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Species-specific traits predict whole-assemblage detritus processing by pond invertebrates

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Abstract

Functional trait diversity determines if ecosystem processes are sensitive to shifts in species abundances or composition. For example, trait variation suggests detritivores process detritus at different rates and make different contributions to whole-assemblage processing, which could be sensitive to compositional shifts. Here, we used a series of microcosm experiments to quantify species-specific coarse and fine particulate organic matter (CPOM and FPOM) processing for ten larval caddisfly species and three non-caddisfly species in high-elevation wetlands. We then compared trait-based models including life history, dietary, and extrinsic traits to determine which traits explained interspecific variation in detritus processing. Finally, we compared processing by mixed caddisfly assemblages in microcosms and natural ponds to additive predictions based on species-specific processing to determine if single-species effects are additive in multi-species assemblages. We found considerable interspecific variation in biomass-specific CPOM (13-fold differences) and FPOM (8-fold differences) processing. Furthermore, on a mass-specific basis, amphipods, chironomids, and caddisflies processed similar amounts of detritus, suggesting non-shredder taxa could process more than previously recognized. Trait models including dietary percent detritus, development rate, body size, and wetland hydroperiod explained 81 and 57% of interspecific variation in CPOM and FPOM processing, respectively. Finally, species-specific additive predictions were strikingly similar to mixed-assemblage processing in microcosms and natural ponds, with the largest difference being a 15% overestimate. Thus, additivity of species-specific processing suggests single-species rates may be useful for understanding functional consequences of shifting assemblages, and a trait-based approach to predicting species-specific processing could support generating additive predictions of whole-assemblage processing.

Keywords Caddisflies · Chironomidae · Detritus processing · Diversity · Ecosystem function · Functional traits · Trichoptera · Whole-assemblage

Introduction

The majority of vascular plant material is not consumed as live tissue; instead, it enters food webs as detritus (Cebrian 1999). Animal detritivores play an important role in determining the fate of detritus as they accelerate breakdown, generate fine particulates, enhance microbial colonization, and remineralize detrital nutrients through excretion and egestion (Gessner et al. 2010). In aquatic systems, and particularly in streams, the detritivore assemblage's effect on detritus processing is well recognized (Wallace and Webster 1996), whereas there is considerably less known about species-specific processing beyond the effects of large- versus small-bodied detritivores (Bradford et al. 2002). However, some detritivores consume and process more detritus than others, suggesting low functional redundancy (Boyero et al. 2007; Dangles et al. 2011). Understanding species-specific contributions to detritus processing is important because whole-assemblage processing is likely to change due to compositional shifts in detritivore assemblages driven by global change (Wardle et al. 2011). Nevertheless, our

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understanding of how detritus processing rates vary among species, as well as which traits are associated with that variation, remains limited.

Linking detritivore traits to species-specific detritus processing could provide a powerful framework for predicting a taxon's contribution to whole-assemblage processing. For example, a taxon's processing could be influenced or controlled by intrinsic traits such as mouthpart morphology, physiology, diet composition (Merritt et al. 2017), body size (Tonin et al. 2018), growth rate and developmental phenology, or extrinsic traits such as preferred microhabitat. In turn, although functional traits of biomass-dominant species often regulate ecosystem processes (Grime 1998), functional trait diversity within species assemblages ultimately determines whether or not ecosystem processes are sensitive to shifts in relative abundance or assemblage composition (Suding et al. 2008). Thus, subdominant taxa can make functional contributions disproportionate to their biomass (Tatarko and Knops 2018). Consequently, diversity effects on ecosystem processes, including detritus processing, can only arise given interspecific variation in key traits (Gessner et al. 2010). Indeed, trait diversity is likely more useful than taxonomic diversity for identifying and studying the mechanisms responsible for diversity effects on ecosystem processes such as detritus processing (McKie et al. 2008; Schindler and Gessner 2009). By extension, establishing links between species' traits and their functional contributions offers generalizable predictive utility across ecoregions with different assemblages, in contrast to a species-based approach which would require new measurements for each new species (Fukami et al. 2005; Webb et al. 2010).

Although the relationship between detritivore traits and interspecific variation in detritus processing is well recognized in streams (Frainer et al. 2014; Tonin et al. 2018), this link is less established in wetlands where species-specific processing rates have been quantified for fewer species. Although detritivore species classified as shredders are absent from many wetlands, species in other functional feeding groups such as collector-gatherers are often critical wetland detritivores (Batzer and Ruhí 2013). Nevertheless, when shredders are present they can make large contributions; in montane Colorado wetlands, coarse (> 1 mm) detritus breakdown is 2–3 × faster in the presence of larval caddisflies (Wissinger et al. 2018). However, the extent to which individual caddisfly species and other detritivores, including those that are not classified as shredders, contribute to the breakdown of coarse detritus remains unclear.

A lack of knowledge of the role of animal detritivores and potentially fewer detritivore species make wetlands ideal systems for exploring species- and trait-based effects on detritus processing. The Colorado wetland system used in this study, and previously extensively studied by Wissinger et al. (2018), is an exemplar because within the closely related caddisfly guild (Ruiter et al. 2013) there is considerable interspecific variation in body size and life history strategies (Wissinger et al. 2003), diet (Wissinger et al. 1996, 2018), and stoichiometric traits (excretion, body C:N:P; Balik et al. 2018). Furthermore, closely related organisms are often presumed to be functional equivalents, but this is not always the case (Balik et al. 2018). Thus, our primary objective was to quantify species- and mass-specific detritus breakdown (mass loss of coarse [> 1 mm] particulate organic matter, CPOM) for ten larval caddisfly taxa and identify which intrinsic and extrinsic traits best explain variation in detritus breakdown. From 2011 to 2020, we conducted five microcosm experiments to measure detritus processing of all ten taxa. These data were used to test the prediction that caddisfly species would process CPOM and FPOM at different rates. We also expected that trait-based models would better explain interspecific variation in detritus processing than species identity-based models because consumers with similar traits (i.e., dietary and life history) will presumably exhibit greater similarity in detritus processing.

