

plausible mechanism for the maintenance of adult differentiated cell types. More broadly, these results showcase the power of explorative single-cell RNA-seq and point the way toward future whole-brain and even whole-organism cell type discovery and characterization. Such data will deepen our understanding of the regulatory basis of cellular identity, in development, neurodegenerative disease, and regenerative medicine.

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#### SUPPLEMENTARY MATERIALS

[www.sciencemag.org/content/347/6226/1138/suppl/DC1](http://www.sciencemag.org/content/347/6226/1138/suppl/DC1)  
Materials and Methods  
Supplementary Text  
Figs. S1 to S11  
Tables S1 and S2  
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#### FRESHWATER ECOLOGY

# Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems

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**Nutrient pollution of freshwater ecosystems results in predictable increases in carbon (C) sequestration by algae. Tests of nutrient enrichment on the fates of terrestrial organic C, which supports riverine food webs and is a source of CO<sub>2</sub>, are lacking. Using whole-stream nitrogen (N) and phosphorus (P) additions spanning the equivalent of 27 years, we found that average terrestrial organic C residence time was reduced by ~50% as compared to reference conditions as a result of nutrient pollution. Annual inputs of terrestrial organic C were rapidly depleted via release of detrital food webs from N and P co-limitation. This magnitude of terrestrial C loss can potentially exceed predicted algal C gains with nutrient enrichment across large parts of river networks, diminishing associated ecosystem services.**

**N**utrient pollution of freshwater ecosystems is pervasive and strongly affects carbon (C) cycling. Excess nutrients stimulate the production of C-rich algal biomass but can also stimulate C loss through increased organic C mineralization that releases CO<sub>2</sub> instead of supporting production of higher trophic levels and other ecosystem functions (1, 2). Production of aquatic life in freshwater ecosystems is based on algae and organic C of terrestrial origin. Currently, consideration of nutrient effects on C cycling in inland waters has focused on enhancement of algal C sinks in lakes and less on fates of terrestrial C that may experience accelerated loss in river networks (3–5).

The processes that lead to nutrient stimulation of algal C production and terrestrial C mineralization are fundamentally different. Algal production increases relatively predictably with the availability of growth-limiting nutrients (1, 6). In contrast, mineralization of particulate organic C (POC) is the more complex result of activity by multiple trophic levels consisting of microbial decomposers and detritivorous animals (hereafter detritivores) (7). Inputs of leaves and wood are the main sources of POC in many rivers, supporting production of animals and uptake of inorganic pollutants (8–10). Nutrients stimulate microbial processing of POC, which results in increased losses of CO<sub>2</sub> to the atmosphere (2, 11). Consumption of microbially colonized POC by detritivores further contributes to its breakdown and conversion to smaller particles, which affect its subsequent transport and processing downstream (7).

To determine how moderate nutrient pollution affects terrestrially derived POC at stream-

