

Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability

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Abstract

1. Extreme disturbances, those high magnitude events that are statistically rare in a particular system, may affect consumer resource use through multiple mechanisms, such as differential consumer mortality and modified resource availability and quality. Documenting the ecological importance of these rare events is difficult, but essential, as the frequency of extreme events is predicted to increase under many climate change scenarios.
2. We quantified changes in stream insect resource use following intense, nonseasonal flooding in the Rocky Mountains of northern Colorado during September 2013. We hypothesised that taxonomic identity, functional feeding group membership and disturbance-caused alterations in resource quantity and quality (C:N ratios) would determine consumer reliance on autochthonous and allochthonous resources and community structure following the disturbance.
3. In summer 2014, we collected basal resources and stream insects for carbon, nitrogen and deuterium bulk stable isotope analysis, and community composition. Basal resource quantity and quality (C:N ratios) were collected at seven headwater streams along a 2013 flood intensity gradient.
4. Using stable isotope mixing models, we analysed consumer autochthony. We also used baseline community composition data from 2011 to compare functional feeding group abundance prior to and following the flood events.
5. We found that consumer resource use was primarily associated with detrital resource quantity, which was positively correlated with disturbance intensity and elevation. Functional feeding group membership did not predict resource use. However, consumers in functional feeding groups did experience differential mortality following flooding. Herbivore relative abundance significantly declined along the disturbance gradient, and predator relative abundance generally declined across all streams from 2011 to 2014.
6. Our results suggest that changes in resource quantity from extreme disturbances can be associated with shifts in consumer resource use. Following this flood event, detritus standing stocks increased, resulting in a concomitant increase in consumer reliance on allochthonous sources.

KEYWORDS

disturbance, functional feeding groups, resource use, stable isotopes, stream insects

1 | INTRODUCTION

Extreme disturbance events, defined as those values that fall at the tails of a statistical distribution of a weather or climate variable at a particular site (Seneviratne, 2012), may result in correspondingly large biotic responses. However, due to their rare nature, extreme events are difficult to observe and characterise in ecological systems, except for sites that are intensively and continuously monitored over long time periods (Fisher, Gray, Grimm, & Busch, 1982; Woodward, Bonada, Feeley, & Giller, 2015). With projected changes in hydrologic regimes due to climate change and water demands (Adam, Hamlet, & Lettenmaier, 2009; Vörösmarty et al., 2010), we need empirical studies examining how stream communities respond to extreme events (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). In particular, the frequency of extreme flooding events is already increasing (Milly, Wetherald, Dunne, & Delworth, 2002). We realise that ecological impacts of extreme events are context-dependent (George, Baldigo, Smith, & Robinson, 2015) and complex, necessitating further mechanistic research (Ledger & Milner, 2015).

Extreme flooding causes extensive stream insect mortality and alters stream geomorphology (Death, Fuller, & Macklin, 2015; Robertson, Brown, Klaar, & Milner, 2015; Woodward et al., 2015). Yet, we do not fully understand how extreme events influence resource availability and food-web dynamics. Disturbance can alter subsidy relationships, both directly by decreasing or strengthening flows of energy between ecosystems, and indirectly by influencing the functional community composition of recipient ecosystems (Pickett & White, 1985). Floods and droughts shorten food chains in aquatic systems (McHugh, McIntosh, & Jellyman, 2010; McHugh, Thompson, Greig, Warburton, & McIntosh, 2015; Sabo, Finlay, Kennedy, & Post, 2010), but we know less about how these disturbances shift stream insect reliance on autochthonous compared to allochthonous resources. Because floods restructure benthic habitat, resetting the geomorphic template, they might have strong bottom-up effects on stream food webs by making food resources less patchy while simultaneously decreasing resource quantities (Death et al., 2015). Due to our knowledge gaps around the effects of such extreme events on stream food webs (Woodward et al., 2016), we expect complex effects of flood disturbance on consumer resource use.

Flooding may either increase or decrease the quantity and quality of detrital inputs and thus consumer resource use, depending on the timing and severity of high flows. Less severe flooding that solely scours the stream channel and not the surrounding riparian zone may flush out conditioned, high-quality detritus already in the stream, but not introduce fresh, low-quality detritus (Jones & Smock, 1991; Wallace et al., 1995), causing an overall decrease in detrital availability. In contrast, extreme flood events can increase lateral linkages, with material moving from the catchment into the channel (Lake, Bond, & Reich, 2006). In some cases, extreme precipitation and flood events result in a net increase in allochthonous organic carbon (leaf litter, soil carbon and woody debris) in stream channels

(Rathburn et al., 2017). However, in New Zealand streams, levels of particulate organic matter were not associated with substrate disturbance (Death & Zimmermann, 2005), demonstrating that flood effects on detrital resources can be context-dependent. Flood timing is also important as seasonal timing can affect resource fluxes (Abelho, 2001). Floods occurring shortly after leaf-fall in temperate regions may decrease detrital stocks, while flooding occurring during other seasons may introduce and amplify detrital inputs (Acuña, Giorgi, Muñoz, Uehlinger, & Sabater, 2004; Wallace et al., 1995). Therefore, we expect flood effects on detrital resource quantity and quality and consumer resource use to be contingent on timing and severity of flooding.

Flooding also controls the availability of high-quality autochthonous resources. Consumers rely more on in-stream primary production following major flooding that impacts the riparian zone, especially if insolation increases (Julian, Seegert, Powers, Stanley, & Doyle, 2011; Mihuc & Minshall, 2005). Even small changes in canopy cover along a stream reach can decrease allochthonous resource availability and cause concomitant consumer shifts towards more autochthonous resource use (England & Rosemond, 2004). However, in disturbance-prone systems, scouring and sloughing of algae can more strongly control autochthonous resource availability than light (Uehlinger, Bühner, & Reichert, 1996). In addition, if extreme flows introduce large amounts of detritus into a stream reach, that detritus can also shade and suppress algal growth (Melody & Richardson, 2004), resulting in a reduction in algal standing stocks. Thus, flooding effects on algal production depend on riparian zone impacts, stream bed stability, and the quantity of detrital inputs.

Flooding effects on resource quantity and quality can drive consumer–resource interactions. However, consumer identity (Mihuc & Minshall, 2005) and vulnerability to disturbance (Lepori & Malmqvist, 2007) also determine consumer–resource dynamics. Although stream insects are often classified in specific functional feeding groups, these taxa exhibit greater plasticity in their diet than feeding group classification implies (Collins, Kohler, Thomas, Fetzer, & Flecker, 2016; Mihuc, 1997). We hypothesise that the flexible nature of stream insect feeding habits may cause food webs to shift in response to extremely high flows, even if taxa are not lost from the community.

We studied small streams in the Rocky Mountains of northern Colorado following a rare extreme flooding event to test the following predictions:

1. Major flooding and concomitant shear stress acting on the streambed are associated with a decrease in epilithon quantity at streams that experienced higher disturbance intensity.
2. Detrital resources increased in quantity, possibly due to overbank flows recruiting floodplain debris. The higher quantity of detrital resources is associated in higher consumer reliance on allochthonous resources at more highly disturbed streams.
3. In addition to resource availability (i.e., quantity), quality (as measured by C:N ratios) is associated with resource use, with consumers relying more on higher-quality resources. Detritus quality

is negatively related to shear stress, as the leaf litter at lower disturbance streams spent more time being conditioned by fungi and microbes and was not newly introduced to the stream by the floods. Epilithon quality is positively related to shear stress as diatoms and other early succession algal taxa have lower C:N ratios.