Our secondary objective was to contextualize species-specific caddisfly detritus processing in pond communities. To compare caddisfly detritus processing to other detritus-associated taxa commonly found in the same habitats, we quantified processing by larval chironomids (mixed taxa in proportion to their relative abundance; see Wissinger et al. 1999), snails (Lymnaeidae), and amphipods (mixed; *Gammarus* and *Hyalella*). We expected that larval caddisflies would have greater mass-specific processing than the non-caddisfly taxa which are primarily not considered shredders. Chironomids can be collector-gatherers (Wissinger 1999; Merritt et al. 2017) and snails scrape epidetrital biofilms (Brady and Turner 2010; Stoler et al. 2016). Although amphipods are important shredders elsewhere (Little and Altermatt 2018), their diets can vary (MacNeil et al. 1997) and the extent to which they utilize detritus in this system is unclear. Next, to further contextualize individual caddisfly taxa's processing, we measured processing in mixed caddisfly assemblages to explore how intraguild species interactions (e.g., facilitation and intraguild predation) could modulate processing. We expected that mixed-assemblage processing would exceed additive predictions (e.g., summing the products of each species' mass-specific processing and biomass) because positive species interactions tend to counteract negative interactions and result in net-positive effects on ecosystem function (Hooper et al. 2005). Finally, to determine if species-specific rates measured in microcosms provide additive predictions of processing by multi-species caddisfly assemblages in ponds, we compared additive predictions (using larval caddisfly abundance in natural ponds and species-specific microcosm processing rates) to previously collected in situ measurements of caddisfly assemblage detritus processing (Wissinger et al. 2018).

Materials and methods

Study system

Since 1990, annual censuses of the invertebrate communities in kettle-pond wetlands near the Rocky Mountain Biological Laboratory (RMBL; Gunnison, CO, USA) have indicated that mixed assemblages of case-making caddisflies (Limnephilidae and Phryganeidae) represent 30–70% of aquatic animal biomass along a hydroperiod gradient from permanent ponds that never dry to vernal ponds that dry every summer (Wissinger et al. 1999, 2016). Previous work demonstrated that processing is 2–3 × faster in their presence (Wissinger et al. 2018) and species-specific processing is density-dependent (Klemmer et al. 2012). The sedge, *Carex aquatilis,* is the dominant detrital source in all wetlands throughout the region, with annual inputs ranging from 74 to 167 g dry mass/m^2 (Balik et al. 2021).

Beaver pond wetlands in the area contain an additional limnephilid caddisfly genus, *Ecclisomyia*, and a high abundance of amphipods (*Gammarus* and *Hyalella*), which are absent from most kettle-pond wetlands (Wissinger et al. 1999). Chironomids (e.g., *Paratanytarsus*, *Psectrocladius*, *Tanytarsus*, and others) are abundant in all wetlands, and can equal or exceed larval caddisfly biomass in permanent kettle-ponds. Other common taxa include omnivorous snails (Lymnaeidae) and tadpoles (*Pseudacris*) that can consume detritus, predators (Odonata, Dytiscidae, Hemiptera, and Chironomidae), and collector–gatherers of fine particulate organic matter (FPOM) with low abundances (e.g., Culicidae larvae; see food webs in Wissinger et al. 1999).

Experimental design

We quantified invertebrate species-specific detritus processing using five microcosm experiments (Appendix S1: Table S1) conducted in a white plastic tent (WeatherPORT, Hansen WeatherPORT, Delta, CO) at the RMBL. All experiments were conducted mid-summer (i.e., late June through early August) and used 0.25 m^3 (51 × 36 × 13 cm) plastic bins as replicate microcosms. Experimental designs were similar across all five experiments (Appendix S1: Table S1). For all experiments, sedge detritus (*Carex aquatilis*) was collected from montane (2850 m elevation) kettle-pond wetlands near the USFS trail #401 south of the RMBL. Sedge was air-dried for 72–96 h, then 20–25 g were added to each microcosm along with ~ 9 L pond water. Microbial inoculum was collected by scrubbing submerged rocks, wood, and sedge from source ponds. All microcosms received equal volume aliquots of filtered (1 mm) inoculum and incubated for 4–5 days to encourage biofilm growth on re-hydrated sedge.

After incubation, invertebrates collected from nearby ponds were added to microcosms. A treatment with *Limnephilus externus* was included in all experiments as a reference treatment (Appendix S1: Table S1) because it was the most common caddisfly species and after the 2011 experiment it was suspected to be the most effective detritivore. The microcosm density of *L. externus* corresponds to the inflection point (100 individuals/m^2) of an asymptotic detritus processing response reported in a previous in situ experiment wherein *L. externus* density was manipulated in littoral cages (Klemmer et al. 2012). Similar densities were used when stocking caddisfly taxa with 5th (final) instar masses comparable to *L. externus*, but proportionally greater densities were used for taxa with smaller final instars (e.g., Table 1, Appendix S1: Table S1). Likewise, densities in mixed caddisfly assemblage treatments (2011, 2013 and 2015) were scaled to match total biomass of the *L. externus* treatment. Mixed caddisfly assemblage compositions included co-occurring taxa. When available, 3rd instar caddisflies were used to stock treatments. Otherwise, later instars were used. We did not match *L. externus* biomass in 2020 for amphipods, snails, or chironomids because we did not have prior average individual mass data for these taxa. Finally, a set of replicate microcosms without any invertebrates (no-invertebrate control) was used to quantify losses from ambient leaching and microbial processing.

Experiments or specific treatments ended when larval caddisflies began to pupate or if mortality was observed (11–42 days; Appendix S1: Table S1). Macroinvertebrates were removed, and in 2019 and 2020 were counted, dried at 60 °C for < 48 h, and weighed to measure average individual final mass. Detritus remaining in each microcosm was washed through a 1 mm net or sieve. Detritus > 1 mm was classified as CPOM and oven dried (60 °C for 72 h) to estimate CPOM dry mass. In 2013, 2019, and 2020, detritus < 1 mm–63 µm was also collected, dried, and weighed to estimate fine particulate organic matter (FPOM) dry mass.

