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Litter decomposition across multiple spatial scales in stream networks

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Abstract Spatial scale is a critical consideration for understanding ecological patterns and controls of ecological processes, yet very little is known about how rates of fundamental ecosystem processes vary across spatial scales. We assessed litter decomposition in stream networks whose inherent hierarchical nature makes them a suitable model system to evaluate variation in decay rates across multiple spatial scales. Our hypotheses were (1) that increasing spatial extent adds significant variability at each hierarchical level, and (2) that stream size is an important source of variability among streams. To test these hypotheses we let litter decompose in four riffles in each of twelve 3rd-order streams evenly distributed across four 4th-order watersheds, and in a second experiment determined variation in decomposition rate along a stream-size gradient ranging from orders 1 to 4. Differences in decay rates between coarse-mesh and fine-mesh litter bags accounted for much of the overall variability in the data sets, and were remarkably consistent across spatial scales and stream sizes. In particular, variation across watersheds was minor. Differences among streams and among riffles were statistically significant, though relatively small, leaving most of the total variance (51%) statistically unexplained. This result suggests that variability was generated mainly within riffles, decreasing successively with increasing scale. A broad range of physical and chemical attributes measured at the study sites explained little of the variance in decomposition rate. This, together with the strong mesh-size effect and greater variability among coarse-mesh bags, suggests that detritivores account, at least partly, for the unexplained variance. These findings contrast with the widespread perception that variability of ecosystem characteristics, including process rates, invariably increases (1) with spatial extent and (2), in stream networks, when analyses encompass headwaters of various size. An important practical implication is that natural variability need not compromise litter decomposition assays as a means of assessing functional ecosystem integrity.

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Introduction

Explicit consideration of spatial scale is a key aspect of comprehending ecosystem structure and processes (Schneider 2001; Turner 2005; Urban 2005). This notion has two interrelated components: recognition that patterns emerge at certain scales but not others, and identification of the factors that determine structures and govern processes at different scales. While accounting for variation in patterns and processes across scales is highly relevant for the analysis of all ecosystems (Wiens 1989), the inherently hierarchic nature of some lends itself to elucidating the significance of spatial scale in ecosystem analyses. One promising model system to address this issue is stream networks (Benda et al. 2004; Thorp et al. 2006) in which a series of successively smaller geomorphic units are nested within each other (Frissell et al. 1986; Lowe et al. 2006). For example, riffles and pools are nested within stream reaches, which are nested in whole streams, and the streams in watersheds.

Scaling theory predicts that variance increases when critical thresholds are approached in a system (Allen and Starr 1982; Cooper et al. 1998; Schneider 2001). Discontinuities arising across geomorphic units of different size should therefore result in increased variance of features influenced by environmental factors that vary systematically with size of the units. In the case of streams, these could be hydrological, geomorphic and other features such as water chemistry. For example, small forest streams with low discharge and coarse substrate are likely to both receive and retain more plant litter supplied by riparian vegetation, with consequent effects on resident detritivore communities and transformations of organic matter. The consequences of such scale relations for analyses of biological community structure have been repeatedly assessed (Downes et al. 1993; Steffan-Dewenter et al. 2002; Boyero 2003). However, the significance for ecosystem processes is essentially unknown.

Decomposition of plant litter is among the most fundamental processes in many ecosystems, both terrestrial and aquatic, including forested streams (Aerts 1997; Webster and Benfield 1986; Gessner et al. 1999; Norby et al. 2001). Litter-feeding invertebrates and microbial decomposers contribute to the process (Webster and Benfield 1986; Hieber and Gessner 2002), and one way to assess their respective roles is to use litter bags made of coarse-mesh and fine-mesh screen that either allows or prevents these detritivores access to the plant material (Boulton and Boon 1991). Litter bags have been used for examining decomposition patterns across broad areas in forests (Meentemeyer 1984; Wardle et al. 2003; Parton et al. 2007) and streams (Minshall et al. 1983; Irons et al. 1994) and also for assessing influences of landscape characteristics on litter decomposition

(Austin and Vitousek 2000; Sponseller and Benfield 2001). However, systematic assessments of variability in decomposition rates across multiple spatial scales have not been performed (Royer and Minshall 2003). Such an approach, when taken in tandem with measurements of environmental variables, may inform how the controls of decomposition vary across spatial scales.

