UiT The Arctic University of Norway

Department of Arctic and Marine Biology

Arctic Shrub Expansion: Implications for Stream Benthic Invertebrate Community Structure & Function

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From the River

Acknowledgments

First of all, thank you benthic invertebrates. Without you little creatures, this study would not have been possible. Although you have been difficult to identify at times, I feel like I have gotten to know you a lot better. I'm sure we'll meet again sometime in the future.

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Abstract

The Arctic is rapidly warming and this increase in temperature has been found to drive range expansion of tall shrubs in the Arctic tundra ecosystems. Although the consequences of shrub expansion have been studied in the terrestrial tundra, effects on tundra stream ecosystems remain understudied. Riparian tall shrubs, such as willows, can provide stream ecosystems with leaf litter and shade, enhancing food availability and habitat complexity. This can alter the abundance, diversity, and community composition of benthic invertebrates. These aquatic species provide important ecological functions such as organic matter processing and oxygenation of the sediment, and reflect the health and resilience of streams. To assess the effects of the tall shrub expansion on Arctic tundra stream functioning, benthic invertebrates were sampled in ten tributaries of the Komag River. I compared the abundance, diversity, community composition, and diet of the benthic invertebrates between streams with and without tall shrubs. The abundance and diversity of the invertebrates showed no relationships with tall shrub presence, but species composition shifted in the presence of tall shrubs. Despite the observed change in species composition, functional composition was similar in all streams. Further, stable isotope analysis revealed that many benthic invertebrates, regardless of tall shrub presence, were feeding on food sources more depleted in ^{13}C than willow or periphyton. My results indicate that the leaf litter from tall shrubs in the stream may not be as extensively used by benthic invertebrates as in boreal and temperate streams. Rather, energy pathways in Arctic tundra streams seems dependent on autochthonous sources, such as filamentous algae, moss, or possibly methanogenic bacteria. The shift in species composition might be induced by tall shrub-associated factors besides leaf litter input. As climate warming continues, the Arctic tundra is predicted to more closely resemble boreal ecosystems, likely increasing allochthonous matter supply to streams. The results of this study increase understanding of the responses of Arctic stream benthic invertebrate communities to tall shrub expansion.

Table of Contents

1 Introduction

The Arctic is warming nearly four times as fast as the rest of the Northern Hemisphere (Serreze & Barry, 2011; Rantanen et al., 2022), which makes Arctic ecosystems particularly vulnerable (Holland & Bitz, 2003; IPCC, 2023). The increase in temperature caused by fossil fuel burning and the use of synthetic fertilizers in agriculture, particularly in the USA and Western Europe (IPCC, 2023), has been identified as the primary driver of the circumpolar range expansion of tall shrubs, commonly referred to as “Arctic greening”, “shrubification”, or “woody encroachment” (Tape et al., 2006; Myers-Smith et al., 2011; García Criado et al., 2020). This encroachment has ecological consequences, replacing native tundra species such as lichen, mosses, forbs, and grasses, and thereby homogenizing the landscape (Stewart et al., 2018). Leaf litter accumulation and changes in vegetation growth forms, due to tall shrubs, alter terrestrial tundra processes including soil organic matter decomposition and energy exchange, particularly in Northern biomes (Hobbie et al., 2002; Cornelissen et al., 2007). The effects of tall shrub expansion in the Arctic tundra have been studied predominantly in the terrestrial tundra, but their effect on adjacent aquatic ecosystems has been neglected so far. This is particularly relevant to low-productive Arctic ecosystems, where small changes in the flow of carbon from terrestrial vegetation into small streams can significantly alter river dynamics (Gounand et al., 2018).

In Arctic and subarctic biomes, snow accumulation and low temperatures during almost all of the year result in a short growing season (CAFF, 2013; Pedersen et al., 2021). Snowmelt in late spring brings nutrients and light to the soil surface and induces a burst of productivity. Low-growing species such as lichen, mosses, and forbs are often found on barren ground, meadow vegetation like grasses and dwarf-shrubs may dominate warmer parts of lower elevation (CAVM Team, 2003), and in some cases, deciduous tall shrubs can be found on warm and moist soils close to major rivers. This is the case along the Komag River, in northern Norway (Sturm et al., 2001; CAVM Team, 2003; Brittain et al., 2009; Pajunen et al., 2010). There, *Salix* species (willows) are found in 0.5-3.5-meter-tall patchy thickets along the main river and the downstream reaches of some tributaries (orders 1 & 2) (Ravolainen et al., 2011, 2013). Currently, the reindeer husbandry in this area has allowed extensive browsing of willow thickets (Ravolainen et al., 2013), which is thought to counter their range expansion (Verma et al., 2020). Despite their limited coverage, willow thickets play significant roles in the terrestrial tundra, by facilitating insect abundance that provides food for insectivorous birds, offering shelter to a variety of species, and protecting understory vegetation from environmental stresses (Totland & Esaete, 2002; Ims & Henden, 2012; CAFF, 2013; Pedersen et al., 2021).

