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# Combined carbon flows through detritus, microbes, and animals in reference and experimentally enriched stream ecosystems

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*Abstract.* Tracking carbon (C) flow through ecosystems requires quantification of myriad biophysical processes, including C routing through microbial and metazoan food webs. Yet detailed organic matter budgets are rarely combined with simultaneous measurement of C flows supporting microbial and animal production. Here, we synthesize concurrent data sets on organic matter, microbes, and macroinvertebrates from two detritus-based stream ecosystems, one of which was subject to experimental nitrogen (N) and phosphorus (P) enrichment. Our synthesis provides new insights into C flow through forest stream ecosystems. Over 3 yr, the reference stream showed a striking balance of inputs and outputs, with a mean surplus of only 7 g C·m$^{-2}$·yr$^{-1}$ (~1% of annual inputs), presumably stored in sediments as fine particulate organic matter (FPOM). In contrast, N and P enrichment over 2 yr resulted in severe deficits of C (−576 g C·m$^{-2}$·yr$^{-1}$ or ~170% of annual inputs), a shortfall presumably met by stored C. Our data set provides an ecosystem-based estimate of the fate of forest litter C at ambient nutrient concentrations: 6.2% was leached as dissolved organic C, 40.6% and 8.5% flowed to litter-associated fungi and bacteria, respectively, 7.5% was consumed by macroinvertebrates, 1.8% was exported as coarse particles, and the remainder (35.4%) was presumably fragmented by biophysical processes. Our calculations also allowed an estimate of inputs into the heterogeneous FPOM pool, which is otherwise difficult to obtain. At naturally low nutrient concentrations, 50.7% was derived from fragmented litter, 39.1% from microbial biomass (mostly fungal), and 10.2% from macroinvertebrate egesta. Nutrient addition drove large changes in C fluxes in the experimental stream, especially in flows of leaf litter to fungi (×1.7 pretreatment) and macroinvertebrates (×2.7), and of FPOM to hydrologic export (×2.6). Our results underscore the key roles of both microbes and metazoans in controlling C flow through detritus-based ecosystems, as well as how release from persistent nutrient limitation may perturb steady-state conditions of C inputs vs. outputs. Our analysis also suggests areas for future research, including assessing the relative importance of stored vs. recycled C in fueling detrital food webs subject to altered nutrient regimes and other global-change drivers.

*Key words: carbon; detritus; energy flow; fungi; micro-organisms; nitrogen; nutrient enrichment; phosphorus; trophic dynamics.*

## Introduction

Carbon (C) dominates flows of material and energy through ecosystems, moving along a diversity of biotic and abiotic pathways that are linked to the availability and cycling of other elements (Lindeman 1942, Odum 1957, Redfield 1958). The routing and magnitude of these C pathways result from complex interactions between the abiotic environment and the combined metabolism of primary producers, heterotrophic microbes, and metazoans in food webs (Reiners 1986). A key abiotic factor driving these interactions is the relative availability of commonly limiting nutrients, such as nitrogen (N) and phosphorus (P), which co-regulate the growth, biomass, and activity of both primary producers and consumers (Sterner and Elser 2002). By relieving stoichiometric imbalance between resources and organismal demand, N and P inputs can accelerate C flow rates through food webs (Cross et al. 2007, Demi et al. 2020). Relative changes to trophic C fluxes in response to elevated nutrients may thus manifest as significant shifts in C routing and flow through ecosystems. Studying such shifts requires detailed measurement of responses to nutrients that fully integrate organic matter (OM) budgets and food-web flows at appropriate spatial

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and temporal scales. Despite calls for such an approach (Marcarelli et al. 2011), few attempts at this level of integration have been made.

Responses of C fluxes and pathways to limiting nutrients are expected to be particularly dramatic in detritus-based ecosystems, because any resulting increase in detrital C processing (and associated loss of organic C) is not expected to be offset by increases in autochthonous primary production (Moore et al. 2004, Rosemond et al. 2015). Such relationships between nutrient enrichment and net C loss have been investigated in some detail in forest stream ecosystems, where the rapid processing of relatively high-quality detritus (i.e., relative to soils) and pervasive hydrologic transport of partially processed detrital particles combine to exacerbate loss of organic C (Benstead et al. 2009, Rosemond et al. 2015). Highly heterotrophic forest streams thus represent excellent model systems for investigating the routing of C through ecosystems, particularly the role played by nutrient availability (Baldy et al. 2007, Demi et al. 2020). This suitability is enhanced by their linear nature and unidirectional flow, which facilitates accurate measurement of C storage and cycling while allowing for experimental manipulation at large spatial scales. Studies of small streams are also relevant: headwater stream networks receive the bulk of terrestrial net ecosystem production, and so act as a key interface for the transfer of organic C into aquatic systems (Cole et al. 2007, Battin et al. 2009). Finally, stream ecosystems are subject to pervasive anthropogenic nutrient enrichment on a global scale, making study of its effects on processing of terrestrial C a research priority (Dodds and Smith 2016, Stoddard et al. 2016, Stets et al. 2020).

To date, forest stream ecosystems have not been subject to detailed C budgets that fully integrate OM and food web flows, presumably because of the effort required to collect concurrent data on responses of microbial, metazoan, and OM components (Cummins et al. 1983, Marcarelli et al. 2011). Here, we combine published concurrent data sets on OM budgets (Benstead et al. 2009), microbial activity (Gulis et al. 2008, Suberkropp et al. 2010), and C flow through macroinvertebrate food webs (Cross et al. 2007) in two intensively studied headwater stream ecosystems. Our previously published OM budget used a relatively coarse approach to quantify dominant OM pools, inputs, and exports (Benstead et al. 2009). We now compile and synthesize a unified data set to ask three questions about C flow through forest stream ecosystems. First, what is the routing, magnitude, and relative proportions of C flow through all major biotic and abiotic pathways in forest streams at naturally low concentrations of N and P? Second, how are these characteristics of C cycling altered by release of biotic C processing from N and P limitation? Last, how can integrated ecosystem-level C budgets inform understanding of the various fates of particulate C that enters streams, as well as the proximate sources of inputs into the heterogeneous and enigmatic pool of organic C that is subsequently stored and transported as fine particulate OM (FPOM)?