To compare invertebrate detritus processing to the no-invertebrate control in each experiment, we first calculated CPOM and FPOM daily rates as

$$\text{mg CPOM microcosm}^{-1}\text{day}^{-1} = \frac{\left[\text{initial sedge (mg)} - \text{final CPOM (mg)}\right]}{\text{treatment duration(day)}}$$

$$\text{mg FPO Mmicrocosm}^{(-1)}\text{day}^{(-1)} = \frac{([\text{FPOM(mg)}])}{(\text{treatment duration(day)})}$$

Next, to compare invertebrate detritus processing among species and across experiments, we first subtracted the daily no-invertebrate control mean from all invertebrate treatment replicates to correct mass-specific invertebrate processing for leaching and microbial breakdown. We then standardized for invertebrate biomass (mg CPOM or FPOM mg^{-1}

Table 1 Summary of species' traits used in trait-based models of detritus processing

Species	Development rate	Body mass (mg)	Habitat	Elevation	Case material	Diet % detritus	Diet % algae	Diet % chitin	*P* Excretion (ug-1 ind-1 d-1)
An. bimaculata	Moderate	18.92	Permanent and semi-permanent	Broad	Sedge	81.02	17.81	1.16	0.05
A. nigriculus	Fast	7.89	Vernal and semi-permanent	Broad	Woody debris	92.82	3.55	3.64	7.98
G. lorettae	Moderate	11.82	Permanent and semi-permanent	Broad	Sedge	91.93	3.77	4.59	14.90
L. abbreviatus	Fast	6.78	Permanent and semi-permanent	Broad	Sedge	77.48	21.93	0.59	9.19
L. externus	Slow	8.54	Permanent and semi-permanent	Broad	Sedge	94.90	3.30	1.90	7.64
L. picturatus	Fast	7.02	Permanent and semi-permanent	Broad	Sedge	90.47	5.25	8.42	17.03
L. secludens	Fast	3.40	Vernal and semi-permanent	Montane	Stone	78.01	0.78	21.35	2.79
L. sublunatus	Fast	4.65	Permanent and semi-permanent	Montane	Sedge	91.00	4.20	2.00	10.10
L. tarsalis	Fast	2.72	Vernal and semi-permanent	Montane	Woody debris	87.70	6.19	6.02	14.94
Ecclisomyia sp.	Fast	5.34	Beaver	Broad	Sedge	19.80	80.20	0.00	0.16
Amphipods	Slow	5.42	Beaver	Montane	No case	75.47	1.72	3.54	11.48
Lymnaeidae	Slow	35.57	All	Montane	No case	51.18	37.70	1.60	4.13
Chironomids	Fast	0.19	All	Broad	No case	92.98	1.55	0.16	0.84

Development rate (fast ≤ 53 days, moderate 53 < x < 77 days, and slow ≥ 77 days) and case material from Wissinger et al. 2003, 2006, Balik et al. 2018, and unpublished data. *P* excretion rates from Balik et al. 2018 and Vanni and McIntyre (2016). *A. bimaculata* and *L. abbreviatus* diet composition were quantified here, *Ecclisomyia* sp. diet from Huryn and Benstead (2019), all other caddisfly taxa from Wissinger et al. (1996, 2018), amphipod (*Gammarus*) diet composition from Acosta and Prat (2011), lymnaeid snails from Kesler et al. (1986), and average chironomid diet composition was calculated using literature values for the three taxa described as regionally "ubiquitous" by Wissinger et al. (1999): *Tanytarsus* from Henriques-Oliveira et al. (2003), *Paratanytarsus* from Jiang et al. (2008), and *Psectrocladius* from Winterbourn (1982). Genus *L. Limnephilus*, *A. Asynarchus, An. Anabolia, G. Grammotalius*

animal biomass d^{-1}). Treatment biomass for each taxon was estimated for 2011, 2013, 2015, and for *L. picturatus* in 2019 as the product of stocking densities (Appendix S1: Table S1) and mean individual final instar masses from prior studies (Wissinger et al. 2003; Balik et al. 2018). For all other treatments in 2019 and 2020, final treatment biomass was measured, but not all individuals were recovered due to pupation or mortality near the end of the experiments. For these taxa, mean individual final body mass was calculated using the recovered animals, then multiplied by initial density to estimate treatment biomass prior to pupation or mortality (Appendix S1: Table S1). Thus, for all experiments, treatment biomass was estimated as a product of initial density and an average final individual mass. Species' per-capita detritus processing was also calculated using treatment initial density (mg CPOM or FPOM $individual^{-1}$ d^{-1}).

We first analyzed daily microcosm detritus processing within experiments to determine if invertebrate treatments differed from the no-invertebrate controls. Shapiro–Wilk normality tests indicated that processing rates were normally distributed in all experiments ($p > 0.05$), so analyses were performed on untransformed data. All statistical analyses were conducted in R 4.0.2 (R Core Team, 2020). For experiments in which both CPOM and FPOM were measured,

multivariate analysis of variance (MANOVA) was used to test for differences among treatments in both response variables due to possible correlation. If the overall MANOVA was significant, univariate analysis of variance (ANOVA) was used to test response variables independently. Likewise, univariate ANOVA was used for experiments in which only CPOM was measured. Following significant univariate ANOVAs, Dunnett's multiple comparison was used to compare each invertebrate treatment to the no-invertebrate control within each experiment.

To compare mass-specific detritus processing among taxa and across experiments, we used linear models with terms for taxon and experiment-year as categorical variables, and their interaction term. Non-significant terms were dropped, then Tukey's honestly significant difference (HSD) was used to identify differences in mass-specific processing among invertebrate taxa. To demonstrate the influence of body size, we also compared per-capita processing among taxa using ANOVA (CPOM or FPOM = taxa). Next, to determine if caddisfly taxa convert CPOM to FPOM at different rates, we used the interaction term in an ANCOVA (FPOM = CPOM + taxa + CPOM*taxa) to test for homogeneity of slopes among taxa CPOM and FPOM processing in mass-specific and per-capita units.

Null expectations for detritus processing in mixed caddisfly assemblage treatments were obtained using each species' mass-specific processing:

$$\text{Predicted mixed assemblage processing } (\text{day}^{(-1)}) = \sum_{\text{all member species}} \left[\begin{array}{c}\text{mg CPOM or FPOM mg}^{-1}\text{ animal tissue day}^{-1} * \\ \text{density in mixed assemblage} * \text{average individual mass (mg)}\end{array}\right]$$

Prior to comparing observed and predicted mixed-assemblage processing with two-tailed one sample *t* tests, we corrected observed values for leaching and microbial breakdown by subtracting no-invertebrate control means.