The establishment of tall vegetation in the riparian zone may govern in-stream processes, primary production, and affect the consumer community (Vannote et al., 1980; Naiman & Décamps, 1997; Meyer et al., 2007). In some temperate areas, riparian vegetation forms a closed canopy, blocking some of the sunlight from penetrating the stream (Dodds & Whiles, 2017). The low light availability limits in-stream primary production and increases the relative importance of allochthonous sources (Warren et al., 2016). These allochthonous resources originate outside the stream and are a source of nutrients, which are essential for headwater and downstream food webs (Dodds et al., 1996, 2015). Moreover, they provide food for stream invertebrates which transfer this energy to higher trophic levels (Wallace & Webster, 1996). It also provides a substrate for primary producer growth and shelter for a variety of organisms. Thus, the input of plant litter enhances food availability and habitat complexity, promoting species diversity. This biodiversity is often positively associated with stream ecosystem health and resilience, as it provides important ecological functions.

Stream benthic invertebrates are often used as indicators of water quality and stream health (Wallace & Webster, 1996; Richarson, 2019; Vaidya, 2019). These organisms are an essential component of the aquatic community and are known to show quick responses to environmental changes. The diversity of benthic invertebrate species also perform diverse ecological functions, such as detritivory (shredders and collectors), herbivory (grazers), and predation (predators) (Cummins, 1973; Covich et al., 1999). The classification of these feeding traits is based on mouthpart morphology and the resources that are consumed by invertebrates. Shredders are notably abundant in shaded streams with high leaf litter input where they accelerate the decomposition process by fragmenting large pieces of plant material (Covich et al., 1999; Graça, 2001; Wallace & Eggert, 2009; Swan et al., 2021). They assimilate nutrients from the consumed leaves and thus contribute to stream nutrient cycling through their digestion and production of faecal pellets (Graça, 2001). The shredded organic matter in addition to faecal pellets and other fine particulate organic matter serve as a food source for another functional group known as collectors. As a result, they are positively associated with shredders, with their abundance and diversity being supported by the abundance and diversity of shredders (Vannote et al., 1980; Cummins et al., 1989; Jonsson & Malmqvist, 2005). In contrast, grazers are less prevalent in areas with tall riparian vegetation, where shade limits autochthonous production, such as periphyton, their primary nutrient source (McNeely et al., 2007; Wallace & Eggert, 2009). Predatory invertebrates are a relatively small group among benthic invertebrates and their presence is not necessarily correlated with the presence of riparian vegetation (Vannote et al., 1980). Changes in abiotic and biotic factors can shift the proportions of different feeding groups within the invertebrate communities resulting in a change in ecosystem processes (Wallace & Eggert, 2009).

The relationships that exist between the different functional groups and their food sources can be identified in more detail using stable isotope analysis. Organisms assimilate nutrients, and the presence of specific stable isotopes can tell which resources have been consumed (Fry, 2006). The proportion of stable isotopes of carbon in a consumer, more specifically, of ^{12}C and ^{13}C, can provide information about the carbon sources present in the diet. This enables us to distinguish between, for example, the importance of periphyton versus that of other carbon sources like willow leaf litter. Stable isotopes of nitrogen (^{14}N: ^{15}N) can reveal information about the trophic position of an organism. These isotopic values from benthic invertebrates can be compared with the food sources present in the environment, allowing for a more detailed understanding of feeding preferences and ecological roles (Fry, 2006). Through this method, we gain knowledge on energy sources within the aquatic food web.

To understand the consequences of the Arctic shrub expansion on stream functioning, I compared the abundance, diversity, and diet of the benthic invertebrate community of Komag tributaries with and without tall shrubs. I asked the following questions:

I. How does the presence of tall shrubs change the benthic invertebrate abundance, diversity, and community composition?

h1.) The abundance and diversity of benthic invertebrates increase in the presence of tall shrubs, reflecting a higher food availability and habitat heterogeneity associated with tall shrub presence in the riparian zone.

h2.) Invertebrate species- and functional composition in streams with tall shrub presence will be different from those without, reflecting feeding modes, such as shredders and collectors, more strongly associated with allochthonous resources.

II. What is the effect of tall shrub presence on benthic invertebrate energy sources?

h3.) The presence of tall shrubs increases the relative importance of leaf litter to the benthic invertebrate diet, whereas the diet of benthic invertebrates in shrub-absent streams reflects a higher dependency on aquatic primary producers.

2 Methods

2.1 Study Area

This study was conducted in the Komag River catchment located north of the Arctic Circle at 70ºN, 30ºE in Varangerhalvøya Nasjonalpark, Finnmark (Fig. 1). The catchment has an area of 321 km^2 where the mean annual air temperature is -0.9 ºC (Brittain et al., 2009). From November – May, temperatures remain under freezing point, snow covers the soil, and the river stays ice-covered. During the period of snowmelt, from May – July, the river is characterized by a high flow regime, with spring flood happening from mid-May to mid-June. In July daily mean air temperatures range from 9 – 12 ºC (Pedersen et al., 2021; MET Norway, 2024). The river has a total length of 52.6 km and is fed by many tributaries. These tributaries are special because extensive tall shrubs only occur in their downstream reaches near the confluence with the main river, and in only some tributaries. Extensive willow thickets are absent further upstream in all tributaries.

