RESEARCH ARTICLE

STREAM ECOLOGY

Human activities shape global patterns of decomposition rates in rivers

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Rivers and streams contribute to global carbon cycling by decomposing immense quantities of terrestrial plant matter. However, decomposition rates are highly variable and large-scale patterns and drivers of this process remain poorly understood. Using a cellulose-based assay to reflect the primary constituent of plant detritus, we generated a predictive model (81% variance explained) for cellulose decomposition rates across 514 globally distributed streams. A large number of variables were important for predicting decomposition, highlighting the complexity of this process at the global scale. Predicted cellulose decomposition rates, when combined with genus-level litter quality attributes, explain published leaf litter decomposition rates with high accuracy (70% variance explained). Our global map provides estimates of rates across vast understudied areas of Earth and reveals rapid decomposition across continental-scale areas dominated by human activities.

Earth's terrestrial ecosystems produce over 100 billion tons of plant detritus annually (*1*, *2*) and the fates of this organic matter—for example, long term storage, mineralization to greenhouse gasses, or incorporation into stream food webs—depend on the rate at which it is decomposed. River ecosystems are carbon-processing hotspots (*3*, *4*), receiving 0.72 billion tons of terrestrial carbon per year (*2*), an amount that is disproportionately important relative to the small fraction of nonglaciated land area (0.58%) that rivers occupy (*5*). Rivers connect terrestrial ecosystems with aquatic storage compartments including floodplains, lakes, and oceans, playing vital roles in the global carbon cycle and functioning both as organic matter conduits and reactors. Despite the widely recognized importance of flowing water in global carbon cycling (*6*–*8*), our understanding of variation in organic matter decomposition rates and their drivers at large spatial scales is still limited (*2*).

Large-scale spatial variation in organic matter decomposition in rivers and streams has been estimated by comparing leaf litter decomposition rates from studies conducted in regions with contrasting climates (*9*, *10*), conducting literature reviews of local field studies (*11*), developing conceptual models (*12*, *13*), and performing meta analyses (*14*, *15*). Coordinated, distributed experiments (*16*–*20*) have been particularly insightful as they generate directly comparable data across broad geographic areas and identify coarse resolution explanatory variables of decomposition rates in rivers, including differences in decomposer communities and biomes. Still, we lack a comprehensive understanding of how drivers such as climate, geology, vegetation, water quality, and soils interact to govern organic matter decomposition at large scales. Such knowledge gaps are particularly evident across the tropics and in lower income economies—ecologically important areas where rivers are grossly understudied relative to those in northern temperate zones. Quantifying patterns and controls of decomposition in these areas is critical, however, as much of Earth's terrestrial plant matter is annually produced in tropical forests (net primary production 16.0 to 23.1 billion tons of carbon) (*21*, *22*), and tropical rivers deliver 48 to 64% of the carbon moving from rivers to the ocean (*23*).

Effectively modeling carbon dynamics at the global scale—including areas where field data are scarce—requires a more mechanistic and process-based understanding of the many environmental and biotic factors that drive organic matter decomposition. Accurate estimates generated by combining existing empirical measurements with fine-scale geospatial and environmental data can provide multiple benefits. They can reduce the need for data collection from remote or difficult to access regions, subsequently generating baseline estimates for decomposition in understudied areas of the world. Global scale predictions also contri to a finer scale understanding of decomposi and support efforts to model planetary carbon dynamics. Models that can accurately predict current in situ decomposition rates across space are particularly valuable, enabling manipulation of environmental drivers in silico to predict impacts under scenarios of future global environmental change.