To determine if species-specific microcosm rates can provide additive predictions of processing by caddisfly assemblages in natural ponds, we made additive predictions for the three ponds studied by Wissinger et al. (2018). Briefly, Wissinger et al. used in situ litter trays with coarse and fine mesh enclosures to quantify larval caddisflies' effect on detritus processing in natural ponds. Fine mesh excluded caddisflies, whereas the change in detritus mass over time in coarse mesh treatments reflected caddisfly assemblage processing. Therefore, we used caddisfly species-specific microcosm processing rates and larval abundances in each pond (Supplemental Table 1 of Wissinger et al. 2018) to predict additive caddisfly assemblage processing:

$$\text{Predicted caddisfly assemblage processing } (\text{m}^2\ \text{day}^{-1}) = \sum_{\text{all larval caddis species}} \left[\begin{array}{c}\text{mg CPOM individual}^{-1}\ \text{day}^{-1}\text{ from microcosm} * \\ \text{abundance per m}^2\text{ in natural pond}\end{array}\right]$$

We used standard errors of species' abundances and mean microcosm per-capita processing to estimate error of predicted caddisfly assemblage processing. We compared predicted to measured caddisfly assemblage processing (litter decay slopes; Fig. 4 of Wissinger et al. 2018) with measured processing error expressed as litter decay slope standard error.

Animal traits predicting detritus processing

Diet composition data for *L. abbreviatus* and *A. bimaculata* were quantified following a protocol previously used for all other larval caddisfly taxa excluding *Ecclisomyia* sp. (Appendix S1: Methods S1; Wissinger et al. 1996, Wissinger et al. 2018). *Ecclisomyia* sp. diet composition data were obtained from Huryn and Benstead (2019), amphipods from Acosta and Prat (2011), and lymnaeid snails from Kesler et al. (1986). Finally, an average chironomid diet composition was calculated using literature values for the three taxa described as regionally "ubiquitous" by Wissinger et al. (1999): *Tanytarsus* from Henriques-Oliveira et al. (2003), *Paratanytarsu*s from Jiang et al. (2008), and *Psectrocladius* from Winterbourn (1982). Phosphorus (P) excretion rates for all larval caddisfly taxa except *Ecclisomyia* sp. were previously collected by Balik et al. (2018); *Ecclisomyia* sp. P excretion rates were predicted using a caddisfly diet composition and molar N:P excretion regression. Excretion traits for other taxa were obtained from Vanni and McIntyre (2016). N excretion and body stoichiometry were not included because they were not available for all taxa.

To explore which animal traits (Table 1) were most informative for predicting detritus processing, we compared trait- and species identity-based models of larval caddisfly processing following methods used in other studies (e.g., Webb et al. 2010, Adler et al. 2018). CPOM models included all 13 taxa, whereas FPOM models only included the 9 taxa for which FPOM production was measured. Since we included body mass as a predictor trait, per-capita rates were used as the response variable. A correlation matrix identified multicollinearity between continuous traits to guide model selection (Appendix S1: Table S2). When two traits

were highly correlated (Pearson's $r > 0.5$), the trait that individually better predicted processing was used (Appendix S1: Table S3). Variance inflation factors (VIFs) also guided trait model selection, with VIF < 3.5 considered acceptable. After minimizing VIFs, the trait models with the lowest Akaike Information Criteria (AIC) were selected. Species-based models included only species identity as a fixed effect predictor and were compared to the selected trait-based models using AIC.

Results

Invertebrate-mediated detritus processing relative to no-invertebrate controls

In all five experiments, there were significant differences in detritus processing among treatments (Appendix S1: Table S4; Appendix S1: Figure S1). In the 2011, 2013, and 2015 experiments, all invertebrate taxa processed more CPOM than their respective no-invertebrate control (Appendix S1: Table S5). In 2019, all taxa processed more CPOM and FPOM than the no-invertebrate control except *L. abbreviatus*, which did not differ (Appendix S1: Table S5). In 2020, CPOM breakdown by all invertebrate taxa was greater than the no-invertebrate control (Appendix S1: Table S5). FPOM in the amphipod, chironomid, and lymnaeid treatments did not differ from the no-invertebrate control, but FPOM was greater in the *L. externus* and *Ecclisomyia* sp. treatments (Appendix S1: Table S5). Although breakdown by a few taxa did not differ from their corresponding no-invertebrate control, we calculated mass-specific breakdown and FPOM production for all taxa because comparing among taxa was central to our primary questions.

Mass-specific and per-capita detritus processing among taxa

Mass-specific invertebrate CPOM breakdown differed among taxa (Fig. 1A; $F_{12,68} = 27.27$, $p < 0.001$), and *L. externus* processed 13.3 × more than *L. abbreviatus*, which processed the least. CPOM differences among taxa were not dependent on experiment-year ($F_{4,68} = 2.02$, $p = 0.101$) or the interaction between experiment-year and taxon ($F_{2,68} = 0.89$, $p = 0.414$). Mass-specific invertebrate FPOM production also differed among taxa (Fig. 2A; $F_{8,44} = 3.27$, $p = 0.005$), and *L. externus* 23.7 × more than lymnaeid snails, which processed the least. FPOM differences among taxa were not dependent on experiment-year ($F_{2,44} = 0.64$, $p = 0.533$) or the interaction between experiment-year and taxon ($F_{1,44} = 0.03$, $p = 0.854$).

Per-capita CPOM also differed among taxa (Fig. 1B; $F_{12,74} = 62.87$, $p < 0.001$), and in contrast to mass-specific breakdown, the larger *A. bimaculata* processed 1.3 × more than *L. externus*. Furthermore, per-capita *A. bimaculata* processed 59.6 × more than chironomids, which processed the least. Per-capita FPOM also differed (Fig. 2B; $F_{8,47} = 19.24$, $p < 0.001$), and *L. externus* FPOM was 54.7 × more than chironomids, which again processed the least.

Within the caddisfly guild, greater CPOM breakdown led to greater FPOM production (Appendix S1: Figure S2; mass-specific CPOM: $F_{1,29} = 81.82$, $p < 0.001$; per-capita CPOM: $F_{1,29} = 100.51$, $p < 0.001$), and this relationship did not differ among species (CPOM*Species; mass-specific: $F_{5,29} = 1.61$, $p = 0.354$; per-capita: $F_{5,29} = 1.05$, $p = 0.407$). However, *L. externus* produced more FPOM than other caddisfly taxa when controlling for variation in CPOM (Species; mass-specific: $F_{5,29} = 2.81$, $p = 0.035$, *L. externus* intercept = 1.25, $t = 2.19$, $p = 0.037$; per-capita: $F_{5,29} = 2.35$, $p = 0.066$, *L. externus* intercept = 10.24, $t = 2.06$, $p = 0.048$).