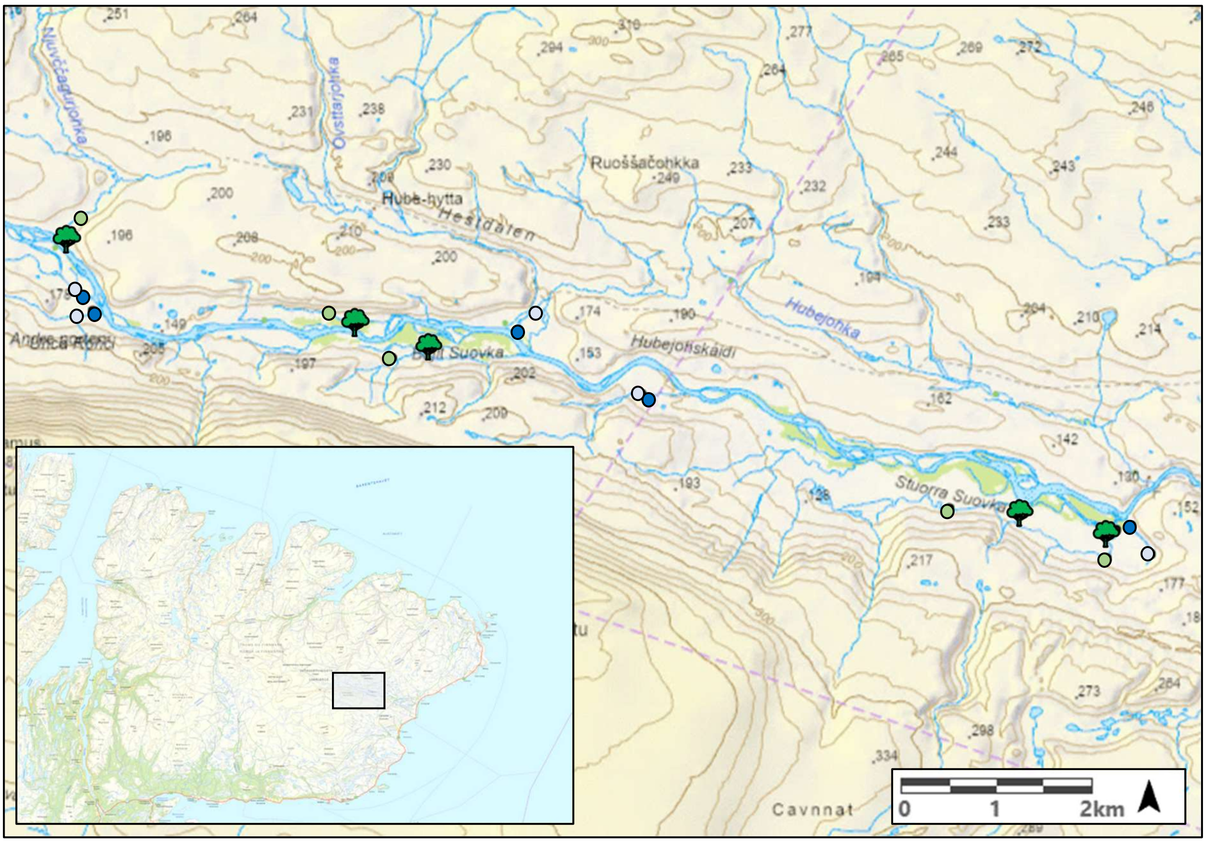

Figure 1 – Sample locations in the Komag River. The blue points on the map represent the meadow streams of which dark blue is the downstream reach and light blue is the upstream reach. The dark green shrub symbol represents the downstream reaches of tall shrub streams and the light green points are the upstream reaches in these streams. The bottom-left map shows the location of the study area within Varanger peninsula. The map layer was obtained in NVE Atlas 3.0 (2021).

2.2 Study Streams

The streams I studied were preselected using ESRI World Imagery on NVE Atlas 3.0 (NVE, 2021) and further assessed for suitability in the field. Ten streams were selected to represent meadow (n=5) and tall shrub (n=5) stream types (Fig. 1) (Appendix 1). All streams are independent tributaries of the Komag River and are situated 22 – 32 km upstream of the Komag River mouth with the Barents Sea. Within each of the 10 selected streams I selected two locations about 260 m (range 82 – 552 m) from each other: one upstream, always characterized by meadow (n = 10), and one downstream either having meadow or tall shrubs in the riparian zone (n = five of each). Meadow streams have little to no presence of tall riparian vegetation in both upstream and downstream locations. Tall shrub streams are characterized by the presence of tall willow shrubs downstream, but not upstream (Fig. 2). This design is important to control for changes that naturally occur when comparing upstream to downstream locations.

