

Cellulose decomposition experiment (CELLDEX) results from four Austin streams

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ABSTRACT

As part of a collaboration with Oakland University, the City of Austin deployed cotton strips at reference stream sites (i.e., sites regionally recognized as being minimally disturbed by anthropogenic influences) in 2015 to estimate microbial decomposition rates. Cotton strips were deployed in two riffles and two adjacent riparian habitats of four streams during the fall, mimicking leaf litter inputs. The cotton strips were tested for tensile strength after three weeks of deployment, with loss of tensile strength reflecting microbially-mediated cellulose decomposition. Data from Austin will be incorporated into the global effort utilizing a standardized method toward the establishment of baseline rates of microbial activity in headwater reference streams. Air temperatures ranged from -1 to 31°C while water temperatures ranged from 11 to 24°C during the deployment period. Streams had specific conductance indicative of high ion concentrations (mean > 500 µs/cm), were basic (mean pH 7.4–8.1), and generally supported high dissolved oxygen concentrations (mean 7.0–9.5 mg/L). Phosphorus concentrations were typically below detection limits, but streams had abundant nitrogen. Relative to control cotton strips, there were significant reductions in the tensile strength of strips deployed in the Barton Creek riparian zone and riffles and Rinard Creek riparian zone. The lack of significant declines in cotton strip tensile strength at the other sites relative to control strips indicates slow degradation of organic matter inputs for those systems.

INTRODUCTION

Microbial decomposition of organic matter in stream and riparian habitats is an important ecological service and can reflect watershed integrity related to nutrient enrichment or disturbance (Ferreira et al., 2015). The City of Austin partnered with Dr. Scott Tiegs at Oakland University (Rochester, MI) as part of a global research project to evaluate decomposition rates using a standardized protocol (Tiegs et al., 2013). Partners deployed cotton strips in riparian and riffle habitats of headwater (1st-3rd order) streams that are minimally impacted by anthropogenic influences. The tensile strength of the cotton strips was determined after field deployment and is inversely correlated with the amount of decomposition that has occurred, thus representing a surrogate for microbial decomposition rates of organic matter (e.g., leaf litter). The Austin streams will be representative of Central Texas and compared with approximately 671 other streams in 50 countries. The goals of the research effort are to describe global variability of:

- organic-matter decomposition in streams and riparian zones of Earth's major biomes

- nutrient content, stoichiometry, and community composition of the microbial biofilms that colonize organic matter.

From this data, the study Primary Investigators hope to establish global data baselines in order to track future changes in a fundamental ecosystem process as the environment changes due to climatic or direct anthropogenic activities.

This data report summarizes the water chemistry data of the study streams as well as the final measured tensile strength of the cotton strips from the riffles and riparian zones of each stream. Broader contextualization of the findings will be completed by Dr. Tiegs as part of a series of future publications.

METHODS

SITES

Cotton strips were deployed at four Environmental Integrity Index (EII) sites known to have minimal development and disturbance within their watersheds: Bull Creek at Franklin (#349; lat/long: 30.1894, -97.81269); Barton Creek at Stark (#44; lat/long: 30.24457, -98.12511); Onion Creek at Hudson (#4595; lat/long: 30.1688, -98.2190); and Rinard Creek at Bradshaw (#233; lat/long: 30.1381, -97.77395) (Fig. 1).

WATER QUALITY

We measured *in situ* water temperature (°C), conductivity (µS/cm), dissolved oxygen (mg/L), and pH hourly with a Hydrotech Hydrolab multiprobe data logging sonde. A surface water grab sample was collected at the beginning (3 November 2015) and end (23 November 2015) of the cotton strip deployment period for: NH₄⁺, NO₂+NO₃-N, total Kjeldahl nitrogen (TKN), orthophosphate (OP), total phosphorus (TP), and SO₄²⁻.

FIELD DEPLOYMENT

The below methods were provided as guidance by Dr. Tiegs and were modified as necessary to accommodate our specific field site conditions. A total of 37 cotton strips were provided by Dr. Tiegs, along with labels, plastic pages with sleeves for return shipping, and the required sterilizing tablets and small centrifuge tubes. At each site a total of eight cotton-strips were deployed (Fig. 2A). Two strips were placed at an upstream and downstream location in riparian leaf litter (Fig. 2B) and two strips were placed in the riffle flow line of the stream (Fig. 2C).

- In the lab, nylon cords were cut to approximately 1 m length and two loops were tied into the cord, one loop near the middle of the cord and the other at the end of the cord. While wearing nitrile gloves, holes were punctured into one end of each cotton strip to accommodate a zip tie. A zip tie was then pushed through the opening in the cotton strip and closed on the cord loop. Cords with attached cotton strips were bundled together in clean zip-lock bags, and bags were labeled for each site.
- Cotton strip riffle deployment. At each riffle habitat we installed rebar into the stream sediment at a point approximately half-way across the wetted stream channel. We then tied the end of a cord with two cotton strips to the base of the rebar, as close to the sediment-water interface as possible. To prevent the cotton strips from flapping in the current, a small rock was placed on the rope immediately upstream from the cotton strip (being careful not to place the rock on the strip itself). The distance between each riffle where cotton strips were deployed was less than 20 m.

- Cotton strip riparian deployment. At the site a coin was flipped to determine which bank the riparian strips would be deployed. In an area adjacent to the riffle location of the in-stream cotton strip placement, we hammered a rebar stake into the soil of the riparian zone. Placement of riparian cotton strips was typically within 1 m of the riffle where leaf litter was thickest, with the exception of Onion Creek where riparian strips were deployed approximately 5 m perpendicular to the riffle. A cord with cotton strips was then tied to the base of the rebar and the cotton strips were laid flat within the leaf litter. This procedure was repeated for the next riffle habitat downstream.
- Control cotton strips. The five remaining control cotton strips were each placed in a sleeve of the provided plastic sheet page. A small sheet of paper labeled “control” was placed in the sheet sleeve with the cotton strip.
- Data logger deployment. A hydrolab was deployed in the up-river riffle of each creek by attaching a chain to the data logger and affixing the chain to a tree, or, if not available, another rebar post hammered into the substrate.
- Sediment size characterization. We visually (qualitatively) characterized the predominant size class of particles in the reach of each stream and entered the classification on the CELLDEX data sheet. Classes were:
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 - o Coarse-sand or smaller (>2 mm diam.)
 - o Fine-Pebble (2-8 mm diam.)
 - o Pebbles (8-32 mm diam.)
 - o Coarse Pebbles (32-64 mm diam.)
 - o Cobbles (64-256 mm. diam.)
 - o Boulders (>256 mm)
- Wetted channel width and depth estimation: We used measuring tape to estimate the mean width of the wetted stream channel (to the nearest 0.1 m) and a meter stick to measure the riffle depth (to the nearest 1.0 cm) at each riffle where cotton strips were deployed. Data were entered on the CELLDEX data sheet.
- Site coordinates. A latitude and longitude of each site was taken near the upriver riffle at each site and recorded on the CELLDEX data sheets.

FIELD RETRIEVAL

- While wearing nitrile gloves, we used a pair of scissors to cut the cord with the cotton strips from the rebar stakes. We then cut the zip tie binder from each cotton strip, handling the strips by gently holding only one end of a strip.
- Cotton strip DNA/RNA sampling: We put distilled water into a centrifuge tube (50 mL) and added a sterilizing tablet. Once dissolved, the scissors were dipped into the centrifuge tube to sterilize, and then thoroughly dried. We cut a 2 cm length from the end of one cotton strip from a

riffle and riparian zone and placed them in a pre-labeled small centrifuge tube containing “RNA Later” solution. The tube was sealed and the procedure repeated at each site.

- In a small bowl we added approximately one centimeter of fresh ethanol. A cotton strip was placed into the alcohol and the strip was gently brushed for 10 seconds to remove adhering sediment and biofilm.
- Each cotton strip was then placed into the center of a small (approx. 10 cm x 10 cm) square sheet of aluminum foil pre-cut in the lab. The sides of the foil were folded over the strip, making an envelope. The strip was kept flat within the foil. A pre-printed label (provided) was added to the foil and then the sample was placed into a small rigid container for transport back to the lab.