4. Because functional feeding groups are only weakly correlated with other traits (e.g., mobility) that confer resilience to disturbance (Poff et al., 2006), members of different functional feeding groups experienced similar mortality following the flood event. However, functional feeding groups predict consumer resource use, with shredders heavily relying on allochthonous resources, herbivores heavily relying on autochthonous resources, and collectors and filterers relying on a balance of autochthonous and allochthonous resources.
5. Taxonomic identity is not strongly associated with consumer resource use because large flood events filter out specialist feeders (Mihuc, 1997), leaving more generalists, with higher feeding plasticity.

To summarise, we expected to see greater autochthony among consumers at streams that experienced lower hydraulic forces during the 2013 flood event due to larger standing stocks of higher-quality algal resources. We also expected functional feeding group membership but not taxonomic identity to constrain consumer autochthony.

2 | METHODS

2.1 | Study system

In September 2013, an extreme precipitation event caused extensive flooding along Colorado's Front Range. Over a period of 8 days, some areas received over 45 cm of rain (Gochis et al., 2014), resulting in severe flooding in the St. Vrain, Big Thompson and Cache La Poudre rivers and their tributaries (Figure 1). Where precipitation was greatest, the exceedance probability of the flooding associated with the 2013 rainfall was estimated to range from 1 in 50 to 1 in 500 years along a gradient of rainfall intensity (Gochis et al., 2014). The timing of this flooding was also unusual; ordinarily, predictably

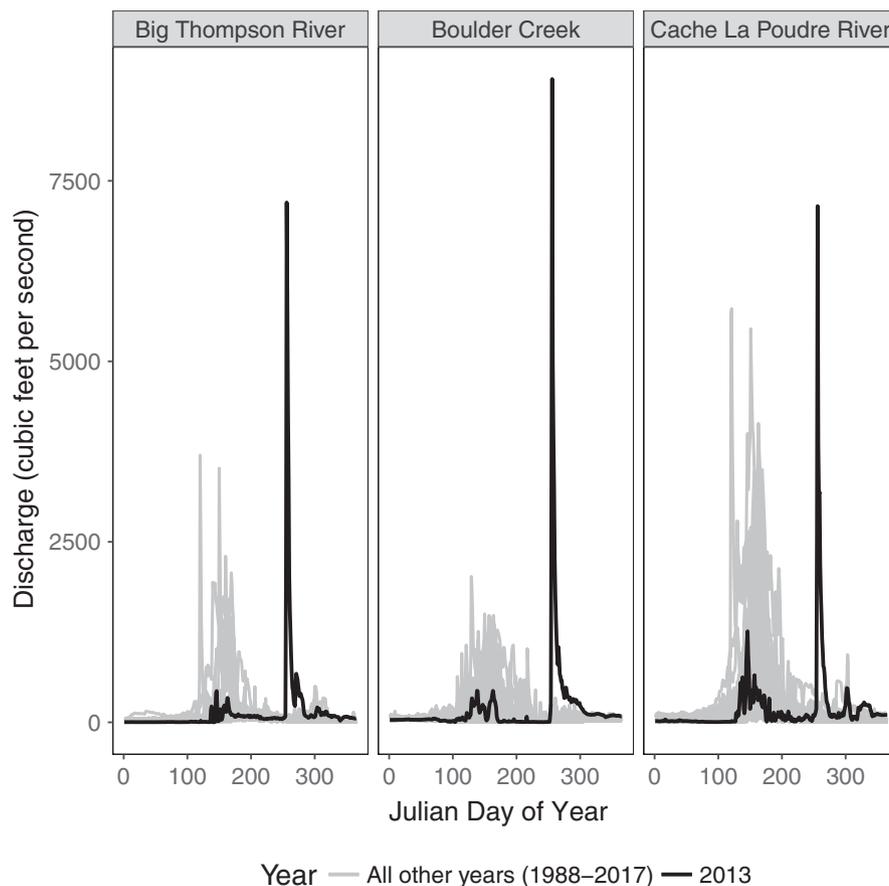


FIGURE 1 Annual hydrographs showing daily means from the period of record (1988–2017) of United States Geological Survey gages at each of our three drainages (Big Thompson, St. Vrain and Cache la Poudre), with the 2013 hydrograph highlighted in black. Boulder Creek, a major tributary of the St. Vrain, is substituted for the St. Vrain gage, which was damaged and discontinued during the 2013 floods, and therefore did not capture the flood peak. Data were accessed and cleaned using the “waterData” package (Ryberg & Vecchia, 2017) in R for the dates from January 1, 1988, to December 31, 2017. USGS gages used in analysis are numbers 06752260 (Cache la Poudre River), 06741510 (Big Thompson River) and 06730500 (Boulder Creek)

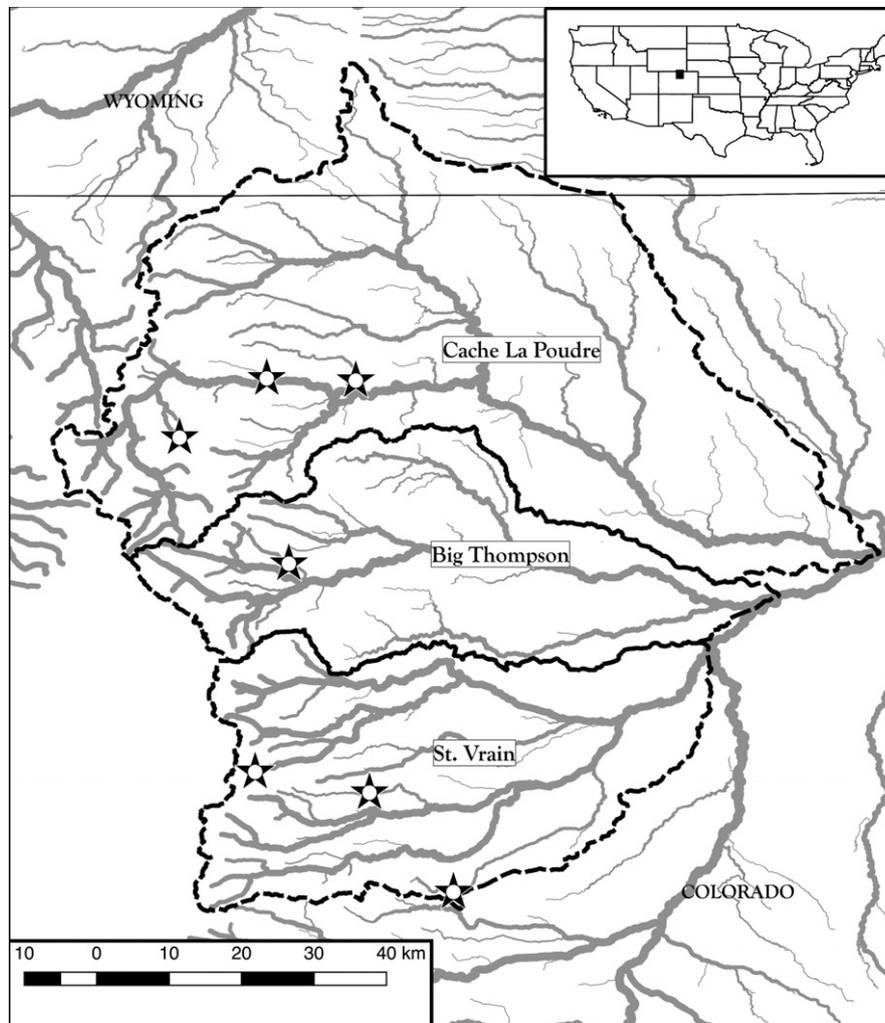


FIGURE 2 Map of study streams. Drainages are outlined by dashed lines, and streams are denoted by stars with white circles, with the size of the point corresponding to the shear stress value at that stream

timed snowmelt run-off in late spring and early summer is the highest flow event of the year (Poff & Ward, 1989). Due to the historic magnitude and timing of the 2013 northern Colorado floods, they are classified as extreme disturbance events, both in magnitude and in timing.