The Komag River catchment is oligotrophic (Sandin et al., 2021) and chosen tributaries were similar in width, depth, dissolved oxygen, pH, conductivity, and temperature at the time of sampling (Table 1). The stream substrate varied from sand to boulders across streams, but not within streams (Appendix 1). At every location within the stream, a riffle habitat was chosen for standardized flow sampling. I attached eleven temperature loggers to boulders in streams from July – September. Stream mean daily temperature was warmest in August and followed a similar pattern with stream temperatures being warmer in July than in September (Appendix 2).

Table 1 – Physical and chemical characteristics of the up-and downstream locations of the meadow and tall shrub streams.

	Tall Shrub		**Meadow**	
Location	Downstream	Upstream	Downstream	Upstream
Width (cm)	80-260	150-450	130-280	250-420
Depth (cm)	7-22	6-35	8-25	6-12
Dissolved Oxygen (mg L^{-1})	105.0-152.2	105.0-147.9	90.0-144.9	106.2-133.2
pH	6.52-7.85	6.84-7.85	6.93-7.33	6.44-7.16
Conductivity (µS cm^{-1})	20-53	20-53	19-54	19-60
Temperature (°C)	6.33-7.87	4.20-7.66	5.05-8.49	5.24-7.84

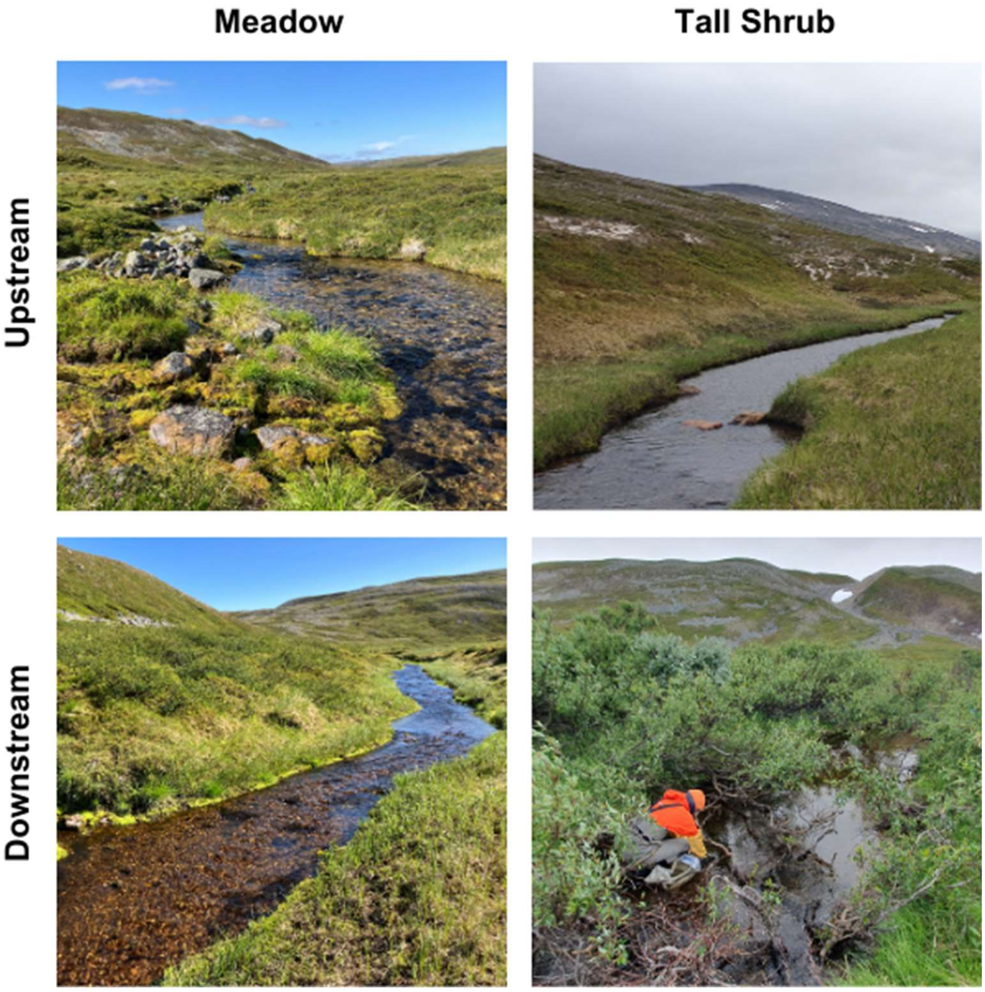

Figure 2 – Overview of stream types (meadow; tall shrub) and locations within each stream (upstream; downstream). The downstream locations of tall shrub streams are characterized by the presence of tall willow shrubs.

