


Increased reliance of stream macroinvertebrates on terrestrial food sources linked to forest management intensity

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Abstract. Our understanding of how forest management practices affect the relative importance of autochthonous vs. allochthonous resource use by headwater stream food webs is relatively poor. To address this, we used stable isotope (C, N, and H) analyses of food sources and macroinvertebrates from 15 streams in New Brunswick (Canada) and assessed how different catchment conditions arising from the gradient in forest management intensity affect the contribution of autochthonous resources to these food webs. Aquatic primary production contributed substantially to the biomass of invertebrates in these headwater streams, especially for scrapers and collector-gatherers (25–75%). However, the contribution of algae to food webs decreased as forest management intensity (road density and associated sediments, water cations/carbon, and dissolved organic matter humification) increased, and as canopy openness decreased. This trend was probably due to an increase in the delivery of organic and inorganic terrestrial materials (dissolved and in suspension) in areas of greater harvesting intensity and road density, which resulted in more heterotrophic biofilms. Overall, results suggest that, despite the presence of riparian buffers, forest management can affect stream food web structure via changes in energy flows, and that increased protection should be directed at minimizing ground disturbance in areas with direct hydrological connection to streams and at reducing dissolved and particulate matter inputs from roads and stream crossings in catchments with high degrees of management activity.

Key words: algae; allochthony; benthic macroinvertebrate; forest harvesting; road; stable isotope analysis.

INTRODUCTION

The source of energy supporting headwater stream ecosystems has been a key question in freshwater ecology for decades. Because primary production tends to be limited by low light conditions in shaded headwater streams (Rosemond et al. 2000, Lesutiene et al. 2014, Collins et al. 2016) and large quantities of allochthonous materials enter these streams (Webster and Meyer 1997), their inputs have been considered the key energy source for these food webs (Vanote et al. 1980). However, recent research has shown that autochthonous (in-stream) production may be more important for these food webs than previously believed. Algae has been reported to contribute more energy than would be

expected based on its small standing biomass relative to detritus (Lau et al. 2009, Hayden et al. 2016, Jonsson and Stenroth 2016, Rosi-Marshall et al. 2016), which is probably the result of algae being of higher nutritional value than detritus for stream benthic macroinvertebrates (Guo et al. 2016a). But with evidence supporting the importance of both aquatic and terrestrial (Wallace et al. 1997, Reid et al. 2008) production as key basal resources for headwater stream food webs, debate over the relative importance of autochthonous vs. allochthonous contributions continues (Brett et al. 2017).

Understanding the relative importance of autochthonous vs. allochthonous resources to headwater stream food webs is necessary for predicting how catchment disturbances may affect the flow of energy from basal sources to top trophic levels (Brett et al. 2017). Forest harvesting has the potential to alter the relative contributions of terrestrial vs. aquatic energy sources by, for example, increasing aquatic primary production due to

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increased light availability and nutrient delivery (Kiffney et al. 2003, Lecerf et al. 2012) or reducing the subsidies of terrestrial organic matter due to vegetation removal (England and Rosemond 2004, Santiago et al. 2011). Of the few studies done in relation to forest harvesting, most report an increase in autochthonous contributions to macroinvertebrate diets (Rounick et al. 1982, England and Rosemond 2004, Göthe et al. 2009; but see Ishikawa et al. 2016). In all of these studies forests were harvested up to the streambanks; yet, such practices are uncommon in most jurisdictions in North America where management practices typically stipulate the retention of riparian buffer zones, areas left unharvested or with modified harvest to protect fish-bearing streams from logging impacts (Schilling 2009, McDermott et al. 2010). Thus, most of the above-mentioned impacts on stream food webs could conceivably be mitigated by the use of riparian buffers (Broadmeadow and Nisbet 2004). Despite their implementation, upland logging may still alter stream food webs by changing biogeochemical processes and water flows in the catchment, and by modifying the delivery of sediments, nutrients, DOC quantity and quality, etc. to streams (Kreutzweiser et al. 2008, Richardson and Béraud 2014, Erdozain et al. 2018). It can be hypothesized that an increased flux of terrestrial materials into streams could be directly (e.g., via invertebrates consuming terrestrial materials) or indirectly (e.g., via microbes recycling terrestrial DOC) incorporated into the food webs, resulting in a more allochthonous food web after forest harvesting. However, to our knowledge, no study has investigated how forest harvesting under best management practices (including riparian buffers) in an intensively managed landscape affects food web structure in streams.

In freshwater ecology, stable isotope analyses of carbon ($\delta^{13}\text{C}$) have been used to identify the contribution of autochthonous and allochthonous food sources to consumers (Finlay 2001, McNeely et al. 2006). $\delta^{13}\text{C}$ is an effective dietary tracer because there are only minor changes in $\delta^{13}\text{C}$ when food C is incorporated into consumers' tissues (Vander Zanden and Rasmussen 2001, Post 2002). However, this effectiveness is conditional upon the terrestrial and aquatic food sources having distinct $\delta^{13}\text{C}$ values, a condition that is not always met in stream ecosystems and limits the usefulness of stable isotopes (Singer et al. 2005, Finlay et al. 2010, Hayden et al. 2016). Other isotopic tracers can increase the separation of food sources and enhance the discriminatory power to detect the contribution of allochthonous vs. autochthonous food sources. More specifically, nitrogen stable isotopes ($\delta^{15}\text{N}$) have been used, provided the prey to predator fractionation is accounted for (Cole and Solomon 2012, Carroll et al. 2016), as well as hydrogen stable isotopes ($\delta^2\text{H}$), which can diverge substantially between terrestrial and aquatic food sources (Doucett et al. 2007, Finlay et al. 2010, Vander Zanden et al. 2016).

Herein, we examined the transfer of energy from aquatic/terrestrial sources to benthic macroinvertebrates by using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ in streams with catchments ranging in forest management intensity in New Brunswick, Canada. Most of the streams were located in the Black Brook (BB) forestry district, which is considered one of the most intensively managed forests in Canada and it is third-party certified as sustainably managed under the Sustainable Forestry Initiative (Etheridge et al. 2005). Considering that forestry has been predicted to intensify in the near future (Creed et al. 2016), and that the need to demonstrate the sustainability of forestry practices is also increasing (CCME 2016), BB provides an opportunity to assess how the potential "forestry of the future" may impact stream food webs. The main objective of this study was to quantify the relative contributions of autochthonous vs. allochthonous sources of energy to headwater stream macroinvertebrates, and to understand how different forest catchment conditions that arise from varying intensities of forest management under best management practices affect those contributions. We predicted that macroinvertebrates would mainly rely on allochthonous resources and that this reliance would increase with increasing forest management intensity owing to elevated delivery of terrestrial materials to streams observed in these streams (Erdozain et al. 2018) and the direct or indirect incorporation of these materials into the food webs.