## Methods

### *Study sites*

Our data set was collected in two adjacent first-order streams (C53 and C54) at the Coweeta Hydrologic Laboratory (CHL) Long Term Ecological Research site, Macon County, North Carolina, USA. The two streams have very similar physical and chemical characteristics (i.e., watershed area, slope, elevation, discharge, temperature, pH). Reach lengths (headwater seep to weir) were 145 m for C53 and 260 m for C54. Discharge was monitored continually at an H-flume at the base of each reach. Annual mean discharge during the 3 yr of the study was below the long-term average, ranging between 0.20 and 0.46 L/s in the reference stream (C53) and between 0.38 and 0.62 L/s in the experimental stream (C54). Water temperature was monitored every 30 min in both streams with Optic StowAway temperature probes (Onset Computer Corp., Bourne, Massachusetts, USA). Temperatures ranged from 1°C to 19°C during the study and did not differ between the two streams. Concentrations of $[NO_3 + NO_2]$–N, $NH_4$–N, and soluble reactive phosphorus (SRP) were measured every 2 wk at the weir of the reference stream and at several locations along the treatment stream. Ambient concentrations of inorganic N and P in these streams are very low ($[NO_3+NO_2]$–N average, 17 μg/L, range, 4–40 μg/L; $NH_4$–N average, 10 μg/L, range, below detection to 30 μg/L; soluble reactive phosphorus [SRP] average, 4 μg/L, range, below detection to 22 μg/L). Vegetation is dominated by mixed hardwoods (primarily oak, maple, and tulip poplar), with a dense understory of *Rhododendron maximum* L. that shades the streams throughout the year.

### *Experimental nutrient addition*

Our study consisted of a 1-yr pretreatment period (July 1999–June 2000) followed by a 2-yr experimental nutrient addition (July 2000–June 2002) to C54. From 11 July 2000, N ($NH_4NO_3$) and P ($K_2HPO_4$ and $KH_2PO_4$) were dripped continuously into C54 along the lower 190 m, permanently flowing reach (see Gulis et al. 2004 for a full description of the flow-proportional, longitudinal dripper system). Concentrations of dissolved inorganic N and P were elevated approximately 6- to 15-fold ($[NO_3+NO_2]$–N average, 309 μg/L, range, 11–1,711 μg/L; $NH_4$–N average, 106 μg/L, range, below 6–566 μg/L; SRP average, 51 μg/L, range, below detection to 268 μg/L).

### *Flows and storage of detrital C*

Methods to quantify OM budgets are described in detail in Benstead et al. (2009). Briefly, inputs of OM

were measured using a combination of litter traps, measurement of dissolved organic C (DOC) at seeps, and estimates of primary production and DOC throughfall. Net primary production is <2% of C inputs under ambient nutrient concentrations, so is ignored here. We only report net DOC export. Storage of OM (leaf litter, nonleaf particulate OM, and FPOM) was estimated from monthly benthic samples (Cross et al. 2006, Suberkropp et al. 2010). Outputs of OM were assessed using continuous FPOM collection by a Coshocton sampler, a coarse particulate OM trap, measurement of DOC exports at the H-flume, and measurements of microbial respiration (see Detrital C flows through microbes section).

### *Detrital C flows through microbes*

We define coarse particulate OM (CPOM) as leaf litter plus nonleaf particulate OM (i.e., mostly small-diameter wood). Annual flows of C to fungi and bacteria associated with CPOM were estimated as the sum of their respective microbial production values and total respiration on each substrate (see Gulis et al. 2008, Suberkropp et al. 2010 for a full description). We assumed that substrate mass-specific bacterial production rates on nonleaf particulate OM represented 25% of total microbial production on that substrate under ambient nutrient concentrations (see Appendix S1: Table S1 for unpublished data from CHL streams). Given that fungal production on leaf litter was strongly (~3×) stimulated by nutrient addition in our experimental streams while bacterial production increased only slightly (Suberkropp et al. 2010), we assumed that bacterial production on nonleaf particulate OM would account for only 10% of total microbial production under nutrient enrichment. Whole-reach respiration and production rates were estimated by summing the mean products of the published estimates of leaf litter, nonleaf particulate OM, and FPOM respiration rates per unit mass and their respective mean storage values (Gulis et al. 2008, Suberkropp et al. 2010, Tant et al. 2013). We assumed that 25% of measured microbial respiration was attributable to bacteria (biomass of fungi on leaf litter and wood is ~70× and 7× higher, respectively, than that of bacteria; Findlay et al. 2002, Baldy et al. 2007, Suberkropp et al. 2010, Tant et al. 2013), a value consistent with the allometry of bacterial vs. fungal metabolism (Aguilar-Trigueros et al. 2017) and with estimated C use efficiencies (CUEs; see Discussion and Appendix S1: Fig. S1). Total areal respiration rates were also corrected by assuming 50% lower rates in the 80% of OM buried >3 cm deep (Findlay et al. 2002, Benstead et al. 2009).

### *Detrital C flows through metazoans*

We estimated annual flows to macroinvertebrates (i.e., consumption) using methods developed by Benke and Wallace (1980) and described in Cross et al. (2007). Briefly, gut contents were analyzed seasonally for dominant primary consumers and averaged over individuals and seasons to obtain estimates of diet composition. Flows of OM (g ash-free dry mass $m^{-2}{\cdot}yr^{-1}$ of leaf litter, wood, fungi, animals, and amorphous detritus) were calculated using annual secondary production estimates (Cross et al. 2006), average diet composition (Cross et al. 2007), and literature-based assimilation efficiencies (see Cross et al. 2007 for a detailed description). Flows to predators from production of primary consumers feeding on FPOM (quantified as amorphous detritus in guts), leaf litter and wood were estimated by assuming that their proportions in predator diets were equal to the relative proportion of these flows to the total flow to primary consumers.