2.2 | Study design

Seven small, wadeable tributaries of the Cache la Poudre, Big Thompson and St. Vrain Rivers were sampled in June–July 2014 for physical characteristics, stream insect communities, quantitative basal resources, and stream insect and basal resource bulk stable isotopes (Figure 2). Stream insect communities at these streams were sampled previously in June–August 2011 (Harrington, Poff, & Kondratieff, 2016), and resampling of stream insect communities in 2014 occurred within 2 weeks of the original sampling date to control for naturally occurring seasonal shifts in stream insect community composition because of strong seasonality in Colorado mountain streams. Because many of the insects in these areas are uni-, bi- or

multivoltine (Poff et al., 2006) and tissue turnover rates of isotopes are slow such that isotope values reflect past diets (McCutchan, Lewis, Kendall, & McGrath, 2003; Ponsard et al., 2004), sampling within 9 months of the flood event still captures flood effects. Our study streams were selected to constitute a gradient of disturbance along latitude and elevation (see Table 1 for stream descriptions and Figure 2 for a map of sampling sites).

At each stream, a 125 m reach was delineated with sampling replicated every 25 m within the sample reach to capture heterogeneity in resource abundance, stream insect community composition and isotope signatures. Transects were sampled by moving from downstream to upstream to avoid disturbing the reach during sampling. In each 125-m stream reach, quantitative coarse particulate organic matter (CPOM) and epilithon samples, and canopy cover densiometer readings were taken every 25 m, for a total of five replicates per stream for quantitative and stable isotope analysis. Four replicate deuterium samples for stable isotope environmental water corrections were collected from the thalweg at the top of the sample reach.

2.3 | Physical habitat data collection

After basal resources and stream insects were collected along the sample reach during 2014 sampling, substrate, channel cross sections, discharge, reach slope and canopy cover were measured. Wetted, bankfull and putative flooded channel profiles were measured five times along the sample reach. Bed slope of the sample reach was also measured along multiple points using a laser rangefinder and a levelling rod. Substrate was measured using the random-walk method (Leopold, 1970), and the three axes of 100 particles were measured within the sample reach.

We estimated relative disturbance intensity during the September 2013 flood event at each stream using an indirect method, because no stream flow gauging data were available for our streams, which are smaller ungaged tributaries of the larger rivers shown in Figure 1. While there are many ways to estimate in-stream disturbance, we selected shear stress, or hydraulic stress, as the most appropriate estimate of disturbance for this study. Shear stress measures the horizontal forces on the streambed that can dislodge or erode material off the bed surface during high flows, even if the coarse bed sediment does not move. Horizontal forces are important when considering longitudinal transport of in-stream detritus and scouring of algae. Using a laser range finder, we reconstructed the flood depth and water surface slope at the stream during the peak flood in September 2013 by measuring the height of the visible flood debris line above the bed at different points along the longitudinal profile of the channel. Dimensionless shear stress (τ^*), hereafter referred to as shear stress, was calculated for each stream (Equation 1) as the ratio of erosive forces (hydraulic depth times the water surface slope of the sample reach) and the resistance forces (size of the coarse substrate fraction, measured as 84th percentile grain size in the pre-flood bed sediment, times the specific gravity of particles in water) (Bagnold, 1980).

$$\tau^* = \frac{\text{Depth} * \text{Bed slope}}{1.65 * D_{84}} \quad (1)$$

The greater the value of this metric, the more horizontal force was applied on the bed and the more likely bed particles were to move during the peak flow event. Shear stress is thus a relative indicator of bed instability that can be compared across streams.

2.4 | Stable isotope sample collection and analysis

We quantitatively sampled basal resources and stream insects for stable isotope analysis during June–July of 2014. Five CPOM samples were collected at the five transect points within the sample reach quantitatively across the full width of the stream, using a 0.25 × 1 m quadrat and a kicknet placed downstream. CPOM was dried in a drying oven at 60°C and then sorted into woody and non-woody components and weighed to calculate CPOM quantity (g/m²) prior to homogenisation for stable isotope analysis. Epilithon samples were collected from three rocks per replicate transect, scrubbing the rocks with a soft-bristled brush. A small subsample from the resulting

algal slurry was filtered for chlorophyll *a* analysis via acidification fluorometry on a TD-700 fluorometer (Turner Designs, Sunnyvale, CA, USA). All chlorophyll *a* filters were frozen at –20°C prior to analysis. The remainder of the slurry was decanted and dried in a drying oven at 60°C prior to homogenisation for stable isotope analysis. Epilithon quantity was measured in g/m². Rocks were photographed with an object of known size, and the area of each rock was then measured in ImageJ (Schneider, Rasband, & Eliceiri, 2012).

Stream insects were collected for stable isotopes throughout the sample reach using kicknet sampling (500- μ m mesh) after basal resource collection was complete. All common taxa were collected live in the field and stored in water for 24 hr to complete gut evacuation. We then identified stream insects to lowest practical taxonomic level under a dissecting microscope and dried them for stable isotope analysis at 50°C. Samples were frozen prior to drying in a –20°C freezer.

For community sampling, we performed a 5-min kick sample (500- μ m mesh) in representative habitat in the sample reach (Harrington et al., 2016). Time spent kicking in each habitat type was proportional to the abundance of that habitat in the study reach. Kick samples were stored in 100% ethanol prior to and after being cleaned and identified to the lowest practical taxonomic resolution. Samples were collected once at each stream during the 2014 sampling. We did not have pre- and postflood community samples at West Fork Sheep Creek, but had sampled a nearby creek, located 2 km away within the same small catchment and at the same elevation (East Fork Sheep Creek) in 2011, so we included data from East Fork Sheep Creek in the community analysis, in place of West Fork Sheep Creek.

All basal resource and stream insect stable isotope samples were analysed for carbon, nitrogen and deuterium stable isotope concentration at the Cornell University Stable Isotope Laboratory. The carbon and deuterium signatures of consumers yield information about resource origin, because terrestrial and aquatic resources differ in their signatures. Nitrogen stable isotope signatures are used to calculate trophic level, which is also important for understanding and accounting for potential enrichment in deuterium and carbon signatures with increasing trophic level (Post, 2002). C and N samples were analysed on a Thermo Delta V isotope ratio mass spectrometer (ThermoFisher Scientific, Waltham, MA) plumbed to a Carlo Erba NC2500 elemental analyser (ThermoFisher Scientific) via a ConFlo II open split interface (ThermoFisher Scientific), with standard deviations of 0.13‰ $\delta^{15}\text{N}$ and 0.06‰ $\delta^{13}\text{C}$. H samples were analysed on a Thermo Delta V isotope ratio mass spectrometer interfaced to a Gas Bench II (ThermoFisher Scientific), with a standard deviation of 2.53‰ $\delta^2\text{H}$. Prior to packing and weighing, all samples were homogenised either using a coffee grinder, mortar and pestle, or a Wiley mill (Thomas Scientific, NJ, USA), depending on the size and toughness of the sample. While our sampling technique for epilithon does not separate out autochthonous and allochthonous components of the epilithon (Collins et al., 2016), we hereafter refer to dietary reliance on epilithon as consumer autochthony, which is customary throughout the aquatic stable isotope literature (Jonsson & Stenroth, 2016).

