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Brown meets green: light and nutrients alter detritivore assimilation of microbial nutrients from leaf litter

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Abstract. In aquatic detrital-based food webs, research suggests that autotroph-heterotroph microbial interactions exert bottom-up controls on energy and nutrient transfer. To address this emerging topic, we investigated microbial responses to nutrient and light treatments during *Liriodendron tulipifera* litter decomposition and fed litter to the caddisfly larvae *Pycnopsyche* sp. We measured litter-associated algal, fungal, and bacterial biomass and production. Microbes were also labeled with ^{14}C and ^{33}P to trace distinct microbial carbon (C) and phosphorus (P) supporting *Pycnopsyche* assimilation and incorporation (growth). Litter-associated algal and fungal production rates additively increased with higher nutrient and light availability. Incorporation of microbial P did not differ across diets, except for higher incorporation efficiency of slower-turnover P on low-nutrient, shaded litter. On average, *Pycnopsyche* assimilated fungal C more efficiently than bacterial or algal C, and *Pycnopsyche* incorporated bacterial C more efficiently than algal or fungal C. Due to high litter fungal biomass, fungi supported 89.6–93.1% of *Pycnopsyche* C growth, compared to 0.2% to 3.6% supported by bacteria or algae. Overall, *Pycnopsyche* incorporated the most C in high nutrient and shaded litter. Our findings affirm others' regarding autotroph-heterotroph microbial interactions and extend into the trophic transfer of microbial energy and nutrients through detrital food webs.

Key words: algae; bacteria; carbon; ecological stoichiometry; fungi; phosphorus; Pycnopsyche.

Introduction

Classic approaches to trophic ecology have focused on delineating energy and material flow between "brown" and "green" food webs (Lindeman 1942, Brett et al. 2017). Brown food webs are driven by inputs of detrital subsidies and subsequent assimilation and mineralization by microbial decomposers (i.e., fungi and bacteria) that are key to detritivore nutrition (Marks 2019). In turn, green food webs are directly influenced by light availability, which regulates autotroph biomass and nutrient content, and therefore influences upper trophic

levels (Sterner et al. 1997). While green and brown food webs differ in their energy basis, they are both limited by the availability of nutrients (e.g., nitrogen and phosphorus (P)) and play major roles in ecosystem-level energy flow and nutrient cycling (Zou et al. 2016, Evans-White and Halvorson 2017).

In brown food webs, detritivores derive nutrition from both detritus and microbial biomass (Marks 2019). The detrital-microbial matrix consists of diverse microbes, predominantly heterotrophic fungi and bacteria, which may differ in nutritional importance for detritivores (Findlay et al. 2002). Detritivores assimilate most of their nutrition from microbial biomass compared to the detritus itself, due to the higher nutritional value of microbial biomass; for example, fungi colonize and assimilate detrital organic carbon (C) and nutrients into a form more palatable for detritivores to ingest

placed into 60 feeding chambers in an environmental chamber at 15°C and a 12 h:12 h light:dark cycle. Feeding chambers were filled with 100 mL Chamber Springs water with constant aeration and a 2-mm mesh for accumulation of egesta. Leaf discs used for feeding were well-conditioned and lost 60–70% of mass during decomposition prior to feeding. Caddisflies were given five unlabeled leaf discs for a 5-d acclimation period prior to feeding on radiolabeled litter. Two days into the acclimation period, we measured consumption and egestion rates (Appendix S2). After the acclimation, all 60 larvae were transferred to a fume hood at 15°C to commence feeding on radiolabeled leaf discs.

