_{wc}$ )?  $ER_{tot}$  represents  
77 reach-scale aerobic respiration from autotrophs and heterotrophs across benthic, planktonic, and  
78 hyporheic zones.  $ER_{sed}$  comprises reach-scale sediment-associated respiration from benthic and  
79 streambed sediments, rooted and submerged plants, and hyporheic zones that are hydrologically

80 connected to the active channel;  $ER_{wc}$  constitutes reach-scale planktonic respiration occurring only in  
81 the water column.

82 We specifically tested the hypothesis that reach-scale  $ER_{sed}$  rates are strongly linked to point-scale  
83 measurements of organic-matter decomposition within streambed sediments. More specifically, we  
84 tested the prediction that cotton-strip-decay rates are best explained by  $ER_{sed}$ , with little additional  
85 variation in decay rates explained by  $ER_{tot}$  or  $ER_{wc}$ . To test our hypothesis and associated prediction we  
86 used field deployments across the Yakima River Basin (YRB). The YRB is an environmentally diverse basin  
87 in southeastern Washington State (USA) that is  $\sim 16,000$  km<sup>2</sup> and with a stream network that culminates  
88 in the 7<sup>th</sup>-order Yakima River. To generate the data needed to test our hypothesis, we used a  
89 combination of sensors and cotton strips across 48 sites in the YRB that collectively spanned a  
90 continuum from small mountainous streams in coniferous forests with little human impact to a large  
91 lowland river in an arid environment surrounded by significant agricultural land use. The resulting  
92 patterns help to fill a fundamental knowledge gap in our understanding of how point-scale organic-  
93 matter-decomposition potential relates to reach-scale respiration and can be used to inform models  
94 that aim to mechanistically integrate biogeochemical processes within and across stream networks.

95

## 96 **Methods**

97 To evaluate the linkages between organic-matter decomposition and stream ecosystem respiration we  
98 took advantage of a prior study (Garayburu-Caruso et al., 2025) that separated  $ER_{tot}$ ,  $ER_{sed}$ , and  $ER_{wc}$   
99 across environmentally divergent locations in the YRB (Fig. 1). Garayburu-Caruso et al. (2025) used  
100 dissolved oxygen (DO) sensors, dark bottle incubations, and the single-station method (Odum, 1956) to  
101 estimate these three components of respiration. In addition, that study deployed sensors to log water  
102 temperature, used here to calculate cumulative degree days as described below. These and associated  
103 contextual data were downloaded from existing data packages (Delgado et al., 2023; Forbes et al., 2023;  
104 Garayburu-Caruso et al., 2023), and methods are described in detail by Garayburu-Caruso et al. (2025).  
105 Data and computer scripts used in the current study are consolidated in Stegen et al. (2025). In brief, DO  
106 timeseries were analyzed via StreamMetabolizer (Appling et al., 2018) to estimate  $ER_{tot}$ . The length of  
107 the reach that a given DO sensor integrates varies across streams and has been estimated to be  
108 roughly three times the turnover length of O<sub>2</sub> (Hall and Hotchkiss, 2017b). As such, integrated  
109 reach lengths likely varied across sites due to differences in reaeration and discharge. Field sites  
110 were located in separate, non-overlapping reaches, helping to minimize potential spatial  
111 autocorrelation between neighboring sites in the estimated metabolic rates. To estimate  $ER_{wc}$ , 2 L  
112 opaque bottles containing a DO sensor were filled with stream water and incubated *in situ*; the rate of  
113 DO drawdown was used as the estimate of  $ER_{wc}$ . The difference between  $ER_{tot}$  and  $ER_{wc}$  was used as an  
114 estimate of  $ER_{sed}$ , which represents all respiration in the stream system that is not directly occurring in  
115 the water column.  $ER_{sed}$  therefore includes respiration in the hyporheic zone, the streambed surface,  
116 and rooted/submerged plants. We note, however, that ER estimates derived from open diel O<sub>2</sub> methods  
117 capture all oxygen-consuming processes, not solely aerobic respiration. These estimates could also  
118 include abiotic oxidation of dissolved Fe(II) or the oxidation of other end products from anaerobic  
119 metabolism (Demars et al., 2015; Piatka et al., 2021), other oxidation processes such as nitrification and  
120 photooxidation of organic matter (Demars et al., 2015; Estapa and Mayer, 2010), or O<sub>2</sub> inputs from  
121 groundwater (Hall and Tank, 2005). Because  $ER_{sed}$  was calculated by the difference between  $ER_{tot}$  and  
122  $ER_{wc}$ , it may be sensitive to these non-respiratory O<sub>2</sub> sinks. However, biological metabolism is generally  
123 considered the dominant O<sub>2</sub>-consuming pathway in streams and we therefore interpret  $ER_{sed}$  primarily

124 as sediment-associated biological O<sub>2</sub> consumption while acknowledging that other contributions may be  
125 captured.

126 To take advantage of the ecosystem respiration study, cotton strips made of Artist fabric (following the  
127 protocol of Tiegs et al., 2013) were deployed at the same time as the DO sensors. They were deployed  
128 upstream of the DO sensors to capture the upstream reach that influenced the DO sensor readings and  
129 prevent disturbance during sensor maintenance. This design prioritized among-reach coverage across  
130 the basin (48 sites) and provided point-scale estimates of decomposition potential at a single location  
131 within each reach.