LAB PROCESSING

- In the lab, each foil envelope was opened minimally and placed in an oven set to approximately 40°C and left to dry for a minimum of 24 h.
- Once dry, the cotton strips were removed from each foil envelope and placed into a sleeve of the plastic sheets along with an identifying paper label. A piece of tape was affixed to each sleeve to ensure the label and cotton strip could not slip out in transit.
- Sleeve pages containing the cotton strips were placed in a rigid envelope and shipped to Dr. Tieg. The small centrifuge tubes containing strip sections and the “RNA Later” solutions were shipped to Dr. Guy Woodward in the United Kingdom for microbial fingerprinting.

RESULTS

Air temperature was downloaded from www.wunderground.com from a station near Bull Creek (lat/long: 30.24, -98.26). The lowest air temperature recorded was -1.3°C and the warmest was 30.5°C. The median and average air temperature over the deployment period was 16.5°C and 16.1°C, respectively.

Median and average water temperatures were similar across all streams ($\approx 18^\circ\text{C}$; Table 1). Highest average pH (8.1) was observed at Onion Creek, followed by Barton Creek, Bull Creek, and the lowest average pH of 7.4 was observed at Rinard Creek. Median conductivity values for all streams were between 522-595 $\mu\text{S}/\text{cm}$ with Barton Creek having the highest average (590 $\mu\text{S}/\text{cm}$); over a three day period in mid-November at the Bull Creek site, abnormally low conductivity measurements were recorded (approx. 4 $\mu\text{S}/\text{cm}$) despite an apparent lack of rainfall and no apparent failure in the other Hydrolab sensors (Table 1). Highest average DO concentrations (9.5 mg/L) were recorded at Onion Creek and lowest average concentrations (7.4 mg/L) were observed at Rinard Creek.

During the deployment period, PO_4^{2-} concentrations were below lab detection limits at all sites; NH_4^+ and TP were also below detection limits at all sites with the exception of Rinard Creek (Table 2). Sulfate, TKN, and $\text{NO}_2 + \text{NO}_3\text{-N}$ concentrations were generally lowest at Bull Creek and greatest at Rinard Creek. Tensile strength measurements indicated greatest decomposition of cotton strips deployed in the riparian and riffle habitats at Barton Creek (Table 3). The pounds required to tear the strips was significantly lower than for the control strips, based on comparison of means and 95% confidence intervals. The tensile strength of strips deployed in the Rinard riparian zone were the only other significantly different

measurements; reductions in tensile strength of strips from the Bull Creek riparian and stream habitats were marginally lower than controls (non-significantly, Table 3).

DISCUSSION

While we do not have results from the global effort, the overall lack of significant degradation of the cotton strips deployed at our stream sites relative to control cotton strips indicates our reference streams are supporting low rates of organic matter decomposition. Rains across the region before the initiation of our study likely contributed to the elevated TKN and $\text{NO}_2+\text{NO}_3\text{-N}$ concentrations measured during cotton strip deployment relative to the end of the deployment period. Rinard Creek was especially turbid during deployment which would have also contributed to the elevated NH_4^+ and TP concentrations. However, low nutrient concentrations, like those observed in our final sampling, are more typical of these stream systems (Clamann et al., 2015). The riffle decomposition rates we observed would be influenced by the low nutrient concentrations of our study systems. Ferreira et al. (2015) found that across a range of studies and stream systems, nutrient enrichment can increase decomposition rates by 50%. Among the sites, we observed the lowest tensile strength (and thus greatest microbial decomposition) at Barton Creek (Table 3). Besides nutrient concentrations, enzymatic activity, and thus decomposition rates, has also been positively related to pH, specific conductance, and dissolved oxygen concentrations all of which were typically greatest in Barton Creek than the other sites (Table 1; Reddy and DeLaune, 2008). Within a site, decomposition rates were marginally lower in the riparian habitats relative to those within the stream riffles. This may be due to the fully aerobic conditions of the riparian zone which promotes faster decomposition (Reddy and DeLaune, 2008). This study has provided a new collaboration and application of a standardized method for the measurement of a difficult to evaluate but important ecosystem service. This work will allow us to place Austin's creeks, heretofore characterized as being in a "good" condition (Clamann et al., 2015), into a global context in terms of nutrient status and microbial activity. It is hoped that in the future, creeks in a degraded condition can be evaluated with the same methods. Additionally, should there be any changes in the trophic status of any of the creeks used in this study, we now have additional baseline data for evaluating biological responses.

References

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Tables

Table 1. Summary statistics of parameters measured hourly from the riffles of four Austin streams over a three week period. Abbreviations: Temp. – temperature; Sp. Cond. – specific conductivity; DO – dissolved oxygen; N – total sample number; Min – minimum value recorded; Max – maximum value recorded; CI – confidence interval (at $\alpha = 0.05$); Std. dev. – standard deviation.

Creek	Statistic	Temp. (°C)	pH	Sp. cond. (µS/cm)	DO (mg/L)		Creek	Statistic	Temp. (°C)	pH	Sp. cond. (µS/cm)	DO (mg/L)
Bull	N	472	472	472	472		Onion	N	472	472	472	472
	Min	14.59	7.61	4.00*	6.91			Min	11.02	7.88	203.00	8.17
	Max	21.44	7.85*	577.00	8.28			Max	23.20	8.12	555.00	11.91
	Median	18.52	7.68	559.00	7.68			Median	17.84	8.06	522.00	9.58
	Mean	18.54	7.69	439.42	7.67			Mean	18.05	8.04	505.71	9.53
	95% CI	0.12	0.01	17.51	0.02			95% CI	0.20	0.00	4.76	0.06
	Std. dev.	1.34	0.06	194.12	0.26			Std. dev.	2.25	0.05	52.71	0.68
Barton	N	472	472	472	472		Rinard	N	472	472	472	448
	Min	11.98	7.78	512.00	7.68			Min	11.77	7.25	325.00	4.32
	Max	22.97	8.01	625.00	10.60			Max	23.58	7.62	614.00	9.26
	Median	18.42	7.90	595.00	8.78			Median	18.57	7.40	532.00	7.36
	Mean	18.48	7.90	590.19	8.81			Mean	18.72	7.41	521.32	7.40
	95% CI	0.18	0.00	2.41	0.05			95% CI	0.20	0.01	5.21	0.08
	Std. dev.	2.03	0.04	26.71	0.50			Std. dev.	2.24	0.08	57.79	0.90
<p>*There was a 0.72" rain event on 17 Nov 2015 that appears to have significantly impacted Bull Creek specific conductance and pH for a 3-4 d period.</p>												

Table 2. Water chemistry measured at deployment (11/3/2015) and collection (11/23/2015) of cotton strips in four Austin streams. If the constituent concentration was below the laboratory reporting concentration, the limits of detection concentration are given in parenthesis.

Creek	Date	Parameter					
		PO ₄ ²⁻ (mg/L)	TP (mg/L)	SO ₄ ²⁻ (mg/L)	NH ₄ -N (mg/L)	TKN (mg/L)	NO ₂ +NO ₃ -N (mg/L)
Bull	11/3/2015	<0.01 (0.004)	<0.02 (0.008)	14.3	<0.02 (0.008)	0.19	0.27
	11/23/2015	<0.01 (0.004)	<0.02 (0.008)	16.2	<0.02 (0.008)	<0.10 (0.04)	0.15
Barton	11/3/2015	<0.01 (0.004)	<0.02 (0.008)	30.9	<0.02 (0.008)	0.18	0.24
	11/23/2015	<0.01 (0.004)	<0.02 (0.008)	41.4	<0.02 (0.008)	0.14	0.08
Onion	11/3/2015	<0.01 (0.004)	<0.02 (0.008)	18.7	<0.02 (0.008)	0.27	0.50
	11/23/2015	<0.01 (0.004)	<0.02 (0.008)	25.4	<0.02 (0.008)	0.17	0.27
Rinard	11/3/2015	<0.01 (0.004)	0.08	53.9	0.12	0.96	0.50
	11/23/2015	<0.01 (0.004)	<0.02 (0.008)	79.3	<0.02 (0.008)	0.43	0.64

Table 3. Summary statistics from cotton strip tensile strength measurements from four Austin streams. Upstream and downstream blocks were combined for each stream reach. Abbreviations: n – total sample number; Std. dev. – standard deviation; CI – confidence interval (at $\alpha = 0.05$).