We present a predictive model fitted with global data from the Cellulose Decomposition Experiment (CELLDEX), a coordinated, distributed experiment on cellulose decomposition in rivers designed to reveal previously undocumented patterns in decomposition rates and the key factors driving this fundamental ecosystem-level process. Decomposition of cellulose—the most abundant organic polymer on the planet and a main constituent of plant litter—was quantified by more than 150 investigators using a common and well-established cellulose decomposition assay (*24*). The "cotton strip assay" is a standardized approach for measuring decomposition by using a readily available woven cotton fabric (artist's canvas), comprised of 95% cellulose. The loss of tensile strength of the fabric is measured, a process that is strongly correlated with the microbial catabolism of cellulose (*25*). We performed the assay in 514 flowing water ecosystems at georeferenced field sites on all seven continents, spanning 135° of latitude and each of Earth's major terrestrial biomes (*19*, *20*). We used high resolution (15 arcsecond) climate, soil, geology, vegetation, and physicochemical data (101 explanatory variables total) in a boosted regression tree algorithm to develop the first global, high-resolution predictive model of organic matter decomposition in rivers. We then tested the utility of the cellulose model by using predicted cellulose decomposition rates and genus-level leaf litter chemistry traits to explain 895 leaf litter decomposition estimates from studies conducted at 559 locations across the globe. We found that cellulose decomposition rates are an excellent proxy for litter decomposition rates. Further, our models indicate the physicochemical factors at river and watershed scales interact with characteristics of the organic matter being decomposed (e.g., leaf litter chemistry) to create heterogeneous spatial patterns in riverine decomposition across the planet.

Climate, geology, soils, and water quality explain cellulose decomposition rates

Climate, geology, soil, and water quality variables explain 81% of variance in field measurements of cellulose decomposition. Because a standardized cellulose substrate was used at all field sites, observed variation in decomposition rates can be attributed unequivocally to the activity of microbial communities and environmental drivers. Prior efforts have explained broad variation in decomposition rates

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across riverine ecosystems as a function of exogenous factors such as temperature (*14*, *19*) and concentrations of dissolved nutrients (*17*, *20*, *26*), as well as litter traits (*15*, *27*, *28*). Our model supports those findings and shows that climatic and water quality parameters are among the most important explanatory variables of decomposition rates (Fig. 1). However, a relatively large number of explanatory variables (*n* = 26) have importance values greater than 1.0 (table S1), and no single variable contributes >15% to the explanatory power of the model (table S1). This result reveals the complexity of the many drivers that influence organic matter decomposition at the global scale.

Top explanatory variables of cellulose decomposition include expected attributes like mean daily water temperature [importance value (IV) = 14.0; Fig. 1A], nitrogen and phosphorus availability (IV = 6.7 and 4.9, respectively; Fig. 1, C and D), and mean annual air temperature (IV = 2.5; Fig. 1F). Our data and approach also highlight watershed-level characteristics that have been given little attention previously, such as sub-watershed lake area (limnicity) (IV = 6.9; Fig. 1B), actual evapotranspiration in the watershed (IV = 4.4; Fig. 1E), and the chemical and physical properties of soil (table S1). Subwatershed lake area was a high ranking variable and its negative relationship with decomposition rates may be explained by the disproportionately greater abundance of lakes at high northern latitudes where water temperatures are low (Fig. 1B). Alternatively, lower nutrient concentrations and suppressed hydrological variability may have also contributed to the negative influence of limnicity on decomposition. Although our study sites were selected to have minimal human impacts relative to their region of study (*19*), variables associated with anthropogenic development such as dissolved nutrient yields, cropland extent (IV = 2.0), population count (IV = 1.3), and river regulation (IV = 1.3) still emerge as important (table S1). Notably, relationships between explanatory variables and decomposition rates are frequently nonlinear, revealing thresholds beyond which there are abrupt changes in decomposition rates (e.g., Fig. 1, B, D, and E). Water temperature has a strong positive effect on cellulose decomposition (Fig. 1A) and there is an optimal range (5 to 13°C) of annual air temperature with estimated lower rates in both cooler and warmer watersheds (Fig. 1F).

