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A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration

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Abstract

The decomposition of plant litter is one of the most important ecosystem processes in the biosphere and is particularly sensitive to climate warming. Aquatic ecosystems are well suited to studying warming effects on decomposition because the otherwise confounding influence of moisture is constant. By using a latitudinal temperature gradient in an unprecedented global experiment in streams, we found that climate warming will likely hasten microbial litter decomposition and produce an equivalent decline in detritivore-mediated decomposition rates. As a result, overall decomposition rates should remain unchanged. Nevertheless, the process would be profoundly altered, because the shift in importance from detritivores to microbes in warm climates would likely increase CO_2 production and decrease the generation and sequestration of recalcitrant organic particles. In view of recent estimates showing that inland waters are a significant component of the global carbon cycle, this implies consequences for global biogeochemistry and a possible positive climate feedback.

Keywords

Carbon cycle, climate change, detritivores, global analysis, latitudinal gradient, litter decomposition, microbial decomposers, streams, temperature.

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INTRODUCTION

Terrestrial plants produce *c.* 120 billion tons of organic carbon each year (Beer *et al.* 2010), only a small fraction of which is annually sequestered (Battle *et al.* 2000) or removed by herbivores (Cebrián & Duarte 1995). This suggests that the reverse process of plant production – the decomposition of plant litter – is one of the most important ecosystem processes in the biosphere. Therefore, elucidating the spatial patterns and environmental controls of litter decomposition is central to understanding the mechanics of ecosystem functioning both locally and over broad spatial scales. As defined here, litter decomposition involves the biological conversion of dead plant biomass to either CO_2 (mineralization) or to other forms of organic matter, such as fine particulate and dissolved organic matter (Seastedt 1984; Gessner *et al.* 1999), which can then undergo further decomposition.

Given the small spatial extent of inland surface waters, most terrestrial plant biomass is decomposed on land. However, recent estimates have shown that decomposition processes in inland waters (Tranvik *et al.* 2009), including streams and rivers (Battin *et al.* 2008, 2009), contribute significantly to the global carbon cycle as a result of high metabolic rates, facilitated by constant water availability and nutrient supply, especially in flowing waters. At the same time, plant litter is a pivotal component of stream food webs and ecosystem functioning, particularly in forest systems (Wallace *et al.* 1997; Gessner *et al.* 2010). The non-limiting role of water is a key feature that makes aquatic systems a suitable model in which to assess the significance of factors controlling decomposition other than water availability (Lecerf *et al.* 2007). This is particularly true for temperature, which in terrestrial systems is inextricably linked to moisture as a mutually confounding factor. Aquatic systems are thus particularly valuable when assessing effects of climate warming on decomposition.

Climate warming predicted for this century (IPCC 2007) is expected to cause species movements and extinctions, change the composition of communities and alter ecosystem functioning (Mooney *et al.* 2009). As decomposition depends strongly on temperature (more so than primary production – Davidson & Janssens 2006), it is expected to be particularly sensitive to climate warming. A useful approach to predict ecological effects of climate change is to use latitudinal gradients as surrogates for future temperature changes (Parmesan & Yohe 2003). Assessments of litter decomposition rates over large spatial scales are rare, however, with only one truly global study (Wall *et al.* 2008), and they are restricted to terrestrial ecosystems, mostly emanating from a single pioneering experiment (Gholz *et al.* 2000; Parton *et al.* 2007; Tuomi *et al.* 2009; Currie *et al.* 2010). The only aquatic study covering a broad latitudinal gradient was confined to single stream sites in Costa Rica, Michigan and Alaska (Irons *et al.* 1994). It suggested that microbes are the main determinant of decomposition near the equator, whereas litter-consuming detritivores gain importance at higher latitudes. However, the relative paucity of investigations in the tropics, and particularly the lack of a global-scale dataset, has precluded a robust test of this suggestion (Boyero *et al.* 2009). Local studies are not coordinated and so differ in their methods, including the use of litter from different plant species that decompose at different rates, thus confounding comparisons of decomposition rates.