The central aims of this study were to assess levels of overall variability in decomposition rates within a given region, and to determine how this variability is partitioned among hierarchical levels of the major geomorphic units in stream networks. Additionally, we tested whether upstream–downstream changes result in systematic differences in process rates among stream reaches belonging to streams of different size, as would be expected if the physical discontinuities arising where tributaries join a larger channel have an influence on ecosystem processes (Benda et al. 2004). Our first hypothesis was that increasing spatial extent adds significant variability in decomposition rates at each hierarchical level within stream networks ranging from riffles to watersheds. The rational was that the likelihood of encountering additional sources of variability increases with the area covered (i.e., with spatial extent) when grain size (here individual litter bags) is kept constant. Our second hypothesis was that stream order is an important source of variability, based on the assumption that environmental characteristics and biological communities vary with stream size. We tested these hypotheses by conducting two litter decomposition experiments at 24 sites distributed systematically across four watersheds, and by analyzing the data at three spatial scales that spanned five orders of magnitude.

Methods

Site characterization

We conducted two experiments to evaluate spatial patterns of litter decomposition in stream networks. Study streams were located between 477 and 870 m a.s.l. in four forested fourth-order watersheds in the southern Black Forest in southwestern Germany (47° 50′N, 8° 48′E). Sites were contained within a mountainous area of approximately 600 km^2, which is homogeneous in geology and land cover and drains into the Rhine River. Streams were circumneutral and softwater. We included only sites with similar mixed-deciduous riparian vegetation. Major tree species were *Alnus glutinosa* (L.) Gaertn., *Salix fragilis* L., *Fraxinus excelsior* L. and *Acer pseudo-platanus* L. All sites were free of intensive human impacts such as upstream dams or agriculture. We measured a wide range of morphological and chemical site characteristics in the fall of 2004 in order

to relate litter decomposition rates to environmental conditions (Table 1).

Experimental procedures

We used a litter-bag approach to determine decomposition rates (Boulton and Boon 1991). Freshly fallen poplar (*Populus nigra* L.) leaves were gathered from the ground of a single location during autumn leaf fall. The leaves were transported to the laboratory where the long and easily broken petioles were removed with scissors to increase homogeneity of the leaf material. Thorough mixing of the entire leaf material improved homogeneity further. We chose poplar because this species is common along larger rivers but did not occur in the riparian vegetation of the study streams, and so any bias among streams resulting from the choice of the leaf species could be avoided. The leaf material was air-dried, weighed into 4.0 ± 0.1 g portions, remoistened to make the leaves pliant, and enclosed in mesh bags. We used both coarse-mesh and fine-mesh bags (10 mm and 0.5 mm mesh size, respectively) to allow or prevent access by detritivores to leaves and thus provide estimation of microbial and detritivore contribution to litter mass loss (Boulton and Boon 1991).

Coarse-mesh and fine-mesh bags were placed in stream riffles on similar substratum and in similar flow conditions.

They were fixed to the stream bed by tying them to an iron bar that was hammered into the substratum. Bags were installed in early November of 2004 to coincide with autumn leaf fall and removed after 47 days. This retrieval date corresponded to the time when approximately 50% of the initial litter mass was lost. We chose this 50% target to strike a balance between sufficient mass loss to have occurred for any existing differences to emerge and mass loss being too far advanced, because variance among replicates increases with time and absolute differences diminish owing to the typically exponential decay of leaves in streams. The timing of litter-bag retrieval was determined based on visual examination of the bags in situ, and by deploying and periodically retrieving additional litter bags that were not included in the data analyses. After retrieval of the samples and transport to the laboratory, the leaves from each litter bag were gently cleaned to remove adhering debris and invertebrates, then dried and weighed to determine the percentage of the original leaf mass that remained.

