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Supplementary Materials

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Continental-Scale Effects of Nutrient Pollution on Stream Ecosystem Functioning

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Excessive nutrient loading is a major threat to aquatic ecosystems worldwide that leads to profound changes in aquatic biodiversity and biogeochemical processes. Systematic quantitative assessment of functional ecosystem measures for river networks is, however, lacking, especially at continental scales. Here, we narrow this gap by means of a pan-European field experiment on a fundamental ecosystem process—leaf-litter breakdown—in 100 streams across a greater than 1000-fold nutrient gradient. Dramatically slowed breakdown at both extremes of the gradient indicated strong nutrient limitation in unaffected systems, potential for strong stimulation in moderately altered systems, and inhibition in highly polluted streams. This large-scale response pattern emphasizes the need to complement established structural approaches (such as water chemistry, hydrogeomorphology, and biological diversity metrics) with functional measures (such as litter-breakdown rate, whole-system metabolism, and nutrient spiraling) for assessing ecosystem health.

Nutrient enrichment from organic inputs and agricultural run-off is placing the world's vulnerable fresh waters in a precarious position (1–4). Far-reaching environmental legislation has been introduced to redress human impacts on aquatic communities (5, 6), yet the consequences of nutrient loading for stream ecosystem functioning remain poorly understood (4, 7, 8). This is worrying because key ecosystem services (such as maintenance of viable fisheries as a provisioning service, and organic matter decomposition as a supporting service) ultimately depend on ecosystem processes, such as leaf-litter breakdown and other processes involved in nutrient cycling (3, 9).

Many aquatic ecosystems are supported by plant litter inputs (10–12). This includes streams, where terrestrial leaf breakdown—which is driven by resource quality; the abundance, diversity, and activity of consumers; and environmental factors—is a key ecosystem process (10, 13, 14). Moderate nutrient enrichment of streams can accelerate breakdown by stimulating microbial con-

ditioning and invertebrate consumption (15, 16). However, a wide range of responses along nutrient gradients has been reported in field studies, suggesting environmental drivers beyond elevated nutrient supply. For instance, wastewater discharge can induce anoxia, mobilize heavy metals, and physically smother benthic organisms (17, 18). Litter breakdown by invertebrates (19) appears especially sensitive to nutrient pollution relative to that mediated by microbes (20) and, because invertebrates often attain their highest densities in moderately enriched streams, a hump-shaped breakdown rate response might be expected along long nutrient gradients (5).

We hypothesized that breakdown rates are constrained by microbial nutrient limitation at the low end of nutrient pollution gradients and by the effects of environmental degradation on invertebrates at the high end. Most studies, however, have been unable to detect this pattern because they have been conducted over relatively short nutrient gradients and small spatial scales (5, 7).

Here, we report a field experiment in 100 European streams spanning 1000-fold differences in nutrient concentrations, as proxy measures of nutrient loading by direct and indirect inputs (21). The validity of this approach is highlighted by the positive relationship between biochemical oxygen demand (BOD₅) and nutrient concentrations in more than 8000 European streams, and the comparable frequency distributions of nutrient concentrations between these and our sites (fig.