### *Calculations and data analysis*

All flows were converted to units of g $C{\cdot}m^{-2}{\cdot}yr^{-1}$. Net DOC export was calculated as the difference between DOC inputs and measured DOC outputs and assumed to be largely derived from the leaching of CPOM (Meyer et al. 1998). The flow of fragmented particles from CPOM to the FPOM pool was the difference between CPOM input and all other outputs. The same approach was used for microbial production, the FPOM pool and the CPOM pool where necessary. In the latter two cases, a negative difference indicated use of stored C.

In order to infer differences between pre- and post-treatment periods (and potential effects of nutrient addition on C pathways in the experimental stream) we calculated log response ratios for all the major C flows (>10 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$) in the reference and experimental stream ecosystems that were directly estimated. We did not calculate response ratios for flows estimated by difference or for the flow of macroinvertebrate egesta derived from CPOM ingestion to the FPOM pool, which was calculated as a fixed proportion of CPOM ingestion (i.e., same response ratio). Response ratios for each flow were calculated for each stream separately as the natural logarithm of the following quotient: mean response value during the 2 yr period of nutrient addition to the experimental stream divided by the mean response value during the 1 yr pretreatment period.

## Results

### *C flow at low ambient nutrient concentrations*

The reference stream was highly retentive of annual CPOM inputs, losing only ~2% to hydrologic export. An additional ~6% was lost to net export of DOC (Fig. 1a). Almost half of the remaining CPOM (41% or 192 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$) flowed to fungal metabolism, with smaller amounts fueling metabolism of bacteria (40 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$) and macroinvertebrates that fed on CPOM (35 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$). The CPOM remaining after

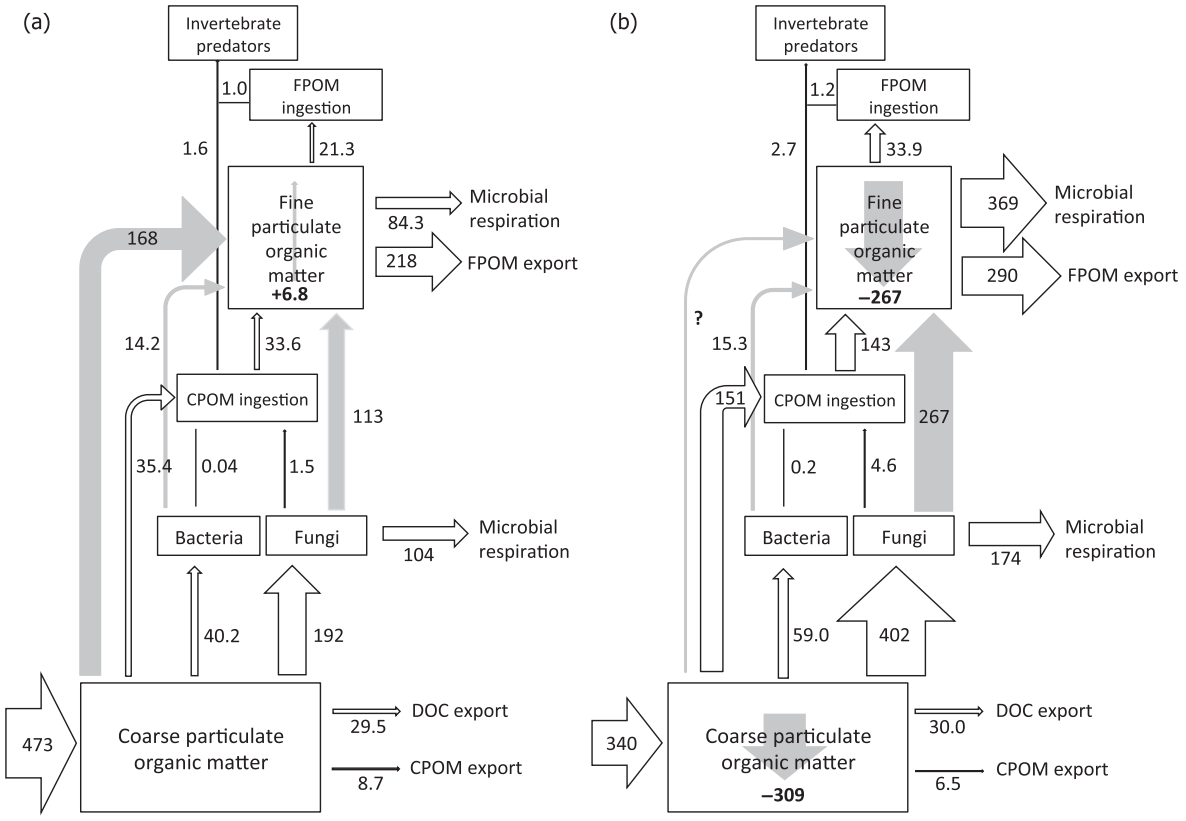


FIG. 1. Flows of C through the (a) reference and (b) experimental stream ecosystem. Values on or beside arrows represent flows in g C·m$^{-2}$·yr$^{-1}$ and are based on the average of 3 yr in the reference stream and 2 yr of N and P addition in the experimental stream. Arrow widths are scaled to flow magnitude. Gray arrows in each diagram indicate flows that were calculated by difference between inputs and outputs into the respective C pool. All other flows are direct estimates. The flow from coarse particulate organic matter (CPOM) to CPOM ingestion labeled with "?" in (b) is undefined because it could not be calculated by difference (i.e., outputs from the CPOM pool exceeded inputs—see Discussion). For some flows fungi were assumed to contribute 75% of the respiration of CPOM-associated microbes (see Discussion and Appendix S1: Fig. S1). Box size is not scaled to magnitude of storage. Flows do not exactly balance due to rounding error. FPOM, fine particulate organic matter; DOC, dissolved organic C.