Remaining conditioned leaf discs from each of the four diets were assigned to one of three radiolabel methods to label different pools of microbial C and P, using dual ^{14}C and ^{33}P labeling, prior to feeding (Appendix S2). Briefly, we used ^{14}C-bicarbonate to label autotrophic C (0.05 μCi/mL; 4 h labeling), and ^{14}C-acetate to label slow-turnover heterotrophic (predominantly fungal) C (0.33 μCi/mL, 0.25 mmol/L acetate; 3-d labeling) or fast-turnover heterotrophic (predominantly bacterial) C (0.33 nCi/mL, 0.25 μmol/L acetate; 1-h labeling). The lower acetate concentration and short duration of fast-turnover label should favor uptake by fast-turnover bacteria, rather than fungi, because bacteria exhibit high affinity for low concentrations of dissolved organic compounds, relative to fungi, which are slower-turnover organisms and less competitive for uptake at low concentrations (Newell 1984). All radiolabel solutions also contained ^{33}P-PO4 at 0.01 μCi/mL to label mid-, slow-, or fast-turnover microbial P, respectively. Labeling took place at 15°C and 300 μmol photons·m^{-2}·s^{-1}. One killed control was from each diet and radiolabel method to correct for non-biological uptake. Killed controls exhibited low radiolabel uptake, indicating minimal influence of non-biological uptake (Appendix S2). Radiolabeled discs were rinsed four times with unlabeled water and either frozen to quantify initial ^{14}C and ^{33}P, or immediately fed to caddisflies (five discs per chamber) from acclimated diet treatments, randomly assigned one of the three radiolabel methods.

Caddisflies were provided radiolabeled discs in a fume hood for 36–48 h. Residual leaf material was frozen to determine post-consumption radiolabel remaining. We filtered accrued egesta onto 25-mm glass fiber filters and froze the filters to determine egested ^{14}C and ^{33}P. Concluding the feeding study, we provided caddisflies with 100 mL fresh stream water and five unlabeled leaf discs for a 24-h period to egest excess radiolabel (Chung and Suberkropp 2009). Accumulated egesta were again collected. Caddisflies were pulled from feeding chambers, removed from their cases, rinsed three times with stream water, blotted, weighed, and frozen. Samples were then processed to determine total ^{14}C and ^{33}P disintegrations per minute (DPMs) (Halvorson et al. 2016; Appendix S2).

Calculations and data analysis

Total ^{14}C and ^{33}P DPMs consumed by each caddisfly was calculated from the total of each radioisotope fed to caddisflies (average DPMs per disc, multiplied by five discs), minus ^{14}C and ^{33}P of residual material. Total DPMs egested and incorporated were determined as ^{14}C or ^{33}P DPMs in egesta and caddisfly samples, respectively. We calculated ^{14}C- and ^{33}P-specific assimilation efficiencies using

$$\text{Assimilation efficiency} = \frac{\text{DPMs consumed} - \text{DPMs egested}}{\text{DPMs consumed}} \quad (1)$$

and ^{14}C- and ^{33}P-specific incorporation efficiencies using

$$\text{Incorporation efficiency} = \frac{\text{DPMs incorporated}}{\text{DPMs consumed}}. \quad (2)$$

We used a mixing model to quantify assimilation and incorporation efficiency for bacterial and fungal C separately (Appendix S2). We used microbial biomass and production rates, along with *Pycnopsyche* consumption rates and efficiency of assimilation and incorporation of microbial C, to quantify C flows to *Pycnopsyche* on each diet (Appendix S2).

Effects of light and nutrient treatments on conditioned leaf litter microbial biomass and production rates were analyzed using a full factorial two-way analysis of variance (ANOVA). Acclimation consumption and egestion rates were analyzed similarly. Diet effects on larval ^{33}P- and ^{14}C-specific assimilation and incorporation efficiencies were also assessed using two-way ANOVA (separate ANOVA for each radiolabel method). Finally, we used one-way ANOVA to analyze differences in assimilation and incorporation efficiency of microbial C and P across radiolabel pools (algal, bacterial, or fungal C and slow-, mid-, or fast-turnover P). Tukey's Honestly Significant Difference tests were used to compare groups when treatment effects were significant. Response variables were log-transformed as necessary to improve variance homogeneity. All analyses were conducted using the statistical program R, version 3.4.3 (R Core Team 2018).