Experimental designs

In Experiment 1, we used a hierarchical design to assess the variability of litter decomposition in streams across three spatial scales: 4th-order watersheds, 3rd-order streams

Table 1 Summary of methods used to characterize riffles, streams and watersheds. *TPN* total particulate nitrogen, *TPP* total particulate phosphorus. See electronic supplementary data (Appendices 1 and 2) for summary data

Variable	Scale at which replicated	Variable description/methodology
Stream order	Stream	After Strahler (1952); topographic map (1:50,000)
Stream links	Stream	Number of 1st order streams draining to site, topographic map (1:50,000)
Drainage area (km²)	Stream	Topographic map (1:50,000)
Channel slope (%)	Stream	Topographic map (1:50,000)
Elevation (m)	Stream	Topographic map (1:50,000)
Perimeter/area (1/m)	Stream	Watershed perimeter/area (1:50,000)
Riffle length (m)	Riffle	Single field measurement
Temperature (°C)	Riffle	Temperature data logger, hourly readings
Channel width (m)	Within riffle	Field measurement, 4 widths per riffle
Channel depth (m)	Within riffle	Field measurement, 9 depths per riffle
Flow velocity (m/s)	Within riffle	Velocity meter, recorded approximately 2 cm above each litter bag
NH_4^+ (µg/l)	Riffle	Spectrophotometry (indophenol-blue method)
$NO_2^- + NO_3^-$ (mg/l)	Riffle	Spectrophotometry
TPN (mg/l)	Riffle	Spectrophotometry (after alkaline digestion)
PO_4^{3-} (µg/l)	Riffle	Spectrophotometry (molybdenum-blue method)
TPP (µg/l)	Riffle	Spectrophotometry (molybdenum-blue method after acid digestion)
pH	Riffle	pH meter
Conductivity (µS/cm)	Riffle	Conductivity meter (at 20°C)
Mg^{2+} (mg/l)	Riffle	Ion chromatography
Ca^{2+} (mg/l)	Riffle	Ion chromatography
Alkalinity (mmol/l)	Riffle	Titration with 0.1 M HCl

within those watersheds, and riffles within those streams. These scales approximate the hierarchical river sub-systems described by Frissell et al. (1986). Within each of the four selected 4th-order watersheds, we identified three replicate 3rd-order streams, and in each 3rd-order stream we nested four replicate riffles (Fig. 1). In three of the 4th-order watersheds we sampled the entire population (*n* = 3) of 3rd-order streams. In the Dreisam watershed, three 3rd-order streams were chosen randomly among a possible five streams. When access to a chosen site was restricted, another stream was chosen. Riffles were separated by a distance of between 60 and 80 channel widths from one another, with the number of channel widths chosen at random. The resulting distances varied from approximately 50 m to 500 m, depending on stream size. We placed a total of eight litter bags (four coarse-mesh and four fine-mesh) within each riffle. Thus, the design consisted of four watersheds, three streams per watershed, four riffles per stream, and eight litter bags per riffle (four per mesh size),

corresponding to a total of 384 bags. All but six lost bags were retrieved at the end of the experiment.