subtraction of these flows (168 g C·m$^{-2}$·yr$^{-1}$ or ~35% of detrital C inputs) was assumed to be fragmented by biophysical action and to enter the FPOM pool (i.e., none was assumed to be buried as CPOM). Of the C flows to fungi and bacteria, trivial proportions were diverted to macroinvertebrates feeding on CPOM, and total microbial respiration (104 g C·m$^{-2}$·yr$^{-1}$) and loss of bacterial and fungal production to the FPOM pool (total of 127 g C·m$^{-2}$·yr$^{-1}$; calculated by difference) accounted for the remainder. Egesta of macroinvertebrates feeding on CPOM was the last, relatively minor source of FPOM (34 g C·m$^{-2}$·yr$^{-1}$; Fig. 1a).

Output flows from the FPOM pool were dominated by hydrologic export (218 g C·m$^{-2}$·yr$^{-1}$) and microbial respiration (84 g C·m$^{-2}$·yr$^{-1}$), with only 21 g C·m$^{-2}$·yr$^{-1}$ being ingested by macroinvertebrates. Mass balance of the FPOM pool dictated a negligible surplus of 7 g C·m$^{-2}$·yr$^{-1}$, which we assumed entered storage in sediments. The final flux to be considered was to macroinvertebrate predators from prey production attributable to consumption of CPOM and FPOM. This flow amounted to only 2.6 g C·m$^{-2}$·yr$^{-1}$, or ~0.5% of annual detrital C inputs (Fig. 1a).

### *C flow under experimental N and P enrichment*

Mean inputs of CPOM to the experimental stream declined after the pretreatment year (Figs. 1b, 2a and Appendix S1: Fig. S2), averaging 340 g C·m$^{-2}$·yr$^{-1}$ during the 2 yr of nutrient addition, or only ~72% of the mean inputs to the reference stream. The experimental stream was similarly retentive, however, losing only 11% of C inputs (37 g C·m$^{-2}$·yr$^{-1}$) to hydrologic export of CPOM and DOC (Figs. 1b, 2b). Nutrient addition had clear effects on subsequent flows of retained C. Of these, large responses were seen in flows of CPOM to fungal metabolism (production plus respiration = 402 g C·m$^{-2}$·yr$^{-1}$) and to macroinvertebrates feeding on CPOM (151 g C·m$^{-2}$·yr$^{-1}$; Fig. 1), which represented two- to fourfold increases relative to the reference stream (Fig. 1) and the experimental stream during the pretreatment period (Figs. 2c, d). The flow of CPOM to