132 The cotton strips were deployed in the shallow hyporheic zone for 35 continuous days at 48 sites across  
133 the YRB (Fig. 1). At each site, deployment locations were selected to be representative of the reach in  
134 terms of sediment size, flow velocity, and substrate composition. In larger river systems (e.g., 7th-order  
135 reaches), deployments were limited to wadeable areas near channel margins. Deployment and retrieval  
136 days varied across four days, but all strips were deployed for 35 days: deployments were from July 25<sup>th</sup>  
137 to July 28<sup>th</sup>, 2022 and retrievals were from August 29<sup>th</sup> to September 1<sup>st</sup>, 2022. Cotton strips were cut  
138 from bolts of 12-ounce, heavy-weight cotton fabric composed of 95% cellulose (Style 548; Fredrix,  
139 Lawrenceville, GA, USA). Each strip was 27 threads wide and cut to 8.0 cm by 2.5 cm (after Tiegs et al.  
140 2013). Each cotton strip was laid flat in a stainless-steel mesh cage (10.8 x 4.5 cm, RSV Jumbo Mesh Herb  
141 Infuser) to minimize physical damage and feeding by macroinvertebrates, thereby emphasizing microbe-  
142 based decomposition. At each site, four cages with one strip each were attached to the underside of  
143 clay bricks (20 x 10 x 5.5 cm) with stainless steel wire. The brick/cage/strip setup was nestled into  
144 streambed sediment such that the cages/strips were within the sediments and the brick was at the  
145 sediment/water interface. The four cages were next to each other. This setup kept the cotton strips out  
146 of direct light and within the sediments while allowing water to flow past the cotton strips.

147 After the 35-day incubation period, cotton strips were carefully removed from cages and gently brushed  
148 with gloved hands in stream water for approximately 10 s to remove large debris. Cleaned cotton strips  
149 were placed in 50 mL conical centrifuge tubes with 70% ethanol. Tubes were capped and rolled  
150 approximately 10 times before ethanol was removed. After completing this step, clean 70% ethanol was  
151 added to the 50 mL tube to minimize further microbial-based decomposition. Cotton strips were  
152 transported in the ethanol filled tubes on blue ice to Pacific Northwest National Laboratory in Richland,  
153 WA. At the laboratory, the ethanol was removed from the tubes and cotton strips were air dried  
154 overnight prior to further drying in an oven at 40 °C for at least 24 hours. After drying, cotton strips were  
155 stored in air-tight containers with desiccant.

156 Dried cotton strips were shipped to Oakland University, Rochester, MI for tensile-strength analysis  
157 following the protocol in Tiegs et al., (2013). A tensiometer was used to estimate tensile strength (Mark  
158 10 MG100 with a Chatillon TCM 201 with roller jaws). The tensiometer pulled each cotton strip at a rate  
159 of 2 cm/min. Some of the cotton strips were completely degraded such that there was no material to  
160 measure, while other cages only contained fragments that were too small to measure tensile strength.  
161 These non-detect strips accounted for 5.4% of all deployed strips. In both cases, a limit of detection was  
162 assigned as the lowest tensile strength calculated in Tiegs et al. (2019) divided by 2, resulting in a final  
163 value of 0.05. This was done to avoid statistical artifacts that can arise when simply introducing a value  
164 of 0 (i.e., the natural log transformation in Equation 1 would be undefined). Removing these strips  
165 entirely would bias the analyses away from conditions with very fast decomposition.

166 Tensiometer data were converted into decay rates using tensile loss calculated via Equation 1 (as in  
167 Mancuso et al., 2022).

$$168 \quad K = \frac{-\ln(T_s/T_{sc})}{Time} \quad \text{Equation 1}$$

169 Here, K is the decomposition rate,  $T_s$  is the post-incubation tensile strength of the deployed cotton  
170 strips, and  $T_{sc}$  is the mean tensile strength of control strips that were not incubated in the field. The time  
171 variable was calculated as either the number of chronological deployment days (i.e., 35 days) or the  
172 number of degree days. Using degree days as the time variable accounts for variation in temperature  
173 across field sites and was estimated separately for each site as the sum of mean daily river temperature  
174 over the incubation period. We use  $K_{cd}$  and  $K_{dd}$  to represent decay rate per chronological day or per  
175 degree day, respectively. The values of  $K_{cd}$  and  $K_{dd}$  were estimated for each individual cotton strip and  
176 then replicates were averaged to provide a single site-level value for  $K_{cd}$  and  $K_{dd}$ .

177 We examined both  $K_{cd}$  and  $K_{dd}$  to evaluate whether the connection between decomposition and reach-  
178 scale respiration rates depends on accounting for temperature variation across the study basin. This is  
179 particularly relevant in the YRB because our field sites ranged from colder headwater streams to warmer  
180 low-gradient rivers. To test our hypothesis, we conducted both univariate and multivariate regression-  
181 based analyses. We used ordinary least squares regression to examine the strength of univariate  
182 correlations between  $K_{cd}$  or  $K_{dd}$  and  $ER_{tot}$ ,  $ER_{wc}$ , or  $ER_{sed}$ . We complemented this univariate analysis with  
183 multiple regression analysis to find an optimized model to explain variation in either  $K_{cd}$  or  $K_{dd}$ .

184 Further, to explore how other system variables may explain variation in decomposition rates, a LASSO  
185 (Least Absolute Shrinkage and Selection Operator) regression model was built using physical, chemical  
186 and environmental variables (Table S1) as inputs, and  $K_{cd}$  or  $K_{dd}$  as the response variables. Variables were  
187 cube root transformed and z-score normalized to reduce the impact of high leverage points in the  
188 regression analysis and to equally weight all variables. The LASSO regression was performed over 100  
189 iterations, each with a different random seed using the `cv.glmnet` function in the `glmnet` R package  
190 (Friedman et al., 2010).  $\beta$  coefficients were normalized to the maximum  $\beta$  coefficient for each iteration,  
191 then averaged over the 100 iterations for the final reported value. Both the raw and normalized mean  $\beta$   
192 coefficient and standard deviation are reported in addition to the  $R^2$  (Table 2).