In Experiment 2, we assessed the variability of decomposition rates along a stream-size gradient. We selected a single 1st, 2nd, 3rd and 4th order stream in each of the four 4th-order watersheds used in Experiment 1. Stream selection was determined by a combination of accessibility of stream sites and the need to create an arrangement of sites that ensured spatial independence among streams of different orders, thereby minimizing situations in which an upstream lower-order stream flowed into a larger stream downstream. The desired spatial arrangement was accomplished with the exception of one watershed where both the 2nd and 3rd-order stream flowed into the 4th-order stream (Fig. 1). We identified four riffles within each of the selected streams as described above, and placed a single coarse-mesh and fine-mesh bag in the center of each riffle. Thus there were 16 streams, four riffles per stream, and two litter bags per riffle (1 per mesh size), resulting in a total of 128 litter bags.
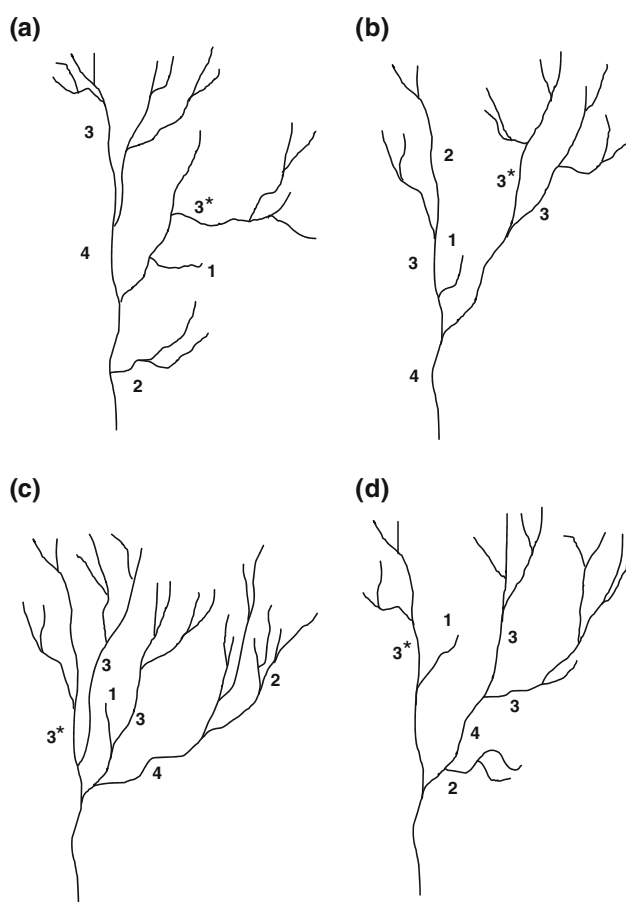
Data analysis

To facilitate comparison with published data, we calculated decay rate coefficients, *k*, for each individual litter bag under the assumption that litter decomposition followed first-order kinetics (i.e., an exponential decay model). However, we used litter mass remaining as the response variable in the data analysis. Before statistical analyses, we examined the data from both experiments for normality (frequency distributions of percent litter mass remaining) and similar variances (comparison of standard deviations) and found them to be suitable for applying parametric tests. To assess the variability in decomposition across spatial scales in Experiment 1, we performed a partially nested analysis of variance (ANOVA) on the percentage of initial leaf mass remaining in litter bags. Riffles were nested within streams, and streams within watersheds. This analysis was performed for the entire data set of Experiment 1 combined and separately for data from coarse-mesh and fine-mesh bags. To analyze data from Experiment 2, we used a two-way ANOVA to test for differences in decomposition rates among the four stream sizes and mesh sizes of litter bags, with watershed treated as a blocking factor. Mesh type was used as a fixed factor (detritivore access either permitted or not) in both experiments; other factors were treated as random factors.

To characterize the stream sites, we performed a principal component analysis (PCA) on the physical and chemical data gathered from each riffle, stream and watershed in Experiments 1. Subsequently, we calculated correlations to evaluate potential relationships between leaf-mass loss and the five most important factors of the PCA (Eigenvalues >1). We used Statistica (StatSoft, Tulsa, OK) to calculate

Fig. 1 Spatial arrangement of the selected study sites across four watersheds. **a** Wiese, **b** Kleine Wiese, **c** Dreisam, **d** Wehra. *Numbers* indicate stream order and the locations of study sites. The 3rd-order streams used in both Experiment 1 and Experiment 2 are indicated with *asterisks*. Sketches of watersheds are not drawn to scale

nested ANOVAs and SYSTAT 10 (Systat Software, Point Richmond, CA) to perform the two-way ANOVA and PCA.

Results

In Experiment 1, mean percent leaf mass remaining among all 378 leaf bags retrieved was 49.7%, with a standard deviation of 7.2%. This corresponds to an exponential decay coefficient of 0.0152 ± 0.0035 day^{-1} (mean $\pm$ SD). Percent leaf mass remaining across all litter bags ranged from 15 to 66%, corresponding to exponential decay coefficients of 0.0410–0.0087 day^{-1}.

