

**Flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs**

Andre R. Siebers<sup>1</sup>, Amael Paillex<sup>1</sup>, Christopher T. Robinson<sup>1,2</sup>

<sup>1</sup>Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Sciences, Überlandstrasse 133, 8600 Dübendorf, Switzerland

<sup>2</sup>Institute of Integrative Biology, ETH-Zürich, 8092 Zürich, Switzerland

**Corresponding author:** Andre R. Siebers, Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Sciences, Überlandstrasse 133, 8600 Dübendorf, Switzerland. E-mail: [andre.siebers@eawag.ch](mailto:andre.siebers@eawag.ch)

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### Abstract

Alpine streams can exhibit naturally high levels of flow intermittency. However, how flow intermittency in alpine streams affects ecosystem functions such as food web trophic structure is virtually unknown. Here, we characterized the trophic diversity of aquatic food webs in 28 headwater streams of the Val Roseg, a glacierized alpine catchment. We compared stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) trophic indices to high temporal resolution data on flow intermittency. Overall trophic diversity, food chain length, and diversity of basal resource use did not differ to a large extent across streams. In contrast, gradient and mixing model analysis indicated that primary consumers assimilated proportionally more periphyton and less allochthonous organic matter in more intermittent streams. Higher coarse particulate organic matter (CPOM) C:N ratios were an additional driver of changes in macroinvertebrate diets. These results indicate that the trophic base of stream food webs shifts away from terrestrial organic matter to autochthonous organic matter as flow intermittency increases, most likely due to reduced CPOM conditioning in dry streams. This study highlights the significant, yet gradual shifts in ecosystem function that occur as streamflow becomes more intermittent in alpine streams. As alpine streams become more intermittent, identifying which functional changes occur via gradual as opposed to threshold responses is likely to be vitally important to their management and conservation.

### Keywords

Macroinvertebrates, stable isotopes, organic matter, allochthonous, glacier, high altitude ecosystem

## Introduction

Intermittent rivers and ephemeral streams (IRES) experience recurrent periods without surface flow (Datry et al. 2017). These periodic drying events regulate the structure and diversity of aquatic communities, alter cycles of organic matter and nutrients, and govern the connections between freshwater and terrestrial ecosystems (Larned et al. 2010, Datry et al. 2014, Leigh et al. 2016). IRES likely make up at least 50% of the world's waterways (Datry et al. 2014), and flow intermittency is further increasing in extent and duration in response to changes in climate and land use (Leigh et al. 2016). Despite a continually growing body of research on IRES (Datry et al. 2016), substantial knowledge gaps of flow intermittency-ecosystem function relationships still exist (Leigh et al. 2016, Stubbington et al. 2018). In particular, little is known regarding the ecology of intermittent alpine streams, which can experience up to 90% intermittency in fluvial networks (Robinson et al. 2016). Alpine catchments are expected to experience a significant change in flow intermittency in the future, as increased temperatures and temporal shifts in precipitation (Horton et al. 2006, IPCC 2014) influence seasonal patterns of glacial melt, snow melt, and groundwater contributions to streams (Brown et al. 2003, Malard et al. 2005, Robinson et al. 2016). These changes in flow intermittency will substantially influence ecosystem properties and processes (Milner et al. 2009, Slemmons et al. 2013, Cauvy-Fraunié et al. 2015). A comprehensive understanding of how flow intermittency structures and maintains alpine fluvial ecosystems is thus critical to the conservation of biodiversity and ecosystem function in alpine, as well as other, catchments.

Food webs characterize the energy flow through communities, thus integrating both biodiversity and ecosystem functioning (Thompson et al. 2012). Flow reduction results in habitat contraction in rivers and streams, which in turn results in smaller and less complex food webs due to restrictions on body size, dispersal, productivity, and interaction strengths (Rolls et al. 2012). An essential component of food webs is trophic diversity, reflecting the range of dietary niches occupied within a web (Bearhop et al. 2003). In IRES, trophic diversity is strongly affected by drying through the exclusion of large, mobile, and obligate aquatic predators (i.e., fish; Sabo et al. 2010, McHugh et al. 2015) that generally occupy the highest trophic levels in freshwater ecosystems (Post 2002a, Takimoto and Post, 2013). IRES trophic diversity is thus hypothesized to be consistently limited in vertical dimensions (i.e., food chain length) by the lack of consumers able to fill higher-order trophic niches (Sabo et al. 2010, McHugh et al. 2015).

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Experimental studies also have shown that the overall diversity of basal resource use within freshwater food webs is largely unaffected by flow intermittency, sometimes despite large changes in biomass flux and consumer mortality (Ledger et al. 2013, Boersma et al. 2014, Vander Vorste et al. 2016). Consequently, trophic diversity in IRES might not vary greatly across gradients of flow intermittency or hydrological isolation (McIntosh et al. 2017), somewhat contrary to the general theory that trophic diversity, particularly food chain length, should scale along gradients of ecosystem size and disturbance (Post 2002a). However, these results may reflect the large proportion of studies investigating trophic diversity or food-web size relationships that focused on reaches containing fish (Takimoto and Post 2013). Fish are strongly limited in body size and trophic position by the size of aquatic habitat (McIntosh et al. 2018), and, being largely intolerant to drying events, may actively avoid reaches that dry even briefly (McHugh et al. 2015). In contrast, the macroinvertebrate fauna of IRES have many adaptations that confer resistance or resilience to drying events (Bogan et al. 2017). An increase in predatory semi-aquatic or terrestrial macroinvertebrate taxa also is common within drying channels, possibly maintaining overall trophic diversity despite the loss of obligate aquatic taxa (McIntosh et al. 2017).

Consequently, while aquatic habitat size may be the most important determinant of overall trophic diversity in ecosystems with fish (Takimoto and Post 2013), macroinvertebrate communities may respond to ecosystem “size” or disturbance at a different scale, e.g., the frequency and duration of drying events. For example, McHugh et al. (2015) found that while food chain length was lower in fishless reaches overall, macroinvertebrate-dominated food chains contributed to an overall relationship between habitat size and trophic diversity in intermittent streams. Further, Hette-Tronquart et al. (2015) showed that much of the difference in food chain length between streams with differing variability in water temperature was due to the trophic position of filter feeders and shredders. Finally, in their meta-analysis of determinants of food chain length, Takimoto and Post (2013) found positive effects of ecosystem size on trophic diversity in the macroinvertebrate-dominated pitcher plant ecosystems studied by Baiser et al. (2011). These studies thus show a need for further work to identify the different constraints on trophic diversity that might occur in IRES as opposed to perennial systems, particularly in macroinvertebrate-dominated ecosystems.

In contrast with overall trophic diversity, the proportional contribution of different food sources to consumers in IRES is often highly spatially and temporally variable. This functional redundancy through high feeding variability may be a mechanism by which IRES food webs resist high environmental variability (Leigh et al.