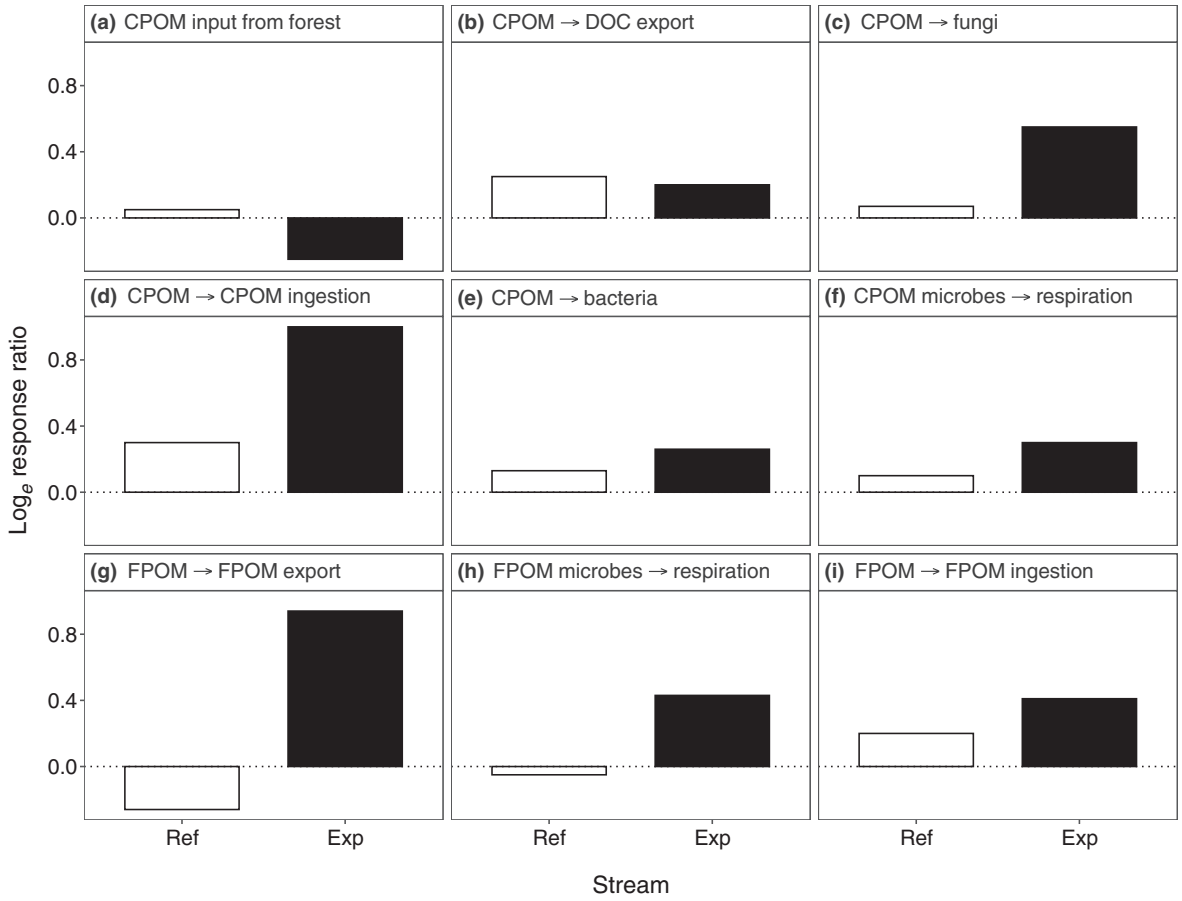


FIG. 2. Log response ratios of directly estimated and major C flows (>10 g C·m$^{-2}$·yr$^{-1}$) in the reference (Ref) and experimental (Exp) stream ecosystems. Not shown are flows calculated by difference and the flow of macroinvertebrate egesta derived from coarse particulate organic matter (CPOM) ingestion to the fine particulate organic matter (FPOM) pool, which was calculated as a fixed proportion of CPOM ingestion (i.e., same response ratio as d). Plot (a) merely illustrates how CPOM inputs differed before and after nutrient enrichment and does not imply a treatment effect. Dashed line at zero indicates no change in the response.

bacterial metabolism was relatively minor (Fig. 2e). Combined, these flows from the CPOM pool resulted in a large mean deficit (−309 g C·m$^{-2}$·yr$^{-1}$) during the 2 yr of nutrient addition, implying a substantial subsidy from a stored C pool. As a result of this deficit, the contribution of fragmented particles to the experimental stream's FPOM pool was undefined (Fig. 1b).

Respiration of litter-associated microbes in the experimental stream exceeded that in the reference ecosystem by almost twofold after enrichment (Fig. 1, 2f). Increased flows of C from fungi and bacteria (total of 282 g·m$^{-2}$·yr$^{-1}$; Fig. 1) were mostly shunted towards the FPOM pool (flow calculated by difference and not shown in Fig. 2). There was a similarly large difference in FPOM inputs from macroinvertebrate egestion (143 vs. 34 g·m$^{-2}$·yr$^{-1}$; Fig. 1). Despite these higher inputs to the FPOM pool, large increases in FPOM export (Fig. 2g) and FPOM-associated microbial respiration (Fig. 2h) combined with the undefined input of fragmented particles to result in an additional and considerable C deficit in the FPOM pool (−267 g C·m$^{-2}$·yr$^{-1}$). The final food-web flows of C involved fluxes of FPOM to macroinvertebrates (34 g C·m$^{-2}$·yr$^{-1}$; Fig. 2i) and of macroinvertebrate prey production (attributable to consumption of CPOM and FPOM) to macroinvertebrate predators (3.9 g C·m$^{-2}$·yr$^{-1}$; Fig. 1). Relative to the reference stream, both of these flows showed modest increases in flow magnitude (×1.6 and ×1.5, respectively) and in their proportions of total C inputs (10% vs. 4.5% and 1.1% vs. 0.5%, respectively).

### *Fates of CPOM and sources of FPOM*

The essentially balanced C budget in the reference stream allowed us to estimate the relative proportions of various proximate fates of CPOM at ambient nutrient concentrations (Fig. 3): 6.2% was leached as dissolved organic C, 40.6% and 8.5% flowed to litter-associated fungal and bacterial metabolism, respectively, 7.5% was consumed by macroinvertebrates, and only 1.8% was

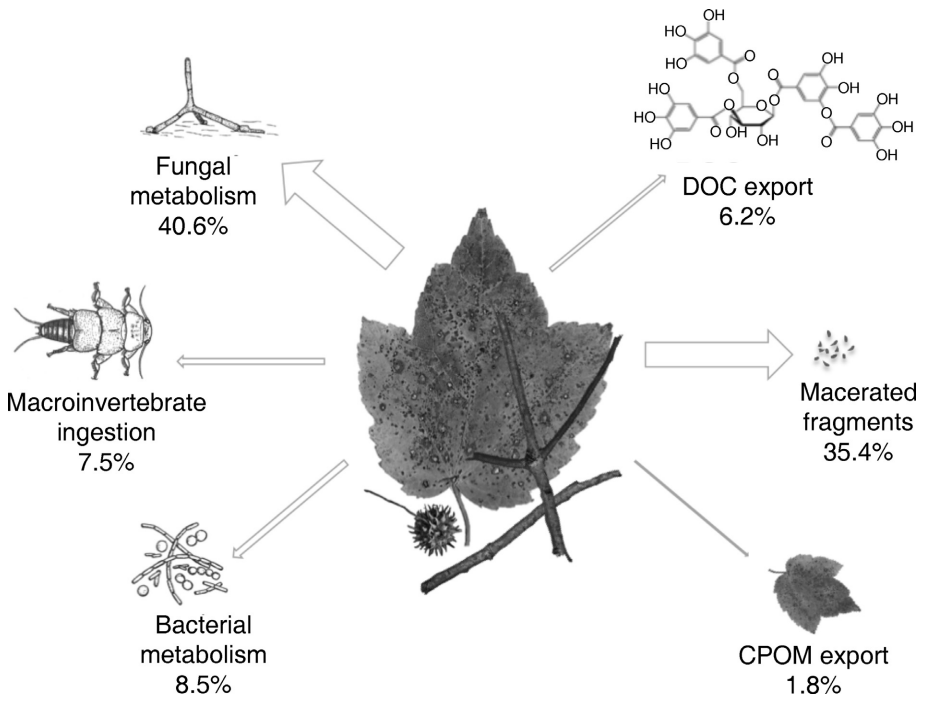


FIG. 3. Summary of ecosystem-level estimates of the fate of coarse particulate organic matter (CPOM = leaf litter, small-diameter wood, etc.) in the reference stream ecosystem under ambient (i.e., low) nutrient concentrations. Arrow widths are scaled to proportion. DOC = dissolved organic carbon (tannic acid molecule shown). Proportional output to macerated fragments was calculated by difference. Images by K. Suberkropp (hyphomycete conidium) and A. Huryn (all others; *Tallaperla* nymph redrawn and modified from Stewart and Stark 2002).