Extrapolating to global patterns of decomposition rates

Our model and map of riverine cellulose decomposition reveals pronounced, large-scale spatial patterns of organic matter processing (Fig. 2). Rates generally increase with decreasing latitude, with rapid rates in tropical regions (e.g., Central America, Amazon basin, Western Africa,

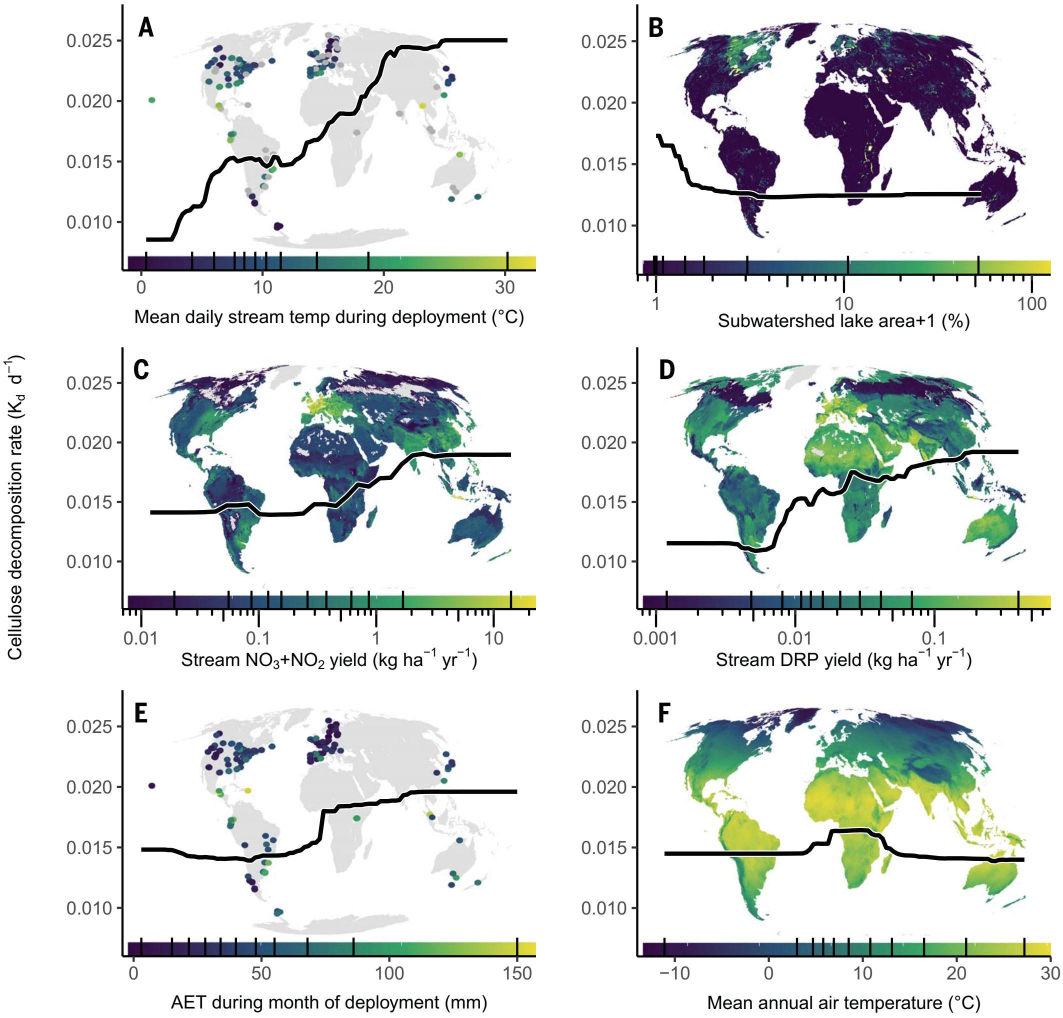

Fig. 1. Partial dependence plots (black lines) of the top variables that explain and predict cellulose decomposition rates (K_d). (**A** to **F**) Background maps show global distributions of explanatory variables in a Mollweide projection. The boosted regression tree model explains 81% of the variance in decomposition rates across the 514 streams used in our study. Most top variables relate to climate and water quality and effects exhibit nonlinear threshold responses. Black ticks above the *x*-axis indicate decile breaks.

Indo Pacific) and areas characterized by volcanic activity and young soils, an effect previously documented only at more local scales (*29*). Notably, fluvial ecosystems in these regions are among the least studied on the planet (Fig. 2, inset) despite having high rates of terrestrial primary production (*22*) and carbon export to the ocean (*23*). Vast areas in middle latitudes with ubiquitous human impacts—central Europe, eastern China, central North America, southeastern South America, and Japan—also support elevated decomposition rates, strongly suggesting continental-scale human impacts on carbon cycling in rivers. By contrast, areas of boreal forests—characterized by short growing seasons, low temperatures, and peaty, acidic, water logged soils—exhibit slower rates of organic matter decomposition, especially in northern Asia, eastern Scandinavia, and northeastern Canada.