Microcosm mixed-assemblage treatment detritus processing

Processing in mixed assemblages was generally similar to predictions calculated by summing the products of each species' mass-specific processing rates and biomass. The 2013 mixed assemblage containing *L. externus*, *A. nigriculus*, and *L. picturatus* processed only 15% less CPOM than predicted (Appendix S1: Figure S3A; $t_3 = 5.660$, $p = 0.011$), whereas the 2011 assemblage containing *L. externus*, *L. sublunatus*, and *L. tarsalis* and the 2015 assemblage containing *L. externus*, *G. lorretae*, *L. picturatus*, and *L. secludens* both processed as much CPOM as predicted (Appendix S1: Figure S3A; 2011 $t_4 = 2.600$, $p = 0.060$; 2015 $t_3 = 2.095$, $p = 0.127$). The 2013 assemblage also produced as much FPOM as predicted (Appendix S1: Figure S3B; $t_3 = 0.552$, $p = 0.620$). Thus, additive predictions were statistically similar to realized processing in the mixed assemblages except for one experiment and response variable (i.e., 2013 CPOM) and this difference was less than 20%.

Predicting caddisfly assemblage processing with additive species-specific microcosm rates

For all three ponds in which Wissinger et al. (2018) measured caddisfly detritus processing with litter trays, in situ caddisfly assemblage processing was similar to additive predictions calculated by summing the products of species' per-capita processing rates and their abundances (Fig. 3). Mean in situ processing was only 8% lower than predicted in Pond K1, 2% higher in Pond K5, and 19% higher in Pond K6. Moreover, standard error bars overlap between in situ and predicted processing in all three ponds, indicating additive predictions were statistically similar to realized processing in these ponds.

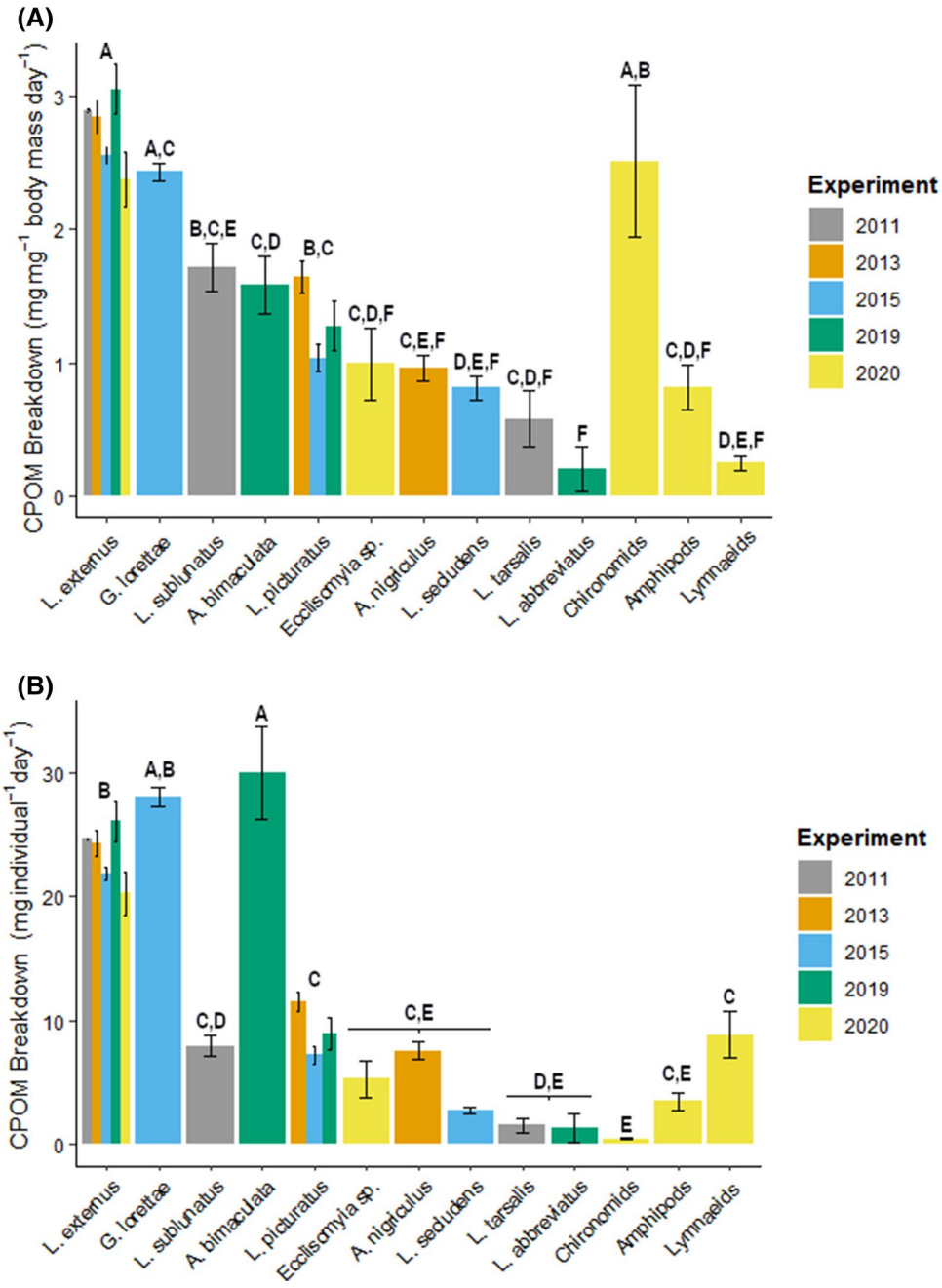

Fig. 1 Mean (±1 SE) invertebrate CPOM processing. Rates expressed in mass-specific (**A**) and per-capita (**B**) units. In both panels, larval caddisfly taxa are sorted by decreasing mass-specific CPOM, followed by non-caddisfly taxa (chironomids, amphipods, and lymnaeids). Fill color indicates experiment-year and Tukey's HSD letter groupings (grand mean for *L. externus* and *L. picturatus*) indicate no significant differences in CPOM processing at the 95% confidence level among species (A: species: $F_{12,70}=29.11$, $p<0.001$; experiment: $F_{4,70}=2.02$, $p=0.1$; B: species: $F_{12,74}=62.87$, $p<0.001$; replicate mesocosms per taxon in each experiment-year: 2011 $n=5$, 2013 $n=4$, 2015 $n=4$, 2019 $n=5$, 2020 $n=6$)

Trait vs. species identity as predictors of detritus processing

Dietary percent detritus, body size, development rate, and habitat's hydroperiod classification were included in the best trait-based models of CPOM processing (AIC = 522.5, $F_{7,79}=95.51$, $p<0.001$, Adj. $R^2=0.81$) and FPOM processing (AIC = 284.96, $F_{7,48}=12.57$, $p<0.001$, Adj. $R^2=0.57$). The species-based models provided AIC-better fits, but both modeling approaches explained similar amounts of variation (CPOM: AIC = 472.5, $F_{12,74}=62.91$, $p<0.001$, Adj. $R^2=0.90$; ΔAIC = 50.0; $\Delta R^2 \leq 0.09$; FPOM: AIC = 259.8, $F_{8,47}=19.27$, $p<0.001$, Adj $R^2=0.73$; ΔAIC = 25.2; $\Delta R^2 \leq 0.16$).