TABLE 1 Stream basal resource characteristics for the seven streams sampled in this study, ordered by increasing shear stress values. Total precipitation, run-off and dimensionless shear stress are values from the 2013 flood event. The pre- and postchange in D_{50} is the difference in the median substrate size between before (2011) and after the flood event (2014). Values for basal resources represent means ± 1 standard error

Stream	Drainage	Dimensionless shear stress	Elevation (m)	Pre- and post-change in D_{50} (mm)	Chlorophyll a (mg/m^2)	% Canopy cover	Epilithon C:N	Epilithon (g/m^2)	CPOM C:N	CPOM (g/m^2)
W. Fk. Sheep	Poudre	0.065	3,206	1.5	18.94 \pm 5.24	12.08 \pm 3.63	10.39 \pm 0.93	47.45 \pm 29.48	20.66 \pm 8.68	2.86 \pm 1.24
Wigwam	St. Vrain	0.120	3,254	-22.5	6.17 \pm 2.89	57.40 \pm 13.24	8.71 \pm 1.38	92.86 \pm 58.27	22.48 \pm 10.09	12.58 \pm 11.37
Elkhorn	Poudre	0.158	2,000	11.5	1.39 \pm 0.16	51.61 \pm 10.36	8.47 \pm 1.68	14.84 \pm 6.85	37.27 \pm 8.96	3.47 \pm 0.93
Fourmile	St. Vrain	0.244	2,180	18.2	1.65 \pm 0.06	48.39 \pm 8.24	7.42 \pm 1.21	8.89 \pm 2.39	37.32 \pm 7.97	4.01 \pm 1.13
Coal	St. Vrain	0.312	2,019	-12.4	4.60 \pm 1.41	35.99 \pm 8.85	7.26 \pm 0.61	54.09 \pm 37.51	38.20 \pm 8.64	11.31 \pm 5.12
Sevennille	Poudre	0.679	2,220	-11	0.74 \pm 0.09	62.55 \pm 6.67	7.95 \pm 0.75	6.90 \pm 0.71	38.05 \pm 3.22	32.03 \pm 8.80
Black Canyon	Big Thompson	1.809	2,435	46.5	1.66 \pm 0.42	22.86 \pm 4.02	7.94 \pm 0.08	8.12 \pm 1.25	55.01 \pm 3.03	28.12 \pm 11.71

2.5 | Stable isotope data analysis

Following methods detailed in Collins et al. (2016) and Solomon et al. (2009), we corrected consumer deuterium values for dietary water, using Equation 2 and published values for ω from Solomon et al. (2009).

$$\delta^2H_{\text{corrected}} = \frac{\delta^2H_{\text{uncorrected}} - \omega\delta^2H_{\text{water}}}{1 - \omega} \quad (2)$$

To account for predator consumption of dietary water via consumers, we applied Equation 3 to calculate ω for each taxa.

$$\omega_{\text{compounded}} = 1 - (1 - \omega)^\tau \quad (3)$$

We calculated trophic position using the equation from Post (2002) (Equation 4), using the mean $\delta^{15}\text{N}$ of grazing or collector mayflies or blackflies as a primary consumer. We then applied the per-trophic-level stable isotope fractionation of $3.4\text{‰} \pm 1.0\text{‰}$ (Post, 2002).

$$\tau = \frac{\delta^{15}\text{N}_{\text{Sample}} - \delta^{15}\text{N}_{\text{Grazer}}}{\Delta_N + 1} \quad (4)$$

We used trophic enrichment factors from Post (2002) for carbon ($0.4\text{‰} \pm 1.3\text{‰}$) and nitrogen ($3.4\text{‰} \pm 1.0\text{‰}$). Because previous studies have not found fractionation of deuterium across trophic levels (Solomon et al., 2009), we did not include deuterium fractionation in our model.

We used a three-source mixing model in the “SIAR” package (Parnell and Jackson, 2013) in R v. 3.3.1 (R Core Team, 2016) to determine the proportion of the diet originating from epilithon compared to coarse particulate matter for each taxon at each stream, using the “siarmcmcdirichletv4” function. This modelling method uses Markov chain Monte Carlo simulations to determine the dietary proportion originating from each source. We set the MCMC to 500,000 iterations and a 50,000 burn-in to allow the model to reach equilibrium.

2.6 | Data analysis

All data analyses were carried out in R v. 3.3.1 (R Core Team, 2016). Mean proportions of the epilithon in the diet for each taxon at each stream from the mixing model simulated output were used as response variables. Only taxa that were found at three or more streams were used for among-stream comparisons. Because many variables can potentially influence consumer allochthony and autochthony, we assessed the relative influence of food quality (C:N ratios) and quantity, taxonomic identity and disturbance intensity on consumer autochthony. Average stream-level information, including per cent canopy cover, C:N content and quantities of epilithon and nonwoody CPOM, elevation and dimensionless shear stress, as well as taxonomic information, including functional feeding group and taxonomic identity, were all used as predictor variables.

We used partial least-squares (PLS) regression using the pls package (Mevik & Wehrens, 2007) in R to determine which variables best predicted the mean dietary proportion originating from epilithon. In

PLS regression, the predictors and response variables are stored as separate matrices and then projected into a new multidimensional space. The PLS model then finds the latent variables (PLS components) in the predictor space that best explain the variance in the response space. PLS regression is robust to both a large number of predictor variables relative to sample size and to collinearity in predictor variables (Carrascal, Galván, & Gordo, 2009) and has been used in similar studies looking at the influence of numerous predictors on consumer autochthony (Jonsson, Polvi, Sponseller, & Stenroth, 2018; Stenroth, Polvi, Fältström, & Jonsson, 2015). Prior to carrying out PLS, the data were normalised using Z scores. A conservative and standard threshold of 1 was set for the variable importance in the projection significance cut-off (Chong & Jun, 2005; Farrés, Platikanov, Tsakovski, & Tauler, 2015).

Linear regression of the change in proportional abundance of functional feeding groups was performed to look at compositional responses of functional feeding groups to the flood disturbance. Finally, we performed PLS regression of epilithon C:N content and quantity, and CPOM C:N content and quantity against shear stress, canopy cover, chlorophyll *a* and elevation to determine the relative influences of different environmental variables in driving basal resource quantity and quality. Because elevation may be an important driver of basal resource quantity and quality, PLS regression allowed us to distinguish between disturbance and elevation effects. PLS regression has been recently adopted by ecologists from the field of chemistry, where it is used to analyse chemical spectra (Carrascal et al., 2009; Stenroth et al., 2015). In studies such as this one, with many correlated predictors and small sample sizes, PLS is a robust method for disentangling the effects of multiple associations with a selected response variable.

3 | RESULTS

3.1 | Disturbance gradient

Disturbance intensity was not correlated with elevation ($r_r = -0.238$, $p = 0.562$). We observed debris wrack lines above the bankfull channel at all seven streams when sampling, indicating overbank flow had occurred at all of our study streams (Table 1). The height of the wrack lines above the bankfull channel varied dramatically among streams and was reflected in the range of dimensionless shear stress values (Table 1, min = 0.065, max = 1.809).

3.2 | Epilithon quantity and C:N content

Epilithon quantity (dry mass, measured in g/m^2) was negatively associated with shear stress (Figures 3 and 4) and positively associated with elevation and chlorophyll *a* (Figure 3). Surprisingly, canopy cover, which ranged from a mean of 12%–63%, was not significantly associated with epilithon quantity (Figure 3). Epilithon C:N was positively associated with elevation and chlorophyll *a* (Figure 3). Shear stress and canopy cover were not significantly associated with epilithon C:N content (Figures 3 and 4).

3.3 | CPOM quantity and C:N content

Nonwoody CPOM quantity, measured as dry mass, was positively associated with shear stress (Figures 3 and 4). CPOM C:N was also positively associated with shear stress and negatively associated with elevation (Figures 3 and 4). Canopy cover was not significantly associated with either CPOM quantity or C:N content (Figure 3). We show only the results from the first component because the identity of important variables in the projection did not change from the first to second component, and in all four PLS regressions, the first component explained a large percentage of the variation: 74.8% for epilithon C:N, 97.9% for CPOM C:N, 46.4% for epilithon quantity and 77.9% for CPOM quantity.