Validating predicted cellulose decomposition rates with leaf litter decomposition rates

Recognizing that the substrate used in our standardized decomposition assay (cellulose as cotton fabric) lacks the chemical complexity of organic matter that naturally enters running waters, we also tested how accurately our modeling approach could explain variation in the decomposition rates of terrestrial leaf litter in rivers reported by ecologists worldwide. To this end we independently validated model forecasts using 895 litter decomposition rates from 559 locations and representing 35 genera of terrestrial plants (*27*). We also used leaf and litter trait data at the genus level (*30*, *31*) and experimental conditions (*14*, *27*) as explanatory variables to account for variation among decomposition estimates resulting from differences in leaf litter quality (e.g., lignin, hemicellulose, tannin, nutrient content) and the feeding activity of invertebrates (Fig. 3A and table S2). Our cellulose decomposition model predictions coupled with litter traits account for 70% of the variation in leaf litter decomposition. Notably, the explanatory power of this model is overwhelmingly driven by predicted rates of cellulose decomposition (IV = 39.5), despite the stark differences in quality between the cellulose substrate and natural litter (Fig. 3A and table S2). These results provide strong support for the critical influence that environmental drivers have in regulating riverine litter decomposition, including those affected by anthropogenic activities.

Prior research at large scales has stressed the importance of litter quality as the predominant control of decomposition rates in rivers (*15*). Our results demonstrate that in addition to leaf litter traits, environmental factors such as temperature and nutrient availability are critically important in regulating decomposition rates at larger spatial scales. Our validation model also reveals that invertebrate access to leaves, as assessed by experimentally manipulating litter bag mesh size, greatly increases the rate of decomposition in all but the fastest decomposing leaves (Fig. 3A). Finally, litter chemistry contributes to the explanatory power of the model in expected ways, with plant genera characterized by high lignin content (IV = 11.9; Fig. 3B) and low litter nitrogen content (C:N, IV = 5.45 and N, IV = 5.23; Fig. 3, C and D), exhibiting slower decomposition.