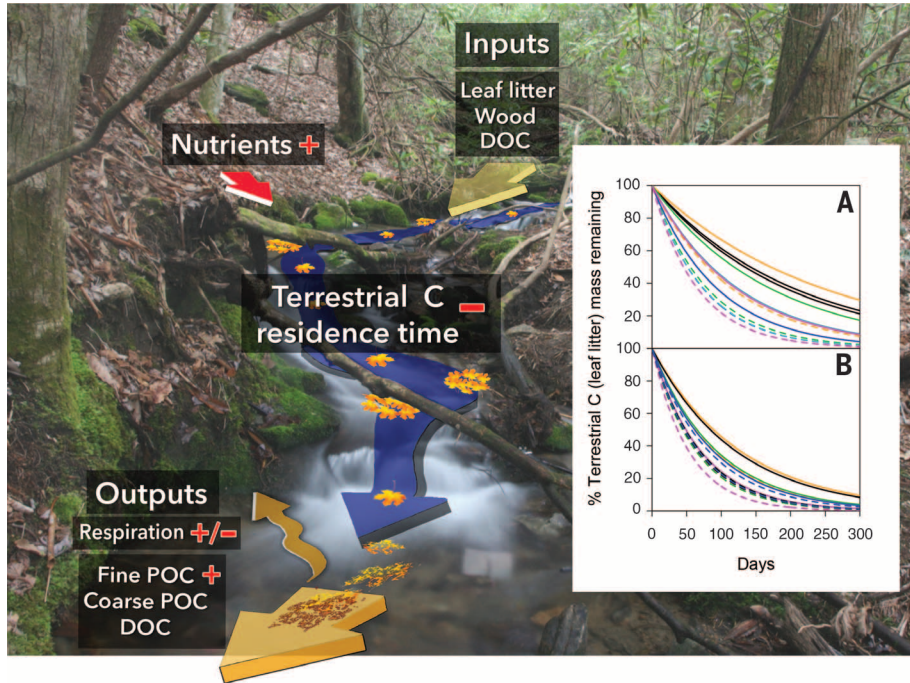
reach scales, we tested how long-term (2- to 5-year), continuous, flow-proportional nitrogen (N) and phosphorus (P) additions affected its loss rates and fates in headwater forest streams (12). We measured the response of terrestrial C loss rates in whole 70- to 150-m stream reaches (tables S1 and S2). Carbon loss rates at this spatial scale are a function of biologically driven breakdown and hydrological export and have not been previously assessed in response to human-influenced stressors (13). We conducted two manipulative experiments at large spatial and temporal scales and focused our measurements on forest-derived leaf litter, because it is the most biologically active pool of terrestrial C in forest streams and is renewed annually (7). After a pretreatment year, we enriched one stream with N and P at a set ratio for 5 years in a paired watershed design (N+P experiment; a second stream acted as a control) and used expanded N and P gradients in a second experiment in five other streams for 2 years after a pretreatment year (N×P experiment) (table S1).

Reach-scale terrestrial C loss rates increased with N and P enrichment across all the concentrations we tested (Fig. 1). Discharge, N, P, temperature, and associated random effects (stream and year) explained 83% of the variation in C loss rates across 27 annual measurements (table S3). Standardized regression coefficients indicated that our moderate additions of N and P contributed roughly three-fourths of the effect on litter loss rates as annual cumulative discharge, which varied 87-fold across streams and years (table S3). Nitrogen and P ( $r = 0.79$ ) and discharge and temperature ( $r = -0.76$ ) were correlated, so their effects and relative significance cannot be teased apart fully. However, roughly similar-sized effects of N and P on loss rates are strong evidence of co-limitation (Fig. 2 and table S3). Comparisons of loss rates from corresponding enriched and reference streams indicate that median C loss rates increased 1.65 times with nutrient enrichment (table S4); the range in these values (1.02 to 4.49 times) reflects variation due to N

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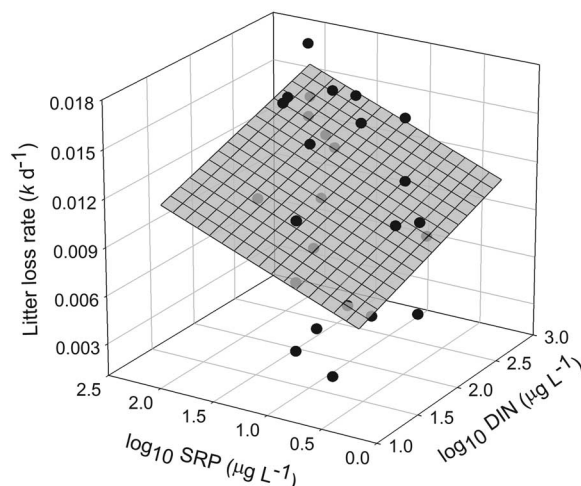
and P concentrations, discharge, and temperature (table S1). Average residence time of terrestrial POC was roughly halved with nutrient

enrichment: from 167 days in reference conditions to 75 days with nutrient addition (median values were 125 and 74 days, respectively). Litter