METHODS

Study sites

A detailed site description is given in Erdozain et al. (2018). Briefly, the study was conducted at two locations in northwestern New Brunswick, Canada, within the Atlantic Maritime ecozone. The 190,000-ha Black Brook District (BB), owned by J. D. Irving, is one of the most intensively managed forest lands in Canada (Etheridge et al. 2005), and Mount Carleton (MC), the reference area, is a Provincial Park ~100 km east of BB with no harvesting history (Appendix S1: Fig. S1). Twelve low-order streams (first to third) were selected in the northern end of BB to capture a range in harvesting intensity (18–100% of the catchment harvested in the last 10 yr), road density (21–89 m of road per ha), stream crossings (0–4), catchment size (77–389 ha), and forest composition (deciduous/mixed/coniferous dominated; Appendix S1: Table S1). Despite being part of a different ecoregion, MC was selected as the reference area because there was an absence of unmanaged catchments closer to BB.

Sample collection

Food resources and consumers were collected within a 60-m stream reach in September 2014 and 2015 to match the timing of natural leaf fall. Both food sources and consumers were collected at the start, middle, and end of the

reach to obtain three subsamples. Macroinvertebrates were collected by electroshocking (HT2000B/MK5 (Halltech Aquatic Research Inc., Guelph, Ontario, Canada); set for 250–350 V DC, 30 Hz and 4 ms pulse width) within a 25 cm wide by 100 cm long rectangular area of the stream for 1 min (three passes of 20 s separated by 10-s breaks). Drifting invertebrates were collected with a 363- μ m mesh drift net placed on the downstream edge of the rectangle, the net rinsed, and the contents emptied into a tray. Macroinvertebrates were also picked from rocks within the rectangle. This procedure was followed at three riffle spots per stream. All the invertebrates were live-sorted to the lowest possible taxonomic level (usually family), stored in bags partially filled with stream water, kept in the dark and on ice, and frozen at the end of each day. For taxa without enough biomass, subsamples were pooled into a single sample; when each subsample contained enough biomass, each was processed separately.

Coarse particulate organic matter (CPOM) was sampled by collecting conditioned leaves from in-stream leaf accumulations. Seston or suspended fine particulate organic matter (FPOM) was sampled by filtering stream water through pre-combusted (500°C for 2 h) GF/F Whatman filters until the filters were saturated (only in 2014), and benthic FPOM was collected by suctioning the top 1 cm of the substrate from depositional areas using a turkey baster (one collection per stream in 2014, three in 2015). Seston samples were not collected in 2015 because 2014 results did not show significant differences in C and N isotope ratios between seston and benthic FPOM samples (data not shown). Biofilm was collected by scraping the surface of artificial substrates (unglazed tiles) and washing the slurry with stream water into bags. These tiles were deployed in three riffles per stream 48–51 d and 37–40 d prior to sampling in 2014 and 2015, respectively. Samples were frozen until further analysis in the lab.

Water samples for H isotope analysis were collected in 2015 from the locations used to collect macroinvertebrates, filtered through a 0.2 μ m PES filter and kept cold and in the dark (three subsamples per stream).

Stable isotope analyses

Coarse particulate organic matter samples were rinsed, oven-dried for 48 h at 60°C and ground to a fine powder. In 2014, biofilm and FPOM samples were filtered through pre-combusted GF/C and GF/F Whatman filters, respectively, and filters were oven dried for 48 h at 60°C. In 2015, biofilm and FPOM samples were freeze dried for 96 h. Processed CPOM, FPOM, and biofilm powder was weighed into tin (3.00–3.20 mg for C and N isotopes) and silver (0.35–0.45 mg for H isotopes) capsules. Macroinvertebrates were identified to genus and classified according to their functional feeding group using Merritt et al. (2008). The taxa that were most widely represented across streams and that captured all five feeding groups were selected for stable

isotope analyses: *Glossosoma* (scraper), Heptageniidae (*Epeorus*, *Heptagenia*, *Rhithrogena*; scrapers), *Baetis* (collector-gatherer/scraper), *Ephemerella* (collector-gatherer), *Leuctra* (shredder), *Parapsyche* and Philopotamidae (*Dolophilodes* and *Wormaldia*; collector-filterers), and *Diura* and *Sweltsa* (predators). Macroinvertebrate samples were freeze-dried for 48 h, ground to a fine powder with a glass rod and weighed into tin (0.40–1.20 mg for C and N isotopes) and silver (0.20–0.30 mg for H isotopes) capsules.

Carbon and nitrogen stable isotope ratios and content were measured at the Stable Isotope in Nature Laboratory (SinLab, Fredericton, New Brunswick, Canada), and the analytical precision of internal standards was $\pm 0.10\text{‰}$ and 0.11‰ on average, respectively. The H isotope ratios of solid samples were also measured at the SinLab, but prior to analysis, samples and standards were left to exchange with local atmospheric H to correct for exchangeable H (Wassenaar and Hobson 2003). The analytical precision of internal standards was $\pm 2.2\text{‰}$ (SD) on average. Water samples were analysed for H isotope ratios at the Colorado Plateau Stable Isotope Laboratory (Flagstaff, Arizona, USA); the analytical precision of internal water standards was $\pm 0.18\text{‰}$ on average. Stable isotope measurements are expressed as delta (δ) parts per thousand (‰) relative to the international standards Vienna PeeDee Belemnite for C, air for N, and Vienna Standard Mean Ocean Water for H, according to the equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000$$

where X is ^{13}C , ^{15}N , or ^2H , and R is the corresponding $^{13}\text{C}:^{12}\text{C}$, $^{15}\text{N}:^{14}\text{N}$ or $^2\text{H}:^1\text{H}$ ratios.

Preliminary studies: acid treatment, gut removal and the feeding experiment.—Preliminary acid treatment and gut removal studies were done to determine whether inorganic C could compromise the accuracy of $\delta^{13}\text{C}$ measurements and whether gut content was affecting stable isotope ratios of predator samples, respectively. Based on the results, acid-treatment and gut removal were not done for the current study (see Appendix S2 for methods and results).