3.4 | Functional feeding group community composition

Two study streams lost a functional feeding group following the 2013 flooding. No shredders were found at Black Canyon in 2014, the stream with the highest shear stress value. Shredders had comprised 6% of the stream insect community there by numbers of individuals in the 2011 sampling, consisting of the nemourid stonefly *Zapada* sp. and the lepidostomatid caddisfly *Lepidostoma* sp., which were not found at the stream during 2014 sampling. At Coal Creek, a low-elevation stream in the St. Vrain drainage, herbivores, which comprised 11% of the pre-flood community, were absent in our 2014 sampling. The ephemereid mayfly *Drunella grandis*, the heptageniid mayfly *Ecdyonurus criddlei* and the glossosomatid caddisfly *Agapetus* sp., all members of the herbivore functional feeding group, were found at the stream in 2011 sampling, but not 2014. Herbivores significantly declined compared to pre-flood abundances in terms of both raw and proportional abundance across the disturbance gradient (*raw*: $b = -641.22$, $t_{(6)} = -5.183$, $p_t = 0.004$, $F_{(1,5)} = 26.87$, $p_F = 0.004$, $R^2 = 0.843$; *proportional*: $b = -0.114$, $t_{(6)} = -2.400$, $p_t = 0.062$, $F_{(1,5)} = 5.758$, $p_F = 0.062$, $R^2 = 0.535$; Figure 5).

Predators also showed a significant decline in both raw and proportional abundance across all streams following the flooding compared to 2011 sampling, but this decline was not significantly related with shear stress (*raw*: $t_{(6)} = -2.3847$, $p_t = 0.054$; *proportional*: $t_{(6)} = -5.9589$, $p_t = 0.001$; Figure 5). No other functional feeding groups showed a significant increase or decrease in raw or proportional abundance from pre- to postflood sampling or along the disturbance gradient in 2014.

3.5 | Autochthonous contribution to consumer diets

Coarse particulate organic matter and epilithon differentiated adequately in their deuterium, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures to satisfy the assumptions of mixing models (Supporting Information Figures S1 and S2). In total, we analysed 21 Ephemeroptera, Plecoptera, Trichoptera and Diptera consumer taxa representing 12 families that

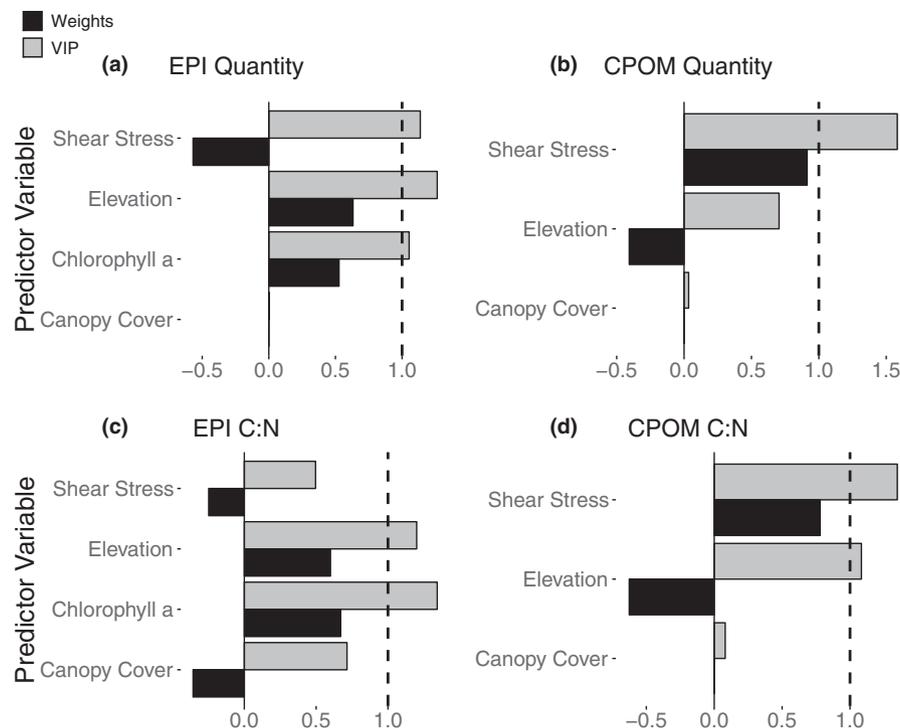


FIGURE 3 Partial least-squares regression results for (a) epilithon and (b) CPOM quantity, C:N content of (c) epilithon and (d) CPOM. Variables considered significant in the model are denoted by having a variable importance in the projection (VIP) score of >1 (grey bars). Loading weights for the first component are given by the black bars

were found at minimum of three streams each (Supporting Information Table S1).

The proportion of the diet derived from autochthonous sources (epilithon) was higher at less disturbed streams. However, taxa exhibited high feeding flexibility both within and across streams. Collector-gatherers, herbivores and predators all showed declines in consumer autochthony with increasing shear stress. Shredders showed no significant relationship with shear stress. Collector-filterer autochthony also did not have a significant relationship with shear stress (Figures 6 and 7).

Shear stress, CPOM quantity and CPOM C:N ratios had a significant negative relationship with consumer autochthony (Figure 7). In contrast, epilithon quantity and C:N ratios, elevation and chlorophyll *a* all had a significant positive relationship with consumer autochthony. Taxonomic identity, functional feeding group and canopy cover were not significantly associated with consumer autochthony. Component 1 explained 74.28% of the variance in proportion of diet derived from the autochthonous sources. Component 2 explained 6.16% of the variance in proportion of the diet derived from autochthonous sources. The significance of predictor variables did not change between Components 1 and 2, and therefore, we did not include results from Component 2 in Figure 7 to simplify interpretation of that figure.

All taxa showed variability in the proportion of their diet derived from autochthonous compared to allochthonous sources across streams (Supporting Information Table S1). Generally, mean consumer autochthony ranged from around 0.25 to 0.5 proportionally of

the diet. Certain taxa, such as the rhyacophilid caddisfly *Rhyacophila angelita* (mean of dietary proportion derived from the epilithon of 0.39–0.48 for their prey across streams), the simuliid blackfly *Simulium* sp. (0.24–0.31), the perlotid stonefly *Megarcys signata* (0.48–0.53) and nemourid stonefly *Zapada* sp. (0.51–0.53), varied little in their resource use across streams. In contrast, the baetid mayfly *Baetis bicaudatis* (0.22–0.52), the perlotid stonefly *Kogotus modestus* (0.28–0.61), and the ephemereid mayflies *Drunella doddsi* (0.26–0.55) and *D. grandis* (0.25–0.42) exhibited more variability in their resource use across streams. Full stable isotope results and biplots are available in Supporting Information Figures S1 and S2.

4 | DISCUSSION

Overall, disturbance-related resource quantity shifts, rather than resource quality (i.e., C:N ratios), predicted consumer resource use. The increase in CPOM along the disturbance gradient occurred with a higher consumer reliance on allochthonous food sources. Due to the complexity of our results, we discuss our findings sequentially in the context of our predictions.