193

## 194 **Results and Discussion**

### 195 **Decomposition in the Yakima River Basin spans globally reported rates**

196 Both  $K_{cd}$  and  $K_{dd}$  exhibited a wide range of values (Fig. 2), effectively spanning the theoretical maximum  
197 of what could have been observed with our deployment setup. This is evidenced by some cotton strips  
198 being completely consumed prior to retrieval (5.4% of all strips,  $K_{cd}$  and  $K_{dd}$  maximized), while others  
199 were largely intact ( $K_{cd}$  and  $K_{dd} \approx 0$ ). This variation is surprising given the relatively small spatial domain  
200 sampled by this study, and emphasizes that environmental heterogeneity can surpass the effects of  
201 spatial extent (Mancuso et al., 2022). The environments studied here ranged from pristine locations in  
202 the mountainous headwaters of the YRB to lowland locations with heavy agricultural influences (Fig. 1;  
203 Laan et al. 2025). This emphasizes the value of environmentally diverse watersheds like the YRB as  
204 useful testbeds to study variation in decomposition rates within single hydrologically connected basins.

205 Comparing decay rates from the YRB to a global dataset from > 500 streams and rivers (Tiegs et al.,  
206 2024) showed that YRB rates spanned nearly the entire global range and had substantial overlap with  
207 the bulk of the global distributions (Fig. 2a,b). Dominant peaks in the YRB rate distributions were shifted  
208 slightly towards faster rates, relative to primary peaks in the global dataset (Fig. 2a,b). This shift towards  
209 faster rates and the wide range in rates are likely due to several factors linked to rates being estimated  
210 in later summer with high temperatures, and established biological communities due to several months  
211 since high-flow disturbances (Collier et al., 2013b; Grimm and Fisher, 1989; Mancuso et al., 2023). The  
212 two decay rates were also closely correlated with each other, though the relationship weakened  
213 towards locations with faster decay rates (**Fig. 2c**). This suggests a weak influence of temperature in the  
214 YRB; a strong influence of temperature should lead to a weak relationship between  $K_{cd}$  and  $K_{dd}$ . These  
215 results contrast previously reported influences of temperature on particulate organic-matter  
216 decomposition (Benbi et al., 2014; Griffiths and Tiegs, 2016), and likely reflect dominance of other  
217 influential factors such as variation in nutrient concentrations (Rosemond et al. 2015). Temperature-  
218 driven decomposition is also expected to lead to a strong relationship between  $K_{cd}$  and summed  
219 temperature, but we observed a very weak relationship despite ~4-fold variation in summed  
220 temperature (**Fig. 2d**). This range in temperature among sites would likely be smaller in other seasons,  
221 and we do not therefore expect a strong influence of temperature to emerge in the YRB by conducting  
222 the study in other seasons. These results emphasize the need to understand factors governing variation  
223 in decay rates across the YRB. This is especially true given that rate distributions within this one basin  
224 span nearly all globally observed decay rates.

225 Across the YRB there appears to be potential for some spatial organization for both  $K_{cd}$  and  $K_{dd}$  (**Fig. 3**).  
226 Visual inspection of the maps suggests that the spatial organization may be stronger for  $K_{cd}$  than for  $K_{dd}$ .  
227 To evaluate this possibility more rigorously, we regressed each decay rate against upstream drainage  
228 area (Fig. 4). In this case, drainage area is meant to reflect position within the YRB. We used drainage  
229 area in preference to stream order because it is a continuous variable directly tied to the spatial domain  
230 a given stream integrates, whereas stream order is categorical and primarily reflects stream network  
231 topology. Associated regressions were significant ( $p < 0.05$ ) with both decay rates increasing with  
232 drainage area (**Fig. 4**). The relationship with drainage area was stronger, in terms of  $R^2$ , for  $K_{cd}$ . Both  
233 relationships were, however, relatively weak with  $R^2$  values of 0.22 and 0.14 for  $K_{cd}$  and  $K_{dd}$ , respectively  
234 (**Fig. 4**). Nonetheless, the existence of a significant relationship after controlling for temperature (i.e., for  
235  $K_{dd}$ ) indicates that spatially structured factors other than temperature influence decay rates. This is not  
236 surprising as studies using cotton strips have found several factors that influence decomposition, such as  
237 nutrient concentrations, turbidity, and many others (Collier et al., 2013b; Pingram et al., 2020; Tiegs et  
238 al., 2024). Before exploring a broad suite of potential explanatory variables, we tested our hypothesis  
239 that decomposition rates will be better explained by sediment-associated respiration ( $ER_{sed}$ ) than by  
240 respiration in the water column ( $ER_{wc}$ ) or by respiration of the integrated stream system ( $ER_{tot}$ ).

241

#### 242 **Respiration in sediments explains little variation in decomposition**

243 Contrary to our hypothesis, we found that both decay rates were most strongly connected to  $ER_{tot}$ , less  
244 so with  $ER_{sed}$ , and not at all with  $ER_{wc}$  (**Fig. 5**). Univariate models using  $ER_{tot}$  were better than multivariate  
245 models using  $ER_{sed}$ ,  $ER_{wc}$ , and their interaction. This is evidenced by univariate models using  $ER_{tot}$  having  
246 AIC values more than two units lower than multivariate models containing  $ER_{sed}$  and  $ER_{wc}$  (**Table 1**).

247 Multivariate models were not used with  $ER_{tot}$  because it contains  $ER_{sed}$  and  $ER_{wc}$ . Garayburu-Caruso et  
248 el., 2025 showed that  $ER_{sed}$  accounted for the majority of  $ER_{tot}$  across most of the YRB, with 88% of  
249 locations showing  $ER_{sed}$  contributions exceeding 50% of  $ER_{tot}$ . The strong correspondence between these  
250 two metrics might explain the similar  $R^2$  values observed. We note, however, that the difference in  
251 explained variance between  $ER_{tot}$  ( $R^2 = 0.29$  for  $K_{cd}$ ;  $R^2 = 0.16$  for  $K_{dd}$ ) and  $ER_{sed}$  ( $R^2 = 0.22$  for  $K_{cd}$ ;  $R^2 = 0.13$   
252 for  $K_{dd}$ ) was modest, and the stronger association with  $ER_{tot}$  should be interpreted cautiously.