A feeding experiment was conducted in 2015 to calculate the fractionation factors for ^{13}C and ^{15}N and the dietary water contribution (ω) to macroinvertebrate tissue $\delta^2\text{H}$ to use for these food webs. At the end of this experiment, ω was 0.27 ± 0.01 for *Leuctra* (mean \pm SD) and 0.17 ± 0.04 for *Zapada* shredders, and 0.17 ± 0.03 for *Glossosoma* and 0.21 for *Epeorus* scrapers. Based on these results and on the literature, we used $\omega = 0.20 \pm 0.1$ to correct for the dietary water contribution to consumers in the mixing models. The $\delta^{13}\text{C}$ fractionation value calculated in this experiment was $0.23\text{‰} \pm 0.66\text{‰}$ for *Leuctra* and $-2.01\text{‰} \pm 1.01\text{‰}$ for *Zapada*. The

$\delta^{15}\text{N}$ fractionation over their food source was $3.88\text{‰} \pm 0.20\text{‰}$ for *Leuctra* and $1.93\text{‰} \pm 0.15\text{‰}$ for *Zapada*. Fractionation values for scrapers could not be calculated (see Appendix S2 for methods and results).

Mixing models

The relative contribution of food sources to the diets of the eight macroinvertebrate taxa was estimated using a Bayesian two-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) 3-source mixing model (“CN model” herein) in 2014 and 2015, and a Bayesian three-isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$) three-source mixing model in 2015 (“CNH model” herein) with MixSIAR (Stock and Semmens 2013) in R. These models allow one to incorporate uncertainty in food source isotopic values as well as in trophic fractionation values. Separate mixing models were performed for each stream and taxon. Convergence of the models on the posterior distributions was determined before accepting the MixSIAR results by using the diagnostic Gelman-Rubin and Geweke tests in MixSIAR.

After plotting the isotope data for each stream, two issues related to biofilm were identified that had to be addressed prior to running the mixing models: (1) some potential food sources were isotopically similar (source overlap) and (2) some fractionation-corrected consumers (namely scrapers) fell outside the mixing polygon defined by food sources. In 2014, biofilm $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ overlapped with values for FPOM in 12 of 15 streams; in 2015, biofilm values overlapped with those of FPOM in 8 streams and of CPOM in 3 streams but was separated from both in 4 streams. This meant that grouping biofilm with another source, or keeping biofilm as a separate source, was problematic. A new marker, $\delta^2\text{H}$, was included in 2015 to get better food source separation, but the overlap between biofilm and other sources remained. This lack of isotopic separation was tied to the second issue, i.e., that scrapers had considerably more negative $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values than biofilms and they fell outside the mixing polygon. Taken together, this evidence suggested that heterotrophic organisms (bacteria, fungi) and terrestrial OM made up the bulk of biofilm biomass and, thus, biofilms were not reflecting the isotopic values of aquatic primary producers (microscopic algae), but that scrapers were selectively ingesting or assimilating this component of the biofilms (McCutchan and Lewis 2002, McNeely et al. 2007, Chessman et al. 2009).

A potential solution for obtaining the isotopic value of primary producers is to use values of herbivores as proxies (Vander Zanden and Rasmussen 1999, Finlay 2001). We estimated algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from *Glossosoma* because this genus (1) had consistently the most negative $\delta^{13}\text{C}$ values, (2) was present in every stream, and (3) is known to feed selectively on microscopic algae on biofilms (Oemke 1984, McNeely et al. 2006, Katano and Doi 2014). $\delta^2\text{H}$ values of algae were estimated by subtracting $170\text{‰} \pm 15\text{‰}$ from stream water $\delta^2\text{H}$, based

on studies showing that primary producers fractionate against ^2H during photosynthesis, resulting in 160–170‰ more negative values than environmental water (Yakir and DeNiro 1990, Solomon et al. 2011, Hondula et al. 2014). Therefore, since biofilms poorly reflected aquatic primary production, and tended to overlap with other food sources (mainly FPOM), they were excluded from mixing models and only three sources were included: algae (autochthonous source; calculated), FPOM (allochthonous source, capturing both FPOM and biofilms in most streams; measured), and CPOM (allochthonous source, mainly representing leaves; measured).

Trophic fractionation values for $\delta^{13}\text{C}$ ($0.4\text{‰} \pm 1.20\text{‰}$) and $\delta^{15}\text{N}$ ($2.3\text{‰} \pm 1.61\text{‰}$) were selected based on published data (McCutchan et al. 2003) and the cage experiment in this study (see *Preliminary studies: acid treatment, gut removal, and the feeding experiment*). Fractionation for $\delta^2\text{H}$ was assumed to be 0 (Solomon et al. 2009). But because a fraction of an organism’s ^2H comes from dietary water rather than assimilated food, this was accounted for by incorporating in the mixing models the dietary water contribution ($\delta^2\text{H}_{\text{WC}}$), which was calculated according to

$$\delta^2\text{H}_{\text{WC}} = \delta^2\text{H}_{\text{cons}} - (\delta^2\text{H}_{\text{cons}} - \omega_{\text{tot}} \times \delta^2\text{H}_{\text{water}}) / (1 - \omega_{\text{tot}})$$

where $\delta^2\text{H}_{\text{water}}$ is the $\delta^2\text{H}$ of stream water, and ω_{tot} is the total contribution of dietary water to consumer $\delta^2\text{H}$ ($\delta^2\text{H}_{\text{cons}}$), calculated according to

$$\omega_{\text{tot}} = 1 - (1 - \omega)^\tau$$

where ω is the per-trophic-level contribution of dietary water to consumers and τ is the trophic level ($\tau = 1$ for primary consumers and 2 for predators). A ω of 0.20 ± 0.1 was assumed based on values from Solomon et al. (2009), Wang et al. (2009) and Wilkinson et al. (2015) and backed by the caging experiment in this study.

Characterization of catchment and reach explanatory variables

Explanatory variables were classified into 10 categories under two spatial scales: catchment variables and reach variables. Catchment variables included those related to harvest, landscape characteristics, and upland and riparian forest condition, and were calculated using LiDAR-derived forest structural metrics, photo-interpreted forest composition and structure data from high-resolution digital stereo imagery (Forest Resource Inventory or FRI), topographic information derived from the LiDAR-based digital elevation model, and harvest GIS layers provided by Irving. LiDAR-derived variables were not available for MC catchments (see Appendix S1: Table S2 for the list of variables available

for BB and MC). Reach variables included those related to stream morphology, sediments, water chemistry, DOM quality, water temperature and biofilms, and were measured within the 60-m sampling reach during a concurrent study (Erdozain et al. 2018). All the variables considered are summarized in Appendix S1: Table S2, but the detailed description of how these variables were measured can be found in Erdozain et al. (2018).

Statistical analysis

Linear mixed models of ANOVA were used to assess the influence of adding a third isotope ($\delta^2\text{H}$, CNH) to 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, CN) mixing models on the calculation of the contribution of each food source to macroinvertebrate diets: mixing model type (CNH/CN) was treated as a fixed factor and stream as a random factor; linear mixed models were conducted for all taxa together, in which taxon was included as a fixed factor in the models and the mixing model type \times taxon interaction was tested, as well as for each taxon individually. Mixed models were run using the lme4 package (Bates et al. 2017) and the significance of the differences were tested using the lmerTest package, with the degrees of freedom calculated based on Satterthwaite's approximation (Kuznetsova et al. 2016). Linear mixed models were complemented with linear regression analyses and assessing the position of data-points in relation to the 1:1 line, which allowed the visual interpretation of how introducing a third isotope influenced the calculations of dietary contributions.