**Fig. 1. Terrestrial C residence time was approximately halved with experimental nutrient enrichment.** Increased nutrient inputs (+) reduced terrestrial particulate C residence time (–) and increased export of fine detrital particles (+) and respiration rates [which increased on C substrates (11) but decreased at reach scales; +/-]. Inset graph: Reach-scale leaf litter loss rates were faster in enriched (dashed lines) than in reference (solid lines) streams; the inverse of these rates is residence time. Colors correspond to the same years in (A) (reference versus enriched streams; N+P experiment;  $n = 12$  annual rates) and to the same streams in (B) (pretreatment versus enriched years; N x P experiment;  $n = 15$  annual rates). Data shown for litter loss are untransformed but were natural log-transformed for analyses and the calculation of loss rates ( $k$ , per day). The larger image depicts terrestrial organic C inputs, which enter as leaf litter, wood, and dissolved organic carbon (DOC), and outputs as hydrologic export (fine and coarse particles, DOC) and respired  $\text{CO}_2$  in deciduous forest streams, using an image of one of the N x P experimental stream sites.

**Fig. 2. Terrestrial C loss rates from stream reaches increased with N and P concentrations.** The surface represents the predicted loss rate ( $k$ , per day) as a function of streamwater dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) at mean discharge rate and temperature for the study period derived from the multilevel model [variance explained by fixed and random effects (conditional  $R^2$ ) = 0.83; parameter estimates are in table S3]. Each data point is the estimated litter loss rate for a particular stream-year derived from the first level of our hierarchical model (12). Mean (range) annual concentrations of nutrients in micrograms per liter tested in our experiments were moderate and reflect concentrations commonly observed due to watershed land-use change: SRP reference: 6 (2 to 12), SRP-enriched: 49 (6 to 117); DIN reference: 53 (13 to 189), DIN-enriched: 347 (66 to 798).

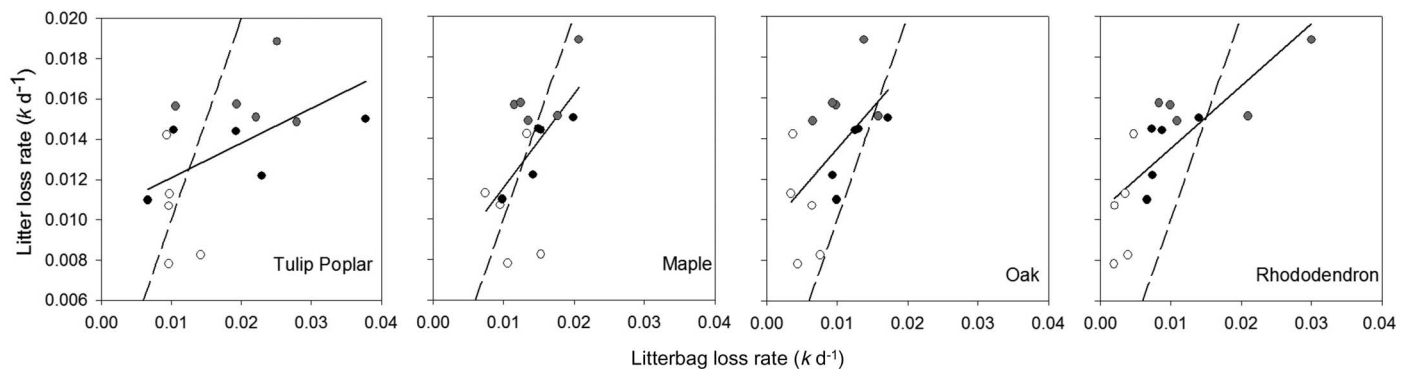


quantity in the streambed was predicted to be 2.8 times and 7.7 times higher in reference versus nutrient-enriched streams after 6 and 12 months, respectively, based on average annual litter inputs and median loss rates in reference and enriched conditions, showing increasing differences in retained C due to nutrient enrichment over time.