253 To interpret these results, we note that cotton strips were deployed a few centimeters into the riverbed  
254 sediments, beneath a brick set flush with the streambed surface. We conceptualized this deployment as  
255 the shallow hyporheic zone, which was a reason we hypothesized that decay rates would be most  
256 strongly connected to  $ER_{sed}$ . However, the results indicate that point-scale decomposition of particulate  
257 organic matter within the shallow hyporheic zone is linked to respiratory processes occurring in both the  
258 sediment and water column. Therefore, our deployment depth might have reflected sediment-water  
259 interface processes in addition to shallow hyporheic zone processes, leading to stronger associations of  
260 cotton strip decomposition with  $ER_{tot}$ . We also note that  $ER_{sed}$  estimates may not exclusively reflect  
261 biological respiration, as non-respiratory  $O_2$ -consuming processes can contribute to these estimates (see  
262 Methods). We propose that if our deployment configuration was complemented with a simultaneous  
263 deployment that enabled growth of benthic algal biofilms on the cotton strips, the combined  
264 decomposition from both deployments could, in some systems, capture more of the processes that  
265 contribute to  $ER_{sed}$ . This would provide a more complete view of sediment-associated biogeochemical  
266 function, potentially leading to a stronger correlation between decomposition rates and  $ER_{sed}$ . While this  
267 remains to be tested, the underlying idea is that primary producers support a large portion of  
268 respiration associated with riverbed sediments, which is supported by recent analyses showing a strong  
269 link between  $ER_{sed}$  and gross primary production across the YRB (Garayburu-Caruso et al., 2025).

#### 270 **Slower rates of $K_{cd}$ and $K_{dd}$ are in streams with coarse sediments, set within wet forests**

271 Given that our hypothesis was rejected and that  $ER_{tot}$  explained only about 29% and 16% of  $K_{cd}$  and  $K_{dd}$ ,  
272 respectively (**Table 1, Figure 5**), we used a discovery-based approach to explore other system variables  
273 that may explain further variation in decomposition rates. LASSO-based modeling indicated that total  
274 dissolved nitrogen (TDN) and the median grain size of sediment texture (D50) were most important for  
275 explaining  $K_{dd}$ , while TDN and aridity were most important for explaining  $K_{cd}$  (**Table 2**). Other variables  
276 were retained in the LASSO models (**Table S1**), but we interpreted TDN, D50, and aridity as the most  
277 important because they consistently had the largest normalized coefficients. This interpretation is based  
278 on these variables having mean normalized coefficients above 0.5—in terms of absolute value—  
279 meaning they were at least 50% as important as the most important variable in the 100 LASSO model  
280 runs. Further, the LASSO coefficients for these variables had a coefficient of variation less than 0.5,  
281 meaning that across the 100 LASSO model runs the values of their normalized coefficients were  
282 relatively stable (**Table S1**). The LASSO modeling also confirmed a relatively weak influence of  
283 temperature, evidenced by relatively small and highly variable  $\beta$  coefficients for summed temperature in  
284 the  $K_{cd}$  model (Table S1); temperature was not used in the  $K_{dd}$  model.

285 Both decomposition rates increased with higher TDN concentrations, while  $K_{dd}$  decreased with larger  
286 D50 and  $K_{cd}$  decreased with higher aridity index values (**Table 1**). To more deeply interpret these  
287 relationships, we examined Pearson-based univariate correlations between these three explanatory  
288 variables and other variables included in the LASSO models. This is important because of strong

289 collinearity among some explanatory variables (**Fig. S1**). In this case, variables identified as being the  
290 most important may be acting as proxies for one or more additional variables. We found that TDN was  
291 most strongly correlated with percent agricultural land cover of the upstream drainage area and sulfate  
292 concentrations in the stream water (**Fig. S1**). Increases in both decomposition rates with TDN may,  
293 therefore, reflect agricultural inputs of nutrients that increase overall microbial activity of the stream  
294 ecosystems we studied. D50 was most strongly correlated with the aridity index, which was most  
295 strongly correlated with percent forest cover; the correlation between D50 and aridity is unlikely to  
296 reflect a causal connection, while aridity and forest cover most likely are causally linked. If the  
297 relationship between decomposition and D50 is causal, it could be mediated by the total surface area  
298 available for microbial attachment. This would, however, influence decomposition only to the extent  
299 that microbial biomass in adjacent sediments impacts microbial activity on the cotton strips. Coarser  
300 sediments have much less surface area, potentially limiting overall microbial activity.

301 Considering the directionality of the univariate relationships, in context of the LASSO outcomes,  
302 suggests slower decomposition—for both rates—in streams with relatively coarse sediments and set  
303 within relatively wet forests. This contrasts with Clapcott and Barmuta (2010) who found faster  
304 decomposition in coarser sediments. The discrepancy is likely because we excluded macroinvertebrates  
305 while they did not, and they interpreted the link to sediment texture as due to greater habitat  
306 availability for macroinvertebrates in coarser sediments. Locations with slower decomposition should,  
307 thus, primarily be in higher elevation, relatively pristine parts of the YRB, while faster decomposition  
308 occurs at lower elevations impacted by agricultural inputs. These results are consistent with previous  
309 work showing greater cotton strip decomposition in impaired streams (Young and Collier, 2009), those  
310 with little natural land cover (Collier et al., 2013a; Webb et al., 2019), and in streams with higher  
311 nutrient concentrations (Ferreira et al., 2015; Pingram et al., 2020; Tiegs et al., 2013). In addition to  
312 differences in nutrient concentrations between higher and lower elevation sites, we expect less light  
313 penetration to streams in higher elevation sites because of more forest cover and smaller streams.  
314 Though not measured here, less light could suppress autotrophic production which may limit  
315 heterotrophic respiration (Bernhardt et al., 2022; Mulholland et al., 2001; Young and Huryn, 1999).  
316 Lower autotrophic production could therefore slow decomposition relative to high-light conditions by  
317 reducing the supply of labile carbon from phototrophs that can prime organic-matter degradation  
318 (Danger et al. 2013; Howard-Parker et al. 2020).