Creek	Statistic	Riparian strips tensile strength (lbs.)	Stream strips: tensile strength (lbs.)
Bull	Mean (n = 4)	65.70	63.10
	Std. dev.	3.73	8.50
	95% CI	3.66	8.33
Barton	Mean (n = 4)	46.38	52.83
	Std. dev.	15.14	11.65
	95% CI	14.84	11.42
Onion	Mean (n = 4)	66.40	68.85
	Std. dev.	11.93	4.74
	95% CI	11.69	4.65
Rinard	Mean (n = 4)	66.48	67.13
	Std. dev.	0.71	6.78
	95% CI	0.70	6.65
Control	Mean (n = 5)	73.36	
	Std. dev.	5.99	
	95% CI	5.25	

Figures

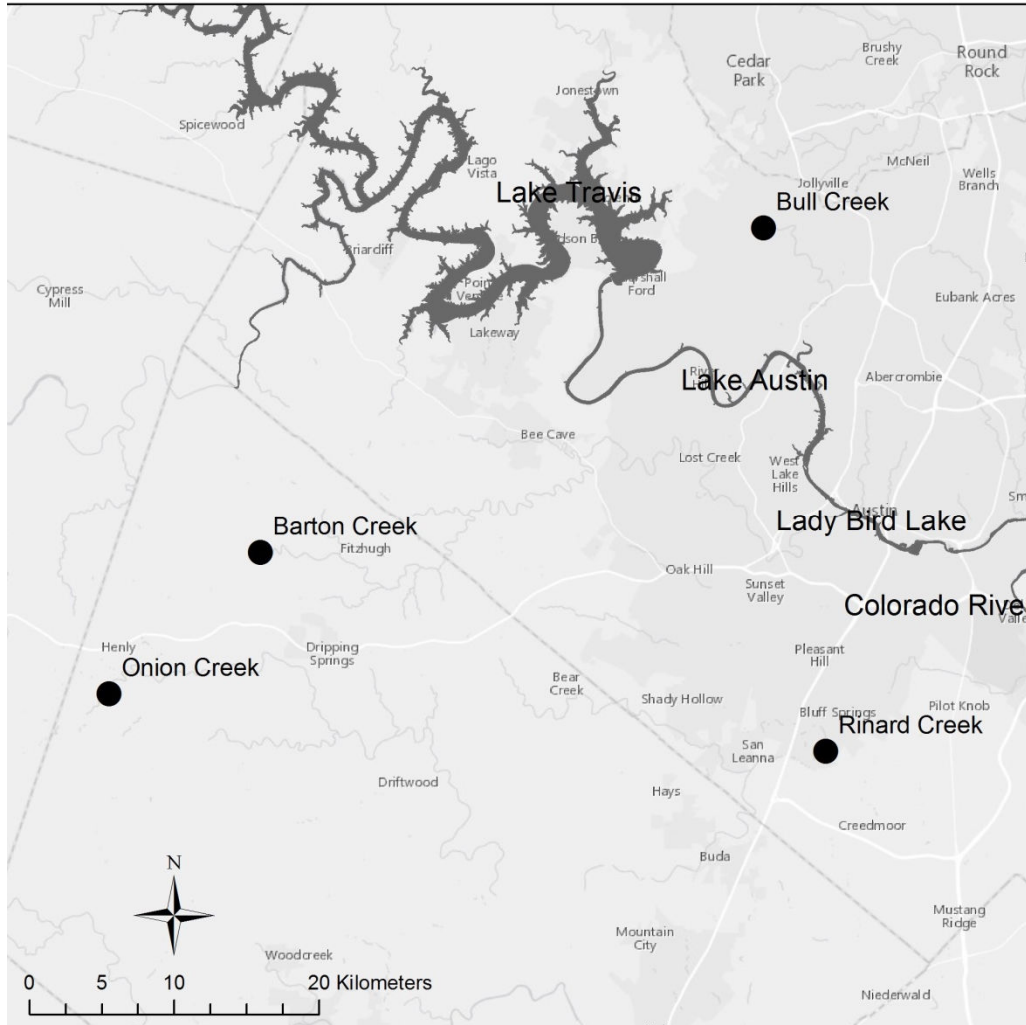


Figure 1. Creek locations around Austin, TX for cotton strip deployment.

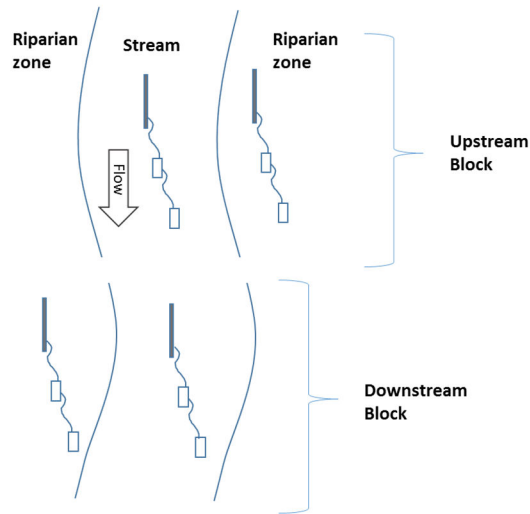


Fig. 2A. Schematic diagram showing the deployment of cotton strips at a site. Four strips total in each stream and each riparian zone will be deployed, and distributed between two blocks: one upstream, and one downstream. The approximate distance from the riparian stakes to the stream stakes will be 5 m.

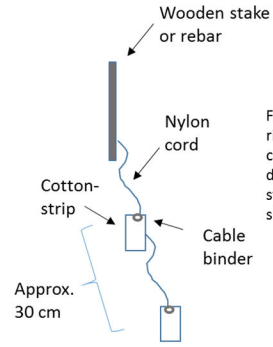
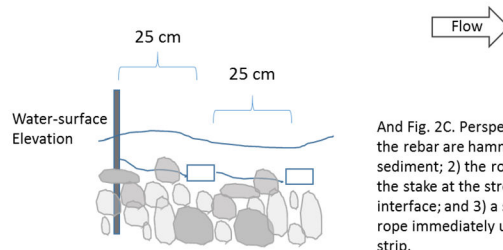


Fig. 2B. Enlargement of the upstream block in the riparian zone showing the attachment of two cotton strips to the stake via a nylon cord. The distance between the stake and the first cotton strip, and the distance between cotton strips, should be approximately 25 cm.



And Fig. 2C. Perspective illustrating that 1) the rebar are hammered well into the stream sediment; 2) the rope is tied to the base of the stake at the stream water-sediment interface; and 3) a small rock is placed on the rope immediately upstream of the cotton strip.

Figure 2. Field deployment protocol for cotton strips provided by Dr. Tieg.

The work of 153 researchers from 40 countries has led to new findings on the effect of climatic factors on river-based ecosystems. The findings are published in the latest issue of the journal *Science Advances*.

The study found that climatic factors, such as temperature and moisture, influenced carbon-cycling rates of river-based ecosystems. Carbon cycling is critical for the functioning of systems across a range of spatial scales, from local food webs to the global climate.

“River ecosystems play significant roles in the global carbon cycle by regulating rates of decomposition and transporting organic matter to the oceans, but we have only a rudimentary understanding of how decomposition rates vary from river to river,” said Scott Tiegs, a biology professor at Oakland University in Michigan, who led the study.

Unlike most previous studies on carbon cycling in streams and rivers, the methodology in this study was identical across all field sites. The study made use of a standardized, easy-to-use bioassay, which enabled a large number of researchers to participate in the study.

“As a result, we were able to quantify decomposition rates in over 500 rivers across the globe, including every continent,” Tiegs said.

The paper noted that the climatic factors that govern decomposition rates are increasingly impacted by human activities. These findings will help researchers establish baselines to quantify environmental impacts to the functioning of ecosystems on a global scale.