exported as CPOM. The remainder (35.4%) was calculated by difference and assumed to be fragmented by biophysical action (i.e., the impact of flow combined with nonconsumptive effects of macroinvertebrates and microbial enzymes, such as sloppy feeding and release of parenchyma cells and fragments via fungal breakdown). The large deficits implied by our calculations from the experimental stream made a similar estimate problematic (i.e., there was no surplus of annual C input to flow to a "fragments" pool). However, any comparison between the two stream budgets suggests that a greater proportion of CPOM must have flowed through microbial and animal consumers, relative to biophysical fragmentation, under nutrient-enriched conditions. Hence, relative inputs of microbial necromass and macroinvertebrate egesta to the FPOM pool were likely much higher under nutrient-enriched conditions.

The budget from the reference stream also allowed us to estimate relative de novo inputs to the FPOM pool. At naturally low nutrient concentrations, we estimate that 50.7% of FPOM was derived from fragmented litter, 39.1% from microbial biomass (overwhelmingly fungal), and 10.2% from macroinvertebrate egesta. Although the undefined flow of CPOM to the FPOM pool via biophysical fragmentation made a similar calculation impossible in the experimental stream, the budgets again indicate that inputs of microbial necromass and macroinvertebrate egesta to the FPOM pool had to be proportionally higher during nutrient enrichment.

## Discussion

We combined published data sets on detritus, microbial production and respiration, and macroinvertebrate production to construct novel budgets that tracked organic C flow along multiple biotic and abiotic pathways. The integrated data set allowed us to compare these flows and to see whether and to what extent they balanced over annual timescales, under ambient nutrient conditions, and in the face of nutrient enrichment. Comparison of the budgets from the reference and experimental streams revealed strong effects of nutrient addition driven by the release of detrital consumers from N and P limitation. Our analysis provides new insights into C flow through forest stream ecosystems, while also raising new questions and uncertainties. We first consider the patterns of C flow at naturally low nutrient concentrations, before examining the consequences of experimental N and P addition for C flow. We then use the budgets to infer the various fates of CPOM and likely sources of FPOM in forest streams. We end by considering some weaknesses of our approach, as well as potentially fruitful avenues for greater understanding of C flow through stream ecosystems.

*Patterns of C flow in the reference stream ecosystem*

The reference stream ecosystem was highly retentive of the CPOM inputs that dominated its C budget, with <2% exported as operationally "coarse" particles (>4 mm in size) and ~40% respired by microbes within the reach, with the bulk of the remainder exported as FPOM and only a small fraction entering storage. The sum of these C outputs was also in marked balance with the stream's C inputs over the 3 yr of study, indicating that C storage was in steady state over this period (i.e., measured C pools were also stable; Benstead et al. 2009). Such steady-state conditions in the reference stream, especially the absence of any significant deficit in FPOM, suggests that our budgets are not missing an important C source (e.g., soil organic particles derived from the catchment). Any lack of evidence for a significant terrestrial subsidy of FPOM suggests that most transported FPOM, at least in small forest streams, is generated by instream processes (also see Wallace et al. 1999). In our study streams, these processes were clearly dominated by the comminution of terrestrial CPOM (see Fates of CPOM and sources of FPOM section).

The high retention of CPOM in the reference stream meant that C flows were dominated by biotic processing within the reach and subsequent C loss via both evasion and advection of respired $CO_2$ and hydrologic export of FPOM. The initial processing of CPOM was overwhelmingly driven by fungi, as demonstrated in other studies (Hieber and Gessner 2002, Gulis et al. 2019), with C flow to litter-associated fungi roughly five-fold higher than to bacteria. Fungi also likely played a disproportionate role in the production of fragmented particles from CPOM via release of partially degraded and macerated plant cells and fragments (Suberkropp and Klug 1980, Chamier and Dixon 1982). Although the flow of C to CPOM ingestion was modest, macroinvertebrates were likely also important in driving the major flow (~35% of CPOM inputs) of fragmented particles to the FPOM pool (i.e., via sloppy feeding; Cummins and Klug 1979). The role of invertebrate feeding in particle generation has been convincingly demonstrated by experimental depression (via insecticide treatment) of macroinvertebrate communities in Coweeta streams, which decreased annual export of FPOM by two-thirds (Wallace et al. 1982, Cuffney et al. 1990). Our budgets indicate that this decrease in export cannot be attributed solely to lower C ingestion and decreased production of egesta by macroinvertebrates, highlighting their nonconsumptive role in fragmenting CPOM, and generating and mobilizing fine particles that are subsequently exported downstream in the single largest C flux we measured in the reference stream.

*Alteration of C flows by N and P addition*

Many patterns of C flow observed in the reference stream were greatly altered by nutrient addition, stressing the role of stoichiometry in driving ecosystem C dynamics via interactions between biotic and abiotic pathways (Battin et al. 2008, Aufdenkampe et al. 2011, Maranger et al. 2018). Of the biotic pathways, flows from CPOM to fungi and macroinvertebrates, and subsequent flows of microbial biomass and egesta to the FPOM pool, showed dramatic responses to nutrient addition (i.e., two- to fourfold higher than the reference stream). Increases in these biotic pathways can be attributed to the release of microbial and metazoan detritivores from pervasive nutrient limitation that typically limits their activity under ambient nutrient concentrations (Suberkropp 1998, Gulis and Suberkropp 2003*b*, Demi et al. 2020). In turn, the resulting higher flows of C into the FPOM pool led to mobilization of C and large increases in its hydrologic export to downstream ecosystems, because of the much longer transport distances of FPOM vs. CPOM, particularly at high discharge (Webster et al. 1999). Hence, our data show that nutrient enrichment does not alter the location of CPOM processing in small streams (because CPOM retention is naturally high). Instead, the budgets show that nutrient addition increases the rate at which C is processed and transported downstream as FPOM, rather than being stored longer (and mineralized more slowly) closer to the location of its original input (also see Rosemond et al. 2015). Thus, by accelerating breakdown and changing the likelihood of transport, increased nutrient enrichment of headwater streams is likely to modify the natural metabolic "footprint" of detritus as it is transported along stream networks (Webster et al. 1999, Webster 2007).