To determine how forest management intensity and other catchment and reach characteristics may influence the diet of macroinvertebrates, the relations between the contribution of algae (ΦA), CPOM (ΦC), or FPOM (ΦF) to each taxon and explanatory variables were assessed. As a first step in model construction and selection, a subset of variables was selected. To reduce the number of explanatory variables within the categories of harvest, upland forest condition, stream morphology, and water chemistry, PCAs were performed for each category with all the variables (on centered and scaled data), and the PCs that captured the main gradients were selected for modeling analyses. The variance explained by each PC as well as the variables correlated with the selected PCs are summarized in Table 1; PCA results for each explanatory variable category can be found in Appendix S3: Figs. S1–S4. For the harvest category, two separate PCAs were done with 2014 and 2015 data because harvesting occurred in some of the catchments between years. For the remaining categories (with fewer variables), only the most representative variables were selected (Table 1) as explained in Erdozain et al. (2018).

To assess the relationship between dietary contributions and explanatory variables, simple linear regressions were conducted between each of the ten explanatory variables and diet metrics, and the coefficient of determination values (R^2) and slope coefficients (only when

regression models were statistically significant at $\alpha = 0.1$) were recorded. These results were complemented with hierarchical partitioning analysis (hier.part package in R; Walsh and Mac Nally 2013) to determine the relative importance of each explanatory variable and separate the independent and joint contributions of each with respect to explaining variation in stream macroinvertebrate richness (Chevan and Sutherland 1991). Separate regression analyses were conducted for each year, and in 2015, for the CN and CNH mixing models.

For model construction and selection purposes, only Black Brook streams were included because the geological and topographical differences between Black Brook and Mount Carleton resulting from these areas being part of different ecoregions could confound the comparison between reference and harvested sites. Therefore, Mount Carleton sites were only used to determine a regional range of natural variation and to compare macroinvertebrate diets in Black Brook to those in nearby unmanaged systems. All statistical analyses were performed in R 3.0.1 (R Core Team 2016).

RESULTS

Contribution of algae, CPOM, and FPOM to macroinvertebrate diets in headwater streams

The dietary contributions of algae (ΦA), CPOM (ΦC), and FPOM (ΦF) calculated from MixSIAR were correlated between different taxa within a functional feeding group, especially in 2015 (Appendix S4: Table S1); therefore, only one taxon per functional feeding group will be presented herein (the taxon that was most represented across streams): *Baetis* (scraper/collector-gatherer), *Ephemerella* (collector-gatherer), *Leuctra* (shredder), *Parapsyche* (collector-filterer), and *Diura* (predator). Based on CN models, algae contributed to 50.0% and 55.6% of *Baetis* diets and 48.4% and 51.1% of *Ephemerella* diets, on average, across streams in 2014 and 2015, respectively (range of median contributions across streams: 25–75%; Fig. 1). FPOM was the main food source for *Leuctra* shredders (72% on average) and *Parapsyche* filterer-gatherers (69.3% and 62.2%; range: 50–90%) compared to algae and CPOM, which constituted <25% of the diet in most streams. The predator *Diura* used all original food sources, with FPOM and CPOM each contributing 35–38% and algae 25% to their diet, on average, across streams and years.

Results from Mount Carleton reference streams tended to fall within the range for Black Brook with respect to the contributions of algae, CPOM and FPOM to macroinvertebrate diets (Fig. 1). The reference stream MC4 tended to have higher algal contribution values than the other two reference streams and most BB streams, whereas MC2 tended to have among the highest ΦC values across all BB and MC streams. The correlation between 2014 and 2015 median dietary contributions across all 15 streams was highest for ΦA ($r = 0.41$ – 0.73)

TABLE 1. Explanatory variables used in regression analyses.

Scale, category, and variable	Description
Catchment	
Harvest	
PC1 (46%), 2014	+: partial harvest (<10, 20, 30 yr); -: recent clearcut (<5, 10 yr)
PC2 (23%), 2014	+: cumulative clearcut (<20, 30 yr) and harvest (30)
PC1 (46%), 2015	+: partial and total harvest (<5, 10, 20, 30 yr)
PC2 (25%)†, 2015	+: clearcut (<5, 10, 20 yr)
Landscape	
Road density	+: stream crossings
Percentage of effective VSA	
Upland forest condition	
FC_PC1 (64%)	+: percentage of deciduous, VCI, P90, CrC2, CrC10, S10; -: percentage of coniferous, S2
FC_PC2 (28%)	+: percentage of mixed, S2; -: percentage of coniferous, CrC2
Riparian forest	
Percentage of riparian conifer	-: percentage of deciduous, percentage of mixed, height
Canopy openness	
Reach	
Stream morphology	
SM_PC1 (40%)	+: percentage of riffle, percentage of cobble, width; -: percentage of run, percentage of pool, percentage of silt, percentage of sand, large woody debris
Sediments	
LIM	leaf inorganic mass: represents inorganic sediment entrainment in leaf biofilms and deposition of fine inorganic sediments
Water chemistry	
PC1 (54%; WC_PC1)	+: Cations (Ca, Mg), C, conductivity, pH; -: SiO ₂
PC2 (24% WC_PC2)	+: DOC, Fe, Al, Cl
DOM quality	
HIX	represents DOM humification; negatively correlated with DOM aromaticity
Temperature	
MAT	maximum August temperature (related to other temperature variables such as average fall temperature)
Biofilm	
Biofilm biomass	ash-free dry mass of biofilm scraped from tiles
Algal biomass	chlorophyll <i>a</i> concentration; positively correlated with autotrophic index

Notes: For principal components (PCs), the variance explained by each PC, the short form, as well as the variables positively (+) and negatively (–) correlated with each PC, have been specified. The values for these explanatory variables can be found in Appendix S1: Table S3.

† The sign (+/–) of the loading of the variables in the principal component has been inverted for consistency and readability.

and lowest for ΦC ($r = -0.04$ to 0.63), but there were no significant differences between 2014 and 2015 in ΦA , ΦC , or ΦF values (Appendix S4: Table S2).