2010, Schriever and Lytle 2016). Omnivory is thus common in IRES food webs, as are high proportions of generalist grazing and gatherer/collector taxa (Sánchez-Carmona et al. 2012, Blanchette et al. 2013). Consequently, while it is predicted that IRES should generally shift their trophic base from allochthonous to autochthonous sources as they dry (McIntosh et al. 2017), evidence for shifts in organic matter sources supporting IRES food webs as they become more intermittent have been largely equivocal. Both algae (Bunn et al. 2003, Dekar et al. 2009, Holgerson et al. 2016, Pettit et al. 2016) and terrestrial detritus (Reid et al. 2008, Leigh et al. 2010, Hunt et al. 2012) have been identified as key sources of the organic matter assimilated by metazoan consumers across intermittent and ephemeral freshwater habitats. Thus, the mechanisms underlying differences in the trophic base of IRES food webs might largely be accredited to differences in additional, regional ecological factors (e.g., riparian vegetation quality) rather than differences in flow intermittency alone (McIntosh et al. 2017). Alpine streams occur along a number of steep environmental gradients that may influence trophic structure in aquatic food webs, such as water temperature, channel stability, and organic matter quality (Brown et al. 2003, Uehlinger et al. 2009, Hotaling et al. 2017). Disentangling the effects of such strong environmental gradients from those of flow intermittency is thus crucial in understanding which aspects of trophic diversity and food-web structure are most affected by changes in the flow regime.

Collection of high-resolution data on flow intermittency is often time and labor intensive (Stubbington et al. 2018). Further, gauging stations are most often placed on large, perennial channels, rather than the extensive upper network of low-order streams that are more likely to dry (Meyer et al. 2007, Snelder et al. 2013). Thus, our understanding of the effects of flow intermittency on ecosystem function has frequently been limited to comparisons of perennial and intermittent reaches, rather than along a gradient of flow intermittency (Leigh et al. 2016). In this regard, ecosystem responses to flow intermittency might follow a ramp, threshold, or stepped pattern (Boulton 2003, Lake 2003), which comparisons of perennial and intermittent reaches alone might not identify. Aquatic communities also are structured as a response to antecedent conditions (Sponseller et al. 2010), and may represent variability to antecedent flow conditions rather than conditions at the time of sampling. In this context, IRES exhibit wide variation in the frequency, timing, and duration of flow intermittency (Costigan et al. 2017). Thus, characterizing the fine-scale spatial and temporal patterns of flow cessation could provide important insights into mechanisms of food-web variation in relation to flow

intermittency gradients (Sánchez-Montoya et al. 2018), particularly when flow intermittency affects fluvial ecosystems in conjunction with other environmental stressors.

In this study, we quantified the trophic structure of naturally fishless alpine stream food webs along a fine-scale gradient in flow intermittency. We used high spatial and temporal-resolution data on flow cessation from electrical resistance sensors to explain variation in stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) composition of food webs among headwater streams of a glacierized alpine catchment. We expected that the increase in resolution of flow intermittency data would allow us to identify that (i) overall trophic diversity might decrease across more intermittent streams, largely driven by a reduction in food chain length; that (ii) macroinvertebrate diets would show a change from allochthonous to autochthonous sources, without an overall reduction in basal resource diversity; and (iii) that measures reflecting common limiting alpine environmental gradients, such as elevation and variation in water temperature, would interact strongly with flow intermittency as explanatory variables for trophic diversity.

## Material and Methods

### *Site description and sampling design*

The Val Roseg is a glacierized river valley located in the Bernina massif in the eastern Swiss Alps. The catchment is hydrologically complex, with flow regimes affected by seasonal and topographical combinations of glacial meltwater, rainfall, and snowmelt (Malard et al. 2005). Meltwaters from two valley glaciers primarily feed a second-order braided river along the valley floor, while numerous headwater tributaries drain into the floodplain along valley side slopes. A high proportion ( $\geq 75\%$ ) of the headwater channel network is likely to have intermittent surface flow (Zah et al. 2001b, 2003, Malard et al. 2005, Robinson et al. 2016).

Vegetation in the valley consists of European Larch (*Larix decidua*) and Stone Pine (*Pinus cembra*) forest along with shrubs (*Juniperus communis* subsp. *alpina*, *Rhododendron ferrugineum*) and small trees (*Alnus viridis*, *Salix* spp.), alpine herbs, grasses and sedges (*Festuca* spp., *Carex* spp.).

A field survey was carried out in June 2017 and used to identify intermittent streams within the fluvial network of the upper Roseg catchment (after Robinson et al. 2016). Based on the survey, 28 headwater streams within the upper catchment were selected for study. These streams were identified as being likely to express a range of flow intermittency from perennial to frequent (weekly to daily). Study streams were distributed both laterally (valley side slopes) and longitudinally across a gradient of altitude, and encompassed headwaters varying in flow (intermittency, water source) and environmental conditions (temperature, altitude,

aspect, slope, vegetation). HOBO Pendant Temperature/Light 64K data loggers (Onset Computer Corporation, Bourne, MA, USA) modified to record electric conductivity and temperature were installed in each stream. The loggers continually recorded (hourly) the presence and absence of surface flow and temperature, thus providing detailed information on flow intermittency (Chapin et al. 2014). Loggers were downloaded in early October 2017 to provide information on the antecedent flow regime for all streams.

#### *Food web sampling*

All streams were sampled in autumn (September 2017) for assessing aquatic food webs. All samples were collected from a 20-30 m reach of stream where loggers were installed. Benthic macroinvertebrates for stable isotope analysis were collected by repetitive kick-sampling (mesh size: 250  $\mu\text{m}$ ) at several sites within each study stream and included main substrate types present (e.g., cobbles, sediments, woody debris, mosses). 3 kick-sample sweeps were conducted per stream, and additional sweeps were conducted targeting rare or smaller species if additional mass to conduct isotope analyses ( $\sim \geq 0.5 \text{ mg}$ ) appeared necessary.

Macroinvertebrates were hand-picked from kick-net samples and immediately sorted into 50ml plastic vials containing stream water, separating non-predator and predator taxa (with large predators further separated from each other), and left alive for ca. 8 h to void stomach contents. Macroinvertebrates were then identified and sorted to family, and individual samples stored at  $-20^{\circ}\text{C}$  until analysis. Fish are not present in the Val Roseg and thus not included in food web analyses.

We collected potential basal resources (i.e., organic matter) as material homogenized from several individuals, colonies, or accumulations from at least 3 locations along the sampling reach of each stream (see Jardine et al. 2014). Leaves of riparian plants and aquatic mosses were collected from living plants. Riparian plant samples were separated by species. Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) were collected directly from the stream. Periphyton was collected as epilithon, scrubbed with a wire brush and rinsed from a minimum of 3 replicate stones. All samples were stored at  $-20^{\circ}\text{C}$  until analysis.