We overcame these drawbacks in a global decomposition experiment at multiple stream sites on six continents, spanning a latitudinal range from 43° S to 48° N, by using standardized methodology and leaves of a single species. As litter in streams forms discrete patches that can be experimentally mimicked and manipulated, decomposition rates and the role of different agents in this process can be quantified. A simple and yet powerful approach to study litter decomposition in the field, widely used in both terrestrial and aquatic systems (Boulton & Boon 1991; Liski *et al.* 2005), is to measure the mass loss of leaves enclosed in mesh bags, which allow water flow and microbial colonization while excluding detritivores or allowing their access, depending on the mesh size of the bags. Distinction between these two agents of decomposition – microbes and detritivores – is important because their activities are partly governed by different factors and result in varying proportions of decomposition products such as CO_2 and dissolved and fine particulate organic matter (Seastedt 1984). Thus, we set out to test, across a broad latitudinal gradient, whether microbial decomposition rates are positively related to temperature (Dang *et al.* 2009), leading to higher rates in the tropics, and whether the commonly observed dearth of litter consumers in the tropics counters this latitudinal pattern, leading to higher decomposition rates in temperate climates (Irons *et al.* 1994).

MATERIAL AND METHODS

Study sites and field work

Twenty-two study streams were located in both hemispheres and in all inhabited continents (Fig. 1), at absolute latitudes ranging from 0.37° to 47.80° (Table S1). Mean water temperature ranged from 1.9 to 26.0 °C and was strongly related to latitude ($y = 24.57 - 0.38\ x$; $r^2 = 0.75$; Figure S1). The pH in all streams was circumneutral (7.06 ± 0.18 SE) and conductivity was low (87 μS cm^{-1} ± 23 SE). The experiment was conducted at the season of maximum leaf litter accumulation, which generally was the dry season at tropical sites and autumn at temperate sites. At each site we chose a single stream reach draining a forested watershed experiencing little human influence.

Senescent leaves (*c.* 3 g) of black alder [*Alnus glutinosa* (L.) Gaertn.] were air-dried, weighed, enclosed in coarse-mesh (10 mm) and fine-mesh (0.5 mm) bags and placed in streams. Choice of this species was motivated by the fact that alders are very important riparian species and that they are widely distributed across, and partly beyond, the North Temperate Zone. Importantly, there is also direct experimental evidence showing that alder leaves are highly palatable not only to temperate but also to tropical stream detritivores (Graça *et al.* 2001).

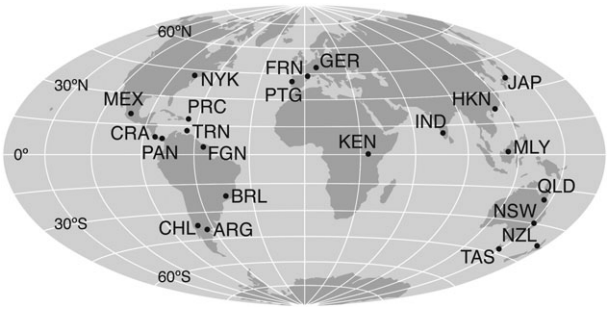


Figure 1 Location of study sites on six continents (ARG, Argentina; NSW, Australia-New South Wales; QLD, Australia-Queensland; TAS, Australia-Tasmania; BRL, Brazil; CHL, Chile; HKN, China-Hong Kong; CRA, Costa Rica; FRN, France; FGN, French Guiana; GER, Germany; IND, India; JAP, Japan; KEN, Kenya; MLY, Malaysia; MEX, Mexico; NZL, New Zealand; PAN, Panama; PTG, Portugal; PRC, Puerto Rico; TRN, Trinidad; NYK, USA-New York).

Three coarse-mesh and three fine-mesh bags were retrieved at each of four dates: day 0 (to determine any weight losses due to handling), and approximately days 14, 28 and 56. Bags were collected with a net (0.5 mm mesh) placed immediately downstream to avoid loss of invertebrates. Leaves were cleaned, oven-dried and weighed.

Data analysis

We used linear mixed models (Pinheiro & Bates 2000; Zuur *et al.* 2009) to test the null hypothesis that decomposition rates do not vary with latitude. To this end, we linearized the simple negative exponential decay model by regressing the natural logarithm of the proportion of litter mass remaining at different sampling dates on the elapsed time (days), latitude of the sampling site (degrees from the equator), elevation (m above sea level), water temperature (°C), mesh size of litter bags (coarse or fine) and the interactions of these factors. To further predict the consequences of climate warming on decomposition rates across latitudes, in a second model we regressed the natural logarithm of the proportion of litter mass remaining on temperature-normalized elapsed time expressed in degree days, latitude, mesh size and their interactions. Degree days were used to normalize for the direct effect of temperature caused by latitude or elevation; they were calculated as time in days multiplied by the average temperature during the experiment, with the threshold set at 0 °C. The slopes of the regression lines were the decay rate coefficient per day or degree day.