Relatively large effects of nutrients on reach-scale loss rates indicated that biological processing had strong effects despite relatively large temporal variation in physical conditions in headwater streams. We further tested the importance of biological versus physical control of C loss rates by comparing the degree to which small-scale (i.e., litterbag) measurements aligned with reach-scale rates, using measurements made at the same time; relatively good alignment between reach-scale and litterbag-scale rates indicates that biological, rather than physical, processes drove reach-scale rates (table S5). Litterbag-scale loss rates of more-labile litter species tended to overestimate and those of more-refractory litter species tended to underestimate reach-scale C loss rates, due to the integration of effects from diverse litter types at the reach scale (Fig. 3). When litterbag-scale rates exceeded reach-scale rates, this suggested strong and increased biological processing of C under nutrient-enriched conditions. Higher C loss rates at the litterbag scale than the reach scale are expected, because litterbags track distinct parcels of C, whereas reaches receive additional C inputs over time. These processes probably outweigh differences due to the retention of smaller particles in litterbags that are not included in reach-scale estimates. Our results generally support the use of litterbags to measure larger-scale C dynamics, but with consideration of differences among litter species and potential divergence in rates due to the degree of biological processing (2, 14).

We quantified the potential alternative fates of terrestrial C to gain insights into the relative role of microbial decomposers that largely drive C losses as respiration, versus detritivores that largely drive C losses as POC export, in contributing to reach-scale C loss rates. Using data from our N+P experiment, we tracked all pools and losses (outputs) of terrestrial C, including litter; C pools declined, and outputs, particularly of fine (<4 mm) POC, increased with enrichment (Fig. 4 and table S6). Pretreatment conditions included higher pools of fine benthic POC and lower export of POC in the enriched stream, due to inherent morphological and hydrological differences between streams [table S6 (12)]. The first 2 years of nutrient enrichment showed that pools of benthic fine and coarse POC declined in the nutrient-enriched stream relative to the reference stream. Reach-scale outputs of C increased as fine POC export, as well as respiration (15). In subsequent years of enrichment, pools of fine and coarse benthic POC were lower in the enriched than the reference stream, as compared to pretreatment conditions, which is consistent with previous findings (15). However, relatively higher outputs from the enriched stream were due more to POC export than to respiration in later years of

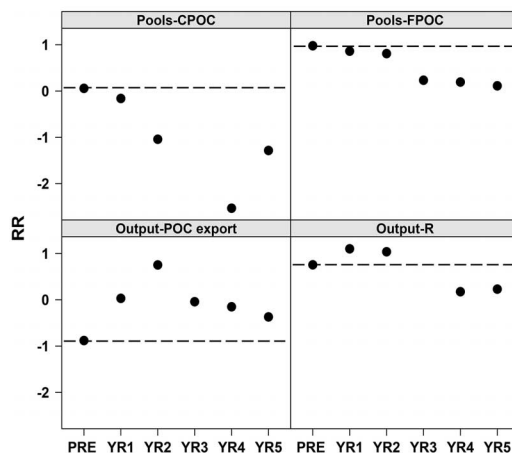




**Fig. 3. Small-scale (litterbag) leaf litter loss rates can predict reach-scale leaf litter loss rates.** Shown are leaf litter loss rates from equivalent streams and years for four leaf litter types across the five streams in the N+P experiment during pretreatment (open circles) and years 1 (gray circles) and 2 (black circles) of enrichment. Litterbag rates were quantified from coarse-mesh bags and represent microbial + detritivore-mediated breakdown (12). The dashed line represents a 1:1 relationship. Equations describing these relationships and those from the N+P experiment are in table S5.