“In addition to providing fundamental information on how river ecosystems function, our results provide baseline data that will enable future researchers to evaluate large-scale ecological responses to warming and other dimensions of global climate change,” said Tiegs.

The research was sponsored by the Ecuadorian Science Foundation.

ECOLOGY

Global patterns and drivers of ecosystem functioning in rivers and riparian zones

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River ecosystems receive and process vast quantities of terrestrial organic carbon, the fate of which depends strongly on microbial activity. Variation in and controls of processing rates, however, are poorly characterized at the global scale. In response, we used a peer-sourced research network and a highly standardized carbon processing assay to conduct a global-scale field experiment in greater than 1000 river and riparian sites. We found that Earth's biomes have distinct carbon processing signatures. Slow processing is evident across latitudes, whereas rapid rates are restricted to lower latitudes. Both the mean rate and variability decline with latitude, suggesting temperature constraints toward the poles and greater roles for other environmental drivers (e.g., nutrient loading) toward the equator. These results and data set the stage for unprecedented "next-generation biomonitoring" by establishing baselines to help quantify environmental impacts to the functioning of ecosystems at a global scale.

INTRODUCTION

Organic carbon that enters river and riparian ecosystems meets one of many fates: It is mineralized and released to the atmosphere as CO₂ or CH₄, incorporated into local food webs, or routed downstream to

join long-term storage pools in marine or lake sediments (1–3). The rate at which organic carbon is processed determines which of these fates predominates and has important implications for the functioning of ecosystems from local to global scales. While rates vary widely over broad spatial scales (4, 5), logistical constraints and standardization issues have hindered elucidation of global patterns and environmental controls. Many investigations have explored organic-matter processing

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in streams and rivers (fig. S1), but methodological differences among studies—especially the use of different substrates—have impeded mechanistic understanding of what drives carbon processing rates at large spatial scales. For example, the quality of leaf litter used in decomposition assays varies systematically across the planet, potentially masking patterns in carbon processing attributable to extrinsic factors such as microbial community structure and environmental conditions—factors that are increasingly affected by human activities. Because different substrates are used across studies, we have an underdeveloped knowledge of the degree to which rates are controlled by substrate quality or by the microbial communities and environmental conditions that characterize a particular location. Overcoming these methodological limitations and filling these knowledge gaps is necessary to gauge large-scale controls on carbon processing, establish baselines for emerging global assessment initiatives (e.g., Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and Intergovernmental Panel on Climate Change), and accurately quantify human impacts to the global carbon cycle (6–8).

To these ends, we report findings from the first global Cellulose Decomposition Experiment (CELLEX), which combines a rigorously

standardized bioassay with a peer-sourced network of research professionals to evaluate carbon processing rates in Earth's rivers and riparian zones. We applied a standardized cotton-strip assay (9, 10) simultaneously in river channels and adjacent riparian habitats to quantify microbial decomposition of cellulose, the most abundant polymer on Earth, the main component of terrestrial plant litter, and an important source of greenhouse gas emissions from riverine ecosystems (11). This assay quantifies the inherent capacity of ecosystems to process organic carbon—their decomposition potential—and integrates the influences of microbial community structure and environmental factors such as nutrient availability, temperature, and moisture on microbial activity. A key advantage of the assay is that it lacks variation in substrate attributes such as nutrient content and toughness. Experimental materials were distributed to 150 researchers in the CELLEX Consortium from ~125 institutions who deployed and retrieved the strips at more than 1000 river and riparian sites. Cotton strips were then returned to the coordinating laboratory for standardized measurements of the degree of decomposition. Field sites spanned 140° of latitude, were located on all continents, and included each of Earth's major biomes (Fig. 1A). Because we used an identical assay across all sites,

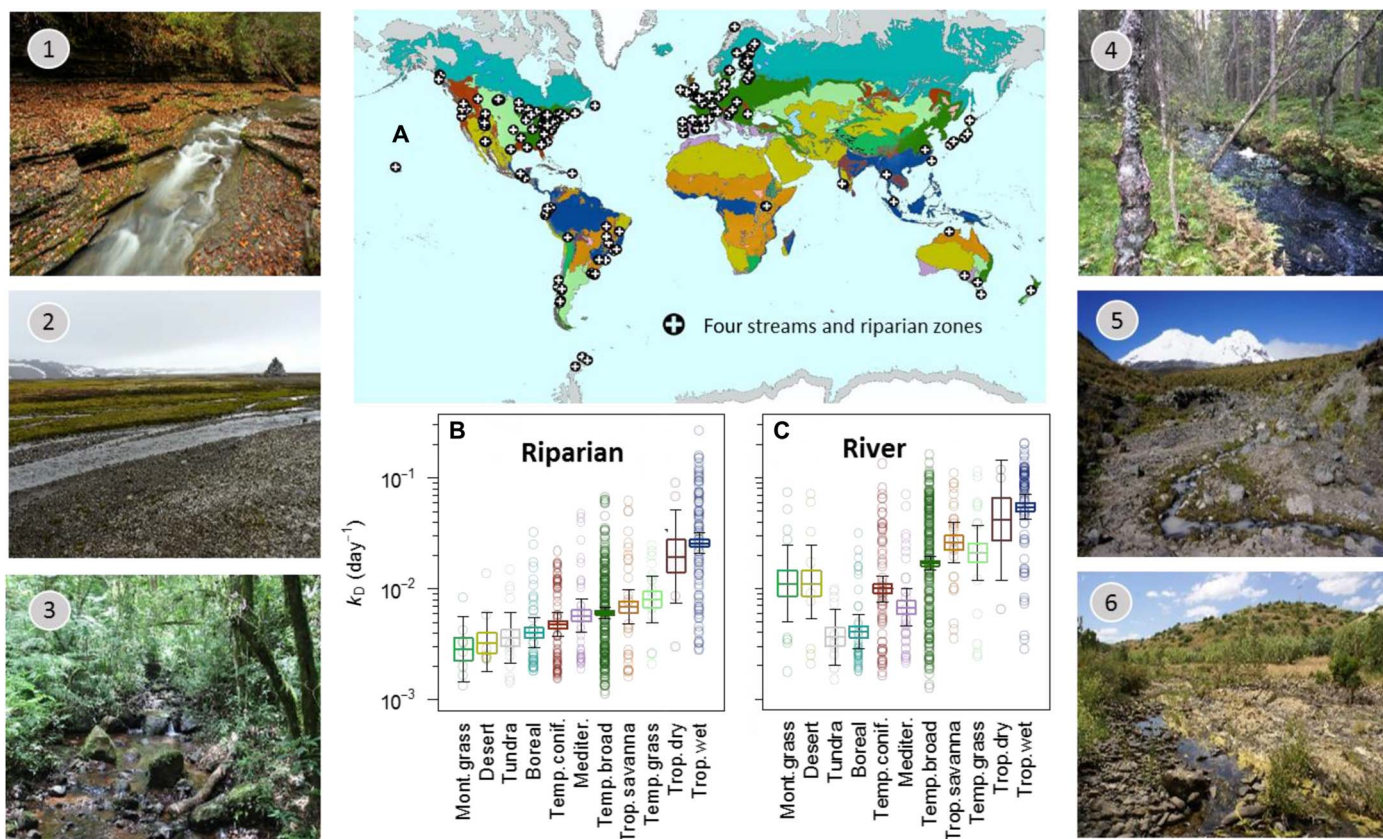


Fig. 1. Global distribution of field sites, mean decomposition rates across biomes, and photos of select field sites. More than 500 river-riparian pairs ($n = 514$ river, $n = 533$ riparian) were located in approximately 40 countries, on each continent, and spanned more than 140° of latitude. Colors correspond to Earth's major terrestrial biomes (A). The estimated mean decomposition rates ($\pm 95\%$ credible intervals) of cotton strips (k_D) varied across biomes in riparian zones (B) and their adjacent rivers (C). Photographs are shown for rivers and zones in temperate broadleaf forests (1), tundra (2), tropical wet forests (3), boreal forests (4), montane grassland (5), and Mediterranean ecosystems (6). Photo credits: Stream 1. Olivier Dangles, Centre d'Ecologie Fonctionnelle et Evolutive, IRD, CNRS. Stream 2. Jerzy Smykla, Institute of Nature Conservation, Polish Academy of Sciences. Stream 3. Luis Hepp, Department of Biological Sciences, Regional Integrated University of Upper Uruguay and Missions. Stream 4. Jukka Aroviita, Finnish Environment Institute (SYKE). Stream 5. Scott Tiegs, Department of Biological Sciences, Oakland University. Stream 6. Manuel Graça, MARE—Marine and Environmental Sciences Centre, University of Coimbra.

we were also able to relate the wide-ranging processing rates that we observed to large-scale environmental drivers of carbon processing in a biogeographical and climatic context.