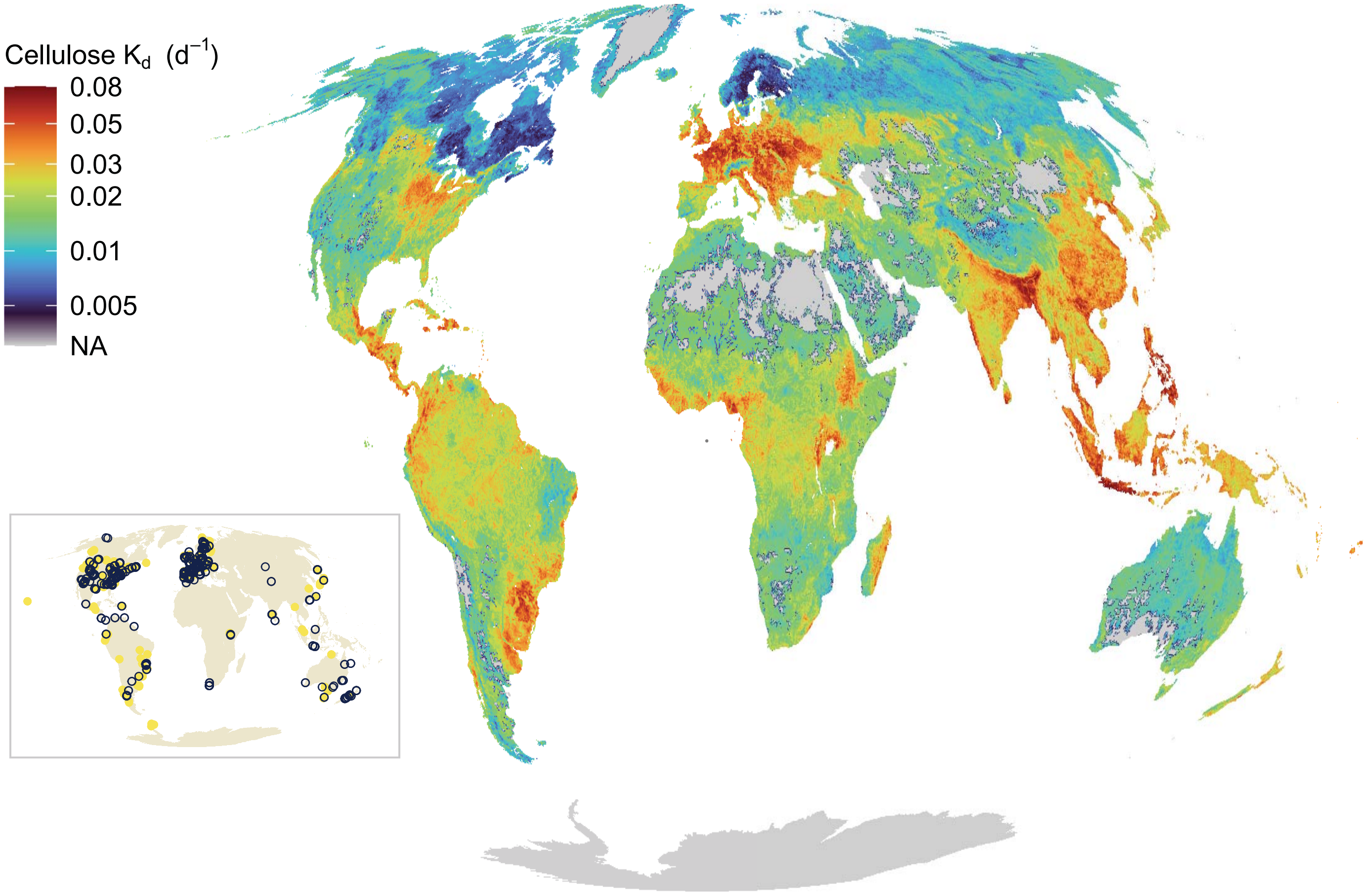

Fig. 2. Predicted mean annual cellulose decomposition rates (K_d) revealing broad spatial patterns in decomposition rates. We did not predict K_d for sub watersheds with ≤10 ha of sub basin area, nor for Antarctica, for which we did not have values for most predictor variables. Inset shows study sites for cellulose (light circles) and leaf litter (dark circles) decomposition measurements. Map and insert are Mollweide projection.