Discussion

Larval caddisflies process detritus at different rates, but several non-caddisfly taxa match or exceed caddisfly processing

Here, we show that closely related larval caddisflies (Ruiter et al. 2013), the biomass-dominant detritivores

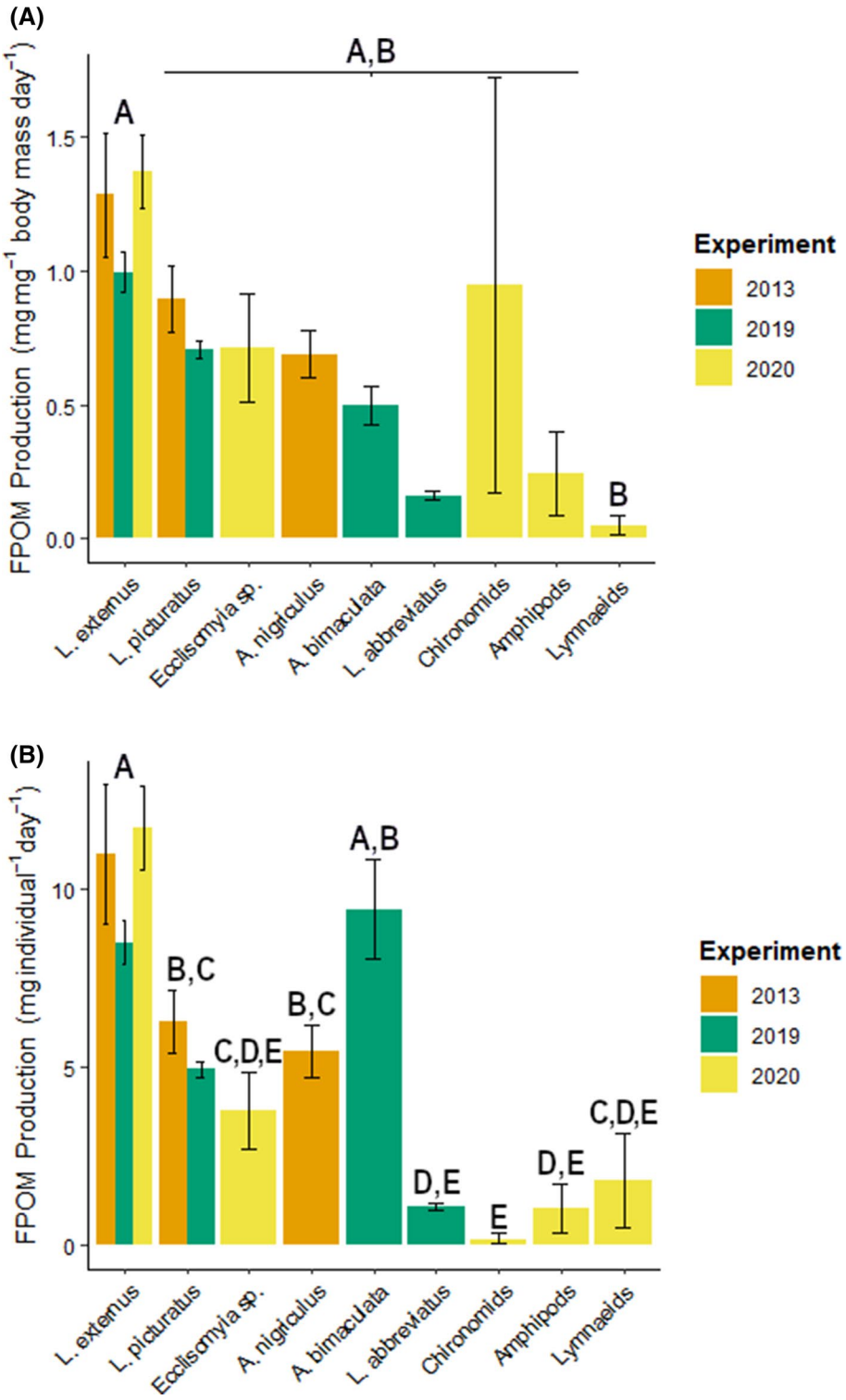

Fig. 2 Mean (± 1 SE) invertebrate FPOM processing. Rates expressed in mass-specific (**A**) and per-capita (**B**) units. In both panels, larval caddisfly taxa are sorted by decreasing mass-specific FPOM, followed by non-caddisfly taxa (chironomids, amphipods, and lymnaeids). Fill color indicates experiment-year, and Tukey's HSD letter groupings (grand mean for *L. externus* and *L. picturatus*) indicate no significant differences in mean FPOM production rates at the 95% confidence level (A: species: $F_{8,45} = 3.339$, $p = 0.004$; experiment: $F_{2,45} = 0.65$, $p = 0.525$; B: species: $F_{8,47} = 19.24$, $p < 0.001$; replicate mesocosms per taxon in each experiment-year: 2013 2019 $n = 5$, 2020 $n = 6$)

in high-elevation ponds (Wissinger et al. 1999), process CPOM at different rates in single-species experiments (Fig. 1). Although mean FPOM production did not differ among taxa (Fig. 2), controlling for covariation in CPOM processing indicates that *L. externus* generates more FPOM than other members of the guild (Appendix S1: Figure S2). This could suggest that *L. externus* is a comparatively sloppy feeder, or that it produces more feces. For *L. externus* and *L. picturatus*, CPOM and FPOM processing were consistent among experiment-years, suggesting that, for at least these taxa, detritus processing is consistent interannually. Furthermore, the magnitude of interspecific variation