RESULTS AND DISCUSSION

We found that Earth's major biomes have distinct carbon processing signatures in both rivers and riparian zones (Fig. 1). Rates are lowest in cold biomes, such as tundra and boreal forests, whereas those in tropical forests (both wet and dry) are up to an order of magnitude greater; most temperate biomes are bracketed by these extremes (Fig. 1, B and C). These patterns suggest that—similar to terrestrial ecosystems—broad-scale climatic factors, temperature and precipitation, are master variables that set the boundaries of carbon processing rates in rivers and riparian zones at the global scale. Biome identity accounted for a similar amount of variance in rivers and riparian habitats (30% versus 28%, respectively); this similarity is notable because the biome concept was originally developed for terrestrial rather than aquatic ecosystems (12). This highlights the close coupling between riverine ecosystems, their catchments and regional climate, and the utility of the biome concept for river and riparian ecosystems.

Knowledge of ecosystem functioning in tropical rivers and riparian zones is poorly developed, even though these rivers constitute >50% of Earth's runoff (12) and form a major carbon input to the global ocean (13). Moreover, tropical rivers are hot spots for CO₂ evasion (14, 15), yet whether the predominant source is instream decomposition of organic matter (dissolved and particulate) derived from terrestrial plants, or CO₂ imported from terrestrial root and soil respiration (14), is largely unknown. Very high terrestrial primary production in tropical forests generates vast quantities of plant litter, and our data show that cellulose—

the most abundant litter constituent—can be very effectively processed by microbial communities in tropical rivers and riparian areas (Fig. 1, B and C). This rapid processing occurred despite the fact that the cellulose substrate does not supply substantial amounts of nutrients (e.g., nitrogen and phosphorus) to facilitate decomposition. Although the cellulose used in our assay differed in quality from the litter that enters tropical rivers, the exceptionally rapid decomposition that we observed is a novel line of evidence suggesting that the microbial processing of plant material is a major CO₂ source (11, 14, 15).

We found clear patterns of processing rates with latitude; both the upper limit of processing rates and variability among rivers and riparian zones decrease with latitude (Fig. 2, A and B). These results are evidenced by the increasing slope of each quantile in these relationships (Fig. 2, A and B, insets), revealing that carbon processing can be slow anywhere on the planet, whereas rapid rates are reached only at low latitudes. Dampening of peak rates with distance from the equator suggests tighter climatic constraints toward the poles—such as temperature limitation—and that additional factors (e.g., nutrient availability, pH, and microbial-community structure) come into play toward the equator.

Across a broad range of quantiles, the slope of relationships between processing rates and latitude is greater in rivers compared to riparian zones, a finding that suggests that rivers are more sensitive to parameters that covary with latitude (e.g., temperature) (Fig. 2, A and B, insets). For sites with the slowest decomposition rates (i.e., quantiles 5 to 10%), the lack of a slope illustrates that slow rates can be found across the broad range of latitudes that we examined, in both rivers and riparian zones. For the majority of the data (quantiles 15 to 80%), the slope of the relationship between rates and latitude is greater in rivers, evidenced by nonoverlapping credible intervals between

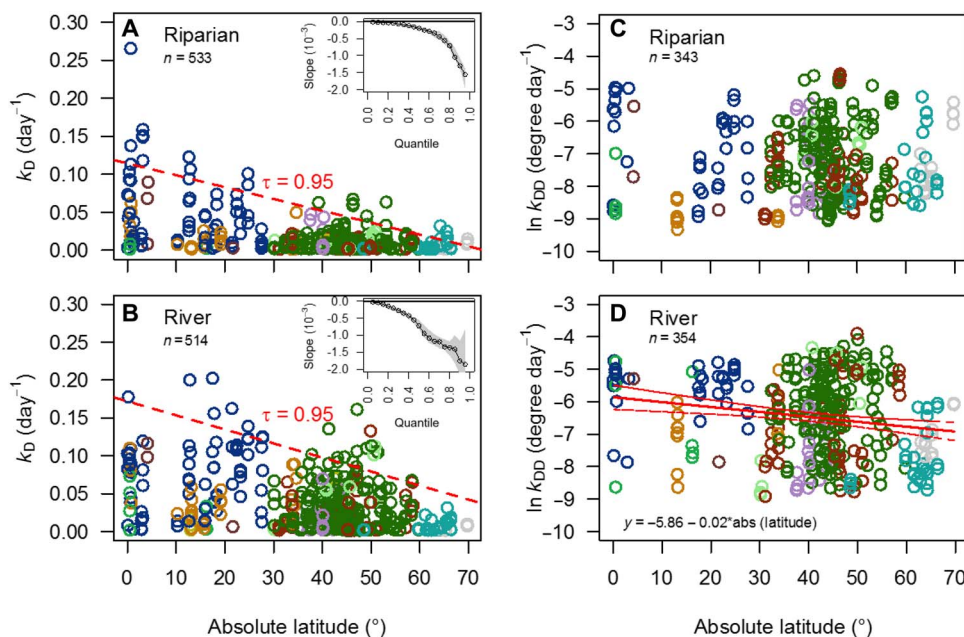


Fig. 2. Relationships between absolute latitude and decomposition rates in riparian zones and rivers. Quantile regression in riparian zones (A) and rivers (B) showing decomposition rates per day (k_D) versus latitude and the 95th quantile (dashed line). Inset panels (A) and (B) show the increasing slope of regression lines with each 5-centile. In each habitat, slow decomposition can be observed regardless of latitude; latitude, however, imposes a strong upper constraint on decay rates. When the effect of temperature is removed by expressing decomposition on a per-degree-day basis (k_{DD}) (C and D), there is no significant relationship between decomposition and latitude in riparian zones (C), and a negative relationship is observed with latitude in rivers (D). Colors match the biomes shown in Fig. 1.

these two habitat types; this greater slope indicates that decomposition in rivers is more sensitive to changes in latitude. For ecosystems that decompose the fastest (i.e., quantiles >85%), the variability among rivers is large and our estimate of the relationships with latitude is not well constrained and is therefore not significantly different between rivers and riparian zones.

In an extensive meta-analysis of data on leaf-litter processing, rates of microbial processing in rivers increased with latitude even after accounting for strong covariation of temperature (5). The proposed mechanism for the increase was physiological adaptation that enables river microbes to remain active during periods of peak litter inputs despite low temperatures. However, our data show that when a standard substrate is used to control for variation in litter quality, temperature-normalized processing rates in rivers decline with latitude (Fig. 2D), with the normalized rates, on average, being 4.1 times greater near the equator than at our highest latitude sites. No relationship was observed in riparian zones (Fig. 2C), suggesting that in these habitats, the environmental variables that covary with latitude are of secondary importance to others, such as moisture limitation as a prime factor. In rivers and riparian zones, we documented considerable variation in temperature-normalized rates across most latitudes, highlighting the variety of environmental conditions that influenced decomposition rates, and the need for additional information beyond geographic location to explain them.

Differences in litter substrate choice are a plausible explanation for contrasting results between our study—which made use of a single standard substrate—and the global meta-analysis—which synthesized studies across many locally collected types of leaf litter. Plant traits vary systematically across large spatial scales (16, 17), as does the quality of riparian leaves and litter (18), both of which increase with latitude. For example, the phosphorus content of leaves increases with distance from the equator (18), a pattern that could foster large-scale adaptations that enable stream microbes to decompose substrates of poor nutrient content, such as litter rich in cellulose and lignin. Together with previous results, ours suggest that, independently of temperature, the inherent capacity of ecosystems to decompose organic matter declines with latitude but that systematic global variation in litter traits might mask these effects and cause apparent decomposition rates to increase with latitude. This highlights the necessity for a standard substrate when using decomposition assays as part of large-scale bioassessment protocols.