### 319 **Point-scale decomposition is associated with processes across the sediment-water continuum and** 320 **land features**

321 Our results collectively indicate that to study shallow hyporheic zone decomposition processes, it is not  
322 sufficient to conceptualize organic-matter decomposition by only considering sediment or water column  
323 processes; one must examine the integrated system. The implication of our analyses is that point-scale  
324 organic-matter decomposition potential was more closely associated with integrated system respiration  
325 than with individual respiration components. Our findings suggest that mechanistic models of stream  
326 ecosystem respiration may benefit from accounting for sediment processes, water-column processes,  
327 and land-cover influences from beyond the stream. Focusing exclusively on the hyporheic zone is  
328 insufficient, even in systems for which the hyporheic zone accounts for most reactions (Boano et al.,  
329 2014; Burrows et al., 2017; McClain et al., 2003). This is further emphasized by previous work showing  
330 that most respiration occurs in the water column of large rivers (Gardner and Doyle, 2018; Roley et al.,  
331 2023). Garayburu-Caruso et al. (2025) also show that fractional contributions of  $ER_{\text{sed}}$  to  $ER_{\text{tot}}$  is often

332 high, but that there is significant variation in those fractional influences across the YRB. This variability is  
333 due to  $ER_{wc}$  being fast enough, in some locations, to account for more than 80% of  $ER_{tot}$  (Garayburu-  
334 Caruso et al., 2025). Similarly, Laan et al. (2025) found substantial overlap between the distribution of  
335  $ER_{wc}$  rates from the YRB and  $ER_{tot}$  from across the contiguous United States. The overall picture is that  
336 decomposition is the result of integrated processes occurring across the sediment-water continuum and  
337 influenced by external factors tied to land cover and land use. We infer that these integrated processes  
338 are influenced by biophysical variation across the YRB (Laan et al., 2025), leading to decomposition rates  
339 within this single basin that resemble global rate distributions and nearly span the global range of  
340 observed rates (Tiegs et al., 2024). Other basins that contain only one ecoregion or have homogeneous  
341 land cover may be expected to have a narrower range of decomposition rates (Webb et al., 2019). We  
342 note that our decomposition estimates represent point-scale conditions at wadeable locations and  
343 should be interpreted as such rather than as reach-integrated measures of decomposition. Capturing  
344 within-reach spatial variability in decomposition across habitats and channel depths would complement  
345 the among-reach approach used here, and may lead to stronger relationships between decomposition  
346 rates and reach-scale ER. Nonetheless, models applied to any stream network that aim to predict  
347 spatiotemporal variation in decomposition rates would be well served by considering processes  
348 throughout the integrated watershed system.

#### 349 **Code and data availability**

350 Data and scripts used to generate the main findings within this manuscript can be found at  
351 <https://data.ess-dive.lbl.gov/view/doi:10.15485/3008446> (Stegen et al., 2025). Other data collected  
352 during the field efforts (i.e., sensor data; surface water chemistry data; and geospatial information,  
353 metadata, and maps for 2021 Spatial Study sampling event) can be accessed on ESS-DIVE at  
354 <https://data.ess-dive.lbl.gov/datasets/doi:10.15485/1987520> (Garayburu-Caruso et al., 2023),  
355 <https://data.ess-dive.lbl.gov/datasets/doi:10.15485/1969566> (Delgado et al., 2023), and  
356 <https://data.ess-dive.lbl.gov/datasets/doi:10.15485/1923689> (Forbes et al., 2023).

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368 Validation: MB and JCS

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## 372 **Competing interest**

373 The authors declare that they have no conflict of interest.

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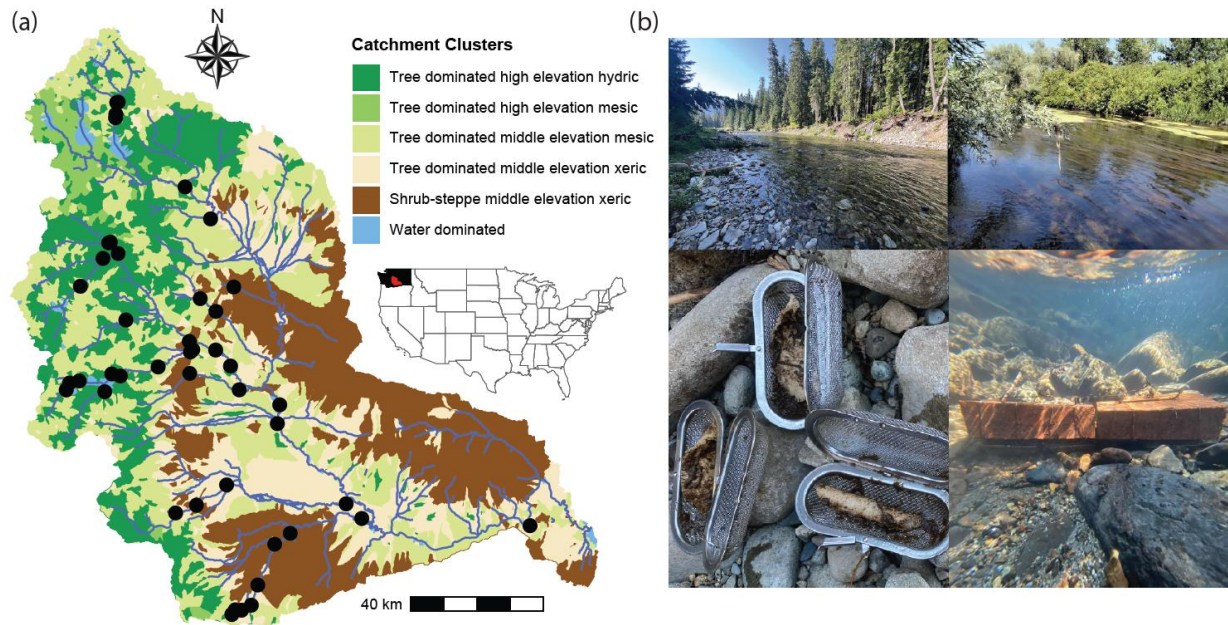
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599 **Figures**