Our C budget for the experimental stream could only be balanced by assuming a large deficit (i.e., total outputs were 576 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ higher than inputs) of CPOM and FPOM sustained by the processing and export of stored detrital C stocks. This mean deficit represented ~170% of mean annual CPOM inputs over the 2 yr of nutrient addition, raising the question of whether such a shortfall could be met by stored C. Our results implied a minimum CPOM deficit of −309 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$, whereas the measured cumulative decrease in CPOM storage during 2 yr of nutrient addition was only 54 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$, or roughly 17% of the deficit implied by our flow calculations (Benstead et al. 2009, Suberkropp et al. 2010). Assuming the minimum CPOM deficit above, our budget from the experimental stream also indicated an FPOM deficit of −267 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$, while measured losses of this pool over the 2 yr of enrichment were 69 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$, or roughly 26% of the calculated deficit (Benstead et al. 2009). Processing of even more stored CPOM than the minimum of 309 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ would direct more C to the FPOM pool, decreasing the amount required to balance this deficit. Overall, changes in pools of CPOM and FPOM in the experimental stream were consistent with the sign implied by our flow calculations, but did not match them closely in magnitude. This disparity may be explained by

difficulties in accurately quantifying total storage of OM in even low-order stream ecosystems, large proportions of which may be buried deeply in channels, especially as wood or interstitial FPOM.

### *Fates of CPOM and sources of FPOM*

Our ecosystem-level budgets allowed us to partition the components of two processes that are otherwise relatively difficult to estimate: the proximate fates of CPOM in forest streams and the contribution of various sources to the poorly characterized FPOM pool. Partitioning the various proximate fates of leaf litter has been tackled using different methods in the literature and at a variety of scales (Gessner et al. 1999, Marks 2019). Perhaps the most common approach combines the patch scale of single-species litter bags with measurement of microbial and shredder production and assumption of bioenergetic efficiencies (e.g., Cuffney et al. 1990, Hieber and Gessner 2002, Baldy et al. 2007). Such studies typically provide estimates of fates that differ substantially from those we present here. For example, contributions of shredding macroinvertebrates to breakdown are usually much higher in litter-bag studies (e.g., 28% across four litter species in Cuffney et al. 1990 and 64% of alder in Heiber and Gessner 2002 vs. 7.5% in our study). Conversely, estimates of flows of CPOM to fungi from studies based on litter bags are typically lower than we calculated here (8–35% in Hieber and Gessner 2002 and 29–39% in Pascoal and Cassio 2004 vs. 40.6% in our study). Attempts to calculate the proximate fates of CPOM at large spatial scales such as entire reaches are scarcer in the literature (Fisher and Likens 1973, Fisher 1977, Webster and Meyer 1997). Discrepancies between estimates at the different scales can perhaps most easily be explained by differences in the mean quality of the C substrates under study (Marks 2019). Our reach-scale budgets integrated C processing across much of the CPOM spectrum (i.e., all leaf litter of varying traits plus small-diameter wood, etc.) and so encompassed the entire range of CPOM quality. In contrast, litter-bag studies typically use single litter species that are often relatively palatable (e.g., alder, willow, and red maple) and that may act as resource "islands" to shredders, likely biasing the relative contributions of major flows to shredders vs. microbes (also see Rosemond et al. 2015 for comparisons of single-species litter-bag breakdown rates with those of whole-reach litter loss).

Our integrated budgets also enabled some new inferences about the broad proximate sources of particles entering the heterogeneous FPOM pool that is otherwise challenging to study. Under reference conditions, ~10% of inputs to the FPOM pool was egesta derived from consumption of CPOM by macroinvertebrates, approximately 40% originated from litter-associated microbial production, and our data suggest that the remainder (~50%) of the inputs to the FPOM pool was composed of macerated detrital fragments derived from CPOM (i.e., comminuted but not yet metabolized). Non–steady state of C in the experimental stream complicated equivalent calculations of its FPOM sources, but our data indicate a far greater contribution of egesta and microorganisms to the FPOM pool under enriched conditions, likely fueled by increased processing of macerated fragments of formerly coarse material. It is also worth noting that our estimates of proximate *inputs* into the FPOM pool cannot speak to the subsequent processing and outputs of that material. Previous studies of FPOM ingestion by stream benthic macroinvertebrates indicate that consumptive demand for the FPOM pool can exceed 100%, suggesting reingestion of egested C (Fisher and Gray 1983, Grimm 1987, Romito et al. 2010). Our budgets are not entirely consistent with such active recycling of the entire FPOM pool, but our data may underestimate feeding on FPOM by only quantifying it as amorphous detritus in macroinvertebrate gut contents and because of our assumption of a relatively high assimilation efficiency for this material (10%; Cross et al. 2007). Direct measurement of assimilation efficiency of FPOM by chironomid midges in CHL streams produced estimates of 1.7–2.5% (Romito et al. 2010), suggesting that ingestion of FPOM by macroinvertebrates may be underestimated in our study. Hence it is possible, and indeed likely, that the FPOM actually exported from our study reaches differs greatly in composition from our estimates of proximate inputs to the FPOM pool, as a result of successive cycles of microbial processing and macroinvertebrate ingestion.