#### *Sample preparation and isotope analysis*

All moss and CPOM samples were triple-rinsed with distilled water. Terrestrial plant and aquatic CPOM samples were air dried at  $60^{\circ}\text{C}$  for 72 hours and then mechanically ground and homogenized. Periphyton and FPOM samples were centrifuged for 15 min to separate out any residual CPOM and invertebrates. Periphyton, FPOM, moss, and invertebrate samples were freeze-dried for 48 hours in a Lyovac GT 2-E lyophilizer

(STERIS GmbH, Hürth, Germany). Moss and invertebrate samples were finely chopped and homogenized after drying. We weighed ~ 0.5 – 1.5 mg plant and animal samples and combusted them in a Vario PYRO Cube elemental analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany) connected to an IsoPrime isotope ratio mass spectrometer (GV Instruments Ltd., Wythenshawe, U.K.) for measurement of total C content, total N content,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Reference materials for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  derived from NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2 were provided by Biogeochemical Laboratories, Indiana University. Analytical precision was 0.01‰ for  $\delta^{13}\text{C}$  and 0.02 ‰ for  $\delta^{15}\text{N}$ .

#### *Data analysis*

Flow intermittency of streams was determined from a principal components analysis (PCA) based on four metrics of flow intermittency derived from the logger data from 5 July to 11 October 2017. Flow metrics included the presence/absence of dry periods, total duration of dry periods (hours; range, 0 to 1429), length of individual drying periods (hours; range of means, 0 to 211), and the timing of dry periods (occurrence of first drying period, August to October 2017). The PCA values ordinated sites along a gradient of flow intermittency from permanently flowing streams to streams with multiple drying events (range; 1 to 15) throughout the specified period (supplementary material Appendix 1 Fig. A1). Axis-1 explained 59% of the variation, and was associated with the occurrence, total duration, and average length of individual drying periods. Axis-2 explained 29% of the variation, and was associated with the timing of drying events. Total drying duration was linearly correlated with the average length of drying periods ( $R^2 = 0.84$ ). We thus used PCA Axis-1 values as a proxy for the main components of flow intermittency (FI value) in further analyses. We first transformed Axis-1 data by reversing signs (see supplementary material Appendix 1 Fig. A1) so that progressively more intermittent streams had higher FI values, then applied a natural log transformation ( $\ln \text{FI value for site minus minimum FI value across sites}$ ) to improve normality.

We further calculated a number of environmental variables which are well-described drivers of ecological change in alpine environments (Brown et al. 2003, Hotelling et al. 2017). Stream temperature data derived from the loggers were used to calculate average water temperature (°C) and the coefficient of variation (c.v.) for each stream over the study period (Hette-Tronquart et al. 2013). Temperature readings from dry periods were thus excluded. Stream elevation was taken from the swissALTI3D digital elevation model (swisstopo 2018a) and tree cover (100-m radius of each site) from the swissTLM3D large-scale topographical landscape model (swisstopo 2018b) using the GIS software package QGIS 2.16.3 (Quantum GIS Development Team,



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http://qgis.osgeo.org). Distance from the head of the catchment to each site (as a proxy for stream age since loss of glacier cover; see Malard et al. 2005, Robinson et al. 2016) was calculated as Euclidean distance (m) based on World Geodetic System (WGS84) coordinates. Finally, CPOM lability was measured by calculating C:N ratios from total C and N content. While these measures do not encompass all aspects of habitat heterogeneity, elevation in particular is closely correlated with several important habitat characteristics (e.g. riparian cover, slope and step-pool morphology, channel stability) across alpine catchments and thus may be considered a general proxy (Brown et al. 2003, Hotelling et al. 2017).

We used complimentary approaches to determine changes in food-web structure along environmental gradients. First, we characterized the trophic niche space occupied by assemblages (i.e., trophic diversity of macroinvertebrate food webs) using complementary metrics. We calculated overall trophic diversity as stable ellipse area (SEAc) (Jackson et al. 2011), maximum height of food webs as food chain length (FCL) (Post 2002b), and basal resource diversity as the  $\delta^{13}\text{C}$  range of consumers ( $C_{\text{range}}$ ) (Layman et al. 2007) at each site (supplementary material Appendix 1 Methods A1).

Second, we used a gradient-based approach from  $\delta^{13}\text{C}$  values of macroinvertebrates and measured basal resources. Given consistent  $\delta^{13}\text{C}$  values of basal resources across streams, changing  $\delta^{13}\text{C}$  values of macroinvertebrates indicate an increasing reliance of consumers on different basal resource pools.

Conversely, gradients of change in  $\delta^{13}\text{C}$  values of consumers equivalent to those of certain resources indicate a consistent reliance on that source (Rasmussen 2010). We separated primary from secondary consumers by comparison of trophic position (TP; supplementary material Appendix 1 Methods A1). We selected a cut-off point of  $\text{TP} \leq 2.5$  for primary consumers as the point at which well-described predators (Buffagni et al. 2018) began to occur in the dataset. Lastly, we used isotope mixing models to estimate the dietary contributions of basal food resource groups to primary consumers. After assessment of the suitability of the possible range of isotopic mixing models (Smith et al. 2013), we used the Bayesian mixing model SIAR (Parnell et al. 2010) to produce probability distributions of the contributions of basal resources to primary consumer isotope values (supplementary material Appendix 1 methods A2).

We used generalised additive models (GAMs) to identify whether SEAc, FCL,  $C_{\text{range}}$ ,  $\delta^{13}\text{C}$ , and median estimated dietary contribution values (supplementary material Appendix 1 Methods A1, A2) varied across streams in response to gradients of flow intermittency and other measured environmental variables. First, we explored correlations between trophic diversity indices and flow intermittency as a single predictor variable

using GAMs. Next, we identified the amount of additional variance explained by including additional environmental variables in the models. GAMs were built using a single variable in addition to flow intermittency (Table 1) and we calculated the difference in deviance explained (%) between these models and the model with flow intermittency alone. Significant differences in deviance explained were identified using Wald likelihood ratio tests. We did not include an autocorrelation term based on the geographical coordinates of pools, as exploratory data analysis revealed no correlation between residuals and geographic coordinates (Zuur et al. 2009). We restricted GAM predictors to 4 knots to avoid over-interpolation of models. All models were created using the package mgcv in R 3.4.2 (R Core Team 2017).

## Results

### *Food-web structure and trophic diversity*

Periphyton was the most isotopically distinct basal resource, with higher  $\delta^{13}\text{C}$  (mean  $\pm$  SD;  $-24.1 \pm 4.6$  ‰) and lower  $\delta^{15}\text{N}$  values ( $-3.0 \pm 1.9$  ‰) than POM (Fig. 1). CPOM had similar  $\delta^{13}\text{C}$  ( $-28.1 \pm 1.8$  ‰) and  $\delta^{15}\text{N}$  values ( $-2.4 \pm 1.7$  ‰) to terrestrial plants and mosses, while FPOM had intermediate  $\delta^{13}\text{C}$  values ( $-26.5 \pm 2.2$  ‰) to CPOM and periphyton but was enriched in  $\delta^{15}\text{N}$  ( $-1.6 \pm 2.4$  ‰) relative to both (Fig. 1).