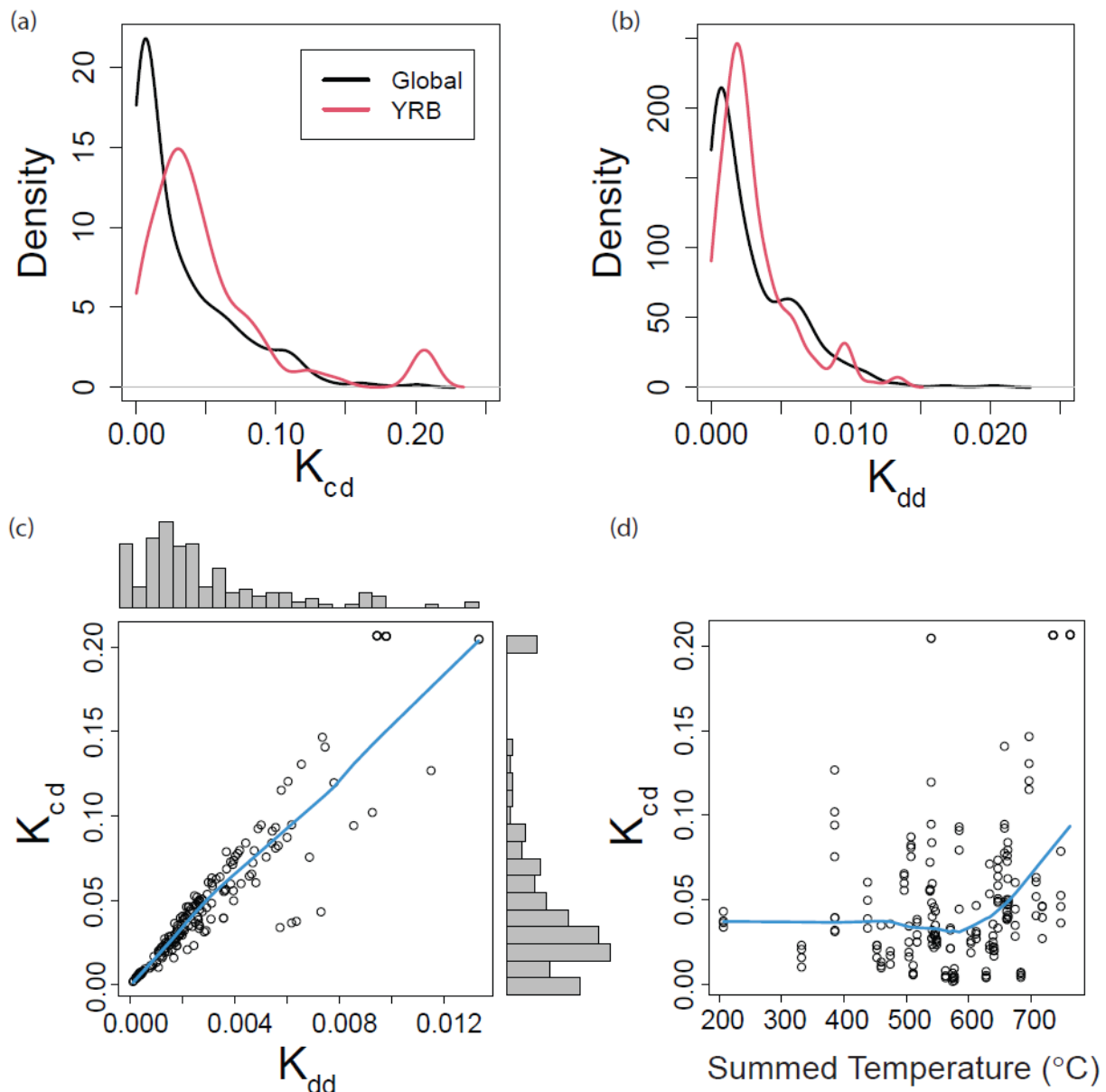


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601 **Figure 1. Biophysical clusters, sampling locations, and example conditions across the YRB.** (a) The inset  
602 map shows the location of the YRB within the contiguous United States, with black indicating  
603 Washington State and red indicating the YRB. The YRB is shown with multiple colors, which correspond  
604 to biophysical clusters, as presented in Laan et al. (2025) and summarized briefly in the legend. Black  
605 circles are locations where decay rates were estimated. (b) Photos provide examples of the breadth of  
606 conditions studied across the YRB, post-incubation states of cotton strips, and deployment of the cotton  
607 strips.