Models were fitted by generalized least squares (GLS) using restricted maximum likelihood (REML) procedures implemented in R 2.10.0 ('nlme' package for mixed effects modelling: R Development Core Team 2009). Diagnostic plots were inspected to assess deviations from the assumptions of the analysis (Pinheiro & Bates 2000). To account for heterogeneity in variances with increasing time, days or degree days [divided by the maximum value because of the wide range of values (Zuur *et al.* 2009)] were used as the variance covariate, and a power transformation of it yielded the lowest Akaike information criterion and satisfactory diagnostic plots of residuals (Pinheiro & Bates 2000; Zuur *et al.* 2009). Water temperature was also included as a variance covariate in the first model. The need for random terms was established using a likelihood ratio test between the GLS and linear mixed effects model, and the fixed effects were tested by comparing nested models estimated using maximum likelihood and likelihood ratio tests (Zuur *et al.* 2009). Once the simplest fixed effects structure was found, the final, reduced mixed model was re-fitted with REML and diagnostic plots inspected again (Zuur *et al.* 2009).

Relationships between temperature and decay rate coefficients obtained by the above mixed-model analyses were also explored based on the metabolic theory of ecology (MTE), which provides a framework to assess the relationship between temperature and biological activity in quantitative terms (Gillooly *et al.* 2001; Brown *et al.* 2004; Allen *et al.* 2005). Accordingly, the natural logarithm of the decay rate coefficient was regressed against the inverse of absolute temperature (T) in degrees Kelvin and the Boltzmann constant (k) (Brown *et al.* 2004). We first used ordinary least-squares regressions but also down-weighted or excluded outliers by means of both robust regressions and the least-trimmed-squares regression procedure implemented in SYSTAT 12 (SYSTAT software, Erkrath, Germany).

RESULTS AND DISCUSSION

Patterns across the latitudinal temperature gradient were strikingly different between microbial decomposition in fine-mesh litter bags and combined microbial activity and detritivore feeding in coarse-mesh bags (Appendix S1). Microbial decomposition rates clearly increased along the latitudinal temperature gradient (decay rate coefficient of 6.75×10^{-3} at 0 °C with an increase of 1.76×10^{-3} for each °C), notwithstanding considerable scatter across sites (Fig. 2a). Furthermore, when temperature is expressed in the terms of the MTE, then a negative slope results with a coefficient of