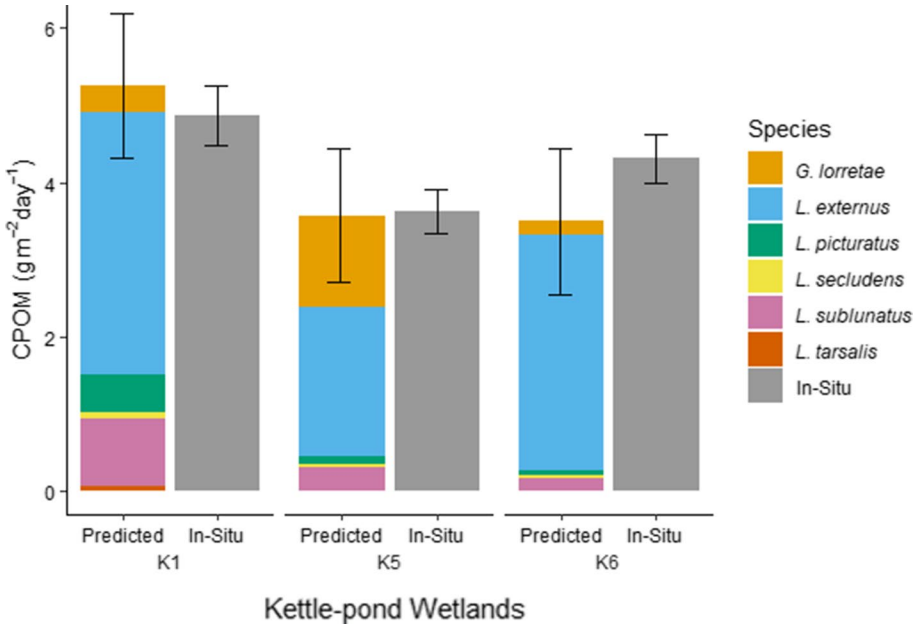

Fig. 3 Caddisfly assemblage detritus processing in ponds K1, K5, and K6, measured in situ with litter trays by Wissinger et al. 2018 (grey fill; Fig. 4 in Wissinger et al. 2018) and additive predictions calculated by summing products of species' mean per-capita microcosm processing and their abundance in natural ponds at the beginning of the litter tray experiment (Supplemental Table 1 in Wissinger et al. 2018). Bar height represents mean in situ and predicted caddisfly assemblage processing. For in situ, error bars represent ± 1 SE of detritus decay slopes (Fig. 4 of Wissinger et al. 2018). For Predicted, the products of species' abundance SE (Supplemental Table 1 of Wissinger et al. 2018) and mean per-capita microcosm processing rates were summed to estimate error

in mean mass-specific processing (13-fold for CPOM and 8-fold for FPOM) is comparable to that of their nitrogen and phosphorus excretion (8-fold for N and 7-fold for P; Balik et al. 2018). Thus, there could be low functional redundancy among members of this guild in terms of their contributions to multiple ecosystem functions including detritus processing, energy flow, and nutrient cycling.

Although chironomids are generally regarded as primarily FPOM collector-gatherers in these wetlands (Wissinger 1999), their mass-specific CPOM breakdown was similar to that of *L. externus*, *G. lorretae*, *L. sublunatus* and *L. picturatus*, and exceeded that of six other caddisfly taxa (Fig. 1A). Their mass-specific FPOM production was also similar to that of all caddisfly taxa (Fig. 2A). Indeed, chironomids are biomass-dominant detritivores in other ecosystems, as Rosemond et al. (2001) found chironomids mediated top-down and bottom-up effects on detritus processing in a tropical river. Even lymnaeid snails, which predominantly scrape epidetrital biofilm (Brady and Turner 2010; Stoler et al. 2016) had similar CPOM processing to five of ten caddisfly taxa, but processed less FPOM. Although amphipods are not found in many lentic habitats within this system, they are abundant in some beaver ponds. Amphipods are important shredders elsewhere (Little and Altermatt 2018), but their diets are highly variable (MacNeil et al. 1997) and the extent to which they feed on sedge detritus in this system was unknown. Amphipods had statistically similar mass-specific CPOM and FPOM processing to all caddisfly taxa except *L. externus*, which processed 3.4 × more CPOM. However, 4 of 5 caddisfly taxa with statistically similar rates had means nearly double that of amphipods. These comparisons among shredder caddisfly taxa and other invertebrates classically organized into other functional feeding groups suggest that the importance of non-shredder taxa for processing CPOM may be greater than previously recognized in these ponds and perhaps other systems. However, sedge detritus was the only dietary resource in experimental microcosms; it is possible that in natural ponds shredders would outcompete non-shredder taxa for access to sedge, or that non-shredders would preferentially select other resources such as FPOM or biofilms. Nevertheless, our results indicate that non-caddisfly taxa can process as much or more detritus as caddisfly shredders.

Life history and diet composition predicts detritus processing

We expected that diet composition, especially percent detritus, would be a useful trait for predicting per-capita detritus processing. Diet excels at predicting other functional traits such as nutrient excretion (Moody et al. 2015). However, percent detritus, algae, or chitin in the diet did

not individually explain significant amounts of interspecific variation in CPOM or FPOM processing. In contrast, when only larval caddisfly species were considered, percent detritus in the diet explained 34 and 72% of interspecific variation in CPOM and FPOM processing, respectively. Thus, some intrinsic traits such as relative diet composition may be predictive of functional traits within orders, but not across. Nonetheless, our trait-based model selection yielded a model of all species' CPOM processing that included percent detritus in the diet as a predictor trait, suggesting that other traits provided complementary predictive information for the non-caddisfly taxa.

For example, body size and development rate were also included in the best trait-based models of CPOM and FPOM processing. Smaller organisms typically grow proportionally faster than larger organisms (Peters 1986); within this guild, taxa with the largest body sizes generally have slow or moderate growth rates. Interspecific differences in body size or development rate could cause different metabolic demands for tissue maintenance or growth, and subsequently prompt different resource consumption and detritus processing rates.

Finally, the best trait-based models of CPOM and FPOM processing also included the taxon's preferred wetland habitat hydroperiod classification (permanent and semi-permanent, semi-permanent and vernal, beaver pond, or any). Taxa preferring permanent and semi-permanent habitats generally had greater processing rates, which is perhaps consistent with greater availability of sedge detritus in those habitats (Balik et al. 2021), compared to temporary habitats that experience additional aerobic decomposition during vernal dry phases that likely reduces detrital stocks (DelVecchia et al. 2019).