Macroinvertebrate consumers generally had higher  $\delta^{15}\text{N}$  values ( $-0.6 \pm 2.6$  ‰) than basal resources, and large predatory Diptera larvae (Empididae, Brachycera, Athericidae), Planariidae, and adult diving beetles (Dytiscidae) occupied the highest levels of food webs (Fig. 1). Periphyton (mean  $\pm$  SD; C:N =  $7.4 \pm 1.1$ ) and FPOM (C:N =  $9.0 \pm 2.0$ ) generally represented more nutritious resources than CPOM (C:N =  $21.5 \pm 8.3$ ). Overall trophic diversity (SEAc), food chain length (FCL), and basal resource diversity ( $C_{\text{range}}$ ) did not significantly change along the gradient of flow intermittency (Fig. 2). Adding average water temperature as an additional predictor resulted in models explaining an additional 20% or more of the variation in all isotopic niche indices (Table 1). Overall trophic diversity (SEAc) decreased (GAM range; 34.0 to 3.5) when streams were both warmer and more highly intermittent (Fig. 3a). Food chain length (FCL) did not significantly change (GAM range; 0.6 to 1.6) across the gradients of flow intermittency and water temperature (Fig. 3). Basal resource diversity ( $C_{\text{range}}$ ) decreased (GAM range; 10.7 to 1.8) in warmer streams (Fig. 3c).

### *Trophic base of food webs*

Macroinvertebrate primary consumers had higher  $\delta^{13}\text{C}$  values in streams with more intermittent flow regimes (GAM range;  $-29.9$  to  $-24.2$  ‰) (Fig. 4a). There was no corresponding change in  $\delta^{13}\text{C}$  values for CPOM (-

28.3 to -27.9 ‰), FPOM (-27.3 to -24.9 ‰), and periphyton (-27.2 to -20.6 ‰) along the gradient of flow intermittency (Fig. 4b, c, d).

Median predictions for the estimated contributions of CPOM to primary consumer diets declined (GAM range; 0.62 to 0.30) with increasing flow intermittency (Fig. 5a, b), while predicted contributions of periphyton to primary consumer diets rose (0.10 to 0.38) with increasing flow intermittency (Fig. 5c, d). Estimated contributions of FPOM were, in contrast, relatively consistent (0.24 to 0.33) across flow intermittency gradients (Fig. 5e, f).

In addition to flow intermittency, CPOM C:N ratios were the best additional predictor for primary consumer  $\delta^{13}\text{C}$  values (Table 1). Primary consumer  $\delta^{13}\text{C}$  values increased (GAM range; -31.5 to -24.0 ‰) as both flow intermittency and CPOM C:N ratios increased (Fig. 6a). Elevation explained more of the variation in estimates of periphyton consumption (Table 1). Estimated periphyton consumption increased (GAM range; 0.02 to 0.46) with increasing flow intermittency but peaked at intermediate elevations (Fig. 6b). Elevation, CPOM C:N ratios, and distance along the catchment contributed most to explaining CPOM diet contributions (Table 1). Estimated CPOM consumption decreased (GAM range; 0.78 to 0.26) with flow intermittency and CPOM C:N ratios (Fig. 6c), but increased (GAM range; 0.11 to 0.78) with elevation (Fig. 6d). Estimated CPOM consumption also reduced as streams were located further along the catchment (supplementary material Appendix 1 Fig. A2). Elevation and CPOM C:N ratios also contributed to further explaining estimated FPOM consumption (Table 1). FPOM consumption was lowest (GAM range; 0.61 to 0.18) at lower elevations (supplementary material Appendix 1 Fig. A3).

## Discussion

We observed little change in food-web trophic diversity across gradients of flow intermittency in 28 alpine headwater streams. In contrast, there was an increase in macroinvertebrate primary consumer  $\delta^{13}\text{C}$  values with increasing flow intermittency. This pattern did not match any corresponding changes in organic matter  $\delta^{13}\text{C}$  values, suggesting differences in diet were the cause of changing consumer isotopic signatures. While mixing model results for primary consumer diet proportions indicated multiple environmental factors were affecting invertebrate diets, models suggested that there was a greater proportion of periphyton and a lower proportion of CPOM being consumed as intermittency increased. Importantly, these results suggest that macroinvertebrates changed the proportional contributions of basal resources in their diets as streams became more intermittent, without necessarily changing the overall diversity of resources being consumed. As CPOM

C:N values were a significant predictor of both increasing primary consumer  $\delta^{13}\text{C}$  values and estimated CPOM consumption, CPOM lability appears to be the driving mechanism behind differences in trophic structure. Thus, this study shows that fundamental ecosystem properties can change gradually as streams become more intermittent, rather than only exhibiting substantial changes at hydrological thresholds.

*Flow intermittency consistently limits overall trophic diversity*

Flow intermittency was generally a poor predictor of trophic diversity. In this respect, our study adds to a growing body of evidence suggesting that trophic diversity, particularly food chain length (FCL), is consistently low across any level of flow intermittency (Sabo et al. 2010, McHugh et al. 2015). However, average water temperature provided a significant increase in the amount of variability explained in trophic diversity. Higher average temperatures might act to affect trophic diversity through increased body mass and energy availability, allowing for larger predators at higher trophic levels (Woodward et al., 2010). However, our results do not provide conclusive evidence of such patterns, and instead suggest that trophic diversity decreases as these alpine streams warm through a reduction in basal resource diversity (Fig. 3). Trophic diversity also might change as higher temperatures increase productivity through enhanced decomposition and mineralization of organic matter together with higher periphyton productivity (Friberg et al. 2009). Our results thus suggest that in these alpine streams temperature might have a greater effect on trophic diversity than flow intermittency, possibly through metabolically-costly adaptations to colder environments (Hotelling et al. 2017) and resource limitations (Uehlinger et al. 2009) that might possibly require macroinvertebrates to feed across a wider range of lesser quality basal resources to obtain enough energy. These effects also may lessen at lower altitudes, as species assemblages shift towards taxa with higher ranges of thermal tolerance (Hotelling et al. 2017).

The mechanisms behind limits on trophic diversity are often due to the habitat requirements of fish; which as mobile, obligate aquatic organisms are highly and consistently affected by drying events (McIntosh et al. 2018). Food webs in Val Roseg are instead dominated by macroinvertebrates, which have a multitude of mechanisms for resisting drying events (e.g., diapause, desiccation tolerance) (Bogan et al. 2017). In Val Roseg, these mechanisms might include hyporheic refuge use (Plecoptera, Ephemeroptera), desiccation resistance (Diptera), and semi-aquatic taxa (adult Dytiscidae) (Shama and Robinson 2009, Perić and Robinson 2015, Leys et al. 2017). The effects of high flows on trophic diversity in IRES, such as disturbance or resource subsidies, also are likely to be stronger for fish than macroinvertebrates (Sabo et al. 2010, Warfe et

al. 2013, Ruhí et al. 2016). However, indicators of different water sources (e.g., temperature variability, distance along catchment) that should drive differences in flow across streams (Brown et al. 2003) were not predictors of trophic diversity in this study.