RESULTS

Microbial biomass and activity

On conditioned litter, algal biomass was significantly greater in the light compared to the shade ($F_{1,12} = 78.0$; $P < 0.001$), but did not differ between nutrient treatments (Fig. 1A). Algal production rates similarly increased in the light treatment ($F_{1,12} = 125.0$, $P < 0.001$), but also responded positively to higher nutrients ($F_{1,12} = 35.8$, $P < 0.001$), resulting in the greatest rates in the high-nutrient light treatment (Fig. 1B). Bacterial biomass did not
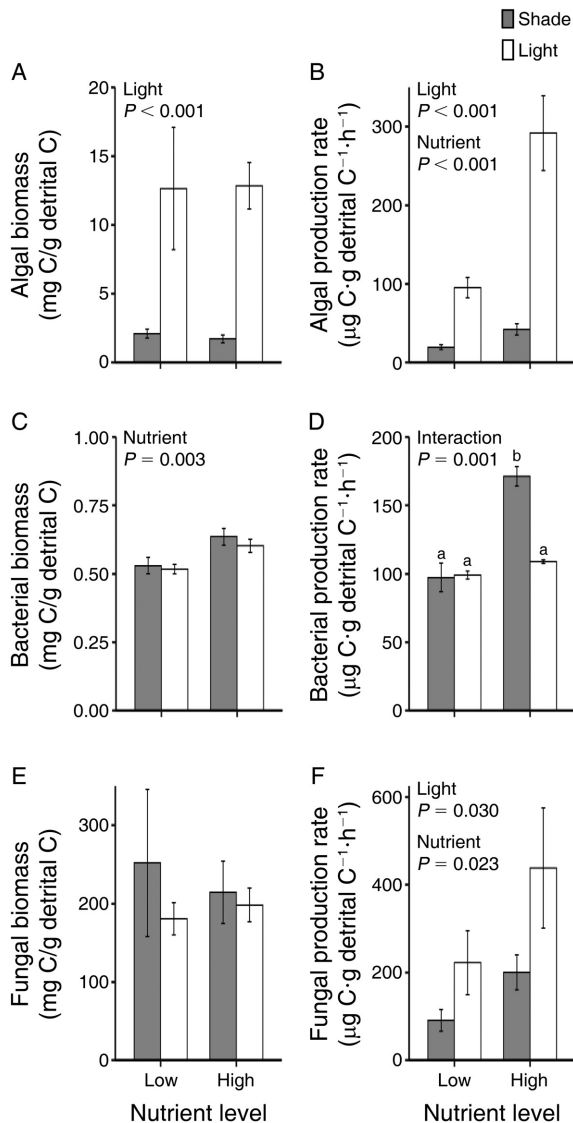
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FIG. 1. (A) Algal biomass, (B) algal production rates, (C) fungal biomass, (D) fungal production rates, (E) bacterial biomass, and (F) bacterial production rates on *Liriodendron tulipifera* leaf litter conditioned under contrasting light and nutrient treatments. Values are mean ± SE. Treatments and *P* values within each panel indicate significant effects (ANOVA, *P* < 0.05) and lowercase letters designate group differences across treatments (Tukey HSD, *P* < 0.05) where interactions were significant.

differ between light treatments, but increased in the high-nutrient treatment ($F_{1,12} = 13.5$, $P = 0.003$; Fig. 1C). Bacterial production rates exhibited a significant light–nutrient interaction ($F_{1,12} = 18.1$, $P = 0.001$) with the high-nutrient shaded treatment showing higher bacterial production (Fig. 1D). Fungal biomass did not differ across light or nutrient treatments (Fig. 1E) but, much like algal production rates, fungal production exhibited positive additive effects of both light and high nutrients ($F_{1,12} = 6.1$,

$P = 0.030$ and $F_{1,12} = 6.8$, $P = 0.023$, respectively; Fig. 1 F). High-nutrient litter exhibited greater percent P but similar percent N contents compared to low-nutrient litter (Appendix S1: Table S2). Litter algal communities in the light treatment were composed primarily of green algae (Chlorophyta, e.g., *Oedogonium*) and diatoms (Heterokontophyta, e.g., *Navicula*; Appendix S1: Table S3).