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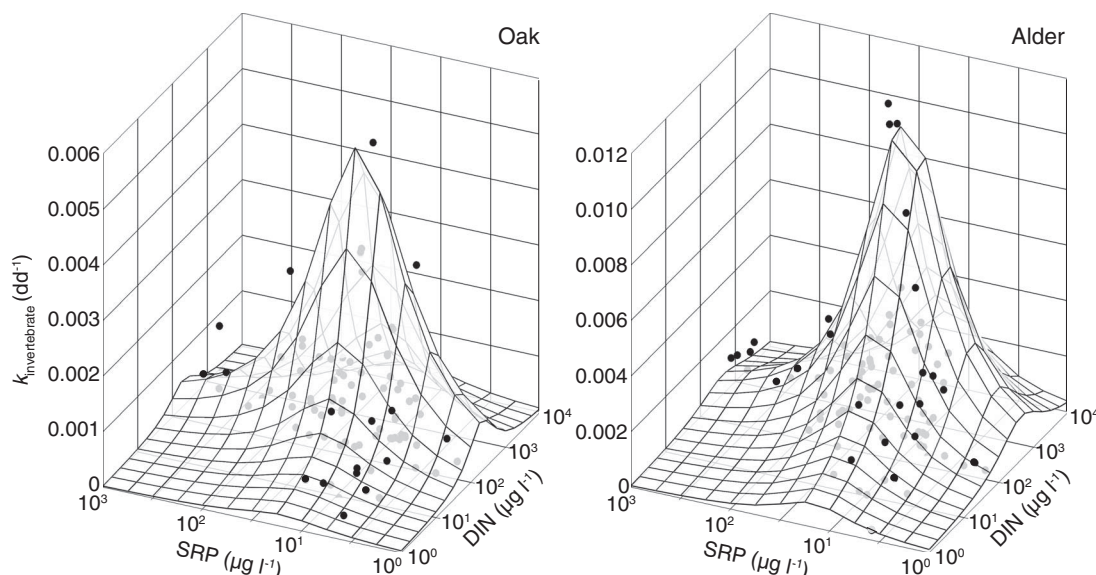
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Fig. 1. Rates of invertebrate-mediated breakdown as a function of SRP and DIN concentrations for oak (Left) and alder (Right) leaves. Each data point represents a temperature-corrected rate [expressed in degree days⁻¹ (dd⁻¹)] for a single stream. Three-dimensional volume-filling relationships between nutrient gradients and breakdown rates with unimodal Lorentzian surfaces are fitted as bounding envelopes to maxima within categories of nutrient concentrations (per 0.5 log₁₀ division of SRP and DIN in μg l⁻¹); R^2 values of the fits to these maxima are 0.85 for oak and 0.77 for alder, respectively (randomization tests were carried out to rule out any potential influence of different sample sizes setting the bounding envelopes along the nutrient gradients) (figs. S4 and S5) (21). Data points above and below unimodal Lorentzian surfaces are displayed in black and gray, respectively.



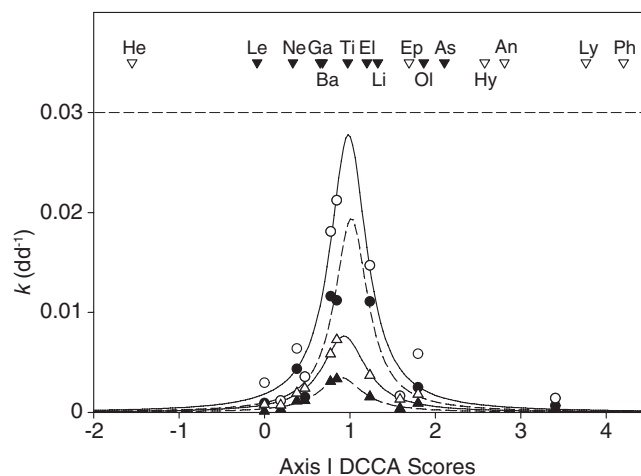
S1). We deployed 2400 experimental litter bags made with fine or coarse mesh to determine total, microbially mediated, and invertebrate-driven breakdown rates of litter from two common tree species: slow-decomposing pedunculate oak (*Quercus robur* L.) and fast-decomposing black alder (*Alnus glutinosa* [L.] Gaertn.), both widespread across Europe and with closely related species that are common throughout the Holarctic region.

Both litter types exhibited hump-shaped responses for invertebrate-driven breakdown rates as a function of soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) concentrations (Fig. 1 and figs. S2 and S3). Rates were always low at the extremes, but low-to-high at intermediate nutrient concentrations. Within a given range of nutrient concentrations, the spread of breakdown rates was almost equal to the maximum (there was an upper, but not a lower, limit) (figs. S4 and S5), supporting the idea that factors beyond nutrients alone modulated consumer activity (14). Although a similar pattern emerged for total breakdown with highest rates at intermediate enrichment levels, this response was not as clear as for invertebrate-mediated breakdown (fig. S2).