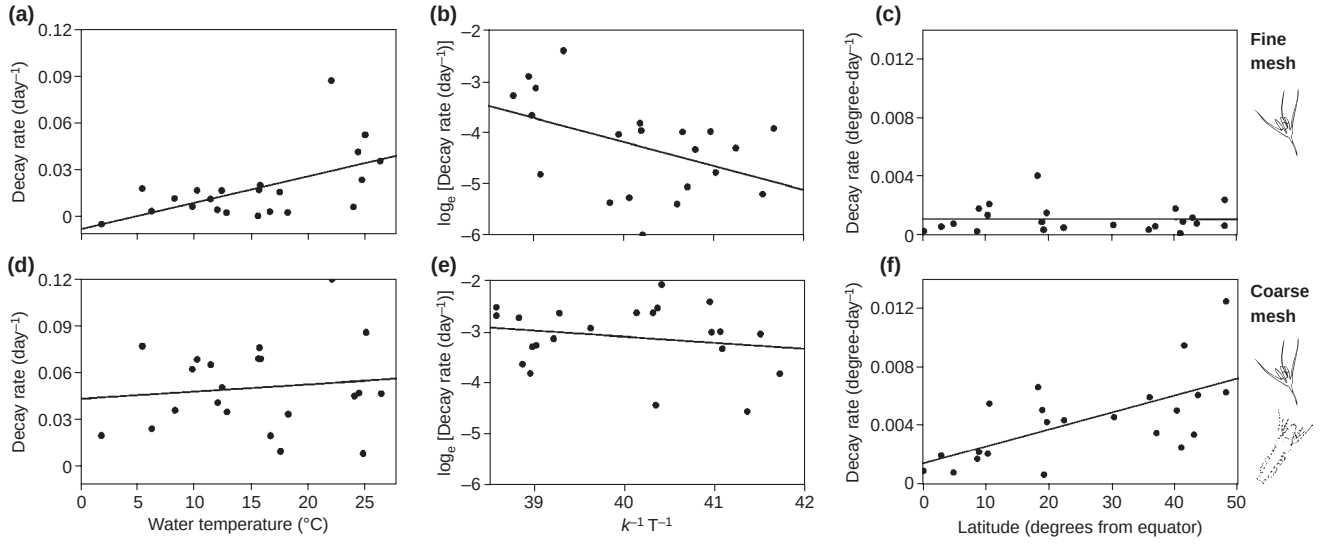


Figure 2 Variation in decomposition rates of litter in fine-mesh (a, b, c) and coarse-mesh bags (d, e, f) across 22 globally distributed study sites. Relationships between decomposition coefficients and stream temperature in °C (a, d), between the natural logarithm of decay rate coefficients per day and stream temperature expressed in the terms of metabolic theory of ecology (MTE) as the inverse of absolute temperature (T) in Kelvin and the Boltzmann constant (k) in eV/k (b, c) and between temperature-normalized decay coefficients per degree day with latitude (e, f). Icons represent a spore of an aquatic fungal decomposer (drawing: E. Chauvet) and a litter-consuming caddisfly larva (drawing: A. Cairns, with permission).

0.46 ± 0.21 (mean ± SE) (Fig. 2b); down-weighting or excluding outliers increases the slope up to 0.58 (robust $r^2 = 0.40$). These estimates compare well with the theoretically expected slope of 0.6–0.7 (Brown *et al.* 2004), indicating that the relationship between microbial decomposition rate and temperature also conforms to theory in quantitative terms. This conclusion is supported by the disappearance of the latitudinal gradient in decomposition rates when these are normalized for temperature by applying a degree-day model that assumes that biological activity ceases below the freezing point (Fig. 2c). This normalization results in a common decay rate coefficient of 1.21×10^{-3} per degree day.

While the above pattern for microbial decomposition is not unexpected, the distinct latitudinal patterns of decomposition in coarse- and fine-mesh bags indicated that the contribution of detritivores to decomposition was opposite to that of microbes; that is, it was at odds with theory on relationships between temperature and biological activity (Appendix S1). Specifically, regression lines for litter in coarse-mesh bags were flat when decomposition rate coefficients, or their logarithm, were plotted against water temperature (Fig. 2d; common decay rate coefficient of 5.16×10^{-2} per day) or against the inverse of water temperature and the Boltzmann constant (Fig. 2e). In contrast, a significant positive slope emerged when temperature-normalized decay coefficients for litter in coarse-mesh bags were regressed against latitude (Fig. 2f). This was strikingly different from the pattern seen for fine-mesh bags and resulted in a decay rate coefficient of 9.55×10^{-4} per degree day at the equator and an increase by 1.37×10^{-4} per degree day for each degree of latitude north or south. Thus, the observed decline in microbial decomposition rate along the latitudinal temperature gradient was balanced, on average, in coarse-mesh bags. The most parsimonious explanation for this pattern is that litter decomposition mediated by detritivores increases with latitude – whether caused by higher detritivore densities, higher individual feeding capacities related to body size, or a combination of both. In line with this explanation, detritivore densities found in natural leaf packs at half of our study sites (sites for which we have appropriate data, and situated from 41° S to 43° N) increased with latitude ($\log_e$ detritivore density = $1.36 + 0.10 \times$ latitude, $r^2 = 0.50$, $P = 0.015$; L. Boyero, R. G. Pearson, R.J. Albariño, M. Callisto, A. Ramírez, E. Chauvet, D. Dudgeon, M. Arunachalam, A.J. Boulton, J. Helson & M.A.S. Graça, unpublished data).

Our results provide a basis for predicting the effects of climate change on litter decomposition in streams. First, they suggest that microbial decomposition rates in a warmer world can be forecast largely on the basis of projected water temperature. Accordingly, a temperature rise would increase microbial decomposition rates, whose magnitude can be derived from our models. As temperature is projected to rise less near the equator (IPCC 2007), warming could have greater effects on microbial decomposition in temperate areas. Second, it appears that total decomposition rates involving invertebrates are determined by the interplay between water temperature and the occurrence of litter-consuming detritivores, with the balance of these two driving forces resulting in unchanged total decomposition rates in a warmer world. This conclusion is only valid under the premise that climate warming leads to relatively rapid range shifts of detritivores according to the new thermal regimes that establish. There is good reason to believe, based on the current distribution and evolutionary history of litter-consuming detritivores, that poleward retractions will indeed occur in response to climate warming (Parmesan & Yohe 2003). Densities of these detritivores are currently higher at higher latitudes (see above) and at higher elevations in the tropics (Yule *et al.* 2009), suggesting that water temperature plays a major role in their distribution. Moreover, many common litter-consuming detritivores belong to insect orders (Plecoptera, Trichoptera) that evolved in cool waters more than 200 million years ago and are still largely restricted to these cool habitats (Wiggins & Mackay 1978; Balian *et al.* 2008). Hence, they are unlikely to respond to climate warming by rapid adaptation or acclimatization, and retraction towards higher latitudes and elevations is much more likely.