#### Fig. 4. Nutrient enrichment affected pools and outputs of terrestrial C in the N+P experiment.

Data shown are natural log-transformed response ratios (RRs) through time for C pools and outputs as POC export and respiration (R). Dashed lines are based on pretreatment-year (PRE) conditions; RRs were calculated as enriched: reference during the PRE and each year of experimental enrichment. We quantified in-stream benthic pools of fine POC (FPOC) and coarse POC (CPOC) and outputs of POC export and estimated reach-scale respiration (12). Data from PRE and enrichment years 1 and 2 have been previously published (15). Benthic pools of CPOC shown consist of leaf CPOC; wood CPOC is additionally shown in table S6. Export of POC consisted primarily of fine particles; coarse fractions typically made up <4% of total POC export (table S6).



enrichment. Specifically, nutrient enrichment affected both outputs, but on a reach scale, POC export increased, whereas respiration declined (Fig. 4). Relatively lower reach-scale respiration despite higher substrate-specific microbial respiration rates (11) was a function of smaller pools of POC, from which the areal respiration estimates were calculated, in the enriched stream (table S6).

Increased POC export in the enriched stream was due to nutrient-stimulated particle generation from a combination of microbial decomposition and detritivore feeding (11, 16–18). These transformations alter the normal balance of the fates of C inputs to greater respiratory losses, more POC export as fine particles, and less C storage. Transport distances of POC are variable, but they are much longer for smaller than larger particles (7, 19). Thus, in a given nutrient-enriched stream reach, less C remains to contribute to annual storage and associated ecosystem services (8). Whether microorganisms or animal feeding have relatively greater influence on the processing of terrestrial C affects how much C is transported downstream or lost primarily as CO<sub>2</sub>. In agricultural streams with diminished abun-

dance of detritivores, nutrients stimulate largely microbial breakdown of crop residues that enter streams (20). Similarly, greater CO<sub>2</sub> flux than export due to increased microbial, but not detritivore, processing of terrestrial C is predicted with elevated temperature (21). When animals are reduced in streams due to biogeographic or land-use factors, nutrients or temperature accelerate losses of C, but primarily via CO<sub>2</sub>, not export of particles. Thus, populations of detritivores in streams play complex and important roles: They may limit terrestrial C loss as CO<sub>2</sub> and maintain downstream C export, but contribute to depletion of local C resources (22, 23).

Our results suggest that N and P co-limit terrestrial C loss rates in streams, for which there is a growing body of evidence (2, 24, 25). Algal C production is similarly co-limited by N and P in many systems (6, 26). The similarity in the magnitude of C loss to general patterns of C gain, despite fundamentally different processes, is significant. Average autotroph responses to N and P additions in freshwater and marine environments are roughly three times and two times higher than controls, respectively (6); however, the range in responses is highly variable (27). Organic C

pools are dominated by terrestrial sources in small streams but shift to greater contributions of autotrophic C in larger streams and rivers (28). We compared simple first approximations of the potential effects of nutrient enrichment on decreases in benthic POC relative to increases in autotrophic C across the larger river network where our studies were conducted and found a potential for terrestrial POC losses that are greater than estimated autotrophic C gains in first- through fourth-order stream channels (12) (table S7). Estimated losses for entire stream networks were greater than autotrophic C gains when summed across total streambed area in streams as large as sixth-order; nutrient-driven increases in autotrophic C production in the largest river channel (seventh-order) outweighed these losses (12). For stream ecosystems in which nutrient pollution results in net C losses, the local ecological effects of lower C availability, as well as the implications for downstream systems, may be substantial.