As in other intermittent catchments, food webs in Val Roseg consist largely of generalist grazers (Ephemeroptera) and gatherers (Chironomidae), with many omnivorous taxa (Zah et al. 2001a). Changes in food-web breadth, or basal resource use diversity, are more often related to the loss or gain of specialist taxa (Layman et al. 2007). Most macroinvertebrates in Val Roseg have aerial dispersal in the adult stage and headwaters are seldom farther than a few hundred meters from relatively perennial habitats. Consequently, there exists a regional/catchment level pool of taxa that are able to disperse across both perennial and intermittent sites (Shama et al. 2011, Leys et al. 2016), overriding local effects on species richness or trophic diversity (e.g. Warfe et al. 2013). Thus, the Val Roseg likely represents a highly-linked metacommunity rather than isolated stream ecosystems (Tonkin et al. 2018). Here, the absence of fish, the high resilience and resistance of macroinvertebrates to drying, a high proportion of generalist/opportunistic taxa, and a closely-linked catchment species pool may all be interacting to drive the poor relationship between trophic diversity and flow intermittency. These mechanisms likely act as co-adaptations to both flow intermittency and the relatively harsh environmental conditions of alpine catchments (Füreder et al. 2003, Clitherow et al. 2013, Cauvy-Fraunié et al. 2015), which might largely restrict food webs to a consistent maximum size.

#### *Flow intermittency affects the trophic base of alpine stream food webs*

Trends in  $\delta^{13}\text{C}$  values of macroinvertebrates and basal resources, together with estimates from the isotope mixing models, suggested that food webs were supported to a greater extent by periphyton in streams that dried more often. Autochthonous production and processing of OM usually peaks with time after flooding and aquatic habitat contracts (Humphries et al. 2014). Autotrophic microbial biomass can also recover rapidly following rewetting events in IRES, despite large changes in elemental stoichiometry during drying (Timoner et al. 2012). The incorporation of algal resources into IRES food webs is thus expected to increase as drying progresses, while CPOM is expected to represent a relatively constant resource across drying gradients (McIntosh et al. 2017). Importantly, we observed strong interacting effects between both flow intermittency and CPOM C:N ratios on the trophic base of food webs. In dry channels, C:N ratios of terrestrial plant litter increase as non-structural compounds are photodegraded or leached (Dieter et al. 2011, Datry et al. 2018). Litter breakdown by micro-organisms and shredding invertebrates also is greatly reduced under dry

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conditions; i.e., terrestrial CPOM lability in streams is reduced under dry periods (Austin and Vivanco 2006, Corti et al. 2011, von Schiller et al. 2017). As such, litter conditioning during aquatic stages, particularly when algae are included, is a major driver of terrestrial OM uptake into aquatic food webs (Brett et al. 2017). Here, increasing flow intermittency may have ultimately caused reduced lability of terrestrial plant litter in streams, leading to lower assimilation of CPOM by food webs upon rewetting.

CPOM use in IRES food webs is dependent on its lability, consequently the increased consumption of periphyton may partly be a response to allochthonous resource “scarcity” rather than increases in autochthonous productivity. The relative importance of allochthonous and autochthonous resources to macroinvertebrate food webs is a long-standing issue, and the generality of conceptual models is often dependent on the characteristics of the study systems (e.g. seasonality of leaf litter inputs) (Thorp et al. 2006, Tank et al. 2010). For example, increased consumption of periphyton might be driven by algal productivity in IRES that have disconnected surface water pools (e.g. Bunn et al. 2003, Dekar et al. 2009). These pools likely act as refuges for aquatic biota and as biogeochemical “reactors” allowing continued production and decomposition of OM through otherwise dry periods (Larned et al. 2010). This geomorphic context highlights the increasing importance of local scale factors as IRES dry and contract (Fisher et al. 1998, Larned et al. 2010, Humphries et al. 2014).

The interacting effects of elevation and CPOM C:N ratios on macroinvertebrate diet proportions may largely arise through the distribution of our streams along altitudinal gradients. In alpine environments, elevation should correlate with periphyton productivity through light attenuation, as vegetation gradients shift to shrubs, herbs and grasses. But in alpine catchments, elevation also can restrict periphyton productivity through decreasing temperature, increasing turbidity and scour disturbance, and low nutrient concentrations (Uehlinger et al. 2009). These factors may thus correspond to the intermediate effect of elevation on periphyton consumption in Val Roseg. Elevation also corresponds with a lower mass of terrestrial OM inputs, although higher elevation vegetation (alpine shrubs, herbs) may have greater lability than lower elevation forests (pine, larch) due to lower proportions of structural compounds in plant tissue. Further, alpine trees also exhibit higher concentrations of non-structural compounds at higher elevations (Hoch and Körner 2012), thus high elevation food webs might rely on relatively labile terrestrial inputs as well as periphyton.

*Ecosystem responses to increased flow intermittency*

Globally, rivers and streams are expected to become more intermittent as temperatures rise and rainfall decreases or becomes more variable (Döll and Schmied 2012). These changes in flow intermittency are likely to have substantial ecological impacts in areas with complex environmental gradients, such as alpine and montane environments (Cauvy-Fraunié et al. 2015). Predicting the response of stream ecosystems to increased flow intermittency is difficult due to the threshold nature of many ecosystem responses and the high inherent variability of IRES food webs. Dramatic changes in food-web structure and function can occur once certain thresholds in flow cessation are reached (e.g., food chain length, biomass flux) (Ledger et al. 2013, McHugh et al. 2015). However, these thresholds can be precipitated by changes in other ecosystem properties, such as the energetic base of food webs (Bestelmeyer et al. 2011). Gradual changes in trophic dynamics may be obscured by the high overlap of feeding traits and functional resistance of IRES taxa to drying and contraction of aquatic habitats (Leigh et al. 2010, Boersma et al. 2014). In this context, our study shows that shifts in the trophic base of IRES can occur as gradual, ramped changes, and these shifts can be identified if flow intermittency is characterized at a fine scale.

A number of ecosystem functions might change gradually along gradients of flow intermittency, rather than exhibiting clear and dramatic threshold shifts upon increased drying. For example, aquatic macroinvertebrates can increase in density as habitats contract without species loss (Acuña et al. 2005, Dewson et al. 2007, Walters and Post 2011), but substantial losses of diversity follow thresholds of water loss (e.g., loss of lateral connectivity, loss of surface water) (Boulton 2003). Threshold changes in ecological function might occur when drying occurs as a supra-seasonal event (*sensu* Lake 2003) on the intrinsic scale of the organisms affected; i.e. the same level of flow intermittency might represent a seasonal disturbance for drying-adapted IRES taxa (Boersma et al. 2014) but a supra-seasonal disturbance for perennial stream taxa (Ledger et al. 2013), resulting in substantially different magnitudes of response in assemblage and food-web structure.

Whether changes in the trophic base of IRES food webs lead to fundamentally different food-web structure and function post-drying (Bogan and Lytle 2011, Cauvy-Fraunié et al. 2016) is an important avenue of further research. We therefore emphasize that aquatic ecosystem function may not be maintained or stable until thresholds in flow intermittency are reached, but might instead change fundamentally but gradually with even small increases in drying frequency or duration. As Alpine streams become more intermittent, identifying these gradual ecological changes is likely to be vitally important to management and conservation aimed at avoiding dramatic, threshold changes in ecological function.