Decomposition was remarkably consistent among watersheds in both coarse-mesh (Fig. 2) and fine-mesh (Fig. 3) litter bags, such that watershed represented less than 1% of the total variability in the data set (Table 2). Decomposition among streams was also similar, although less so than among watersheds (Figs. 2, 3), resulting in a significant difference among streams (Table 2). When the mass-loss data from coarse-mesh and fine-mesh bags were analyzed separately, no differences were observed among streams in leaf-mass remaining in fine-mesh bags ($F_{8,36} = 1.69$, $P = 0.13$). Among-stream differences in decomposition rates of leaves in coarse-mesh bags were marginally significant ($F_{8,36} = 2.23$, $P = 0.048$). Like streams, differences in

decomposition among riffles (Figs. 2, 3) were also significant (Table 2), accounting for 10% of the total variance. As for streams, the riffle effect was significant for the coarse-mesh ($F_{36,142} = 1.86$, $P = 0.006$) but not the fine-mesh ($F_{36,140} = 1.06$, $P = 0.39$) bags. Furthermore, the overall variance in the coarse-mesh data set was 40% higher. Leaves placed in coarse-mesh bags also decomposed significantly faster than those in fine-mesh bags (Figs. 2, 3). This mesh effect was relatively strong and consistent across watersheds, with much of the overall variance in the data set related to mesh size (Table 2). Nevertheless, variability among individual litter bags within individual riffles (i.e., the error term) was the largest source of variability, representing 51% of the total variance.

In Experiment 2 decomposition rates of leaves placed in 1st-order to 4th-order streams were remarkably consistent and ranged from 43 to 46% of the initial leaf mass remaining in coarse-mesh bags, and from 50 to 54% in fine mesh bags. No significant difference was observed among stream sizes ($F_{3,114} = 1.00$, $P = 0.40$) (Fig. 4). Mesh size was a highly significant factor affecting leaf mass loss ($F_{1,114} = 43.3$, $P < 0.0001$), whereas the interactions between mesh size and stream size was not significant ($F_{3,114} = 1.27$, $P = 0.29$), nor was watershed as a blocking factor ($F_{3,114} = 0.26$, $P = 0.85$).

Morphological and physico-chemical characteristics of the studied streams and riffles are summarized in the