Dietary effects on acquisition of microbial C and P

Pycnopsyche consumption rates were greater on high-nutrient litter ($F_{1,56} = 6.3$, $P = 0.015$), but declined on light-conditioned litter ($F_{1,56} = 5.8$, $P = 0.019$; Appendix S1: Fig. S1A). Egestion rates closely reflected consumption rates and responded positively to nutrients ($F_{1,56} = 7.1$, $P = 0.010$), but light treatment effects were not statistically significant (Appendix S1: Fig. S1B).

Pycnopsyche assimilated algal C more efficiently on low-nutrient litter compared to high-nutrient litter ($F_{1,16} = 10.2$, $P = 0.006$; Appendix S1: Fig. S2A), and incorporated algal C more efficiently on the shade litter compared to the light treatment litter ($F_{1,15} = 9.4$, $P = 0.008$; Appendix S1: Fig. S2B). Assimilation of bacterial C was more efficient on the shade litter ($F_{1,16} = 16.1$, $P < 0.001$; Appendix S1: Fig. S2C) while efficiency of incorporating bacterial C was significantly higher on the low-nutrient litter ($F_{1,16} = 5.4$, $P = 0.033$; Appendix S1: Fig. S2D). Neither assimilation nor incorporation efficiencies of fungal C differed across litter treatments (Appendix S1: Fig. S2E, F).

Pycnopsyche assimilated and incorporated fast- and mid-turnover microbial P similarly across treatments (Appendix S1: Fig. S3A–D). Light-nutrient interactions affected *Pycnopsyche* assimilation ($F_{1,15} = 5.2$, $P = 0.038$) and incorporation ($F_{1,16} = 13.1$, $P = 0.002$) of slow-turnover microbial P. Assimilation efficiency was lowest and incorporation efficiency was greatest for slow-turnover microbial P on the low-nutrient shade litter (Appendix S1: Fig. S3E, F).

Microbial C and P flows to Pycnopsyche

Results from one-way ANOVA indicated that, across all diets, *Pycnopsyche* assimilated fungal C significantly more efficiently compared to assimilation of algal or bacterial C, equating to 19.0% and 27.2% greater efficiency, respectively, of assimilating fungal C ($F_{2,57} = 19.9$, $P < 0.001$; Fig. 2A). By comparison, *Pycnopsyche* incorporation efficiency of microbial C was markedly lower among all microbial pools, and *Pycnopsyche* incorporated bacterial C significantly more efficiently compared to fungal or algal C, representing 12.0% and 16.5% greater efficiency, respectively, of incorporating bacterial C ($F_{2,56} = 11.8$, $P < 0.001$; Fig. 2B).