Rivers and their riparian zones are closely connected through reciprocal exchanges of organic carbon, and processes in one habitat have ramifications for the other (19, 20). To better understand their relative functioning, we evaluated the log ratio of carbon processing rates in paired river-riparian sites. We found that rivers have rates (k_D) that are, on average, nearly twice those of the adjacent riparian habitats (median River k_D /Riparian $k_D = 1.77$, $n = 514$ sites) (Fig. 3). Standardizing for temperature (k_{DD}) does not change the magnitude of this disparity (median River k_{DD} /Riparian $k_{DD} = 1.86$, $n = 314$ sites), reflecting the strong correlation between average air and water temperature. The ratio varies widely across sites, ranging from 70 to 0.05 (fig. S2). Rates in riparian zones of montane grasslands and deserts are extremely slow (Fig. 1B), whereas rates in the adjacent river channels are similar to the global average (Figs. 1C and 3). In contrast, cellulose-decomposition rates in only 2.5% of riparian zones significantly exceeded those in rivers (fig. S2). Given the exchange of carbon between rivers and riparian zones, and their discrepancy in processing potentials between these two habitats, streams are hot spots for carbon processing, while riparian

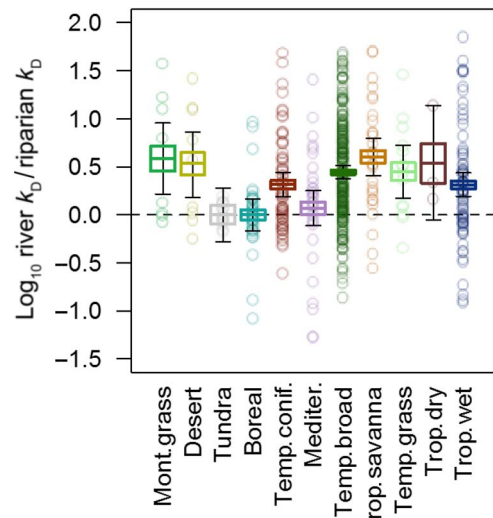


Fig. 3. The log response ratio of river decomposition (k_D) to riparian decomposition (k_D). Bayesian estimates of median ratios are shown as horizontal lines, with 50 and 95% credible intervals of the median as the box and whiskers, respectively. Open symbols show individual riparian-river pairs color-coded by biome ($n = 514$). Values greater than zero (dashed line) indicate significantly more rapid decomposition in rivers relative to their riparian zones.

zones, given their relatively slow carbon turnover, likely serve as sources of organic carbon well past periods of organic matter input (e.g., autumn leaf fall in temperate zones). The magnitude of river/riparian processing rates shows no relationship with latitude (fig. S3A), unless the effects of temperature are removed and then a negative relationship emerges (fig. S3B). This finding indicates that the relative difference in temperature-adjusted processing between habitats is, on average, greater toward the poles. Variation in the relative processing rates of rivers and riparian zones highlights functional biodiversity across broad latitudinal gradients and across Earth's biomes. And in many biomes this variation highlights the importance of local habitat diversity to create heterogeneity in ecosystem functioning at a landscape scale.

The variable relative processing rates in coupled riparian-river habitats may be caused by differential temperature sensitivity between rivers and riparian zones. The significantly greater apparent activation energy calculated for river channels (0.68 eV) shows that, on average, carbon processing in river habitats is far more sensitive to temperature than in riparian zones (0.40 eV; Fig. 4). This terrestrial-aquatic disparity mirrors patterns in a meta-analysis of whole-ecosystem respiration (21) and our river data almost exactly match the theoretically expected activation energy according to the metabolic theory of ecology (22). These disparities suggest that different drivers are at play in river channels and riparian habitats, with water limitation being an obvious contender. This moisture-limitation hypothesis is further supported by similar decomposition rates observed in riparian and river habitats of cool mesic biomes, such as tundra and boreal forests (Fig. 3).

Because different factors constrain carbon processing in riparian and river habitats, responses to environmental change could differ greatly among biomes and habitats. In particular, warming and aridity are both predicted to increase across vast areas of the planet (23), a climatic trend that should increase processing rates in rivers

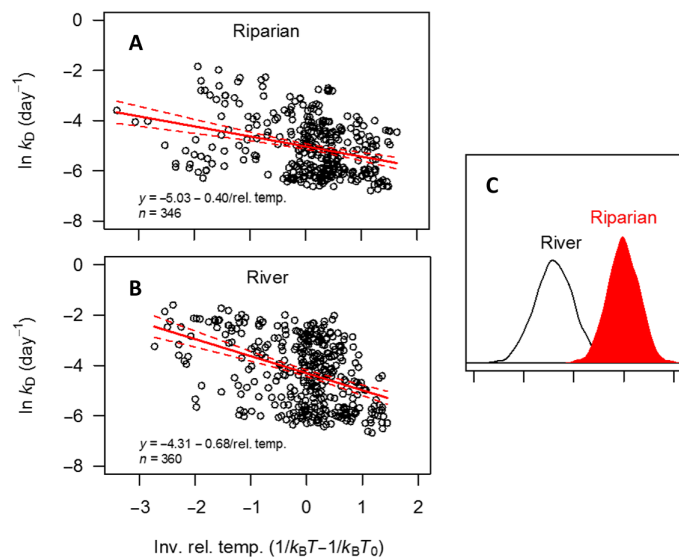


Fig. 4. Temperature sensitivity of cellulose decomposition in riparian zones and rivers. Arrhenius plots illustrating differences in the apparent activation energies of decomposition in riparian zones (A), 0.40 eV and rivers (B), 0.68 eV. (C) Posterior distribution of the slope estimates (i.e., apparent activation energy estimates), indicating that neither of the slopes overlap with zero (i.e., they are statistically significant) and that there is very little overlap between the slope estimates for decomposition in rivers and riparian zones.

yet decrease them in riparian zones. This dimension of relative processing rates between rivers and riparian zones—differential responses of a process between habitats under environmental change—represents a yet-to-be-explored portfolio effect (24) arising from habitat diversity that stabilizes mean processing rates at the landscape scale.

CONCLUSIONS

The >1000 river and riparian sites used in our study were deemed relatively free of human impacts. Consequently, by using an identical assay at all sites, we can unambiguously ascribe the variability that we document to naturally variable environmental conditions and biotic communities. Importantly, these environmental drivers include those that are increasingly affected by human activities such as temperature and moisture availability. This sensitivity to anthropogenically affected variables gives our data added value as a baseline for the biomonitoring of a functional ecosystem property. Moreover, the validated utility of combining a straightforward field assay with a large peer-sourced network of researchers, in tandem with the baseline dataset presented here, sets the scene for gauging ecosystem functioning at large scales to monitor impacts of global environmental change. In doing so, we address pressing needs for effective process-based tools (25) that can be deployed at large scales (6) by emerging international assessment programs (e.g., Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and Intergovernmental Panel on Climate Change) (7).

MATERIALS AND METHODS

Experimental approach

Our coordinated experiment used a peer-sourcing approach whereby each of approximately 150 research teams distributed worldwide de-

ployed a standardized assay in four rivers and their adjacent riparian zones. With this approach, we retrieved samples from 514 rivers and 533 riparian zones (1047 sites in total). Despite the unprecedented global coverage of our field experiment, gaps in spatial coverage exist as a result of a lack of available researchers in some areas (e.g., the Siberian steppe) or scarcity of flowing water ecosystems (e.g., Saharan Africa). Partners were drawn from professional relationships and research networks and by responses to invitations posted on the websites of professional organizations (e.g., the Society for Freshwater Science and Ecological Society of America). Each researcher was sent a kit that contained experimental materials, along with a detailed field and laboratory protocol. The distributed cotton strips were incubated in the field for approximately 4 weeks during 2015 and 2016 and shipped to the Aquatic Ecology Laboratory at Oakland University for analysis.