The mineralization of terrestrial C, similar to the production of algal C, is stimulated at nutrient concentrations that are now common across human-disturbed landscapes (2, 29). Thus, reduced retention and increased export and respiratory losses of terrestrial C are probably occurring in many aquatic systems because of increased nutrient availability, with consequences for ecosystem services. The loss of terrestrial C is not as visually obvious as increased algal biomass. Policies aimed at addressing nutrient effects on C resources, as well as efforts to determine the effects of global change on inland C balances, currently focus largely on the accrual of algal C, not losses of terrestrially derived C (30, 31). Management of nutrient effects on both of these pathways would positively affect riverine health.

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#### SUPPLEMENTARY MATERIALS

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Materials and Methods  
Supplementary Text  
Tables S1 to S7  
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#### POLITICAL ECONOMY

# On the endogeneity of political preferences: Evidence from individual experience with democracy

Nicola Fuchs-Schündeln\*† and Matthias Schündeln\*†

Democracies depend on the support of the general population, but little is known about the determinants of this support. We investigated whether support for democracy increases with the length of time spent under the system and whether preferences are thus affected by the political system. Relying on 380,000 individual-level observations from 104 countries over the years 1994 to 2013, and exploiting individual-level variation within a country and a given year in the length of time spent under democracy, we find evidence that political preferences are endogenous. For new democracies, our findings imply that popular support needs time to develop. For example, the effect of around 8.5 more years of democratic experience corresponds to the difference in support for democracy between primary and secondary education.

Popular support for democracy is critical to the success of a democracy, especially an emerging democracy (1, 2). Will support increase over time when a democracy emerges and the population gains experience with democracy? If so, how quickly? Or are democratic attitudes deeply ingrained in individuals, such that they are hard to change? The latest wave of democratizations in the world, which started in December 2010 in a movement often collectively referred to as the “Arab Spring,” and the subsequent struggles of these countries provide a recent illustration of the importance of these questions. However, a study that uses a clean identification strategy based on an experimental or quasi-experimental setup to identify the causal effect of accumulating experience with democracy on support for democracy in a broad set of countries—or more generally, a study that identifies endogenous preferences for political systems—is missing from the literature.

Indeed, recent research suggests that economic preferences are shaped by individual experiences with markets (3). In particular, preferences regarding fairness, preferences for redistribution, and other types of preferences related to economic behavior vary across societies in a way that correlates with market characteristics (4, 5). A causal interpretation of these correlations and the view that economic preferences are endogenous is founded in theoretical arguments (6–8) and is empirically supported by research based on experimental or quasi-experimental settings, such as the end of communism in Eastern Europe or the stock market return experiences accumulated over a lifetime (9–11).

Regarding the endogeneity of political preferences, research has so far shown a positive correlation between experience with political systems

and political preferences at the country level (12), a positive correlation between attitudes toward democracy and currently living under a democratic system (13), and that a longer democratic experience lowers the probability of exit from democracy and increases the probability of exit from autocracy (12). However, a causal influence of experience with democracy on the support for democracy, which would imply endogeneity of preferences, cannot be established from these correlations. The correlations could (partly) be due to reverse causality (i.e., countries have a democratic history precisely because the electorate supports democratic values); or a third, possibly unobserved, variable, such as historic events or economic conditions, could determine both individuals' support for democracy and the political system in place.

Here, we exploited within-country variation at the individual level in experience with a democratic regime to establish a plausibly causal impact of experience with democracy on preferences for democracy, and thereby contribute to a better understanding of the endogeneity of political preferences. Because we control for country-year fixed effects, the observed differences in attitudes toward democracy do not simply reflect a reaction to differences in the current quality of institutions or political environments, but, under the minimal and plausible identifying assumption that we state below, constitute a change in intrinsic preferences due to differences in the length of exposure to democracy. For example, if democratic institutions or economic conditions improve with the length of time spent under democracy, this might increase the support for democracy directly and not through intrinsic preferences, but it would be captured in our specification by the country-year fixed effects, which control for all country-level unobservables that are specific to a country in a given year. Any remaining correlation between experience with democracy and support for democracy can therefore confidently be attributed to a change in preferences.

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## Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems

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