In addition to our Europe-wide measures of breakdown rates, we characterized the structure of invertebrate communities in 10 Irish streams that spanned the entire continental nutrient gradient (21). Condensing the principal gradient of invertebrate primary consumer relative abundance across these sites into a single ordination axis, via detrended canonical correspondence analysis (DCCA) (22), revealed the typical community response to pollution, from indicators of clean water (such as heptageniid mayflies) to those typical of polluted conditions (such as physid snails) (Fig. 2). This enabled us to plot invertebrate community structure against breakdown rate.

Fig. 2. Axis I sample scores from a DCCA on communities of primary consumers in alder (circles) and oak (triangles) leaf bags at 10 streams in Ireland, plotted against total (white symbols) and invertebrate-mediated (black symbols) breakdown rate (expressed in degree days⁻¹). Unimodal Lorentzian curves have been fitted to the data (alder k_{total} : $R^2 = 0.93$; $P < 0.0001$; alder $k_{\text{invertebrate}}$: $R^2 = 0.88$; $P = 0.0006$; oak k_{total} : $R^2 = 0.97$; $P < 0.0001$; oak $k_{\text{invertebrate}}$: $R^2 = 0.96$; $P = 0.0001$).

Scores of individual invertebrate taxa depicted as letters at the top of the graph show that the largest litter-consuming detritivores, gammarid shrimps and limnephilid caddisfly larvae, are close to the peak of the curves. An, Ancylidae; As, Asellidae; Ba, Baetidae; EL, Elmidae; Ep, Ephemerellidae; Ga, Gammaridae; He, Heptageniidae; Hy, Hydrobiidae; Le, Leuctridae; Li, Limnephilidae; Ly, Lymnaeidae; Ne, Nemouridae; OL, Oligochaeta; Ph, Physidae; Ti, Tipulidae.



The moderately enriched sites exhibited the fastest breakdown and were characterized by the largest consumer taxa (Fig. 2), whose abundance was a strong predictor of breakdown rate (fig. S6). This integrated community gradient yielded clearer unimodal relationships to our functional measure (R^2 all ≥ 0.88 , $P < 0.001$) (Fig. 2) than to either nutrient alone (SRP, $R^2 = 0.66$ to 0.79 , $P = 0.04$ to 0.004 ; DIN, not significant).

The rising part of the unimodal curve likely resulted from nutrient stimulation of microbes and subsequent increased consumption of leaf litter by invertebrates. In contrast, the falling portion probably reflects deteriorating environmental conditions suppressing invertebrate-

mediated breakdown (for example, chemical and habitat conditions associated with high BOD₅) (fig. S1), suggesting that increases in detrimental pollution syndromes (such as oxygen depletion, smothering, or disappearance of sensitive invertebrate taxa) might counteract the stimulating effects of nutrients (23). Because breakdown at moderately enriched sites was released from constraints of both nutrient limitation and stressors accompanying excess nutrient supply, other drivers, including biological community structure (24, 25), clearly assume importance here. This poses challenges—and also provides opportunities—to stream assessment and management because most European streams and rivers lie in this zone of

maximum uncertainty (Fig. 1 and fig. S1). For example, increased breakdown rates in slightly enriched streams would indicate altered ecosystem functioning, although most managers would consider such streams ecologically intact on the basis of traditional assessment criteria. Conversely, low breakdown rates at moderately enriched sites are no guarantee that streams are unaffected, requiring comprehensive assessments based on a range of indicators in order to draw conclusions about ecosystem impairment.