Across all diets, ANOVA results indicated that *Pycnopsyche* assimilated microbial P with similar efficiency across the radiolabel pools differing in P turnover rate ($F_{2,55} = 0.2$, $P = 0.792$; Fig. 2C), with mean ± SE P
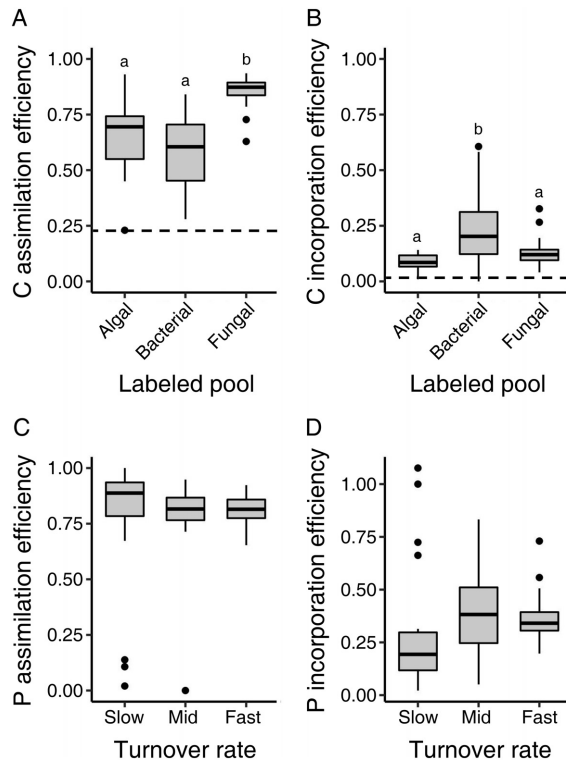
FIG. 2. Box-and-whisker plots of *Pycnopsyche* (A) C assimilation efficiencies, (B) C incorporation efficiencies, (C) P assimilation efficiencies, and (D) P incorporation efficiencies across different labeled microbial C and P pools. Box mid lines show medians, box edges show the 1st and 3rd quartile, whiskers show the range out to maximum 1.5 times the interquartile range, and points show values outlying the maximum whisker range. Horizontal dashed lines in panels A and B reference assimilation and incorporation efficiencies assumed for detrital C (see Appendix S2). Lowercase letters designate statistically significant differences across pools (Tukey HSD, $P < 0.05$).

assimilation efficiency of 0.78 ± 0.03. By comparison, *Pycnopsyche* incorporated microbial P less efficiently (0.35 ± 0.03), and P incorporation efficiency also did not differ across turnover rates ($F_{2,56} = 0.7$, $P = 0.505$; Fig. 2D).

Despite the wide range of C flows within the detrital-microbial matrix and to *Pycnopsyche* assimilation and incorporation of microbial C (Fig. 3), high litter-associated fungal biomass, compounded with the relatively high efficiency of assimilating and incorporating fungal C, resulted in fungal C being consistently the dominant microbial pool contributing to *Pycnopsyche* assimilation and growth. While diet treatment affected algal and bacterial C flows, these flows were always lower than fungal or detrital C flows. Our calculations suggest that *Pycnopsyche* incorporated the most C on the high-nutrient shade conditioned litter.

DISCUSSION

By employing dual tracers to label contrasting pools of microbial C and P, our study helps resolve the nutritional value of detrital microbial biomass and shows bottom-up effects of light and dissolved nutrients on acquisition of microbial nutrients by detritivores. On average, *Pycnopsyche* assimilated and incorporated heterotrophic microbial C at higher efficiencies than autotrophic microbial C, refuting our first hypothesis that autotrophic C would be of greater value compared to heterotrophic C. While incorporation of fast- and mid-turnover microbial P did not show dietary effects, incorporation of slow-turnover microbial P expressed higher efficiencies under shaded low-nutrient conditions, supporting hypothesis 2. Finally, only assimilation of bacterial C was significantly more efficient in the shade treatment, and incorporation of fungal C was on average higher on the light treatment diets, lending weak support to hypothesis 3. The results indicate that microbes differ in bulk C quality, but we acknowledge microbial pools can also be high-quality by providing essential micronutrients such as fatty and amino acids, which were a small proportion of labeled C (Brett et al. 2017, Trochine et al. 2020). Overall, our findings suggest that environmental factors like light and nutrients are bottom-up controls not only on the magnitude, but also the nutritional quality, of detrital microbial biomass, which constrains energy and nutrient flow at the base of brown food webs.