2.2.1 Terrestrial and Aquatic Primary Producers

To quantify tall shrub coverage, I estimated the shrub percentage cover in a 20-meter radius area centred at each sampling location within the stream. I differentiated shrub vegetation from the other types of vegetation on ESRI World Imagery and marked the area to calculate the percentage cover using the package *leaflet* (Cheng et al., 2023) in open-source software R (v.4.3.1, R Core Team, 2023) (Fig. 3) (Appendix 1). To verify accuracy, the same estimation was done using a 40 m radius around the location, which resulted in similar percentages. The tall shrub cover ranges from 15.2% – 100% at the downstream locations of the tall shrub streams. At all other locations, the vegetation cover ranges from 0% – 2%. Other biological stream characteristics moss and filamentous algae coverage were documented. To quantify stream primary production, I measured algal standing biomass on five boulders in $\mu g/cm^2$ using a bbe BenthoTorch (BT) which distinguishes green algae, diatoms, and cyanobacteria in the biofilm based on the intensity of chlorophyll fluorescence.

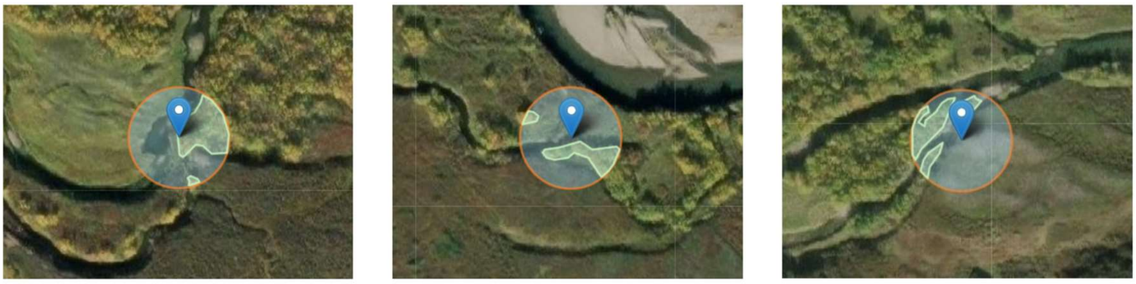

Figure 3 – Tall shrub extent quantification with use of leaflet in R on ESRI World Imagery. Blue markers indicate the centre of each location within the stream, the orange circle around represents the 20-meter radius around the marker, and the highlighted areas are selected tall willow shrubs.

2.3 Benthic Invertebrate Communities

Invertebrate sampling was done July 1st – July 7th, 2023. This sampling time was aimed to allow the assessment of a more complete benthic invertebrate community before the peak of insect emergence. At every sampling location (n=20), three separate sample replicates (A, B, and C) were taken within a 4-meter reach using a Surber sampler with bottom frame dimensions of 25 x 20 cm and a bag mesh size of 500 µm. Within the Surber frame the boulders were brushed clean and the substrate was disturbed for two minutes against the water current. The material contained in the Surber bag was transferred to 500 mL containers containing 96% ethanol and stored at room temperature until lab identification. In the laboratory, the invertebrates were separated from plant material and sand and assigned to the groups Ephemeroptera, Plecoptera, Trichoptera, Diptera, and "other". The first four groups were then identified to species, genus, or family levels using various identification keys (Lillehammer, 1988; Nilsson, 1996; Elliott & Humpesch, 2010; Rinne & Wiberg-Larsen, 2017), counted, and stored for further analyses.

Because the invertebrate species have different feeding traits, I assigned each taxon, when possible, to a 10-point system of functional feedings groups (FFGs) as in Moog (1995) using the database accessed through www.freshwaterecology.info on October 30th, 2023 (v. 8.0, Schmidt-Kloiber & Hering, 2015, eds.). Next, the FFGs were sorted into four traits: shredders, collectors, grazers, and predators, based on Cummins (1973) (Appendix 3).

2.4 Stable Isotope Analysis

Resource samples were taken September 14th – 15th, 2023. This time was chosen as riparian leaf litter will enter the streams in autumn and is an important component of diet during winter, when the streams are ice-covered, and early spring before emergence (Frainer et al., 2014). Due to slow turnover rates (Anderson et al., 2017) the isotope values of the invertebrates sampled in the spring will reflect the isotope values of the resources they fed upon during late winter. The potential litter resources included nearly abscised willow and dwarf birch leaves, and grass. Besides leaf litter, I also collected other resources present in the streams and in the riparian zone and that could constitute part of the invertebrates diet. Fresh moss and filamentous algae were collected from within the stream. All material was dried with a paper towel, and stored in zip lock bags at -18 ºC until further processing. Stream biofilm from 10 boulders randomly chosen at each location and scrubbed with a toothbrush into a tray until clean. This material was transferred into a 250 mL container topped up with stream water and stored on ice for transport. At two locations where boulders were absent, the tray was filled with substrate from the stream and stirred with water. The top layer of water was then transferred into the container. In the laboratory, a 10 mL aliquot of each container was filtered through a 47 mm pre-combusted glass fibre filter and dried at 60 ºC for 24 hours. After drying, the filters were folded in half and packed in tinfoil in a zip-lock bag. The resource and invertebrate samples were dried for 24 hours at 60 ºC and ground to a fine powder. Eight invertebrate taxa were selected for stable isotope analysis based on their distribution across locations and trait classification. Ground samples were weighed on a microbalance with 0.001 mg precision. The target weight is 1.0-1.2 mg for animal samples and 3.0-3.2 mg for plant samples. Encapsulated samples and filters were sent to Stable Isotopes in Nature Laboratory (SINLAB), University of New Brunswick, Canada, and were analysed for stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) using Continuous Flow Isotope Ratio Mass Spectrometry (CFIRMS).