Algal contributions were greater with CNH than CN models (Table 2; Appendix S4: Fig. S1), with this increase being greatest for *Diura* (20.5%) and *Baetis* (19.8%) and lowest for *Leuctra* (4.4%); yet, median dietary contributions obtained from these two mixing models tended to correlate across streams ($r = 0.52$ – 0.85). On the contrary, median ΦF contributions for all taxa were significantly lower by an average of 19.3% when including $\delta^2 H$ in the mixing models but were still correlated between the two mixing models ($r = 0.59$ – 0.85). Median ΦC values were significantly higher with CNH mixing models for *Ephemerella* (by 12.5%), *Leuctra* (13.8%), and *Parapsyche* (12.4%), but lower for *Diura*

(by 6.3%), and correlations between CN and CNH for ΦC were weaker than for ΦA and ΦF ($r = 0.19$ – 0.79).

Relationships between dietary contributions and catchment and reach variables

In general, relationships between the diet of macroinvertebrates and environmental variables were consistent between years and between contributions calculated using CN and CNH models but, sometimes, were only significant in one year or with one model (CN or CNH; Fig. 2). *Baetis* was the taxon with the strongest and greatest number of significant relationships with explanatory variables, as well as the one with the greatest consistency between years and models. At the catchment level, the reliance of *Baetis* on terrestrial food sources,

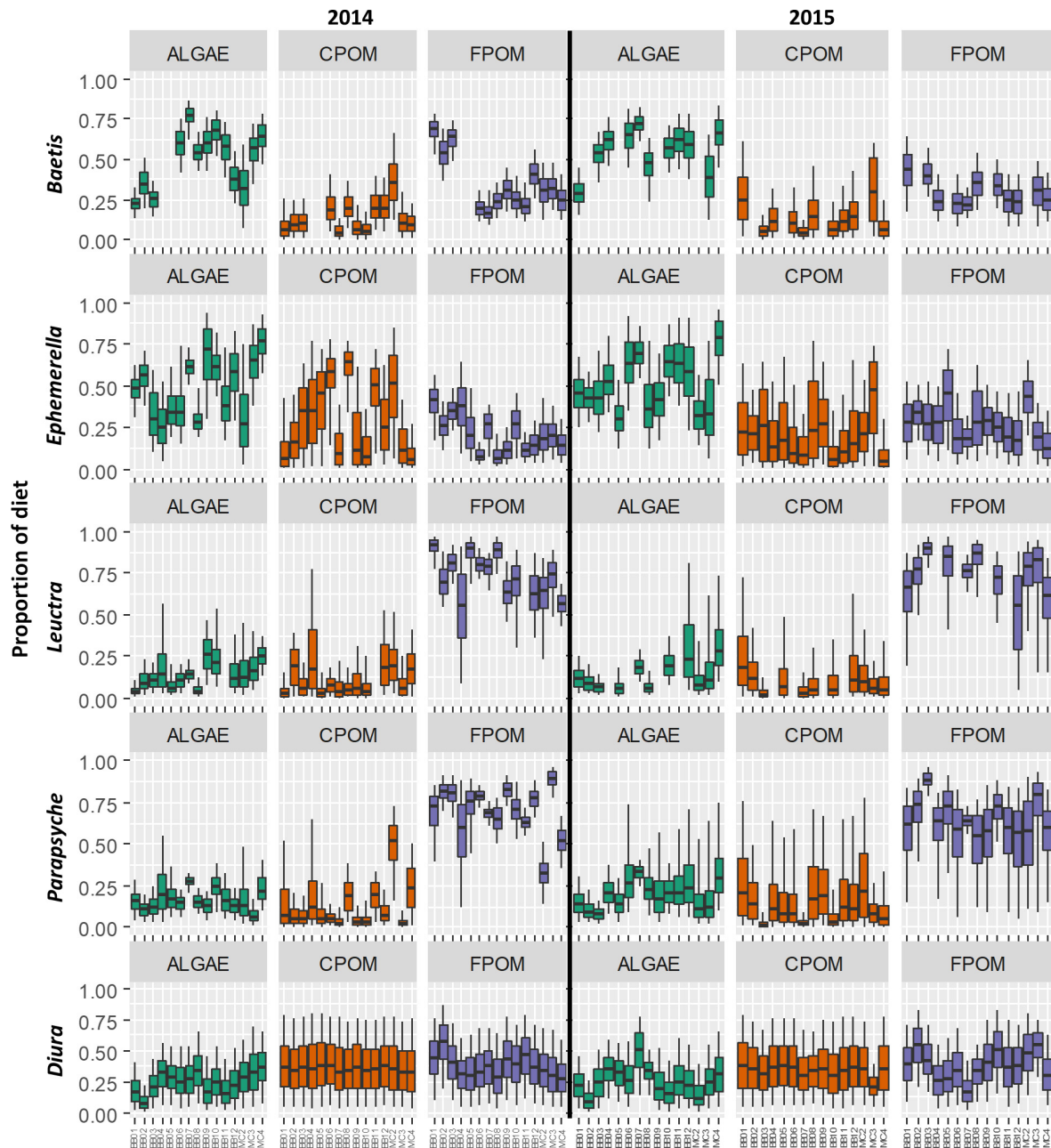


FIG. 1. Box plots showing the dietary contributions of algae (y axis represents proportions between 0 and 1), coarse particulate organic matter (CPOM), and fine particulate organic matter (FPOM) to the diets of *Baetis* (scraper/collector-gatherer), *Ephemerella* (collector-gatherer), *Leuctra* (shredder), *Parapsyche* (filterer), and *Diura* (predator) in 12 harvested (Black Brook, BB01–BB12) and 3 reference (Mount Carleton, MC2–MC4; last three) streams (New Brunswick, Canada) in 2014 and 2015. Dietary contributions were calculated based on Bayesian two-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) mixing models with MixSIAR (The upper and lower hinges of each box correspond to the upper and lower quartiles of the probability distributions calculated with MixSIAR, and the line in between to the median; the whiskers represent 5th and 95th percentiles of the probability distributions).

both FPOM and CPOM, was significantly and positively related to road density, effective VSA and percentage of riparian conifer, whereas the reliance on algae was negatively related to those same variables. Road density tended to be the catchment variable explaining

the highest portion of the variance ($R^2 = 0.40\text{--}0.46$ for Φ_A , $0.32\text{--}0.40$ for Φ_F , $0.37\text{--}0.73$ for Φ_C) but not always highest independent effect (Appendix S5: Figs. S1–S3). At the reach level, inorganic sediments, water cations, organic and inorganic carbon, and DOM humification

TABLE 2. Results of mixed model ANOVA testing for differences between two-isotope (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and three-isotope (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) mixing models to calculate the median contribution of food sources (algae, coarse particulate organic matter [CPOM], and fine particulate organic matter [FPOM]) to the diets of five benthic macroinvertebrate genera collected in 12 Black Brook and 3 Mount Carleton streams in 2015 (New Brunswick, Canada).