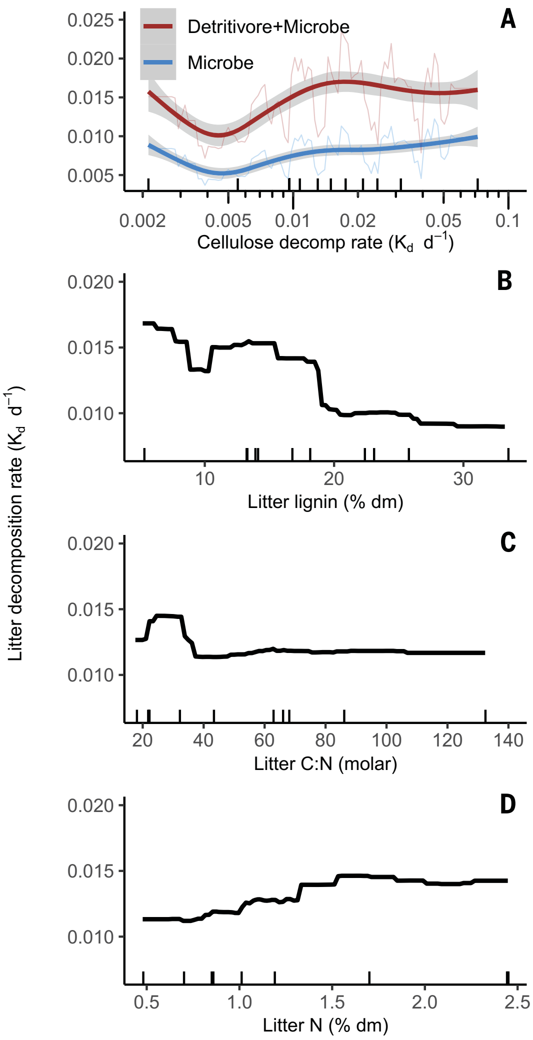

Fig. 3. Partial dependence plots of the top variables that explain leaf litter decomposition rates (K_d). The boosted regression tree model explains 70% of the variance in rates across 895 published values of leaf litter decomposition (*27*). Top explanatory variables included our modeled cellulose decomposition rates, invertebrate access to the leaf material, and attributes related to litter quality at the genus level. Smooth fits (GAM) show the relationship between cellulose decomposition rate and litter decomposition for the two different common litter bag mesh sizes that allow or exclude invertebrates (**A**). The smooth fits capture the general environmental effects on decomposition, whereas the partial dependency plots (thin lines) are noisier due to covariation in leaf quality and environmental conditions (i.e., certain leaf types are used in certain regions). Black ticks above *x* axis indicate decile breaks. Note the change in *y* axis between (A), (**B**), (**C**), and (**D**).

Other litter traits (e.g., P content, cellulose) provide little additional explanatory power and these leaf traits explain no more variation than expected by chance (table S2). It is well-recognized that leaf litter chemistry can vary among individuals within a species (*32*, *33*) and even individual leaves from a single tree (*34*); thus our model may underestimate the importance of individual-level variation in leaf and litter chemistry in driving decomposition. Greater measurement and reporting of litter chemistry, especially nitrogen and lignin content, will improve understanding of endogenous controls at global scales. Despite limitations in available data we show that cellulose decomposition can be an excellent proxy for litter decomposition, and our composite model of environmental drivers makes reliable estimates of litter decomposition at a global scale.

Forecasting decomposition under global environmental change

The high explanatory power of our cellulose and leaf litter decomposition models enables forecasting of decomposition rates under altered climate, land cover, soil conditions, and nutrient loading scenarios. These predictions can identify locations across the globe where decomposition may be particularly susceptible or resistant to global change, thereby informing freshwater conservation efforts. As proof of concept, we examined potential changes in predicted litter decomposition rates associated with changes in pine oak forest composition in Mexican watersheds invaded by pine bark beetle (*Dendroctonus mexicanus*) (*35*). This invasion is expected to be particularly severe in the watershed of the Rio Grande de Santiago, a major conduit of organic matter to the Pacific Ocean in Mexico (Fig. 4). Our forecasts predict that insect-induced canopy replacement from pine to oak would cause decomposition rates to increase and become more variable (2.5- to 3.8-fold increase), with larger increases in decomposition associated with watersheds with greater evapotranspiration and drier soils (fig. S1). To promote the use of our models for forecasting we created an easy-to-use, open-source online application where users can estimate both cotton strip and leaf litter decomposition rates for any river across the globe (https://shiny-bsci.kent.edu/CELLDEX/).

Conclusions and implications

By pairing a distributed field experiment with publicly available environmental data, we created the first high-resolution map and predictions of organic matter decomposition rates in flowing waters worldwide. Our model demonstrates that cellulose decomposition results from diverse, interacting, and nonlinear environmental forcings that can best be described with complex, data-rich models. Although the standard cotton fabric used lacks the biochemical complexity of leaf litter, our relatively simple organic matter substrate is an excellent proxy for leaf litter in decomposition studies, as demonstrated by our model predictions. Simplification of the leaf litter bag assay allowed us to both achieve standardized results and fill extensive geographic gaps in remote and low resourced areas, demonstrating the power of coordinated, distributed experiments (*36*). Although our datasets were large when compared with other studies of organic matter decomposition, the field data used were relatively limited in both space and time, which makes our strong explanatory power all the more valuable. Thus, this work also underscores the power of machine learning algorithms and large geographic databases of environmental data (e.g., HydroBASINS) (*37*, *38*) plus the critical value of temporally and geographically extensive data from simple but standardized coordinated experiments (e.g., CELLDEX).