First, we predicted that flooding would lead to streambed instability, decreasing the abundance of autochthonous food sources at more highly disturbed streams. Epilithon quantity was positively associated with higher concentrations of chlorophyll *a*, reduced shear stress and higher elevations. The negative effect of disturbance on epilithon biomass was surprising, given that our sampling occurred

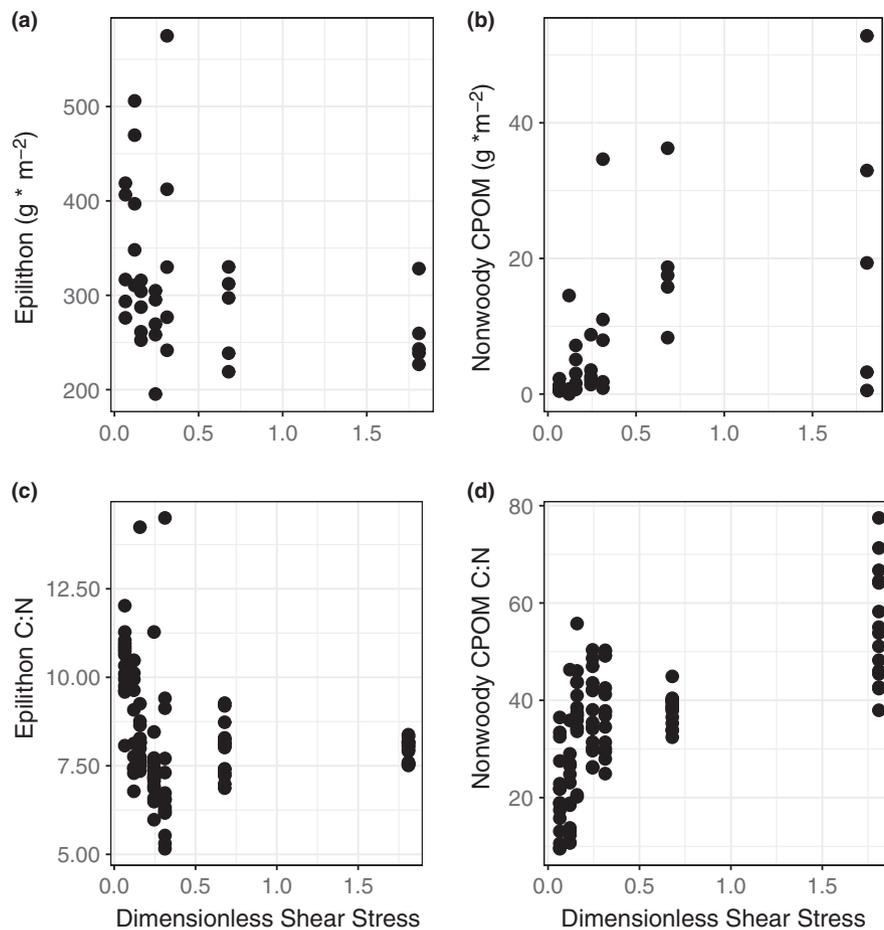


FIGURE 4 Replicate measures of quantity and C:N content of CPOM (b, d) and epilithon (a, c) across streams plotted against shear stress

9 months after the flooding event and algal turnover rates in lotic environments are fast (Peterson, 1996). We ascribe this relationship to elevated and chronic instability of the stream bed following massive flood events (Poff et al., 2018; Segura, McCutchan, Lewis, & Pitlick, 2011), which would have resulted in more scouring during intervening snowmelt spates and other flooding events. Our related work at these streams also found that bed movement during the 2013 floods was lower at high elevations, because of underlying geomorphic stability, and was significantly and positively related to shear stress (Poff et al., 2018). Therefore, our higher elevation streams seem to experience less chronic bed instability, resulting in higher epilithon standing stocks. We also observed large shifts in sediment size distribution following the floods (Table 1), leaving highly disturbed streambeds presumably prone to movement during annual late spring snowmelt run-off in June 2014. Our sampling could have seen this legacy effect of enhanced bed mobility (Poff et al., 2018), which would reduce algal standing crops (Peterson, 1996; Uehlinger et al., 1996), even months after the flood event.

While light can be an important control on consumer autochthony in streams (Collins et al., 2016), we did not find canopy cover to be a significant predictor of basal resource quality and quantity nor of consumer autochthony in the postdisturbance streams. However, the light availability in our streams was high, with

canopy cover values of 12%–63% across streams (Table 1), while Collins et al. (2016) studied streams of 5%–95% canopy cover. Therefore, canopy cover may not be sufficiently dense along our disturbance gradient to cause light limitation at our streams. While higher light availability results in higher algal availability, and subsequently, higher reliance on autochthonous food sources (Collins et al., 2016; Davies-Colley & Quinn, 1998), disturbance can alter this relationship by decreasing reliance on autochthonous materials in favour of reliance on accumulated detritus introduced during the flood from the riparian zone.

Second, we predicted that flooding would amplify detrital inputs to our study reaches, with a concurrent increase in allochthonous resource use (Winterbourn, 1976). Although in-stream detrital standing stocks are often exported during high-intensity disturbances (e.g., Cover, de la Fuente, & Resh, 2010) and may recover slowly, the influence of in-stream and riparian disturbances on detrital resources in streams may be context-dependent (Rathburn et al., 2017). First, higher flood magnitudes would extend water levels further out of the stream channel, entraining more riparian detritus into the stream channel as floodwaters recede. Additionally, tree phenology may play a large role in determining the magnitude and direction of disturbance effects on detrital resource availability. Because the September 2013 flooding occurred before deciduous leaf-fall, leaf-fall would