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## Figure Legends

Figure 1. Mean ( $\pm$  standard error)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for basal resources and macroinvertebrates across the 30 study streams. Large predatory dipteran taxa (Brachycera, Athericidae, Empididae), detritivorous stoneflies (Nemouridae, Leuctridae), and detritivorous caddisflies (Limnephiliidae, Sericostomatidae) are pooled for visual clarity. Values are not corrected for trophic enrichment. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter.

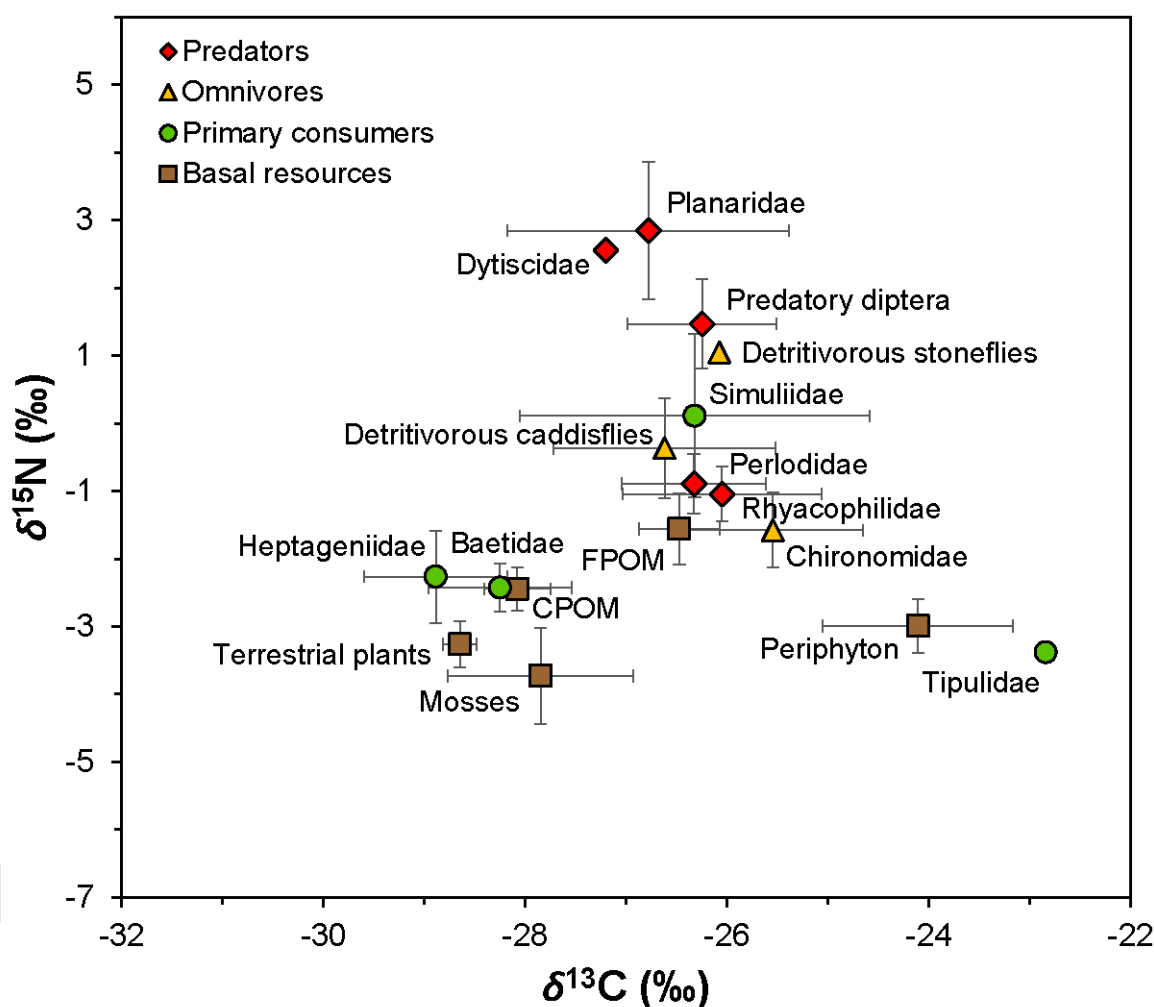


Figure 2. Patterns of isotopic niche space indices describing trophic diversity across flow intermittency gradients. (a) Median estimated overall trophic diversity (stable ellipse area corrected for sample size, SEAc) and associated generalized additive model (GAM). (b) Food chain length (FCL) and associated GAM. (c) Basal resource diversity (consumer  $\delta^{13}\text{C}$  range,  $C_{\text{range}}$ ) and associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines).  $R^2$  values are adjusted for sample size. edf = estimated degrees of freedom.

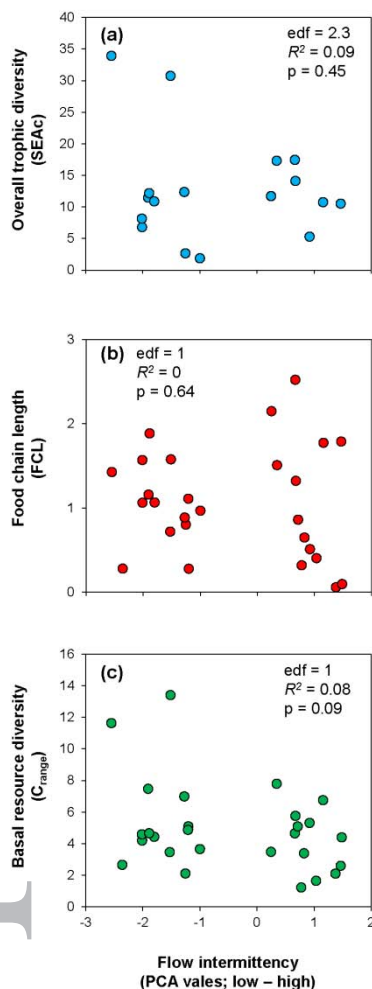




Figure 3. Three-dimensional plots of generalized additive model (GAM) predicting (a) overall trophic diversity (SEAc), (b) food chain length (FCL), and (c) basal resource diversity ( $C_{\text{range}}$ ) relative to flow intermittency with average water temperature ( $^{\circ}\text{C}$ ). Original data points and residuals relative to GAM fitted values are also shown.  $R^2$  values are adjusted for sample size. Temp. = water temperature.