Decomposition assay

The cotton strip assay was chosen because the strips are composed of greater than 95% cellulose—the most abundant polymer on Earth and the main constituent of terrestrially derived leaf litter (15)—and because the assay is readily standardized (9). Such standardization is essential because failure to standardize so blurs large-scale patterns in the capacity of rivers and riparian zones to process organic carbon. For example, among the 2182 studies related to decomposition in riverine ecosystems published since 2000, only a handful have rates that are truly comparable (fig. S1). Even within studies, the attribution of differences in carbon processing rate to variation in environmental conditions is questionable because of the confounding effects that arise from variation in litter quality across space. This is inherently problematic at large spatial scales where there is growing appreciation of variation in leaf traits (16), including riparian litter (18). By using an identical cotton strip assay across all sites, we provide information on the capacity of ecosystems to process organic carbon. Additional reasons for using this assay are its sensitivity to environmental conditions, including temperature and nutrient availability (26), ease of use, suitability for both terrestrial and aquatic habitats, and the fact that dry samples can be readily shipped.

A trade-off of using any standardized organic matter in studies that span large spatial scales is that the quality of the standard organic matter will differ from natural inputs because their quality varies across large scales (18). In addition, because the quantity of organic matter inputs also varies spatially, decomposition assays do not necessarily reflect the quantity of organic matter that is being decomposed. Rather, the cotton strip assay and others (e.g., litter bag assays) are designed to quantify the relative capacity of ecosystems to decompose organic matter (i.e., decomposition potential) (10). Another trade-off is that the cotton strip assay isolates the activity of microbial heterotrophs and does not directly account for decomposition from the feeding activity of invertebrates (9).

The cotton strip assay relies on quantifying tensile strength loss of the cotton fabric, a process that reflects the microbial catabolism of cellulose (9, 10). Individual cotton strips (8.0 cm by 2.5 cm) were prepared from bolts of 12-ounce, heavy-weight cotton fabric (Style 548; Fredrix, Lawrenceville, GA, USA) and were each 28 threads in width (9). Strips were shipped to each partner along with reference strips that were not incubated in the field to obtain estimates of the initial tensile strength and to detect any changes occurring during shipping. Tensile strength was determined by placing each cotton strip in the jaws of a Mark-10 MG100 tensiometer mounted to a motorized test stand and pulling

them at a rate of 2 cm/min (9) until the strips tore. The maximum tensile strength (T_{MAX}) for each strip was recorded (in units of mass) and used for subsequent calculations. Individual T_{MAX} values from control and incubated strips were used in a hierarchical Bayesian model to calculate estimates of carbon processing rates (k).

Field methods

Each partner deployed the assay in four or more reference rivers (i.e., those characterized by minimal human impacts) and their adjacent riparian zones (i.e., the semi-aquatic terrestrial ecosystems immediately adjacent to permanent water bodies) during a time of the year when there were peak inputs of terrestrially derived organic matter (e.g., autumn leaf fall in temperate deciduous forests and the dry season in tropical dry forests). In each river, four replicate cotton strips were attached via cable binders and twine to stakes that were hammered into the river substrate of riffle or riffle-type habitats. This procedure was repeated in the riparian area adjacent to the river habitats where the cotton strips were deployed. In riparian zones, cotton strips were placed on the soil surface to simulate organic-matter input by senescent leaves. The cotton strips were distributed evenly between two locations in each habitat (i.e., each site) (2 cotton strips per location, 2 locations per habitat, 2 habitats, 4 rivers/riparian zones, and 32 cotton strips total per partner) that were separated by a distance of approximately five to seven bankfull channel widths. The strips were removed after approximately 3 to 4 weeks, an amount of time that was estimated to result in approximately 50% tensile strength loss; this degree of decomposition is believed to maximize the sensitivity of the assay to variation in environmental conditions (9).

Temperature data and Geographic Information System

In most instances, a temperature logger was placed in each river and each riparian zone and programmed to record hourly. This protocol yielded temperature data for 352 river and 343 riparian sites. Data from each logger were explored using a Python-based tool that facilitated data preprocessing tasks such as enforcement of a common date format, ensuring that all temperature readings were in centigrade, and transfer and consolidation of raw temperature readings from hundreds of files into a single database. The statistical computing package R was used to develop scripts for data processing, summarization, and plotting. Temperature readings for periods in which the logger was out of the water were removed, as were readings associated with obvious logger malfunctions. Plots and summary statistics were reviewed to confirm that remaining temperature readings were valid. Degree days were computed using positive temperature readings to generate daily mean temperatures and summing them.

Geographic Information System (GIS) and latitude and longitude data were used to ascribe a biome to each field site using a modified classification scheme (27) that was downloaded from the Environmental Systems Research Institute (ESRI) map server. In a small number of instances, field sites were located near transitional areas between two biomes and were noted by project partners as possibly having an incorrect biome classification. For the sake of repeatability, the original GIS-based biome classification method was retained. Latitude and longitude were determined at each river-riparian pair by each project partner using GPS or geo-referenced satellite photographs. A spatial join was performed between the biome layer and that which displayed the geographical location of the field sites. Biomes that do not have rivers and riparian zones (e.g., lakes) were not included in analyses.

Statistical analyses

Decomposition rates (k) were estimated from river and riparian zones separately using a standard exponential decay function and a Bayesian hierarchical model

$$g(k_j, P_j, T^C) = e^{-k_j \times P_j + T^C}$$

$$[k_j, \sigma, T^C, \sigma^C | P_j, y_{ij}, y_l^C]$$

$$\propto \text{lognormal}(y_{ij} | \log(g(k_j, P_j, T^C)), \sigma) \times \text{lognormal}(y_l^C | T^C, \sigma^C)$$

$$\times \text{lognormal}(k_j | -4.35, 2.09) \times \text{lognormal}(T^C | 4.2, 32)$$

$$\times \text{uniform}(\sigma | 0, 100) \times \text{uniform}(\sigma^C | 0, 100)$$

where y_{ij} is the natural log tensile strength measured on the i th replicate strip from the j th site, k_j is the site-specific decomposition rate (k_D , in units of 1/day), T^C is the natural log T_{MAX} of all the replicate incubated control strips (y_l^C), and P_j is the period of exposure in days. Because of the limited number of cotton strips at each site, individual error terms could not be modeled for each river or riparian habitat, but single pooled SD for incubated (σ) and control cotton strips (σ^C) provided adequate fits for all cotton strips. A similar model was used to calculate temperature-corrected decomposition rates (k_{DD} , 1/degree day), where the exposure period (P_j) was the mean daily temperature accumulated over the incubation period ($^{\circ}\text{C} > 0$) and the priors on k_j were $\alpha = -6.57$ and $\beta = 2.24$. Error terms were assigned relatively uninformative priors, but T^C and k were given informed priors. The prior for T^C was derived from data for control strips of the same material used in previous studies, and the inflated β was used to account for any potential handling damage that may have occurred in this unique study. For priors on k , we used a global synthesis of leaf litter breakdown (5) to place constraints on our expectations of decomposition rates (28). Decomposition rates were assumed to be distributed log-normally and were given mean natural log k_D and k_{DD} (α) that matched the values from the literature (5); however, the SD of natural log k_D and k_{DD} (β) was inflated (β prior = $\sigma \ln(k) \times 2$) to slightly reduce the information content of the prior (28), which was done to reflect potential differences in decomposition rates between litter and cotton strips. The ratio of decomposition rates in river and riparian habitats was calculated for each complete river-riparian pair. Bayesian models were implemented in JAGS using the R package rjags. Three parallel chains with different initial conditions were run, chains were evaluated for convergence and mixing, and posterior distributions from 10,000 samples were generated.