Given the broad geographical scope of our study, factors other than temperature and biogeographical patterns of detritivores likely influenced decomposition rates across sites and accounted for the residual variability around the relationships we found. For example, physical fragmentation or abrasion of decomposing leaves could have contributed to litter mass loss at some of our sites. Importantly, however, such physical effects cannot account for the latitudinal patterns we observed, as there is no plausible mechanism by which fragmentation or abrasion would systematically increase with latitude. If anything, streams would be expected to be flashier (i.e. more disturbance-prone) at lower latitudes because of more intense precipitation events (Boulton *et al.* 2008), and this would generate a latitudinal pattern opposite to the one we observed. Even that relation is unlikely, however, given that no high-flow events occurred during our field studies, and flume experiments in controlled flow conditions have shown that physical loss of decomposing leaf mass is barely detectable even at quite high current speeds (Ferreira *et al.* 2006a).

Possible differences in dissolved nitrogen concentrations (Ferreira *et al.* 2006b; Benstead *et al.* 2009) across streams were also likely to be unimportant in our experiment because we had chosen litter of a nitrogen-fixing plant, black alder, that provides a large nitrogen pool to decomposers, making them independent of nitrogen in the environment. Differences in stream phosphorus concentrations could have played a role (Ardón *et al.* 2006), even though our streams had similar basic characteristics and experienced no or relatively little human influence. Other elements, such as sodium, might also have limited decomposition at some locations, as has recently been shown in terrestrial ecosystems (Kaspari *et al.* 2009). Variation in these and other factors (e.g. abundance of leaf litter) across sites may well account for some of the residual variability in our decomposition data set. However, the latitudinal patterns we observed emerged regardless, pointing to the robustness of our findings.

If, as indicated by our results, climate change produces an increase in microbial decomposition and a concomitant decrease in rates of detritivore-mediated decomposition, then total decomposition rates at a given latitude would remain unchanged in response to climate warming. Nevertheless, climate warming could still have substantial consequences for litter decomposition and the food webs and ecosystems depending on this process because microbial decomposers and detritivores have different effects. In particular, microbial decomposition converts a greater proportion of organic compounds to CO_2 (Seastedt 1984; Baldy *et al.* 2007), whereas detritivores tend to generate large amounts of fine particulate organic matter (Ward *et al.* 1994) that is more recalcitrant and more easily exported downstream than the parent leaf material. This implies that CO_2 production through litter decomposition in streams might increase with climate warming, while the generation of recalcitrant organic particles (Yoshimura *et al.* 2008) and sequestration in downstream floodplains, lakes or oceans (where environmental conditions are less conducive to decomposition than in streams) could be reduced.

However, this is only true under the premise that a larger fraction of organic matter than at present is converted to CO_2 on an annual basis. Clearly, projections of climate-change effects on litter decomposition would be improved if future global changes in the nature of riparian vegetation and the amounts and quality of litter inputs were known.

Conventional models of the global carbon cycle describe inland waters as passive pipes of organic carbon from terrestrial ecosystems to the oceans (Battin *et al.* 2009). Recent estimates have shown, however, that streams and rivers receive and transform a sizeable fraction of terrestrial net ecosystem production and thus contribute significantly to the global carbon cycle (Battin *et al.* 2008, 2009). Although this argument is largely based on the turnover of dissolved organic carbon (DOC) received from the watershed, it illustrates the landscape-scale importance of organic matter turnover in stream networks despite their small spatial extent. Plant litter is an important component of organic matter turnover in streams in addition to DOC. Thus, beyond the proof of principle that our study provides, our findings and their implications appear to be directly relevant to global biogeochemistry, with possible positive feedbacks on the climate system (Heimann & Reichstein 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary results.

Figure S1 Relationship between latitude and mean water temperature across 22 stream sites distributed on both hemispheres and six continents.

Table S1 Location of study sites, site codes, latitude, longitude, elevation and average water temperature.