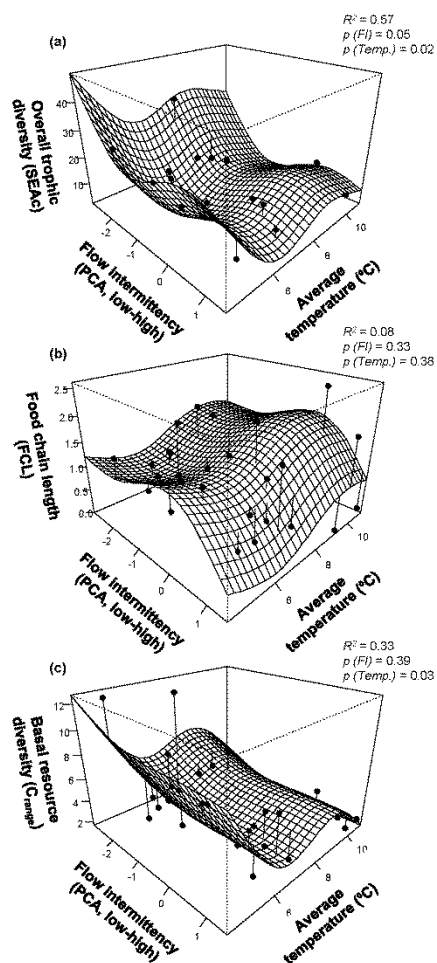
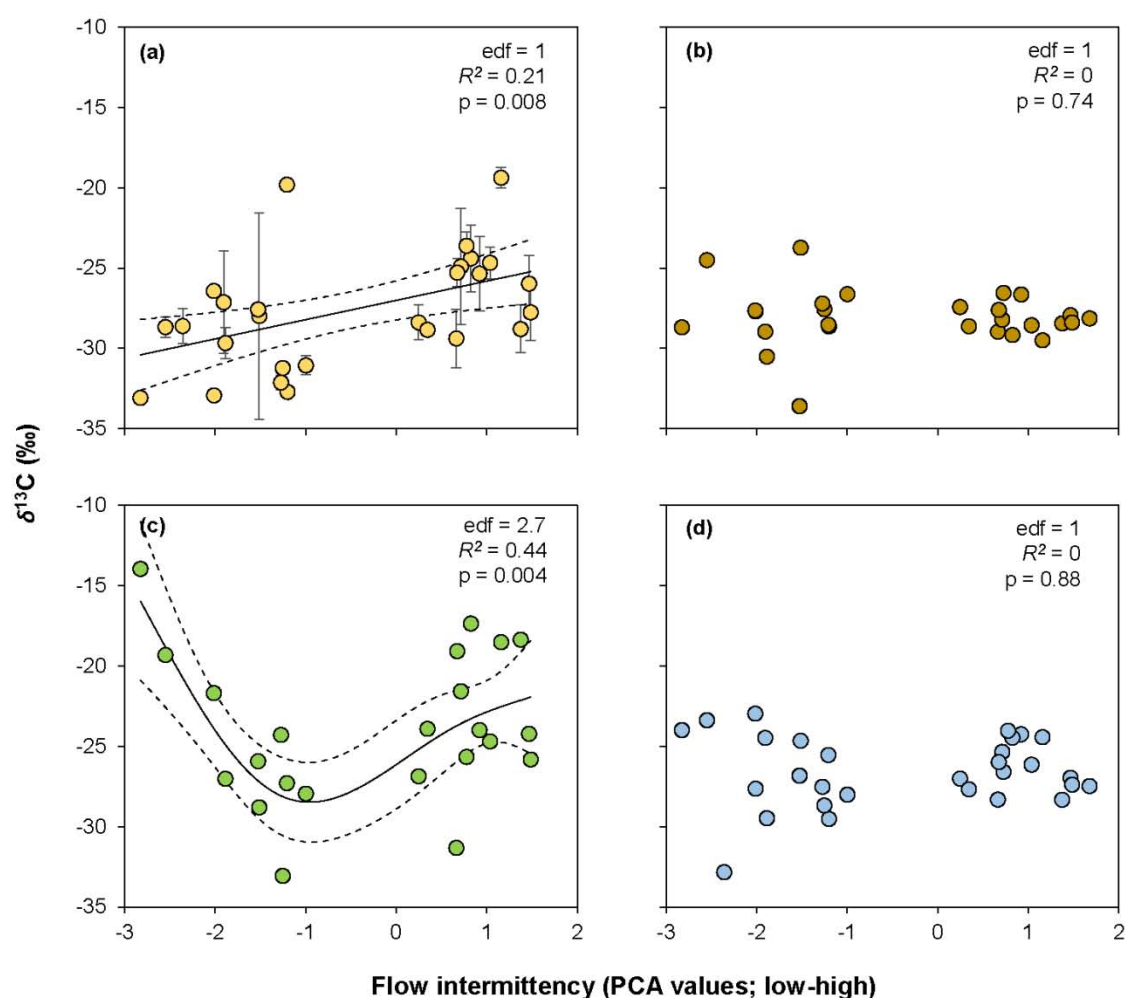


Figure 4. Patterns of organic matter and macroinvertebrate primary consumer  $\delta^{13}\text{C}$  values across flow intermittency gradients. (a) Macroinvertebrate primary consumer  $\delta^{13}\text{C}$  values (site mean  $\pm$  SD) and associated generalized additive model (GAM). (b) Coarse particulate organic matter (CPOM)  $\delta^{13}\text{C}$  values and associated GAM. (c) Epilithic periphyton  $\delta^{13}\text{C}$  values and associated GAM. (d) Fine particulate organic matter (FPOM)  $\delta^{13}\text{C}$  values and associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines).  $R^2$  values are adjusted for sample size. edf = estimated degrees of freedom.



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Figure 5. Estimated dietary contributions (as proportions of total) for 3 basal resource groups to macroinvertebrate primary consumers across flow intermittency gradients. Estimated contributions are shown as 25<sup>th</sup> percentile, median and 75<sup>th</sup> percentile of probability distributions for (a) dietary contribution of coarse particulate organic matter (CPOM), with (b) associated generalized additive model (GAM) predicting medians of probability distributions. (c) Dietary contributions of epilithic periphyton and (d) associated GAM. (e) Dietary contributions of fine particulate organic matter (FPOM) and (f) associated GAM. GAM results are shown as fitted values (solid lines) and 95% confidence intervals for fitted values (dashed lines). Note differences in x-axis scales; streams are ranked by flow intermittency (low-high) for visual clarity in (a), (c), and (e).  $R^2$  values are adjusted for sample size. edf = estimated degrees of freedom.