Our study affirms others' showing that light and dissolved nutrients affect biomass and activity of detrital microbes at the base of the brown food web (Danger et al. 2013). Detrital algal biomass and production increased strongly with light exposure, as did fungal production, suggesting algae directly stimulated heterotrophy, likely by provisioning labile C exudates to fungi (Kuehn et al. 2014, Halvorson et al. 2019). Conversely, bacterial production was higher under shaded and high-nutrient conditions, suggesting bacterial activity was reduced by algal photosynthesis, perhaps due to competition with algae for dissolved nutrients (Wyatt et al. 2019). Together, these findings suggest that algal activity can shift microbial biomass and C flows within the detrital-microbial matrix, potentially affecting detritivore nutrition and growth.

Consumption and assimilation determine the amount of energy and nutrients available to support animal growth. In the present study, *Pycnopsyche* consumption and egestion rates increased on high-nutrient litter compared to low-nutrient litter, consistent with previous findings (Evans-White and Halvorson 2017). This may be explained by a release from nutrient limitation and increased feeding rates and throughput on high-quality microbial biomass. *Pycnopsyche* also decreased consumption rates on light-conditioned litter, suggesting this litter was less palatable, perhaps due to a shift in the fungal assemblage (Arsuffi and Suberkropp 1989), or as a compensatory response to raise assimilation (see similar

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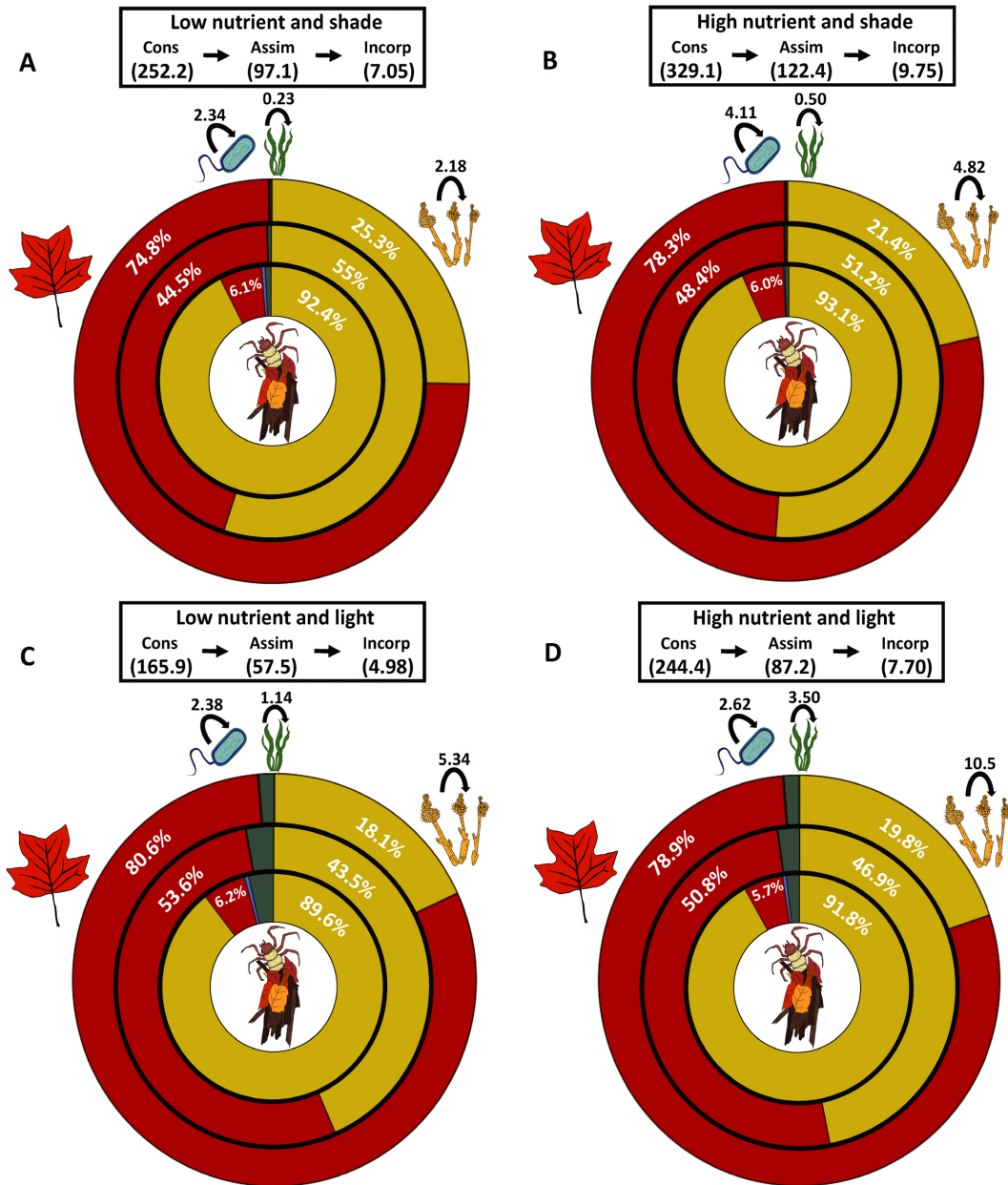
Fig. 3. Summary of C flows within the detrital-microbial matrix and to *Pycnopsyche*. All microbial flows are in units of mg C·g detrital $C^{-1} \cdot d^{-1}$ (production rates; curved arrows). Quantitative total C flows to *Pycnopsyche* consumption (Cons), assimilation (Assim), and incorporation (Incorp) are identified at the top of each panel, associated, respectively, with the outermost, middle, and inner concentric circles in each panel. Flows are designated as detrital (red), bacterial (blue), algal (green), or fungal (yellow) in units of mg C·g *Pycnopsyche* $C^{-1} \cdot d^{-1}$ based on microbial biomass, *Pycnopsyche* consumption rates, and *Pycnopsyche* microbial C assimilation and incorporation efficiency (also see Appendix S1: Table S4). Panels are organized by diet treatment: (A) low-nutrient shade, (B) high-nutrient shade, (C) low-nutrient light, and (D) high-nutrient light. See Methods and Appendix S2 for a description of flow budget calculations.