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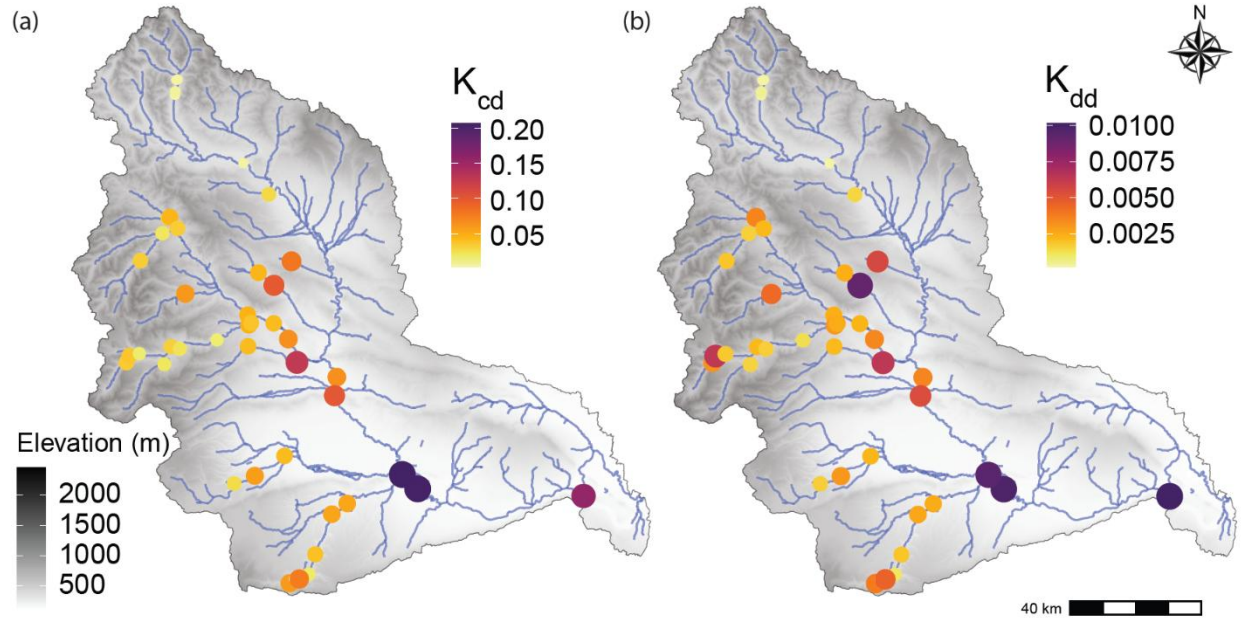


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611 **Figure 2. Decay rate distributions and relationships to each other and temperature.** Kernel density  
612 functions for (a)  $K_{cd}$  and (b)  $K_{dd}$  from a global streams and rivers dataset and from the YRB. (c) Scatterplot  
613 correlating  $K_{cd}$  to  $K_{dd}$ . Histograms summarizing the distribution of each rate are provided on the outer  
614 boundaries. (d)  $K_{cd}$  related to temperature summed across the deployment period; summed  
615 temperature was used to calculate  $K_{dd}$ . Blue lines represent Lowess spline fits as regression analysis was  
616 not required for interpretation.

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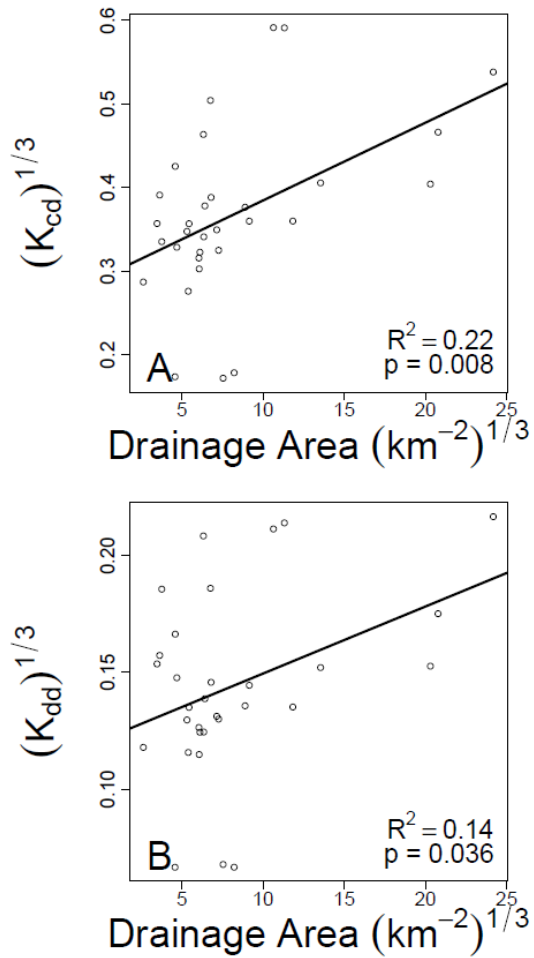
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620 **Figure 3: Spatial distribution of decay rates across the YRB.** Each map shows elevation profiles and  
 621 either  $K_{cd}$  (A) or  $K_{dd}$  (B). Colored circles are field locations where rates were estimated. The color of each  
 622 circle is related to decay rate as indicated in the legends, and circle size is scaled to decay rate to further  
 623 facilitate visual interpretability.