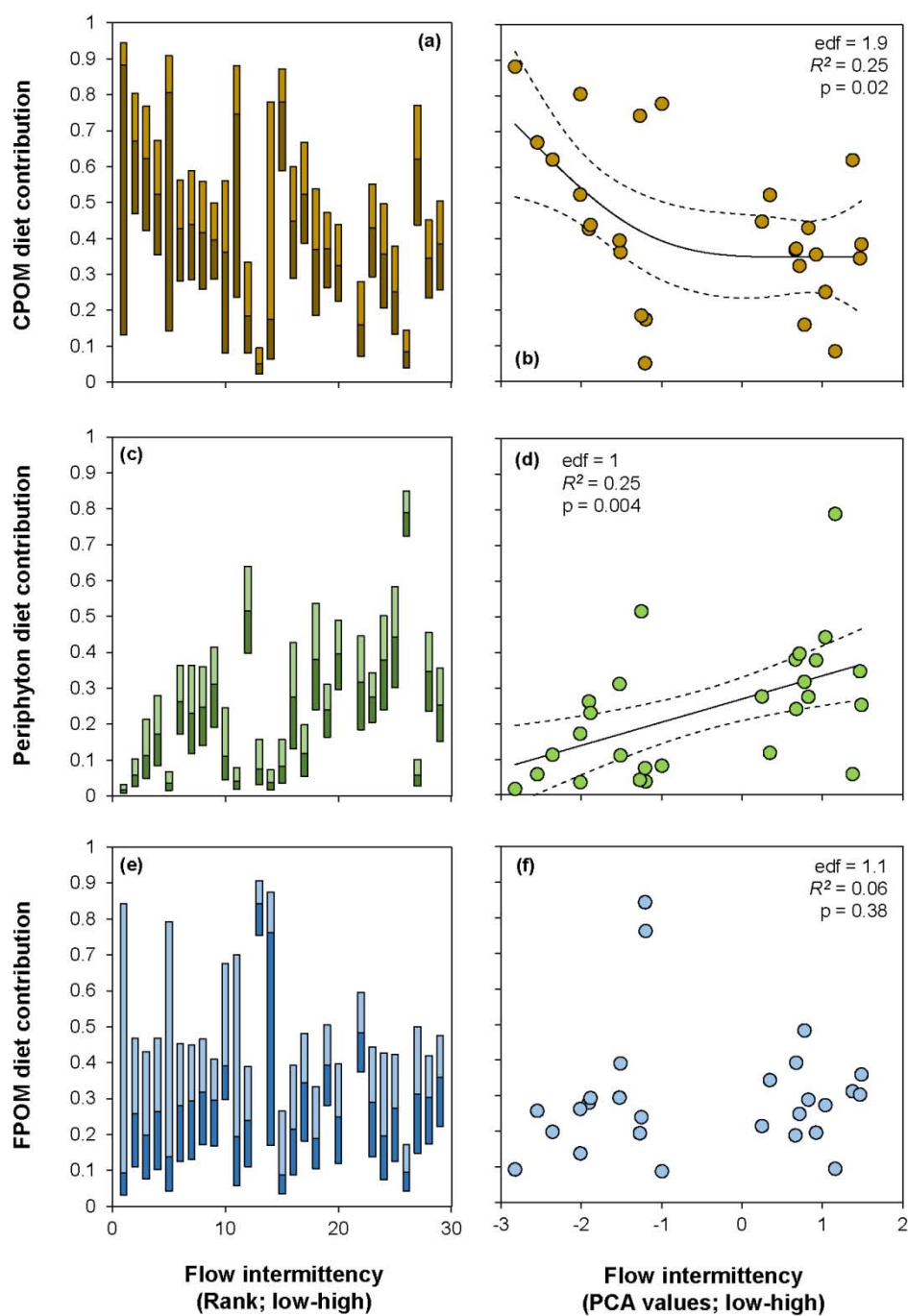
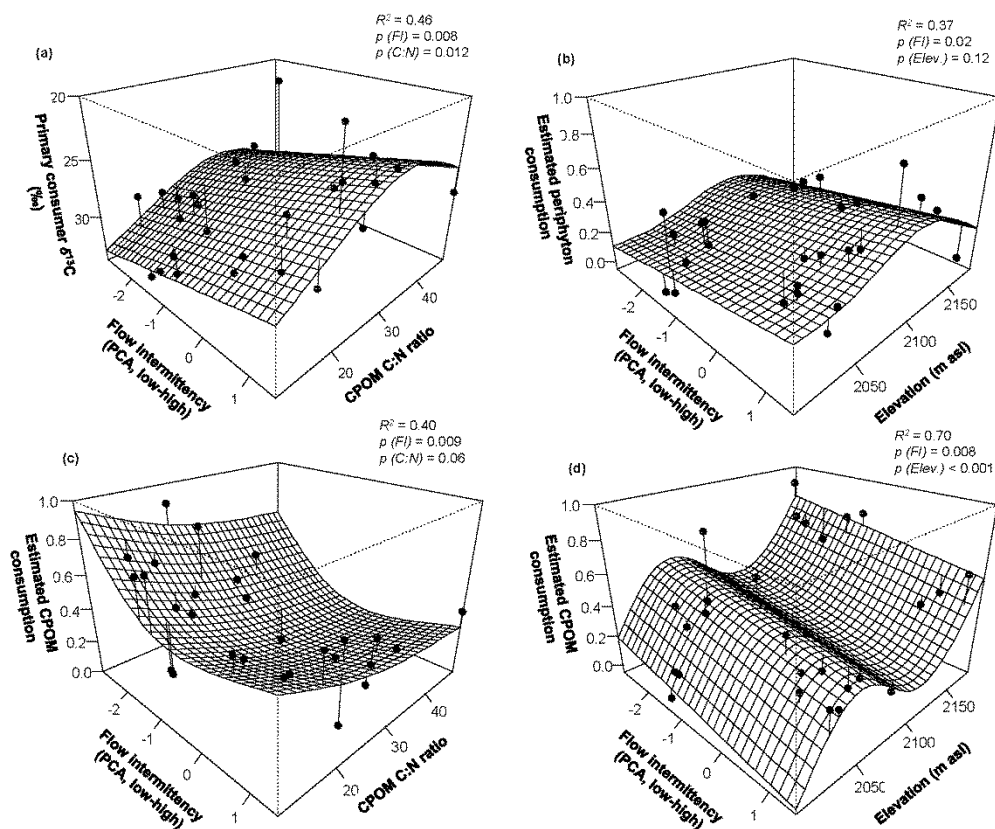


Figure 6. Three-dimensional plots of generalized additive models (GAMs) predicting (a) primary consumer  $\delta^{13}\text{C}$  values and (c) median estimated coarse particulate organic matter (CPOM) consumption by primary consumers in relation to flow intermittency and site elevation, and (b) median estimated consumption of periphyton and (d) median estimated consumption of CPOM by macroinvertebrate primary consumers relative to flow intermittency and site elevation. Original data points and residuals relative to GAM fitted values are also shown.  $R^2$  values are adjusted for sample size. FI = flow intermittency. Elev. = elevation. C:N = CPOM C:N ratio.



# **Table Legends**

Table 1. Differences in deviance explained (%) between models predicting various isotope metrics as a response to flow intermittency, and models including both flow intermittency and an additional environmental variable as a predictor term. † p < 0.10, \* p < 0.05, \*\*p < 0.01, \*\*\* p < 0.001.

Response	Additional predictor					
	Elevation (m asl)	Tree cover (%)	Temperature (°C)	Temp. variability (c.v.)	Dist. along catchment (m)	CPOM C:N ratio
Overall trophic diversity (SEAc)	-1.3	-2.2	48.8***	9.7†	-2.0	-0.8
Food chain length (FCL)	0	2.0	24.6	9.8	0.5	12.9
Basal resource diversity (Crange)	0.2	3.2	33.4*	1.6	0.2	0
Primary consumer $\delta^{13}\text{C}$	11.3	3.1	12.7†	0.5	4.6	28.5***
CPOM consumption	44.1***	2.1	11.3	-0.6	27.3**	17.9*
Periphyton consumption	17.5*	0.3	10.6	2.4	4.5	11.5
FPOM consumption	36.8***	1.0	5.5†	3.7	7.3	10.5*