Decomposition rates from each river-riparian site combination were then used in subsequent analyses to assess patterns in decomposition across biome, latitude, and temperature. Estimates of mean (and 95% credible interval) decomposition rates and ratios of river-riparian rates were compared across biomes using a Bayesian implementation of linear models via the brms function in R. Similarly, linear regressions between k_D and the inverse relative temperature (normalized to 10 $^{\circ}\text{C}$) and k_{DD} and latitude were completed with the brms package. The slope of the relationship between temperature and $\ln(k_D)$ is activation energy (E_a), and values of E_a were contrasted between riparian- and river-incubated cotton strips by comparing the posterior distributions of those parameters. Variance explained (i.e., Bayesian R^2) by a factor (e.g., biomes) was calculated according to published procedures (29). All decomposition rates and river-riparian ratio values were log-transformed before fitting linear models. Standard decomposition rates (k_D) exhibited heterogeneous variance across latitudes, and so we used quantile regression to estimate relationships between k_D

and latitude. We used the `qantreg` package in R to model the linear slope of the k_D versus latitude regression at 5-centile increments.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/5/1/eaav0486/DC1>

Fig. S1. Exponential increase in the number of articles addressing organic matter decomposition in rivers during the past two decades.

Fig. S2. Scatterplot of decomposition rates per day in rivers versus riparian zones and a 1:1 line.

Fig. S3. Relative carbon processing rates between rivers and their riparian zones across latitudes.

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Supplementary Materials. All data presented here and model code are available at <https://github.com/dmcostello/CELLEX2018>. Additional data related to this paper may be requested from the authors.

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Supplementary Materials for

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Fig. S1. Exponential increase in the number of articles addressing organic matter decomposition in rivers during the past two decades.

Fig. S2. Scatterplot of decomposition rates per day in rivers versus riparian zones and a 1:1 line.

Fig. S3. Relative carbon processing rates between rivers and their riparian zones across latitudes.

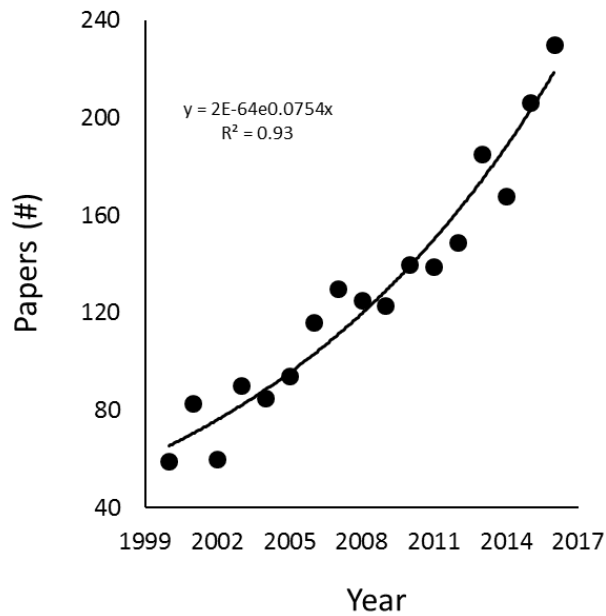


Fig. S1. Exponential increase in the number of articles addressing organic matter decomposition in rivers during the past two decades. Results are based on the Boolean search string “(breakdown OR decomposition) AND (stream OR river) AND (leaf OR organic matter OR litter)” entered in the ISI Web of Science during December 2017. Results revealed 2,182 individual publications from 2000 and 2016, and a strong positive relationship between the number of studies published per year and time ($R^2=0.93$, $p<0.0001$, $n=17$).

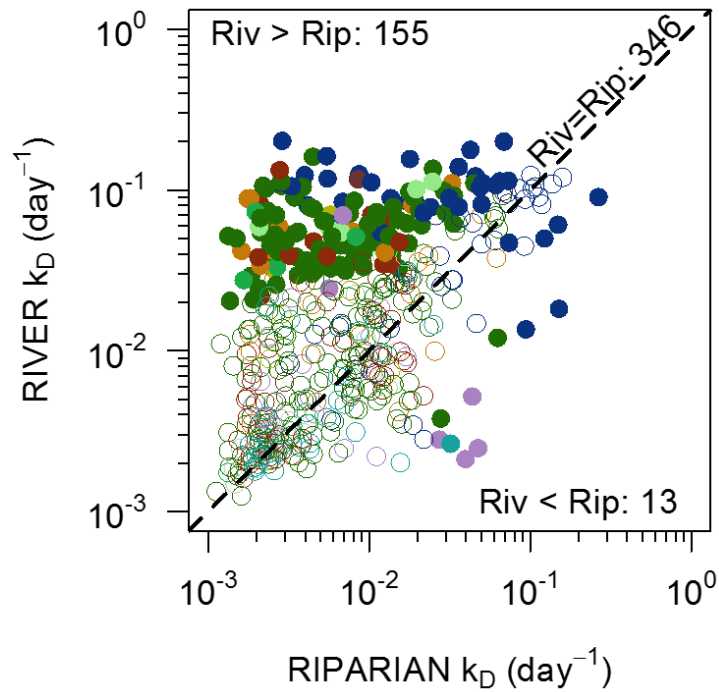


Fig. S2. Scatterplot of decomposition rates per day in rivers versus riparian zones and a 1:1 line. Solid data points above the 1:1 have decomposition rates in rivers that are significantly greater than those in riparian zones (n=155 river-riparian pairs); solid data points below the 1:1 indicate decomposition rates that are significantly more rapid in riparian zones than their rivers (n=13). Open data points overlap with the 1:1 line indicating that decay rates do not differ between these two habitats (n=346). Colors match the biomes shown in Fig. 1.

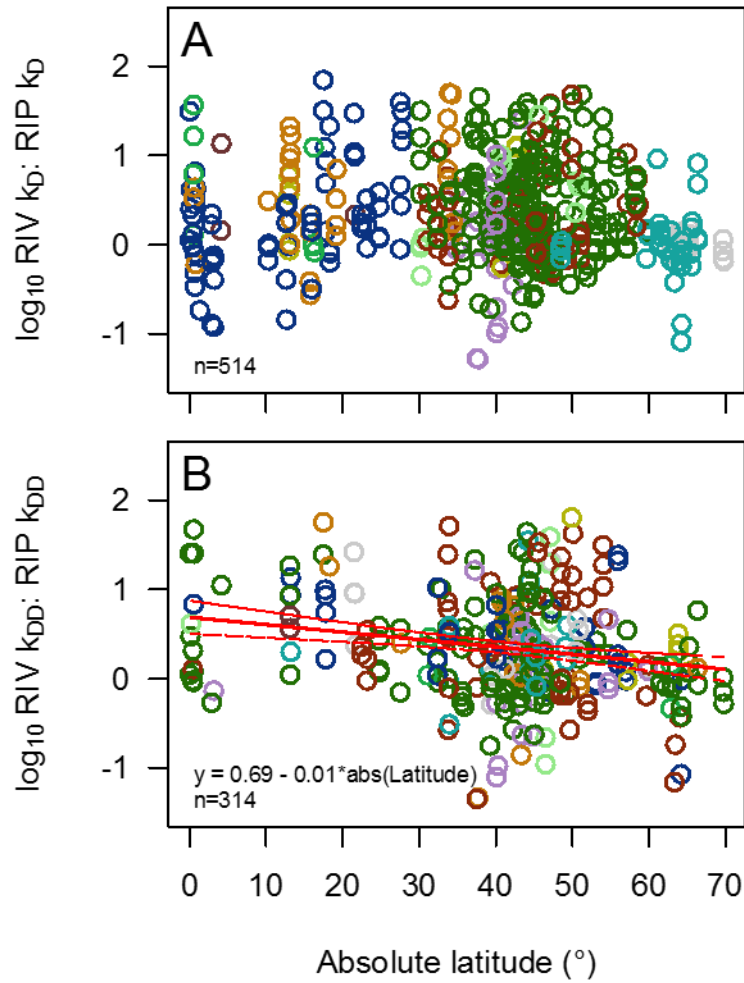


Fig. S3. Relative carbon processing rates between rivers and their riparian zones across latitudes. Rates are expressed as the ratio river:riparian. No relationship was found between decomposition rates expressed on a per day basis and latitude (A), but when temperature-normalized data were examined (i.e., rates were expressed on a per-degree-day basis), a significant negative relationship emerged.