Our results raise fundamental questions about how to determine ecosystem health. First, naturally low-nutrient conditions are the desired state that water resource managers aspire to, and yet breakdown rates in such systems were indistinguishable from those in heavily polluted streams. This suggests that ensuring both low-nutrient water and effective resource use in stream food webs (from leaf litter to detritivores to fish) coupled with high process rates might be irreconcilable goals in stream management. Second, stream managers currently rely primarily on structural measures to assess stream ecosystem health. In particular, changes in biological community structure (invertebrates, fish, and algae) have long underpinned stream bioassessment schemes because they provide a reliable time-integrated response to stressors such as organic pollution or acidification (5), but biogeographical constraints make this approach difficult to standardize at large scales (10). Litter breakdown can help here because biogeography is a minor issue (for example, black alder or similar species of the genus are common throughout most of Europe and the Holarctic), and marked changes in breakdown rate occurred in the rising portion of the pollution gradient, in which established structural measures (such as water chemistry, hydromorphology, and metrics based on fish, invertebrate, or algal communities) are typically least sensitive. Consequently, litter breakdown—and potentially other functional measures such as whole-ecosystem metabolism, nutrient spiraling, or primary production (26–28)—can be used to complement, not replace, established procedures to assess stream ecosystem health. This highlights the need for differential diagnoses in environmental assessment, as is standard practice in medicine. Importantly, litter breakdown and some other functionally based methods can be implemented at relatively little cost or resource input (29) in order to assess effects of pollution and other ecosystem impacts that are of concern to environmental managers and stakeholders.

Increasing human pressure is accelerating environmental change throughout the world, threatening water security for humans and aquatic biodiversity (2). Large stretches of the landscape in Europe and other parts of the world are characterized today by highly industrialized, intensively managed agriculture and the large-scale application of fertilizers. This, in combination with other nutrient sources such as atmospheric deposition, has resulted in widespread nutrient pol-

lution of aquatic ecosystems (2, 5, 8). Our study reveals that along with biodiversity losses, as fresh waters drift away from their natural conditions, ecosystem processes are profoundly changed, too. Impacts on stream functioning may go beyond the effects on litter breakdown because changing litter dynamics can have strong effects on nutrient retention and transformations (27), invertebrate productivity (12, 30), and other functional ecosystem attributes. Given these complexities and large uncertainties surrounding human environmental impacts (5, 24), a critical objective for the future will be to improve concepts and implementation tools to simultaneously manage surface waters sustainably and meet the demands of biodiversity conservation and environmental legislation.

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Supplementary Materials

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Materials and Methods
Figs. S1 to S6
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Databases S1 and S2

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p53 Dynamics Control Cell Fate

Jeremy E. Purvis, Kyle W. Karhohs, Caroline Mock, Eric Batchelor,*
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Cells transmit information through molecular signals that often show complex dynamical patterns. The dynamic behavior of the tumor suppressor p53 varies depending on the stimulus; in response to double-strand DNA breaks, it shows a series of repeated pulses. Using a computational model, we identified a sequence of precisely timed drug additions that alter p53 pulses to instead produce a sustained p53 response. This leads to the expression of a different set of downstream genes and also alters cell fate: Cells that experience p53 pulses recover from DNA damage, whereas cells exposed to sustained p53 signaling frequently undergo senescence. Our results show that protein dynamics can be an important part of a signal, directly influencing cellular fate decisions.

Cells use molecular signaling networks to sense, interpret, and respond to stimuli. Recent advances in time-lapse microscopy have revealed that many signaling molecules show complex dynamical behaviors (1–13). In

some instances, dynamical properties such as oscillation frequency or signal duration, have been shown to alter gene expression (1, 3, 6, 8, 11, 13–16) or to control cellular differentiation (7, 12, 17). These examples point to a rich mode of regula-

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Reading the Leaves

Excess inputs of nutrients—a type of pollution known as eutrophication—threatens biodiversity and water quality in rivers and streams. **Woodward *et al.*** (p. 1438; see the Perspective by **Palmer and Febria**) studied how one key ecosystem process—leaf-litter decomposition—responds to eutrophication across a large nutrient pollution gradient in 100 European streams. Leaf breakdown was stimulated by low to moderate nutrient concentrations but was inhibited at high rates of nutrient loading.

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