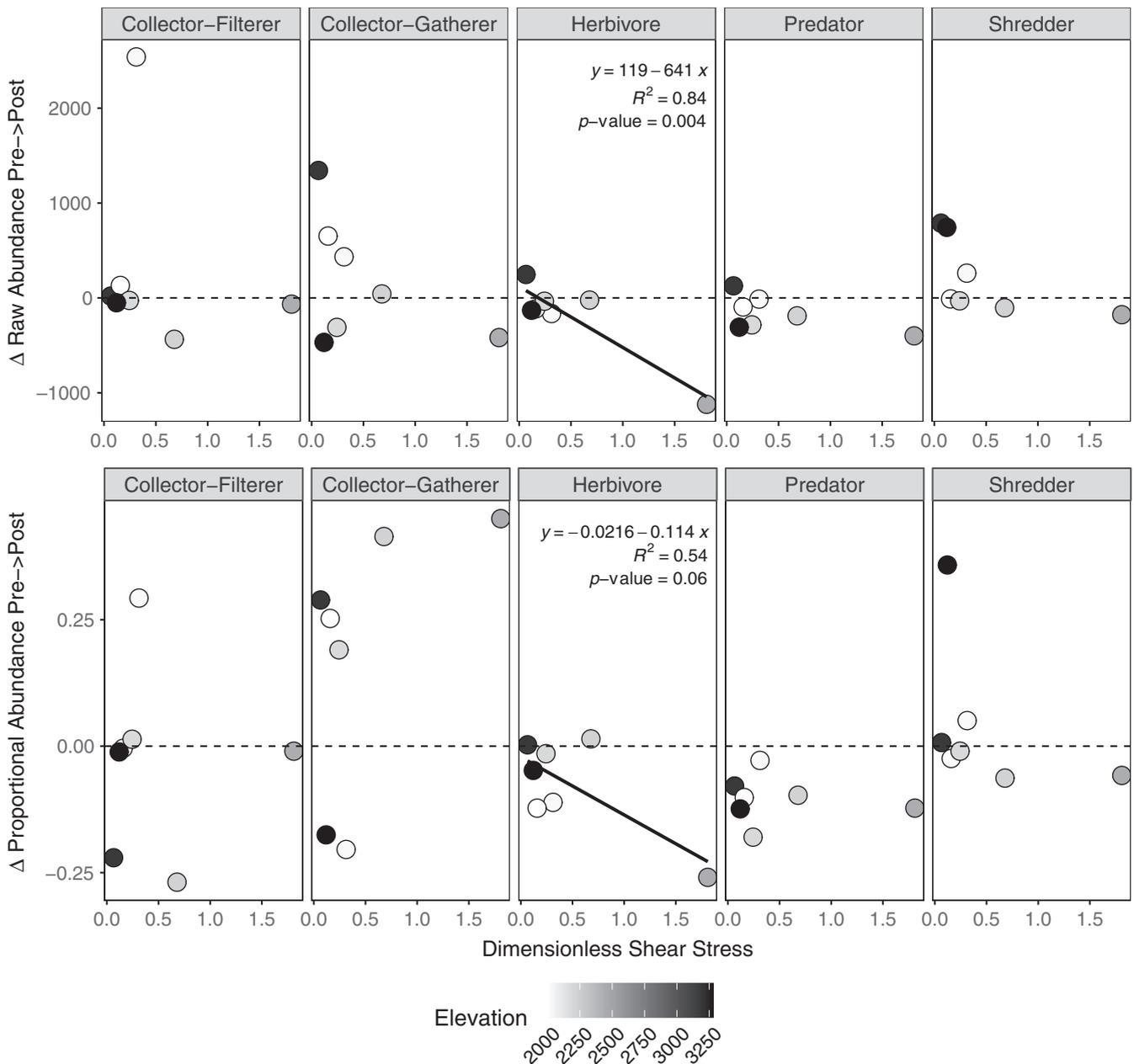


FIGURE 5 Changes in raw and proportional abundance from 2011 to 2014 among functional feeding groups. The dashed line represents the no change line. Only significant regressions are shown by solid lines

add detritus to the stream after water levels had declined. Thus, this particular disturbance may have largely amplified detrital inputs to stream food webs, rather than flushing in-stream conditioned detritus downstream. We propose that, in this case, heavy rains and runoff caused a large pulse of streamside terrestrial detritus into the stream and that detritus load persisted into the next year's sampling. Indeed, in a neighbouring drainage to our three study drainages, the September 2013 floods introduced large amounts of wood and litter into tributaries (Rathburn et al., 2017). Thus, the timing of an extreme event relative to terrestrial litter input determines whether benthic organic matter accumulates or diminishes and whether CPOM will be ample or limiting for consumers in the following year.

Third, we predicted that resource quality would correspond with assimilation of food resources, but we did not find that invertebrate diets tracked higher-quality resources. The positive relationship between shear stress and CPOM C:N indicates low-quality detrital resources (Marcarelli, Baxter, Mineau, & Hall, 2011) were associated with higher disturbance intensity. CPOM C:N was also positively correlated with elevation, which may reflect the higher relative abundance of coniferous compared to deciduous trees in the riparian zones of our high elevation streams. Conifer needles have high C:N ratios compared to deciduous leaves (Sanborn, 2001) and are not a high-quality resource for stream consumers due to their slow breakdown rates (Webster & Benfield, 1986), but they may be more

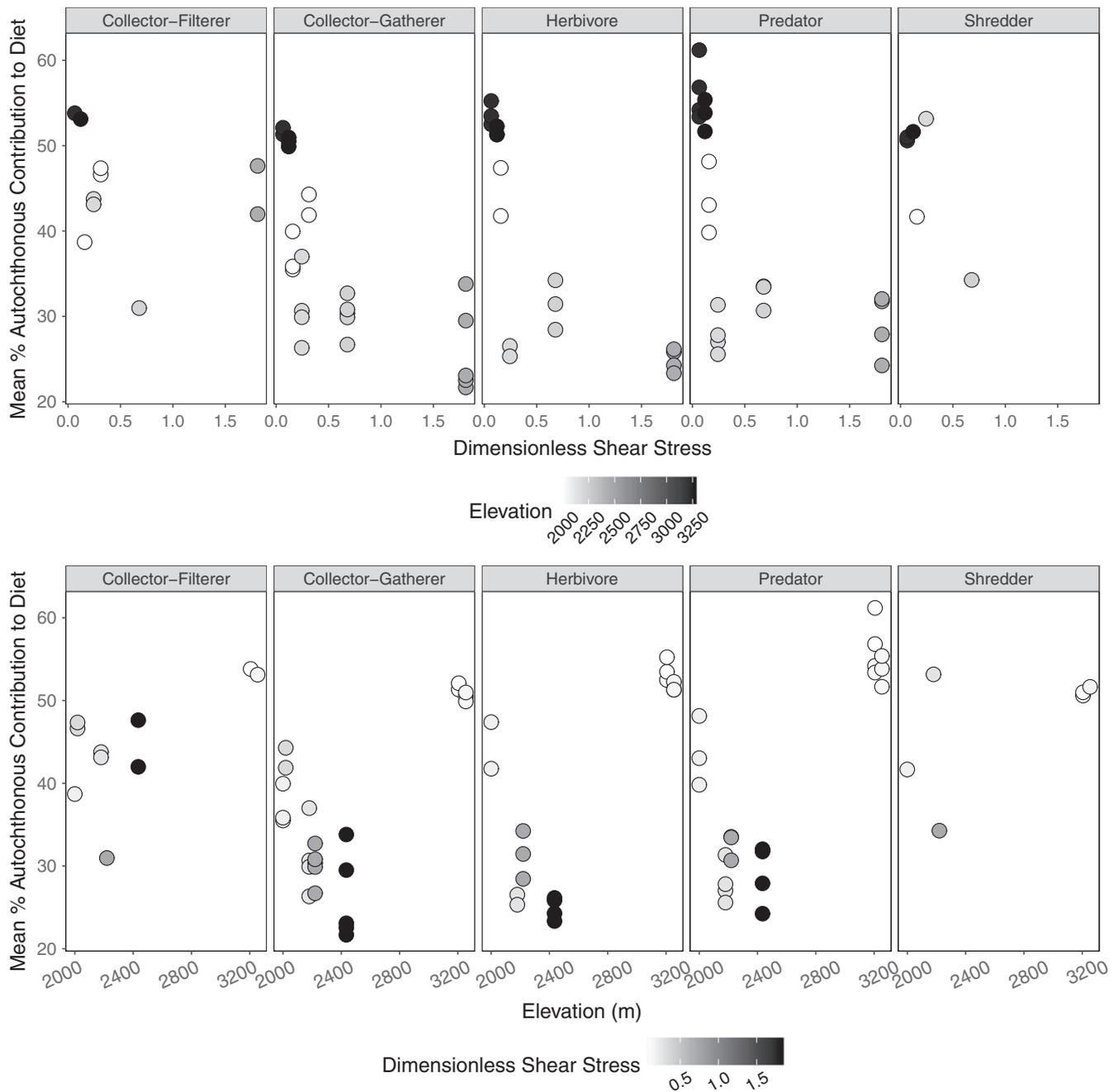


FIGURE 6 Mean autochthonous contribution to the diet for each functional feeding group across streams. Shaded circles are individual taxa. Points aligned on the same vertical line occur at the same stream

consistently available as a food resource than other types of higher-quality detritus (Sakai, Fukushima, Naito, Natuhara, & Kato, 2016). Elevation and chlorophyll *a* were significantly and positively associated with epilithon C:N, while shear stress was not. A previous review found preferential feeding by aquatic invertebrates on higher-quality foods, but while invertebrates use terrestrial resources in lower proportions to their availability, the amount of reliance on allochthonous materials still increases with availability (Marcarelli et al., 2011).