Fig. 2 Percent litter mass remaining (mean $\pm$ 95% CI) in fine-mesh bags across the three spatial scales examined. **a** Watershed, **b** stream and **c** riffle. Standard errors are based on three streams within each watershed, four riffles within each stream, and four litter bags within each riffle
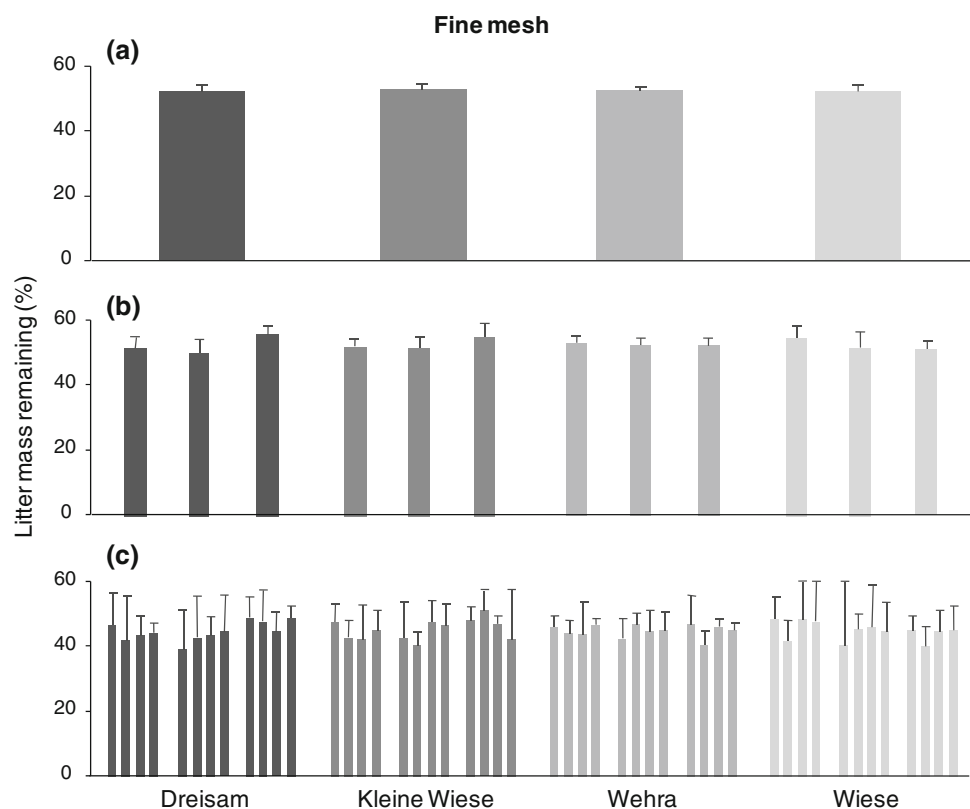
Fig. 3 Percent litter mass remaining (mean ± 95% CI) in coarse-mesh bags across the three spatial scales examined. **a** Watershed, **b** stream and **c** riffle
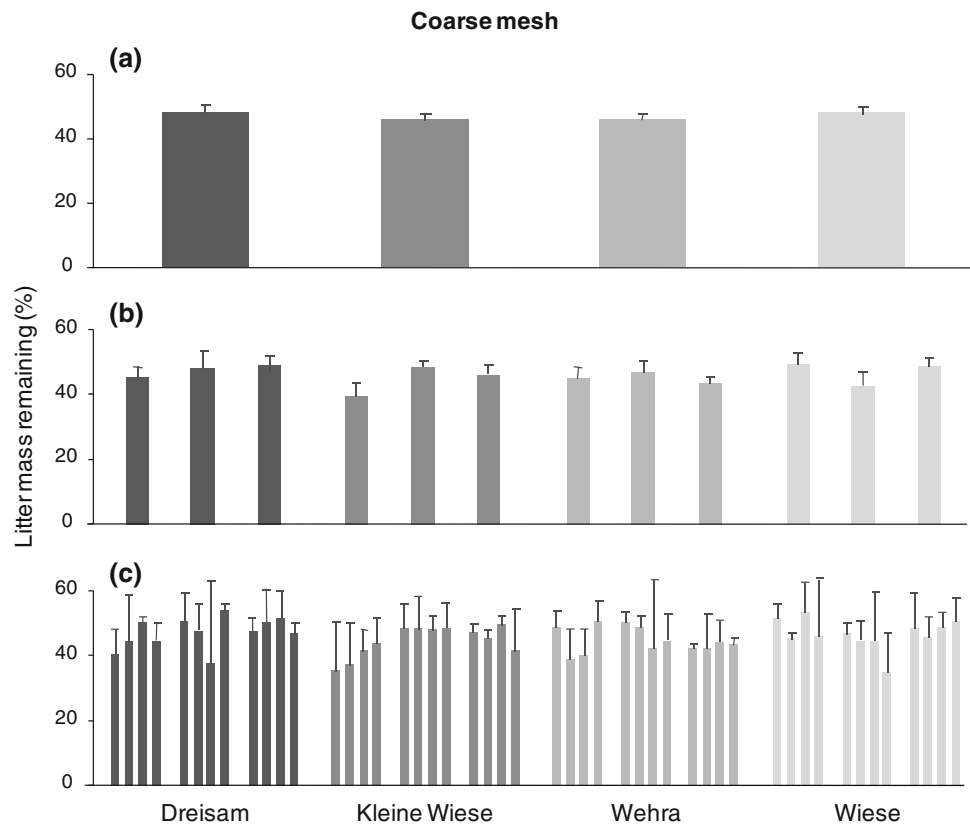

Coarse mesh

Table 2 Results of nested ANOVA to test for effects of mesh size of litter bags, watershed, streams nested in watershed, and stream riffles nested in streams on litter decomposition rates

Source of variation	Sum of squares	Total variance (%)	Numerator degrees of freedom	Mean squares	Denominator degrees of freedom	F	P
Mesh	1,284	19.1	1	1,284	282	104.9	<0.001
Watershed	29	0.4	3	9.7	8	0.20	0.88
Stream (watershed)	381	5.7	8	47.7	36	2.52	0.028
Riffle [stream(watershed)]	682	10.1	36	18.9	282	1.55	0.028
Watershed × mesh	64	1.0	3	21.4	8	0.82	0.52
Stream(watershed) × mesh	209	3.1	8	26.1	36	1.52	0.19
Riffle [stream(watershed)] × mesh	620	9.3	36	17.2	282	1.41	0.068
Error	3,450	51.3	282	12.2			