Given the pressing need for measuring ecosystem functions for biomonitoring and bioassessment (*39*, *40*), our globally distributed experiment provides a template for matching observational data with model predictions. This

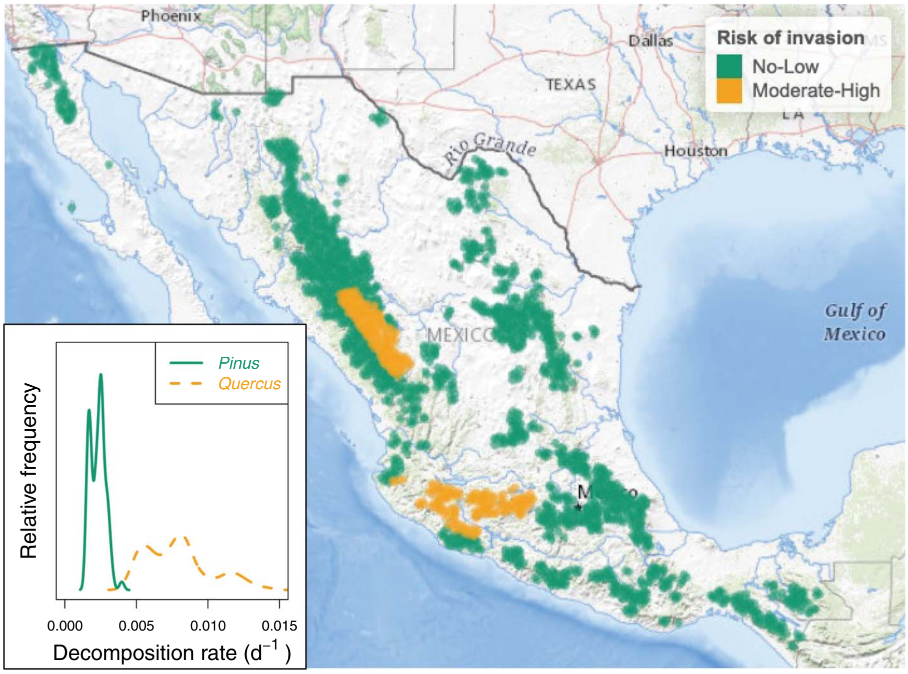

Fig. 4. Distribution of temperate coniferous forests in Mexico (all points) and locations (orange) where there is a moderate to high risk of pine bark beetle (*Dendroctonus mexicanus*) invasion [adapted from (*35*)] that drives a shift from coniferous to deciduous forest. Inset shows the density distribution of predicted litter decomposition rates for streams in areas of moderate to high invasion risk both for pine litter (green solid line) and oak litter (orange dashed line). Our model predicts that full canopy replacement from pine to oak would increase leaf litter decomposition rates 2.5 to 3.8 fold with a greater increase predicted in watersheds with greater evapotranspiration and drier soils. Base from US Geological Survey, The National Map, 2023; Web Mercator projection; created in the R package leaflet 2.2.1 (*44*).

approach provided baseline data for estimated decomposition rates across immense, unstudied areas of the planet and supports the development of biomonitoring networks in areas where they are most needed (*41*). To further advance large scale monitoring and assessment, we have made these modeling approaches accessible through an open-source online mapping tool. Application of the models to current and future environmental threats will enable scientists and natural resource managers to forecast changes in the functioning of river networks at a planetary scale.

Cellulose decomposition is strongly influenced by multiple interacting environmental drivers that continue to be affected by anthropogenic activities. Undoubtedly, climate change, increased nutrient loading, intensified land use modification, and changes in vegetation cover will continue to alter organic matter processing in rivers and streams. Notably, key human influenced drivers of cellulose decomposition—especially nutrient loading and temperature—are positively related to decomposition rates. A critical implication is that in the presence of continued environmental change, organic matter decomposition rates will likely increase in rivers, resulting in declines in shorter-term carbon storage (*42*) and reductions in carbon transfer to longer-term storage compartments, such as reservoirs, floodplains, and oceans.

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SUPPLEMENTARY MATERIALS

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CELLDEX Consortium Authors and Affiliations
Materials and Methods
Fig. S1
Tables S1 and S2
References (*45*–*55*)

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