	Algae					CPOM					FPOM				
	ES	df	F	P	r	ES	df	F	P	r	ES	df	F	P	r
Overall †	0.198	1, 110	58.7	<0.001	0.78	−0.008	1, 110	21.4	<0.001	0.44	−0.193	1, 110	160.3	<0.001	0.89
<i>Baetis</i> ‡	0.198	1, 10	77.8	<0.001	0.82	−0.008	1, 10	0.16	0.69	0.63	−0.193	1, 10	242.8	<0.001	0.85
<i>Ephemerella</i> ‡	−0.012	1, 14	0.1	0.72	0.53	0.125	1, 14	24.9	<0.001	0.55	−0.072	1, 14	15.7	0.001	0.69
<i>Leuctra</i> ‡	0.044	1, 10	3.8	0.08	0.52	0.138	1, 10	53.0	<0.001	0.79	−0.163	1, 10	69.2	<0.001	0.80
<i>Parapsyche</i> ‡	0.161	1, 14	16.1	0.001	0.61	0.124	1, 14	13.8	0.002	0.57	−0.262	1, 14	99.0	<0.001	0.59
<i>Diura</i> ‡	0.205	1, 14	166.8	<0.001	0.85	−0.063	1, 14	5.8	0.03	0.19	−0.135	1, 14	41.5	<0.001	0.67

Notes: Column ES describes the effect size or differences between contributions calculated with CNH and CN mixing models. The row “overall” indicates that all taxa were pooled together in the model; the interaction between method and taxon was significant for all three food sources. Values that are significant at $\alpha = 0.05$ are shown in boldface type. Column *r* shows the Pearson correlation coefficient between CNH and CN.

† Contribution of algae/CPOM/FPOM ~ Mixing model \times Taxon + (1|Stream) model tested.

‡ Contribution of algae/CPOM/FPOM ~ Mixing model + (1|Stream) model tested.

were significantly and negatively related to ΦA , and positively to ΦF and ΦC . Although the strength of the associations varied between years and models, some linear relationships were very strong. For example, both DOM humification and inorganic sediments explained up to 82% of the variance in ΦA for *Baetis* individually. The joint effect was greater than that of the independent one for both variables.

These same catchment and reach variables were similarly and significantly related to the diet of other macroinvertebrate taxa, although the strength of the associations were lower. For example, the significant positive relationship between the reliance on terrestrial food sources and sediments and DOM humification was observed to some extent and with varying strengths for all taxa (Fig. 2). The reliance on terrestrial sources was also positively related to road density in *Ephemerella* ($R^2 = 0.40$ for ΦF in 2014) and *Leuctra* ($R^2 = 0.73$ for ΦC in 2015), and to percentage of effective VSA in all taxa except *Ephemerella* ($R^2 = 0.42$ – 0.67).

Harvesting variables showed significant relationships only with the dietary habits of *Leuctra*. In 2014, their reliance on FPOM was positively related to clearcut and negatively to partial harvest (represented by harvest PC1), whereas the opposite trend was observed for their reliance on CPOM. In 2015, clearcut (represented by harvest PC2) was negatively and positively related to their reliance on algae and FPOM, respectively.

Canopy openness and algal biomass were significantly related to the diet of most macroinvertebrate taxa to varying degrees and, in all instances, they were positively related to ΦA and negatively to ΦF and ΦC . These relationships were especially strong in *Diura* ($R^2 = 0.42$ – 0.57 , $I = 31$ – 32.3% in 2015) and *Parapsyche* ($R^2 = 0.56$ – 0.73 , $I = 30.2$ – 73.6% ; Fig. 2; Appendix S5: Figs. S1–S3). Finally, in most taxa stream morphology PC1 (positively related to percentage of riffles/cobbles and negatively to percentage of runs/silt) was significantly and negatively

associated with the reliance on terrestrial food sources and positively with the reliance on algae.

DISCUSSION

Algal contribution to macroinvertebrate diets in headwater streams

We examined the contribution of different food sources to the diets of macroinvertebrates in 15 streams in northern New Brunswick (Canada), predicting that the greatest contribution would come from allochthonous food sources. However, our results showed that the reliance of some macroinvertebrates on algae was greater than anticipated given the shaded nature of these forest headwater streams (Fig. 1). This supports recent studies that emphasize the importance of aquatic primary producers to consumers in these ecosystems (Hayden et al. 2016, Rosi-Marshall et al. 2016) and shift away from the understanding that mainly allochthonous food sources fuel forested headwater streams (river continuum concept; Vanote et al. 1980). This shift in perspective stems from the need to consider both resource quantity and quality, the latter of which would explain why autochthonous production may contribute more to animal tissue than expected based on its small standing biomass relative to detritus in shaded headwater streams (Marcarelli et al. 2011, Rosi-Marshall et al. 2016). The importance of quantity is also reflected in our results since the reliance on algae increased with algal biomass and canopy openness, suggesting that light is a limiting factor for the autochthony of macroinvertebrates in these streams (Fig. 2).

The reliance of macroinvertebrates on algae was taxon and functional feeding group dependent, but the trends within each taxon remained relatively constant between years. The greatest contribution of algae to a macroinvertebrate's diet was observed in scrapers (*Glossosoma*