Fourth, we predicted that members of different functional feeding groups would not experience differential mortality in the 2013

flood event, but would exhibit differential resource use. We found a consistent decline of herbivores in terms of both raw and proportional abundance along the disturbance gradient. Grazers rely largely on algae and biofilms (Wallace & Webster, 1996), and the decreased availability of algal resources at streams that experienced higher intensity flooding may have resulted in food limitation and subsequent mortality. We also found an overall decline in predator raw and proportional abundance following the 2013 flood event, but with no significant trend along the disturbance gradient. Generally, functional feeding groups showed similar responses in their autochthony across the disturbance gradient, although a lack of

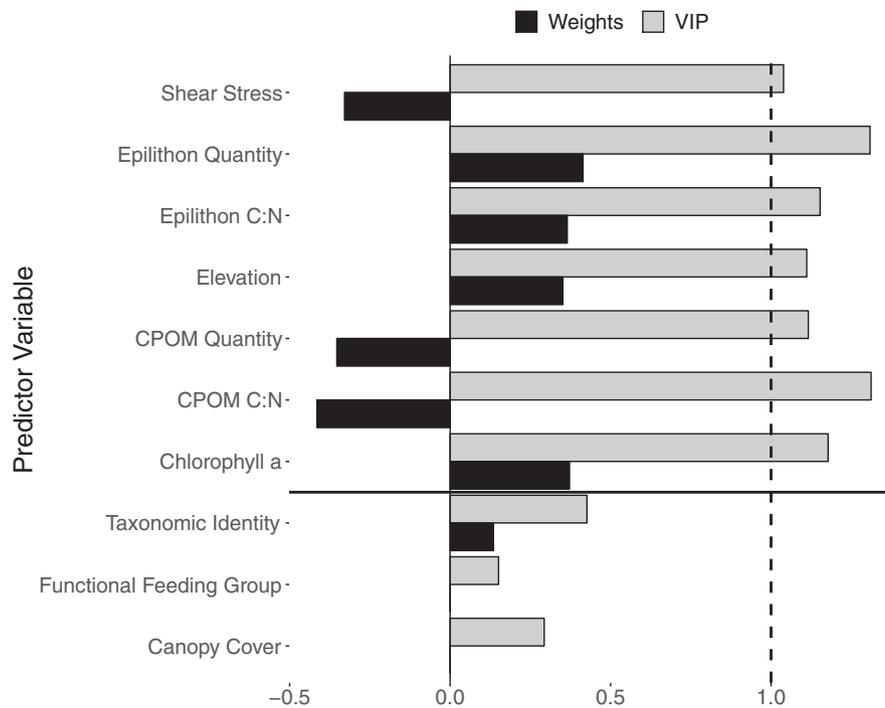


FIGURE 7 Loading weights and variable importance in the projection scores for each variable considered in partial least-squares regression with consumer autochthony as the response variable. Dashed line indicates 1.0—VIP scores above this value are considered significant in the model. All variables above the solid line are significant, and all variables below the solid line are insignificant, based on their VIP scores. Loading weights for the first component are given by the black bars

large-bodied, immobile shredders at the stream that experienced the highest intensity flooding (see Poff et al., 2018) did not allow us fully to assess shredder autochthony in response to disturbance. Shredders may be the most likely to be constrained in their resource use and rely heavily on detrital resources. Therefore, shredders might not shift their reliance on allochthonous resources, even as in-stream algal production increases (Collins et al., 2016). Accordingly, we expect that shredders would exhibit reduced consumer autochthony at highly disturbed streams, where higher postflood detrital loading occurred, but could not fully evaluate this prediction due to the lack of shredders at our high disturbance intensity streams.

Finally, we predicted that taxonomic identity would also be associated with consumer resource use, with some specialist taxa being more restricted in their feeding, and generalist taxa being more plastic. However, consumer autochthony was not explained by taxonomic identity or functional feeding group membership. Rather, environmental characteristics, such as resource quantity and quality and the shear stress experienced during the 2013 event, best explained the relative importance of autochthonous-derived resources. Some taxa, such as the caddisfly *R. angelita*, the blackfly *Simulium* sp., and the stoneflies *M. signata* and *Zapada* sp., do appear to be more tightly constrained than others in their resource use, suggesting some degree of specialisation (Supporting Information Table S1). Because many functional feeding groups are distinguished by their feeding morphologies, rather than actual reliance on specific resources, this result corroborates the idea that feeding morphology and food acquisition traits do not necessarily determine consumer

autochthony, but rather determine the size classes of food that consumers use (Cummins, 1973). Other studies in this system have similarly found a wide variation in autochthonous resource use along an elevation gradient within functional feeding groups (McCutchan & Lewis, 2002). From a food-web perspective, our results robustly demonstrate a shift in consumer resource use along a gradient of disturbance intensity, irrespective of taxonomic identity or functional feeding group membership. Our sampling may have missed trophic specialists with more constrained diets if they were locally extirpated after the disturbance due to a shift in available resources. Therefore, our findings are similar to those in studies that have examined the impact of fires on stream food webs and found that generalists were favoured following disturbance events (Mihuc & Minshall, 1995) and to studies finding that streams with unstable beds are characterised by generalist fauna (Winterbourn, 1997; Winterbourn, Rounick, & Cowie, 1981).

Elevation and snowmelt flooding were potentially confounding variables in our study design, but we still found a signal of disturbance effects on consumer resource use. Our related work at a larger number of streams, including all of the streams used in this study as well as seven additional streams, did find a significant negative correlation between elevation and 2013 flood bed mobility, which also correlated with shear stress (Poff et al., 2018). Thus, higher algal biomass associated with high elevations may reflect reduced disturbance legacy effects at those high elevation streams. While we found that elevation was a significant predictor of consumer autochthony, CPOM and epilithon C:N, and epilithon quantity,

elevation did not significantly predict CPOM quantity, which was a strongly significant negative predictor of consumer autochthony. Therefore, while elevation may have influenced consumer resource relationships, the strongest relationship we observed driving consumer resource use in our system was a flood-related increase in CPOM quantity, leading to higher reliance on CPOM by stream consumers at streams that experienced higher shear stress during the 2013 event.

Annual snowmelt run-off occurred in our streams during the spring of 2014, but we still detected a strong signal from the 2013 floods. The run-off levels in 2014 were above the median long-term snowmelt run-off volumes (NRCS National Water and Climate Center Basin Reports, 2014), but were small compared to the extreme run-off volumes in September 2013, which were estimated to be 1 in 50 to 1 in 500 year events (Gochis et al., 2014; Figure 1). Moreover, snowmelt flooding affected our streams relatively equally based on records of snowpack in the contributing catchments (NRCS National Water and Climate Center Basin Reports, 2014). Thus, our streams experienced a range of extreme flooding intensity during the September 2013 flood event followed by a similar level of moderate snowmelt run-off, strongly suggesting that the differences in consumer autochthony that we see across streams are associated with responses to the 2013 floods.

Although we did find a significant disturbance effect on consumer autochthony, disturbance intensity did not swamp out other factors, such as elevation, that affect consumer resource use. Over the entire disturbance gradient, variation in the per cent contribution of autochthonous resources in consumer diets showed a relatively small range of 22%–61% (Supporting Information Table S1). We would expect a high-intensity, unusually timed disturbance to have a large impact on food webs, but our results suggest that consumer plasticity may compensate for disturbance effects.

Studying the effects of such unpredictable extreme events can mostly occur only on an opportunistic basis. However, better understanding the natural impacts of disturbance events on ecosystem subsidy relationships is important for anticipating how both food-web structure and the transfer of energy and nutrients across and within ecosystems may change. In the future, extreme events are projected to increase in frequency and the loss of snowpack in western regions is predicted to result in more unpredictable rain-driven hydrologies in montane streams (Fyfe et al., 2017). Our finding that the timing of the disturbance likely played a major role in the system response suggests that not all extreme hydrologic events will manifest similarly in terms of basal resource and consumer responses. Developing a more general understanding of the ecological effects of extreme events will require a better understanding of underlying mechanisms, including how individual consumer species are affected by disturbance and interact with resources to drive emergent community-level properties.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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