egestion despite slower consumption rates on light treatments). Increased feeding could have also occurred as a compensatory response on high-nutrient, shaded litter due to an inability of *Pycnopsyche* to increase assimilation efficiency on this litter. Although greater consumption may elevate growth rates, efficiencies of assimilation and incorporation, particularly of high-quality microbial

biomass, ultimately determine energy and nutrient flows toward detritivore growth (Marks 2019).

The assimilation and incorporation efficiency of resources are useful metrics in determining the fate of C in consumer nutritional budgets. Particularly, assimilation efficiency provides information on the energy or C used in rapid metabolic processes. Incorporation

efficiency quantifies nutrients put towards long term structural growth. Comparisons between *Pycnopsyche* assimilation and incorporation across microbial pools allowed us to parcel out the microbial contributions to detritivore energy and nutrient demands between varying treatments. Across all diets, fungal C was the highest-quality for assimilation, but bacterial C was the highest-quality for incorporation. The observed results may be explained by the presence of secondary metabolites produced by fungi to deter animal consumption (Arsuffi and Suberkropp 1989). Secondary metabolites may be energetically expensive for *Pycnopsyche* to metabolize and increase the incorporation of C from bacterial pools. Furthermore, differences in the molecular compounds produced between bacteria and fungi may impact incorporation efficiency. For instance, bacteria may offer a unique suite of amino acids to *Pycnopsyche* that are absent or at lower concentrations in fungal cells (Larsen et al. 2009). Future studies should address differences in microbial taxonomic assemblages between light and nutrient treatments, as this may influence the microbial nutritional quality to aquatic consumers.