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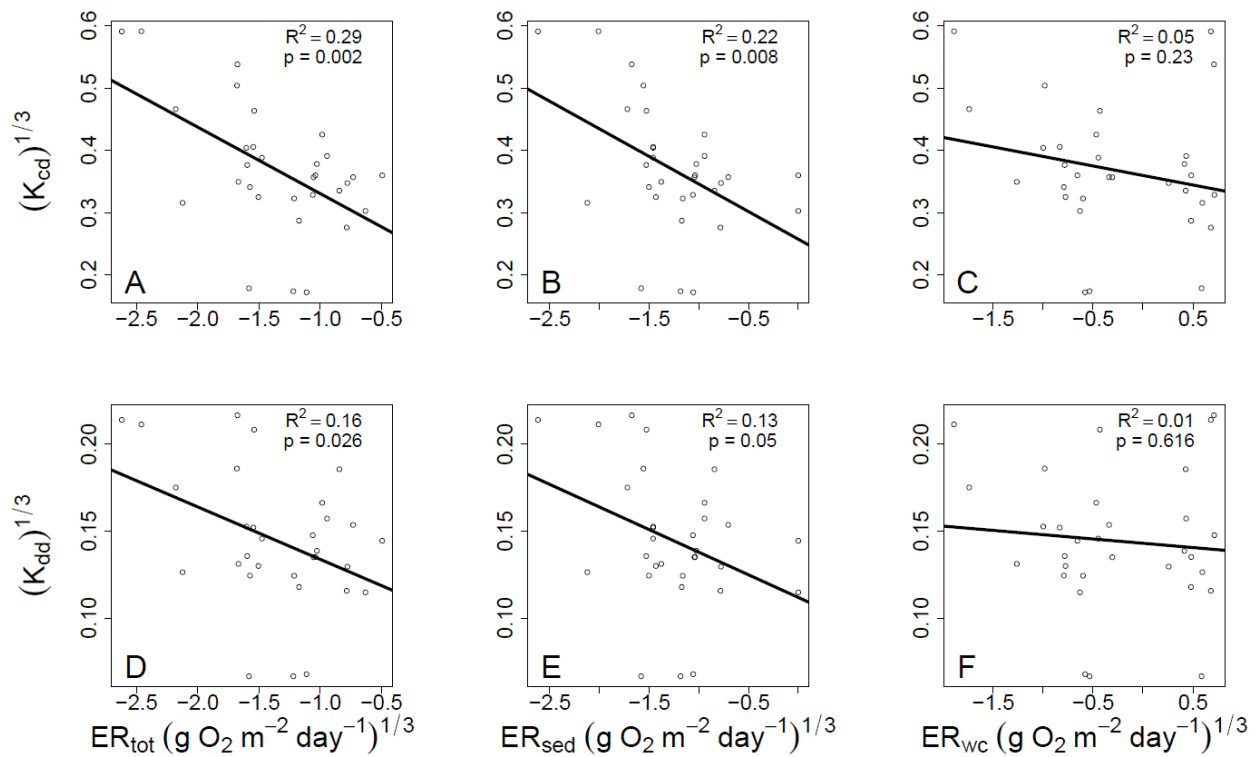


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626 **Figure 4. Decay rates increase with drainage area.**  $K_{cd}$  (A) and  $K_{dd}$  (B) regressed against upstream  
 627 drainage area and fit with an ordinary least squares linear regression. Associated regression models are  
 628 shown as solid black lines and statistics are provided on each panel. Data were cube root transformed to  
 629 improve normality before analysis.

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633 **Figure 5: Decay rates related to each of the three aspects of stream ecosystem respiration.** Both  $K_{cd}$  (A-  
634 C) and  $K_{dd}$  (D-F) show strongest relationships with  $ER_{tot}$  (A,D), weaker relationships with  $ER_{sed}$  (B,E), and  
635 non-significant relationships with  $ER_{wc}$  (C,F). Ordinary least squares linear regression models are shown  
636 with solid black lines and associated statistics are provided on each panel. All variables were cube-root  
637 transformed to improve normality prior to regression analysis.

638

639 **Tables**

640 **Table 1.** Comparison of univariate and multivariate regression models explaining variation in  $K_{cd}$  and  $K_{dd}$ .  
 641 Model structures are indicated, along with change in AIC relative to the best model.  $ER_{tot}$  was not used  
 642 in multivariate models because  $ER_{tot} = ER_{sed} + ER_{wc}$ . Regression statistics for the univariate models are  
 643 provided in Figure 5; only the best performing univariate models, in terms of  $R^2$ , are shown. The models  
 644 with  $ER_{sed}$  and  $ER_{wc}$ , but not the interaction term, are effectively the same as the  $ER_{tot}$  model because  
 645  $ER_{tot} = ER_{sed} + ER_{wc}$ . They are included as a point of reference for the model that also includes the  
 646  $ER_{sed} * ER_{wc}$  interaction term.

Model	$\Delta$ AIC
$K_{cd} \sim ER_{tot}$	0
$K_{cd} \sim ER_{sed} + ER_{wc}$	3.8
$K_{cd} \sim ER_{sed} + ER_{wc} + ER_{sed} * ER_{wc}$	5.7
$K_{dd} \sim ER_{tot}$	0
$K_{dd} \sim ER_{sed} + ER_{wc}$	3.0
$K_{dd} \sim ER_{sed} + ER_{wc} + ER_{sed} * ER_{wc}$	4.8

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648 **Table 2.** Regression coefficients from LASSO models explaining variation in  $K_{dd}$  and  $K_{cd}$ . Explanatory  
 649 variables were cube root transformed to reduce influence from high leverage data points and  
 650 standardized as z-scores to enable direct comparison of the regression coefficients. LASSO models were  
 651 fit over 100 seeds. Regression coefficients ( $\beta$ ) and  $R^2$  values were averaged across the 100 seeds.  
 652 Normalized regression coefficients were calculated by dividing each  $\beta$  coefficient by the maximum  $\beta$   
 653 coefficient in each seed. Standard deviation (sd) is reported for each variables' coefficient over the 100  
 654 seeds and used to calculate the coefficient of variation (cv). Variables shown have an absolute value of  
 655 mean normalized  $\beta$  of  $> 0.5$  and  $cv < 0.5$  to emphasize variables that were consistently important across  
 656 seeds. Results for all variables, both normalized and not normalized, can be found in Table S1.

Response Variable	Predictor Variable	Mean Normalized Regression Coefficient ( $\beta$ )	sd	cv
$K_{dd}$	Water TDN	1	0	0
	D50	-0.699	0.087	-0.124
<b>Mean <math>R^2</math></b>			<b>0.502 (sd = 0.0673)</b>	
$K_{cd}$	Aridity	-0.959	0.065	-0.067
	Water TDN	0.805	0.156	0.193
<b>Mean <math>R^2</math></b>			<b>0.883 (sd = 0.083)</b>	

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