2.5 Data Analysis

All analyses were carried out using the open-source software R (v. 4.3.1, R Core Team, 2023). R scripts can be found at https://github.com/rsa3007/ArcticShrubExpansion.git. Results are reported as “statistically clear” or “statistically unclear” as proposed by Dushoff et al. (2019).

2.5.1 Algal Standing Biomass

I used linear mixed-effects models (LMMs) to test the impact of tall shrub presence on the standing biomass of green algae, diatoms, and cyanobacteria. The model predictors ‘location within stream’, ‘type’, and their interaction were used together with the random effect ‘stream’ in a random intercept model. If the interaction between ‘location within stream’ and ‘type’ did not demonstrate a statistically clear influence on the response variable, I simplified the model by removing this interaction. The LMMs were conducted using the lmerTest package (Kuznetsova et al., 2017).

2.5.2 Benthic Invertebrate Diversity

Data on Chironomidae *spp.* were excluded from all analyses. Their abundance and species / functional diversity are known to be very high, and their identification is very labor-intensive. Including them as one taxon could dilute the possible changes in full benthic invertebrate communities (Rabeni & Wang, 2000). The calculations of community metrics abundance, species richness, Shannon's diversity, and evenness were done using the package *vegan* (Oksanen et al., 2022). Abundance was log-transformed. Shannon's diversity (*H*) was calculated as the Shannon-Weaver Index (Shannon & Weaver, 1963):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where S is the number of taxa and pi is the proportion of taxa i in the community. The species evenness (*J*) was calculated as a measure of equitability from Shannon's diversity (*H*) and the number of taxa S as Pielou's Evenness Index (Pielou, 1975) with:

$$J = \frac{H'}{\log S}$$

FDis was calculated from a matrix of functional groups, an abundance matrix with the "dbFD" function in the *FD* package (Laliberté & Legendre, 2010; Laliberté et al., 2014). Taxa that could not be assigned to FFGs have been excluded from the calculation of the functional dispersion (*FDis*) and the community-weighted means (*CWM*). First the weighted centroid $\boldsymbol{c}$ was calculated as:

$$\boldsymbol{c} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j}$$

where c_i is the mean value of the trait i, a_j is the abundance of species j, and x_{ij} is the attribute of species j for trait i. Following, *FDis* was calculated through the inclusion of z_j, the distance of species j to the calculated centroid:

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

LMMs were used to test the effect of tall shrub presence on the response variables abundance, richness, Shannon's diversity, evenness, and *FDis*. The predictors 'location within stream' and 'type' and their interaction were used together with the random effect 'stream' in a random intercept model. In the case that the interaction between 'location within stream' and 'type' showed no statistically clear influence on the response variable, the model was simplified by removing this interaction. The LMMs were run using the *lmerTest* package (Kuznetsova et al., 2017). After, I ran linear models (ANOVA) with predictors 'location within stream' and 'type' for all response variables to verify the mixed effects model output (Appendix 4).

2.5.3 Species and Functional Composition

Variation in benthic invertebrate species composition of replicates in up- and downstream locations of tall shrub and meadow streams was investigated through Non-metric MultiDimensional Scaling (NMDS) using the Bray-Curtis abundance-based dissimilarity (Bray & Curtis, 1957) in the *vegan* package (Oksanen et al., 2022). The NMDS axes were plotted using the package *ggplot2* (Wickham, 2016) and confidence intervals were plotted using the package *ggpubr* (Kassambara, 2023).

The *CWM* was calculated from the matrix of functional groups and an abundance matrix using the *FD* package (Laliberté & Legendre, 2010) as:

$$CWM = \sum_{i=1}^{S} p_i x_i$$

where *CWM* is the community-weighted mean value of a functional trait using p_i (the relative abundance of species i) and x_i (the trait value for species i; as in Appendix 3) (Garnier et al., 2007). To explore variation in the functional composition of replicates in up- and downstream locations of tall shrubs and meadow streams, NMDS was conducted in the same way as previously described for species composition.

To assess whether the variation of species and functional composition up to downstream in the streams was correlated with the presence of tall shrubs a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed. The PERMANOVAs were done using the "adonis2" function in the *vegan* package with 'stream' included as a first predictor (Oksanen et al. 2022).

2.5.4 Stable Isotope Analysis

To correct for variation in lipid content between the samples, lipid correction was done on the $\delta^{13}C$ values of all samples as described in Post et al. (2007) (Table 2). Biofilm samples with values of amplified N_2 smaller than 0.02 were removed to decrease analytical uncertainty in the isotope plots. To visualize the trophic level and food sources of benthic invertebrates of all streams I plotted the mean and standard deviation of $\delta^{13}C$ against $\delta^{15}N$ grouped by taxon, type, and location within the stream in *ggplot2* (Wickham, 2016). After, I visually inspected the differences between type and location within the stream of all resources separately. If no clear differences were observed in $\delta^{13}C$ and $\delta^{15}N$ within a resource, data were assumed to be similar at the whole-catchment scale and were therefore aggregated in the biplot.