Appendices 1 and 2 in the electronic supplementary material (ESM). A principal component analysis (PCA) of the variables revealed five important factors, which together accounted for 85% of the total variance in the Experiment 1 data set. However, litter mass loss from either coarse-mesh or fine-mesh bags was significantly related to only two of these factors ($P = 0.001$), and both of these negative relationships were weak ($r^2 = 0.053$ and 0.058, respectively). The most important variables defining the first factor (F1) were related to stream size and water hardness. These were, in order of importance, stream links (i.e., the number of 1st order streams upstream of the sampling point), conductivity, calcium concentration, and drainage area. The most

important variables defining the other factor that was significantly related to litter mass loss (F3) was defined primarily by temperature and nutrient concentrations: (in order of importance) mean daily temperature, total particulate phosphorus concentration, elevation, and total particulate nitrogen concentration.

Discussion

Results of the two decomposition experiments, encompassing stream sizes from 1st to 4th order and three spatial scales, from riffles to streams to watersheds, lead to two
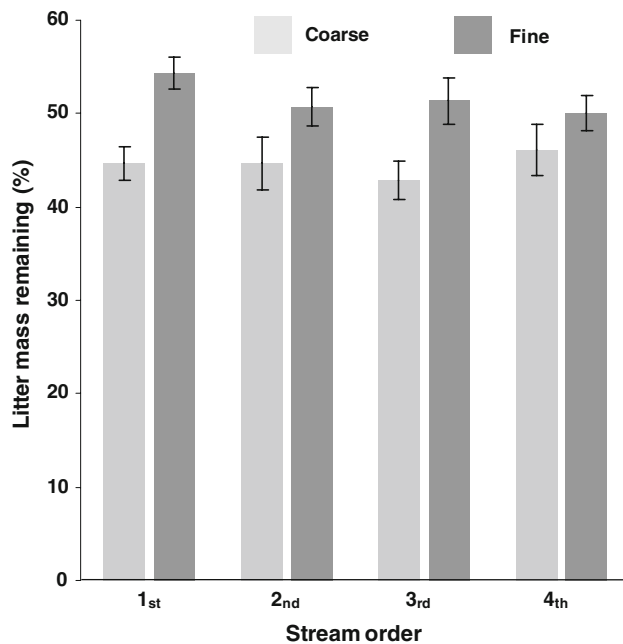
Fig. 4 Percent litter mass remaining (mean ± 95% CI) in coarse-mesh and fine-mesh bags in 1st to 4th-order streams. The effect of mesh size was highly significant (ANOVA; $P < 0.001$), whereas no statistically significant difference was observed among stream sizes (ANOVA; $P = 0.39$), nor was the interaction between both factors significant

important conclusions. First, overall variability in decomposition rate of a standard litter type can be remarkably small across numerous sites within a region with similar general geologic features and riparian vegetation structure. The similarity in decomposition was particularly clear for microbial decomposition, estimated as leaf mass loss in fine-mesh litter bags. These results suggest little variation in the control of decomposition rates, particularly at the watershed scale. This does not mean, of course, that controls beyond the regional scale operate through drivers such as geology and climate (Royer and Minshall 2003). Indeed, variability in decomposition among biomes (Minshall et al. 1983; Irons et al. 1994; Parton et al. 2007) and, in forests, across pronounced climatic gradients (e.g., Meentemeyer 1984; Austin and Vitousek 2000) has been documented.

The second conclusion is that most of the variability observed among sites appeared to be attributable to local factors at particular sites within streams. This is indicated not only by the fact that riffles had the strongest influence on decomposition rate among the three spatial scales explicitly considered, but also by the large proportion of unexplained variance (51%), i.e., among litter bags within riffles, with most of the remainder being related to mesh size (Table 2). A fraction of the unexplained variance might be due to differences in leaf quality in individual litter bags and to variability introduced by handling. However, given the homogeneous quality of the litter batch used in our

experiment, much of the variability likely arose from variation in local conditions within riffles. These observations suggest that an important percentage of the total variability in decomposition rates is generated by mechanisms operating at very fine scales, whereas controls at larger spatial scales (watershed, stream, riffle) were of much lesser or no importance.