			<i>Baetis</i>			<i>Ephemerella</i>			<i>Leuctra</i>			<i>Parapsyche</i>			<i>Diura</i>		
			2014	2015 - CN	2015 - CNH	2014	2015 - CN	2015 - CNH	2014	2015 - CN	2015 - CNH	2014	2015 - CN	2015 - CNH	2014	2015 - CN	2015 - CNH
Catchment	Harvest PC1	ΦA															
		ΦF							-0.50								
		ΦC							+0.49								
	Harvest PC2	ΦA									-0.53						
		ΦF									+0.56						
		ΦC															
	Road density	ΦA		-0.46	-0.40												
		ΦF	+0.32		+0.40	+0.40											
		ΦC		+0.59	+0.37					+0.73							
	Forest condition PC1	ΦA															
		ΦF										+0.36	+0.25				
		ΦC		-0.42						-0.44		-0.41	-0.25				
	Forest condition PC2	ΦA									+0.45						
		ΦF				-0.34											
		ΦC															-0.25
	% effective VSA	ΦA			-0.35								-0.30	-0.34	-0.52		
		ΦF			+0.33										+0.50		
		ΦC		+0.32	+0.37					+0.55	+0.67			+0.50			+0.42
	% riparian conifer	ΦA			-0.41												
		ΦF	+0.32		+0.42	+0.51	+0.27	+0.29									
		ΦC			+0.36												
	Canopy openness	ΦA						+0.48			+0.88	+0.31	+0.34				
		ΦF						-0.36									
		ΦC						-0.48									-0.38
Reach	Stream morphology PC1	ΦA			+0.35									+0.37			
		ΦF	-0.43	-0.41	-0.40	-0.41									-0.27		
		ΦC													-0.48		-0.28
	Sediments	ΦA	-0.30	-0.65	-0.82									-0.25			
		ΦF	+0.51	+0.45	+0.82	+0.50											
		ΦC	-0.32	+0.47	+0.79					+0.61	+0.37			+0.26			+0.24
	Water chemistry PC1	ΦA	-0.49	-0.37	-0.46									-0.30			
		ΦF	+0.62	+0.32	+0.50	+0.53											
		ΦC			+0.41												+0.26
	Water chemistry PC2	ΦA		-0.51	-0.39												
		ΦF			+0.34				+0.33								
		ΦC		+0.50	+0.43				-0.34								
	DOM humification	ΦA	-0.35	-0.82	-0.84												
		ΦF	+0.48	+0.38	+0.82	+0.35											
		ΦC		+0.58	+0.85					+0.60				+0.31	+0.30		
	Temperature	ΦA		-0.59	-0.40										-0.25		
		ΦF		+0.54	+0.39												
		ΦC		+0.31	+0.40									+0.30	+0.29		
	Biofilm	ΦA															
		ΦF	+0.31			+0.37				-0.36	-0.77		-0.31		+0.32		
		ΦC		+0.27		-0.38				+0.55							
	Algae	ΦA	+0.37								+0.57	+0.73	+0.56			+0.57	+0.42
		ΦF														-0.51	
		ΦC	-0.48			-0.36									-0.44		-0.25

FIG. 2. Summary of the simple linear regressions between explanatory variables (rows) and the contribution of algae (ΦA, green), FPOM (ΦF, gray) and CPOM (ΦC, orange) to the diet of five macroinvertebrate taxa in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian two-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian three-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$) in 2015. The + or - signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$ and the number corresponds to the R^2 of those models.

and Heptageniidae) and gatherers (*Baetis* and *Ephemera*), which seemed to be selectively ingesting or assimilating the algal portion of biofilms since they had considerably more negative $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values than those of the biofilms (McNeely et al. 2007, Chessman et al. 2009). The shredder *Leuctra* derived up to 25% of its biomass from autochthonous sources, which agrees with observations that even macroinvertebrates classified as obligate and facultative shredders assimilated energy from algae in shaded streams (Li and Dudgeon 2008, Lau et al. 2009, Hayden et al. 2016). As for allochthonous contributions, FPOM contributed considerably more than CPOM to *Leuctra*'s diet, opposite to what is expected for an obligate shredder. Since FPOM and bulk biofilm had similar isotope ratios in most of the streams in this study, it seems that *Leuctra* was feeding selectively on the biofilm on leaves rather than ingesting the leaves themselves, which would agree with observations from Dangles (2002), who reclassified *Leuctra* as generalist collectors/scrapers after finding that, on average, 50% of their gut content was comprised of FPOM. Predators from the streams in BB and MC seemed to feed on primary consumers that relied on both aquatic and terrestrial resources. It has been suggested that predators select prey based on their quality, and that prey dependent on autochthonous resources are preferred due to a higher content of highly unsaturated fatty acids (Lau et al. 2014). In our study, however, stonefly predators seemed to indiscriminately feed on autochthonous or allochthonous primary consumers. This could be partly explained by the abundance of *Glossosoma* algae feeders in these streams: predators tend to avoid them due to their protective stone cases (Parker 1994), which diverts algal biomass away from predators (McNeely et al. 2007).

Effects of forest management on the contribution of food sources to macroinvertebrate diets

Our results show that, as predicted, the contribution of autochthonous resources to macroinvertebrates decreased as variables associated with forest management intensity increased (see *Relationships between dietary contributions and catchment and reach variables*), which contrasts with several studies that reported an increase after logging (Rounick et al. 1982, England and Rosemond 2004, Göthe et al. 2009). In those studies, harvesting was done right to stream edges, resulting in increased primary production from reductions in canopy cover and in decreased inputs of terrestrial detritus. In BB, however, all streams retained ~30 m wide riparian buffer zones, and harvesting did not have a major effect on stream canopy cover and direct terrestrial detritus inputs (Erdozain et al. 2018). But as described in Erdozain et al. (2018), harvesting promoted higher transport of water-borne terrestrial materials (cations, organic and inorganic carbon, humic DOM) to streams, with the delivery being facilitated by higher road density and stream crossings, and this favored

the growth of more heterotrophic biofilms in these streams. In this current study, we demonstrate that not only did forest management intensity enhance the delivery of terrestrial materials, but that those materials seemed to be incorporated into the food webs.

Such an incorporation was likely mediated by the consumption of more heterotrophic biofilms via (1) ingestion of terrestrial organic matter associated with sediments and entrained in biofilms and/or (2) ingestion of microbes recycling terrestrial DOC. In fact, the increased delivery of carbon associated with forest management intensity could be favoring the heterotrophic organisms in biofilms over the primary producers, because under low light and nutrient availability and high allochthonous C supply, detritivores (bacteria and fungi) tend to competitively exclude algae (Daufresne and Loreau 2001, Danger et al. 2007). Jonsson et al. (2018) also found a positive relationship between forestry and allochthony in stream filter feeders, which they also attributed to influences on terrestrial organic matter inputs. However, it is interesting to note that we did not detect a negative relationship between forest management intensity and algal biomass (Erdozain et al. 2018). This is likely because algal biomass in shaded headwater streams tends to be low, yet of high nutritional quality (namely diatoms) and with fast turnover rates, resulting in consumers readily ingesting the new algal growth (Rosemond et al. 1993) and obscuring our ability to measure the actual amount of algal biomass available to consumers. Therefore, food web structure (i.e., time integrated measure of algae assimilation) was a more reliable indicator than algal biomass (i.e., snapshot in time) to detect the effects of forestry. This was especially true for *Baetis*, which showed the strongest relationships between resource use and forest management intensity, although these were observed for all taxa to some extent.

The positive relationship between percentage of effective VSA (stream-side areas with strong hydrological connectivity) in the catchment and CPOM or FPOM contribution to macroinvertebrate diets suggests that both anthropogenically (via roads) and naturally (via effective VSAs) enhanced hydrological connectivity contributed to the delivery of more terrestrial compounds and consequent allochthony. These streamside areas of high hydrological connectivity have been shown to be contributors of organic materials to streams and are thought to be areas requiring special attention during forest harvesting operations (Laudon et al. 2016).