Table 2 – Lipid correction models for invertebrates, biofilm, and other resources as in Post et al. *(2007).*

	Lipid Correction Model
Invertebrates	$\delta^{13}C = -3.32 + 0.99 \times C{:}N$
Biofilm	$\delta^{13}C = 1.25 + -0.00 \times C{:}N$
Other resources (% C >40%)	$\delta^{13}C = -5.83 + 0.14 \times \%\,C$

3 Results

3.1 Algal Standing Biomass

Diatom mean standing biomass was highest with (mean ± SD: 0.95 ± 1.22 µg/cm^2), followed by green algae (0.72 ± 1.38 µg/cm^2), and cyanobacteria (0.19 ± 0.22 µg/cm^2) (Fig. 4). Linear mixed-effects models (LMMs) indicated that standing biomass of green algae, diatoms, and cyanobacteria was not affected by 'location within stream' (all $p > 0.177$, $F < 1.855$) nor by 'type' (all $p > 0.488$, $F < 0.527$) (Appendix 5).

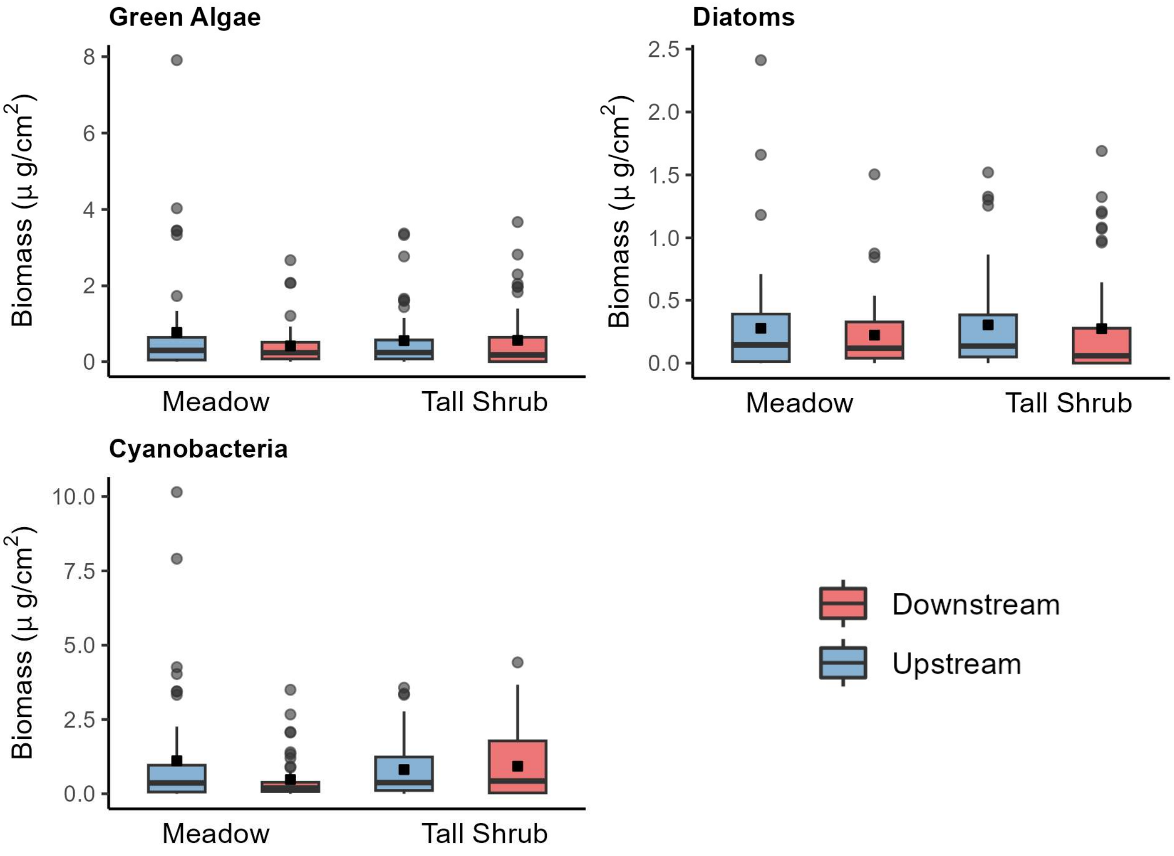

Figure 4 – Boxplots showing median, 25% and 75% quartiles, minimum- and maximum values, and outliers of standing biomass of green algae, diatoms, and cyanobacteria in microgram per cubic centimetre in up- and downstream locations of meadow and tall shrub streams. Mean values of biomass are represented by black squares.