### *Caveats and conclusions*

Our ecosystem C flow analysis includes some important caveats. The first is the relatively high CUEs that our data imply. We assumed that 75% of measured litter respiration was attributable to fungi. Mean fungal CUE (i.e., production/[production + respiration] on leaf litter) in the reference stream can therefore be estimated at ~53%. The equivalent mean fungal CUE in the experimental stream was even higher at 65%. Equivalent estimates of bacterial CUE (assuming bacteria accounted for 25% of microbial respiration on CPOM) in the reference and experimental stream were 25% and 22%, respectively. These microbial CUEs exceed those of some published estimates. For example, Suberkropp (1991) reported a CUE of 35% for litter-associated fungi. However, CUE of stream fungi depends on nutrient availability and has been estimated at 31% vs. 60% at low vs. high dissolved nutrient concentrations, respectively (Gulis and Suberkropp 2003*a*), a range that largely overlaps our estimates. Bacterial CUEs reported from rivers range from 3% to 46% (del Giorgio and Cole 1998), making estimates from our budgets also appear feasible. Given the greatly skewed ratio of fungal to bacterial biomass and production on CPOM, especially leaf litter, these CUE estimates are not likely to be sensitive to realistic ranges in our assumption of

proportions of fungal and bacterial respiration (see Appendix S1: Fig. S1).

A second caveat is that our budgets may simplify the cycling of C within the microbial–detrital complex. For example, our estimates of C flow to fungi and bacteria assumed that all production is based on C from the CPOM substrate, essentially discounting the possibility of recycling of C in microbial biomass that can result in total C demand exceeding initial C input (depending on CUE and retention; Strayer 1988). Our budgets maintained mass balance by shunting all microbial production to other pools, so overlooking recycling could influence the relative magnitude of C flows but not their sum. For example, we measured a fungal C demand of 192 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ in the reference stream. If we assume C recycling under conditions of 50% CUE and 100% retention, this flow could be derived from an initial C input of just 96 g. The unused litter C would instead flow down alternative pathways calculated by difference instead of direct measurement.

Retention of 100% of assimilated C is obviously unrealistic in stream ecosystems, especially of easily mobilized microbial necromass. Nevertheless, the example above illustrates the potential significance of recycling within pools for calculating C flows among them. It also raises questions about the fate of microbial (especially fungal) necromass in streams, which our data show to be a relatively significant C flow. The function of fungal necromass is increasingly recognized in the soil literature (Fernandez et al. 2016, Beidler et al. 2020, Maillard et al. 2020). Unfortunately, other than visual evidence of bacteria growing on fungal hyphae (V. Gulis, *personal observations*) and the known chitinolytic capacity of some bacterial taxa, little is known about degradation of microbial necromass in aquatic environments (Swiontek Brzezinska et al. 2014). We predict that the potential for recycling within the CPOM aggregate is relatively low, because bacteria are implicated in recycling and their C demand on CPOM is a small proportion of total microbial demand (13–17% in this study). Higher potential for recycling exists within the FPOM pool where bacteria have much higher relative importance, but again this would only affect the composition of the FPOM pool (i.e., the degree to which those particles have been processed by microbes) without changing the total magnitude of flows associated with a given amount of respiration.

A final caveat is that our analysis lacks estimate of errors associated with C flows. It is important to note that our budgets mimic the function of forest stream ecosystems by eventually routing all excess particulate C through the FPOM pool. Consequently, any change in the magnitude of a flow affects only the size of the FPOM pool in a strictly proportional way. Such a simple response makes any formal sensitivity analysis relatively uninformative. However, consideration of relative error is still valid. Some of the flows we report here are based on continuously collected fluxes from entire reaches (e.g., outputs of CPOM and FPOM) that, although subsampled for quantification, were presumably subject to relatively low measurement error. Other flows were based on extrapolations from periodic sampling and/or assumptions that could have introduced errors into the respective flow estimates. Of all our measured flows, FPOM respiration is likely to be subject to the highest error, driven by difficulties in quantifying the FPOM pool, variation in mass-specific respiration rates, and the effect of assumptions in our calculations (e.g., lower respiration rates in buried sediments). As explained above, any change to FPOM respiration would affect the FPOM pool in a proportional manner. Future stream C budgets should attempt to refine estimates of storage and biological activity of this important C pool. Despite the uncertainty around our estimates of FPOM respiration, we believe that our overall results are robust. Certainly, the dramatic effects of nutrient addition we summarize here seem unlikely to result from errors in measurement of FPOM respiration or any other flow.

In summary, analysis and comparison of our two integrated C budgets revealed important insights, both into the natural function of forest stream ecosystems and how it can be altered by anthropogenic nutrient inputs. The reference stream was evidently in C steady state over the study period, with inputs almost perfectly balanced by outputs. Our results quantify the key roles played by microbes and metazoans in controlling the internal C flows in the reference stream, with both assimilation and nonconsumptive effects of consumers playing an interactive role in mobilizing C for hydrologic export of FPOM to downstream reaches. Release from persistent nutrient limitation by our 2-yr N and P addition caused substantial deficits that could only have been met by stored C, raising the question of how historical nutrient pollution has altered patterns of detrital C storage in streams and rivers worldwide. Finally, our analysis highlights the importance of additional research into aspects of stream C budgets that are typically treated as "black boxes." These include the role of C recycling in stream food webs, especially within the microbial–detrital complex, and how such recycling is affected by nutrient enrichment. Other topics deserving of attention include accurate assessment of inputs and retention of C in streams that would allow temporal changes to be tracked, as well as the sources, processing, and turnover of the enigmatic and challenging FPOM pool that represents such an important component of elemental fluxes in stream and river ecosystems (Webster et al. 1999, Webster 2007, Maranger et al. 2018).

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