Surprisingly, autotrophic C was assimilated and incorporated with lower efficiency, suggesting that although algae may provide essential micronutrients (Brett et al. 2017; Trochine et al. 2020), algae are likely not the bulk of high-quality C supporting detritivore growth even on light-conditioned litter. Across diets, 89.6–93.1% of estimated *Pycnopsyche* C incorporation was from fungi, whereas bacteria supported 0.2–0.6% and algae supported 0.6–3.6% of *Pycnopsyche* C incorporation (Fig. 3). Although our results indicate fungal C is easily digested, the majority of ingested fungal C is ultimately lost post-assimilation, likely to respiration. Lower assimilation efficiencies of bacterial C may be due to small bacterial cells entrained away from digestive activity within the detrital matrix, lowering assimilation efficiency, or possibly due to low litter bacterial biomass that may cause the *Pycnopsyche* gut to bias digestion of fungal rather than bacterial C. Still, bacterial C appears to be high quality for direct incorporation into animal biomass, as indicated by higher incorporation efficiencies. Overall, our data highlight the quantitative importance of fungal C, relative to bacterial or algal C, in supporting detritivore growth across a range of diets (Chung and Suberkropp 2009).

Detritivore acquisition of microbial P is likely a major constraint on detritivore growth, because microbes provide a major pool of P available to detritivores relative to the P-deplete detrital substrate (Manning et al. 2015, Halvorson et al. 2016). Our ^{33}P labeling methods did not distinguish microbial pools and thus labeled a consortium of microbes simultaneously, but diet treatments and turnover times should have resulted in a wide range of microbial P pools labeled. For example, fast-turnover P pools are more likely associated with cellular growth, such as ribosomal RNA, whereas slow-turnover P pools are more likely associated with P storage molecules such as polyphosphate, which both fungi and algae may store (Rier et al. 2016). Biomass production between the different microbial pools can also lead to changes in the bioavailability of P to aquatic consumers. For instance, competitive interactions between algae and fungi at longer time scales may lead to P storage that is less available for consumer incorporation. The microbial pools may differ in nutritional quality of P molecules and drive the patterns observed in our study, namely a trend of increasing P incorporation efficiency on the low-nutrient shade-treatment diet and among faster-turnover P pools. Future work should address the roles of algal vs. fungal P storage within the detrital-microbial matrix, particularly given P is an important bottom-up control in brown food webs (Demi et al. 2018).

Our study used novel radiolabel methods to untangle interactions within the detrital-microbial matrix under contrasting environmental conditions. As such, we showed that light and nutrient availability influence both microbial interactions and transfer of microbial C and P to detritivores. Fungal C was the largest contributor to detritivore growth, even on light-conditioned litter with substantial algal biomass and activity. Direct algal contributions to C flow into brown food webs may thus be relatively small. Still, algal influence on detrital food webs may be substantial, if indirectly mediated by algal-induced shifts in fungal biomass, activity, or species assemblage (Halvorson et al. 2019). For example, algae may provision labile C to heterotrophs, providing a flow path ultimately supporting detritivores, alternative to detrital substrate C (Kuehn et al. 2014). On average, *Pycnopsyche* assimilated and incorporated microbial P more efficiently than microbial C, highlighting the importance of microbial P for invertebrate growth (Halvorson et al. 2016, Demi et al. 2018). Further work must parcel out biomolecules that explain varying microbial P quality. We acknowledge our assumptions that *Pycnopsyche* did not feed selectively on microbial biomass, and that radiolabel ^{14}C did not transfer across microbial pools during labeling (e.g., label transfer from autotrophs to heterotrophs via exudation, or internal cycling of labeled CO_2; Demars et al. 2020). While these processes merit investigation, the controlled and relatively short labeling conditions, especially of algae and bacteria, should have limited these dynamics during our study. Toward untangling trophic pathways within detrital food webs, our results provide a new, quantitative view into the role of green vs. brown flow paths in driving microbial interactions and trophic transfer in many ecosystems.

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