Which mechanism may have caused the observed variability at fine spatial scales? Differences in the variance of decomposition rates between coarse-mesh and fine-mesh bags may hold a partial answer. Given that decomposition was faster in coarse-mesh bags and that overall variability across coarse-mesh bags was 40% greater than across fine-mesh bags, one plausible explanation of variation at the riffle scale is patchiness in detritivore feeding. It could arise from differences in per capita consumption rates or total shredder abundance or biomass that operate at the stream, riffle and small-patch scale within riffles. Consistent with this interpretation, Abos et al. (2006) reported that aggregation of shredder species in leaf packs was greater than could be explained by chance alone (see also Murphy et al. 1998). Since litter-feeding detritivores vary in their capacity to consume litter (e.g., Anderson and Sedell 1979), aggregation by certain species in some litter bags and different species in others can translate to variable decomposition rates at small spatial scales (Tiegs et al. 2008), even when total detritivore abundance and biomass are similar. Moreover, several studies have observed patterns of variability in invertebrate assemblages (Downes et al. 1993; Crowl et al. 1997; Li et al. 2001; Boyero 2003) and movement patterns (Boyero and Bosch 2002, 2004) that are comparable to those observed for the decomposition rates measured here in that variability was greater at smaller spatial scales.

An alternate explanation for the high degree of within-riffle variability observed in our study is that local hydraulic and related factors, such as current velocity, resulted in patchy physical fragmentation of the leaf material. However, none of such variables was correlated strongly with decomposition rate. For fine-mesh bags, altered environmental conditions (e.g., O_2 concentration or nutrient supply) could slow decomposition and contribute to variability. However, our 0.5-mm mesh still allowed excellent water exchange, and clear relationships between such variables and decomposition rate were not detected, suggesting that notable effects of altered water chemistry in fine-mesh bags are highly unlikely. Collectively, the evidence from our experiment points to spatially variable consumption by litter-shredding invertebrates as one factor responsible for decomposition rates at small spatial scales, and the remaining variation was not related strongly to the site characteristics we examined.

If discontinuities in stream character and communities occur between streams of different size (Benda et al. 2004),

one would expect repercussions for biological communities and hence ecosystem processes. However, our data do not lend support to this idea, since no strong tendency in decomposition rate was observed along our stream-size gradient. Upstream–downstream changes in decomposition rate have been observed in field studies extending over greater stream-order gradients than examined here, as predicted by the river continuum concept (Melillo et al. 1983; Minshall et al. 1983; Jonsson et al. 2001). A key difference, however, is that even our larger streams were fully shaded and received appreciable inputs of terrestrial litter. These results illustrate that variation in the influence on decomposition by either detritivores or microbial decomposers can be rather small among well-characterized streams ranging in size from 1st to 4th order. We posit that, in the absence of human impacts this pattern holds in other regions with homogeneous geology, climate and land cover, including riparian vegetation.

Litter decomposition has been proposed and used as a means of assessing the functional integrity of ecosystems (Christensen et al. 1996; Gessner and Chauvet 2002; Gulis et al. 2006; Young et al. 2008). The results presented here have important implications for implementing such an approach, since natural variability, as a source of statistical noise in litter decomposition trials, poses a major threat to the effectiveness of such assessments if human impacts are to be sensitively detected (Gessner and Chauvet 2002; Ciesielka and Bailey 2007). However, the magnitude of variability in decomposition rate observed across all spatial scales in the present study was small relative to the pronounced impact that anthropogenic activities can have on litter decomposition (e.g., Dangles et al. 2004; Chadwick et al. 2006). Low variability facilitates establishing absolute reference values for decomposition rates within climatically and geologically homogeneous regions without the need for spatially extensive studies such as that presented here. Rather, when stream types are well delineated, reference decomposition rates could be defined based on a small set of sites and yet cover most of the overall natural variability to be expected within the region. This is a clear advantage in the implementation of process-based approaches to ecosystem assessment, where required effort, the related costs, and the lack of suitable benchmarks are often major constraints.

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