Considering the higher nutritional quality of algae than materials of terrestrial origin (Guo et al. 2016a), the reduced use of this resource can result in slower growth of consumers and less efficient energy transfer to upper trophic levels (Goedkoop et al. 2007, Gladyshev et al. 2011), as well as reduced rates of leaf decomposition (Brett et al. 2009, Danger et al. 2013, Guo et al. 2016b). However, the observed values fell within the natural variability observed in the reference streams in this study. Reference streams showed a wide range of algal

contributions to macroinvertebrate diets, with MC4 tending to have among the highest and MC2 among the lowest values across all 15 streams. Probably, the low algal contributions observed in MC2 stemmed from the beaver dam ~1 km upstream from our sampling reach, which may have enhanced the release of terrestrial materials following the inundation of soils (Catalán et al. 2017).

Methodological limitations and contributions

Biofilms.—The main challenge in this study, as well as in most studies that use stable isotopes to track the energy transfer from food sources to consumers in streams (Brett et al. 2017), was to reliably determine the isotopic ratio of the autotrophic fraction of the biofilm. In most of our streams, biofilm overlapped in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with terrestrial sources (mainly with FPOM), which was likely due to biofilms containing considerable amounts of terrestrially derived organic matter and heterotrophic microbes feeding on terrestrial C compared to algal biomass (Jardine et al. 2009, Brett et al. 2017). However, due to the fast turnover of algae (Dodds et al. 2014) and its higher nutritional quality (Guo et al. 2016a), algae can disproportionately contribute to consumers' diets (McCutchan and Lewis 2002), making it important to characterize the autotrophic end member to accurately estimate its use in aquatic food webs. To improve source separation, we first incorporated a third marker ($\delta^2\text{H}$), since the addition of H isotopes to stream food web studies has been shown to increase the resolution of dietary sources (Doucett et al. 2007, Jardine et al. 2009, Finlay et al. 2010), but the source overlap remained. Another solution was to use isotopic values of herbivores as proxies for the isotopic values of algae (Vander Zanden and Rasmussen 1999, Finlay 2001), and we used the ubiquitous *Glossosoma* scrapers, which are known to selectively feed on the algal portion of biofilms (Oemke 1984, McNeely et al. 2006, Katano and Doi 2014), to reflect algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We acknowledge that this approach may have introduced some error in our estimates as it assumes 100% herbivory by *Glossosoma* across streams. That assumption is unlikely to be true, leading to an overestimation of autochthonous contributions. Although there are limitations to this approach, we believe that it was the best available one to elucidate food web structure in these streams considering the described issues (i.e., biofilm samples did not reflect primary producer's isotope ratio values). We have some evidence suggesting little concern with using *Glossosoma* to estimate algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. For example, algal $\delta^2\text{H}$ was estimated independently by assuming a 170‰ depletion in ^2H compared to water during photosynthesis (Yakir and DeNiro 1990, Solomon et al. 2011, Hondula et al. 2014); the cage experiment showed that *Glossosoma* and algal $\delta^2\text{H}$ were similar, suggesting that the assumption of 100% herbivory for *Glossosoma* was appropriate. In fact, values for algal contributions tended to be higher when including $\delta^2\text{H}$ in mixing

models than when only using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Future studies might consider separating algae from the detritus in biofilms via density fractionation in colloidal silica (Hamilton et al. 2005; but see McNeely et al. 2007).

Another potential reason for the lack of overlap between the stable isotope ratios of biofilm and algae-feeders could be that consumers may have not reached isotopic equilibrium with their food source, since both were collected at the same time. However, we believe that this may have played a minor role, because: (1) these invertebrates have very fast isotopic turnover rates (1–9 d half-lives; Jardine et al. 2014, Thomas and Crowther 2015), (2) the variables inducing changes in algal $\delta^{13}\text{C}$ (e.g., flow, source of carbon) are less likely to fluctuate drastically in hydrologically more stable systems such as the streams in eastern Canada (Jardine et al. 2014), and (3) isotope values of detritus tend to be rather stable temporally (McArthur and Moorhead 1996).

Two- vs. three-isotope mixing models.—Algal contribution estimates tended to be ~20% higher and FPOM contributions ~20% lower on average when including $\delta^2\text{H}$ in mixing models (CNH) than when only using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (CN; Table 2). Syväranta et al. (2016) also documented lower allochthony estimates in a lake with CNH than with CN modeling, especially for fish and zooplankton. They hypothesized that this difference could stem from the considerably lower $\delta^2\text{H}$ values of lipids (Sessions et al. 1999), which, unless removed, would lead to underestimations of allochthony (due to algae having lower $\delta^2\text{H}$ values). Currently, unlike for $\delta^{13}\text{C}$, models to correct for the presence of lipids when measuring $\delta^2\text{H}$ values do not exist, and the few studies that have assessed the effect of lipid-extraction on $\delta^2\text{H}$ values present mixed results (Vander Zanden et al. 2016). Therefore, it is difficult to assess whether the mismatch in our CNH and CN model results stems from lipids or other uncertainties associated with H isotope analysis (e.g., percentage of environmental H contribution). Nevertheless, the relative changes in autochthonous resource use by *Baetis* and *Diura* across streams were quite similar when using either CN or CNH in the models, but less so for other taxa (Table 2). Overall, the strength of the associations between dietary contributions and explanatory variables was model (CNH vs. CN) dependent (Fig. 2). Therefore, though using $\delta^2\text{H}$ alone highlights trends in the use of autochthonous resources across streams (Doucett et al. 2007, Wilkinson et al. 2013), including both $\delta^{13}\text{C}$ and $\delta^2\text{H}$ may improve the robustness of the results, especially considering the fundamental uncertainties that still remain regarding the interpretation of $\delta^2\text{H}$ values in the context of food webs (Vander Zanden et al. 2016).

CONCLUSIONS

Although calculating the contribution of algae to the biomass of macroinvertebrates is challenging due to

methodological limitations, our results suggest a substantial contribution in these headwater streams, especially for scrapers and collector-gatherers. However, the algal contribution to food webs decreased as forest management intensity increased. This trend was probably due to an increase in the delivery of organic and inorganic terrestrial materials (dissolved and in suspension) promoted by higher forest harvesting and road density, which resulted in more allochthonous biofilms. Considering the higher nutritional quality of algae, a decrease in its assimilation may result in a slower growth and development of consumers, with potential implications for higher trophic levels and stream functions such as leaf litter decomposition. Therefore, increased protection of stream food webs should be directed at minimizing ground disturbance in areas with direct hydrological connection to streams and reducing dissolved and particulate matter inputs from roads and stream crossings in catchments with high degrees of management activity.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1889/full>

DATA AVAILABILITY

The contribution of food sources to macroinvertebrates can be found in Mendeley Data: <https://doi.org/10.17632/zjv2264cky.1>