Comparisons with species-based models can evaluate how well trait-based models predict organisms' contributions to ecosystem functions. If species identity is interpreted as the aggregate of all known and unknown traits, the comparable performance of trait-based and species-based models (e.g., $\Delta R^2 \leq 0.16$) suggests that the most important traits were included here. Thus, trait-based models are preferred over species-based models for both CPOM and FPOM because they potentially offer generalizable predictive utility across ecoregions with different species assemblages (Webb et al. 2010). However, one important consideration for this approach is that type of detritus could be an extrinsic trait that influences processing rates (Boyero et al. 2021), as other systems may have different or multiple detrital sources.

Negative species interactions can exceed positive interactions in mixed assemblages

Species interactions in mixed assemblages can cause realized ecosystem function to differ from additive predictions of species-specific contributions. Loreau (1998) refers to this difference as the diversity effect. Although classic diversity-function studies predict that the net-positive diversity effects due to niche or resource partitioning and facilitation counteract negative interactions (Hooper et al. 2005), we did not observe a net-positive diversity effect in any of our mixed assemblages. Instead, processing was consistently similar to our additive predictions. However, in the 2013 assemblage of *L. externus*, *L. picturatus*, and *A. nigriculus*, CPOM was 15% lower than predicted but FPOM was as predicted. This small difference is not surprising because *A. nigriculus* engages in intraguild predation (IGP) of *Limnephilus* larvae as well as conspecific cannibalism (Wissinger et al. 1996, 2004, 2006). Here, antagonistic interactions likely counteracted and exceeded any positive effects of facilitation or resource partitioning.

Absence of positive diversity effects is not unprecedented (Maynard et al. 2017). First, positive effects of interspecific complementarity could take years to accumulate because ecosystem feedback effects such as microbial nutrient cycling develop interannually (Reich et al. 2012). Our mixed assemblages were short duration (23–42 days), and more importantly, microcosms were sterile prior to inoculation. Second, although each of the assemblages we tested occur in situ (Wissinger et al. 2003, 2018), our microcosms may not be the correct venue to observe diversity effects because natural ponds have greater habitat and resource heterogeneity, and therefore present greater opportunity for niche and resource partitioning, in addition to greater potential for ecosystem feedbacks. Consequently, positive diversity effects on detritus processing may be more likely to occur in situ than microcosms.

Species-specific microcosm rates provide accurate additive predictions of in situ processing

Although other studies have quantified species-specific detritus processing in laboratory microcosms (Bjelke and Herrmann 2005; Boyero et al. 2007; Dudgeon and Gao 2010), it is often unclear how these rates translate to natural systems (but see Boyero et al. 2006). However, here, prior studies provide points of comparison. First, for some taxa, single-species microcosm and in situ processing are similar. Specifically, *L. externus* and *L. picturatus* microcosm per-capita CPOM processing were, respectively, only 10 and 16% lower than in littoral cages (Klemmer et al. 2012; Shepard et al. 2021). *A. nigriculus* showed a similar pattern, with microcosm per-capita CPOM processing 42% lower than in littoral cages (Shepard, unpublished data). Air-drying sedge detritus and re-setting epidetrial microbial communities during the setup of our microcosm experiments could cause them to under-estimate processing relative to these littoral cage experiments, which utilized wetted detritus. However, positive ecosystem feedbacks (e.g., epidetrial biofilm resource

quality, microbial conditioning, and nutrient supply) absent from the microcosm venue may also promote greater single-species processing in situ.

Second, we demonstrate that species-specific microcosm detritus processing rates provide accurate additive predictions of caddisfly assemblage processing in ponds, measured previously by Wissinger et al. (2018). In situ caddisfly assemblage processing slightly exceeded additive predictions only in Pond K6 (19%), although overlapping standard errors suggest they are similar. Here, the natural pond context and greater species richness suggest that niche or resource partitioning and positive species interactions such as facilitation generally balance any effects of antagonistic species interactions.

However, there are two key considerations regarding additive detritus processing predictions. First, similar to the mass-ratio hypothesis (Grime 1998), the nutrient excretion literature demonstrates that population-level biomass often determines species' contributions to community-wide supply despite considerable interspecific variation in mass-specific excretion (Atkinson et al. 2017). For example, caddisflies account for 30–70% of animal biomass in subalpine ponds in the study area, but in some years and at particular times within each year (i.e., between emergence and egg hatching), chironomids attain similar or greater biomass (Wissinger unpublished data). Thus, chironomid contributions (i.e., mass-specific rate x biomass) to overall processing could occasionally exceed that of any single caddisfly species, including *L. externus*, which has the highest mass-specific processing and is the biomass dominant within the detritivore guild (Wissinger et al. 2003). Although it is unknown if chironomids utilize CPOM in this system when FPOM is available, Rosemond et al. (2001) demonstrated that chironomids were the main processor of CPOM despite ambient FPOM availability in a tropical river.

In addition to a taxon's biomass, the amount of time they spend in the habitat also influences their contribution to functions such as detritus processing (i.e., mass-specific rate x biomass x time) over seasonal and annual time scales. For example, the larval development cycle of *L. externus* is at least 3 weeks longer than that of any other caddisfly in the guild (Wissinger et al. 2003, unpublished data), and consequently, *L. externus* is likely the dominant detritivore in many habitats in this system, excluding beaver ponds where amphipods are more abundant. Thus, a taxon's realized effect on ecosystem processing is sensitive to their system-specific context (Wellnitz and Poff 2001), including all species interactions, their biomass, traits, and the amount of time they spend in the habitat.

Ecologists' understanding of the relationships between properties of species assemblages and their associated ecosystem functions is being tested as we try to anticipate the ecosystem outcomes of species range shifts, invasions, and extinctions in response to global change. Our results suggest that scaling direct measurements or estimates of species-specific processing from trait-based models to additive predictions of whole-assemblage processing is a fruitful path to understanding how shifts in assemblage composition alter key ecosystem functions.

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Author contribution statement SAW conceived the experiments and designed the methodology. JAB conceived the manuscript. With SAW's assistance, experiments were conducted by DMK and MEP in 2011, MV in 2013, SEW and JAB in 2015, and CL, IDS and HSG in 2019. The 2020 experiment was conceived and conducted by JAB, BWT, LMD, BC, AS, and OJW. JAB processed and analyzed data and wrote the manuscript; all the authors contributed critically to the drafts and gave final approval for publication.

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Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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