3.2 Benthic Invertebrate Diversity

I identified a total of 1894 individuals from 33 different taxa (Ephemeroptera, 644; Plecoptera, 358; Trichoptera, 314; Diptera (excl. Chironomidae), 578) from the ten study streams. The Ephemeropteran *Baetis rhodani* was the most abundant species found with 609 individuals, accounting for 32,2% of the total abundance. Another 49,2% of the total individuals is found in four taxa, from highest to lowest abundance: Simuliidae *spp.*, Limnephilidae *spp.*, *Nemoura* *spp*., and *Dicranota spp*.. The taxon Limnephilidae *spp.* represents only *Chaetopteryx spp.* and *Annitella obscurata.* Abundance per replicate ranged from 1 to 198 with a mean abundance of 31.5 (± 34.4) per replicate (Fig. 5). Mean richness per replicate was 5.2 (± 2.1), ranging from 1 to 10 species. Mean Shannon's diversity and evenness were 1.19 (± 0.46) and 0.74 (± 0.22) respectively. A total of 28 taxa were used for the calculation of functional dispersion ($\mu = 4.08 \pm 1.93$). The LMMs fixed effects show no differences in abundance and the different metrics of diversity between stream types (all $p > 0.110$, $F < 3.230$) or locations within streams (all $p > 0.112$, $F < 2.627$), indicating that tall shrubs do not affect benthic invertebrate abundance and diversity.

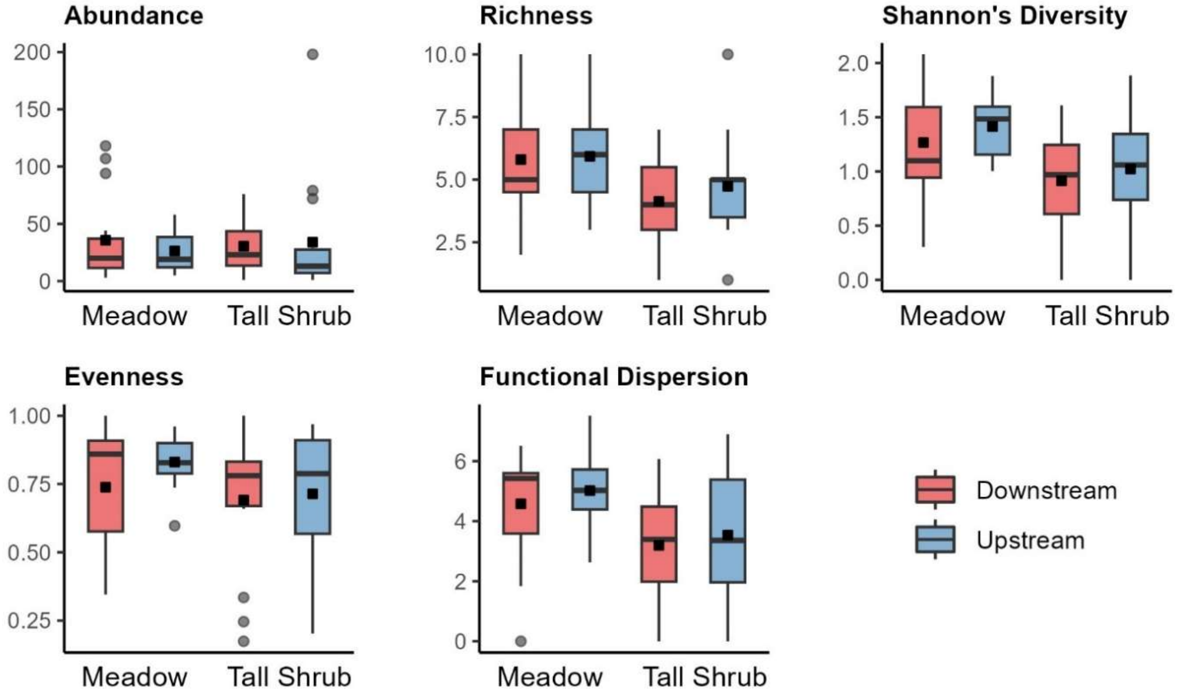

Figure 5 — *Boxplots showing median, 25% and 75% quartiles, minimum- and maximum values, and outliers of biodiversity metrics species abundance, species richness, Shannon's diversity, species evenness and functional diversity of down- and upstream locations (red and blue respectively) of meadow and tall shrub streams. Mean values of the variables are represented by the black square.*

3.3 Species Composition

The NMDS ordination of meadow streams shows no difference in species composition between up- and downstream locations as indicated by the high overlap of replicates across the different locations (Fig. 6A). In tall shrub streams, species composition shows clear differences in species composition between the upstream and downstream locations (Fig. 6B). PERMANOVA results indicate that species composition in meadow streams is not affected by location within the stream (*p* = 0.306, *F* = 1.184), but the species composition in tall shrub streams is (*p* = 0.010, *F* = 2.549) (Appendix 7). This indicates that the presence of tall shrubs affects the benthic invertebrate species composition. NMDS ordinations for all data combined including the position of each separate taxa can be found in Appendix 8.

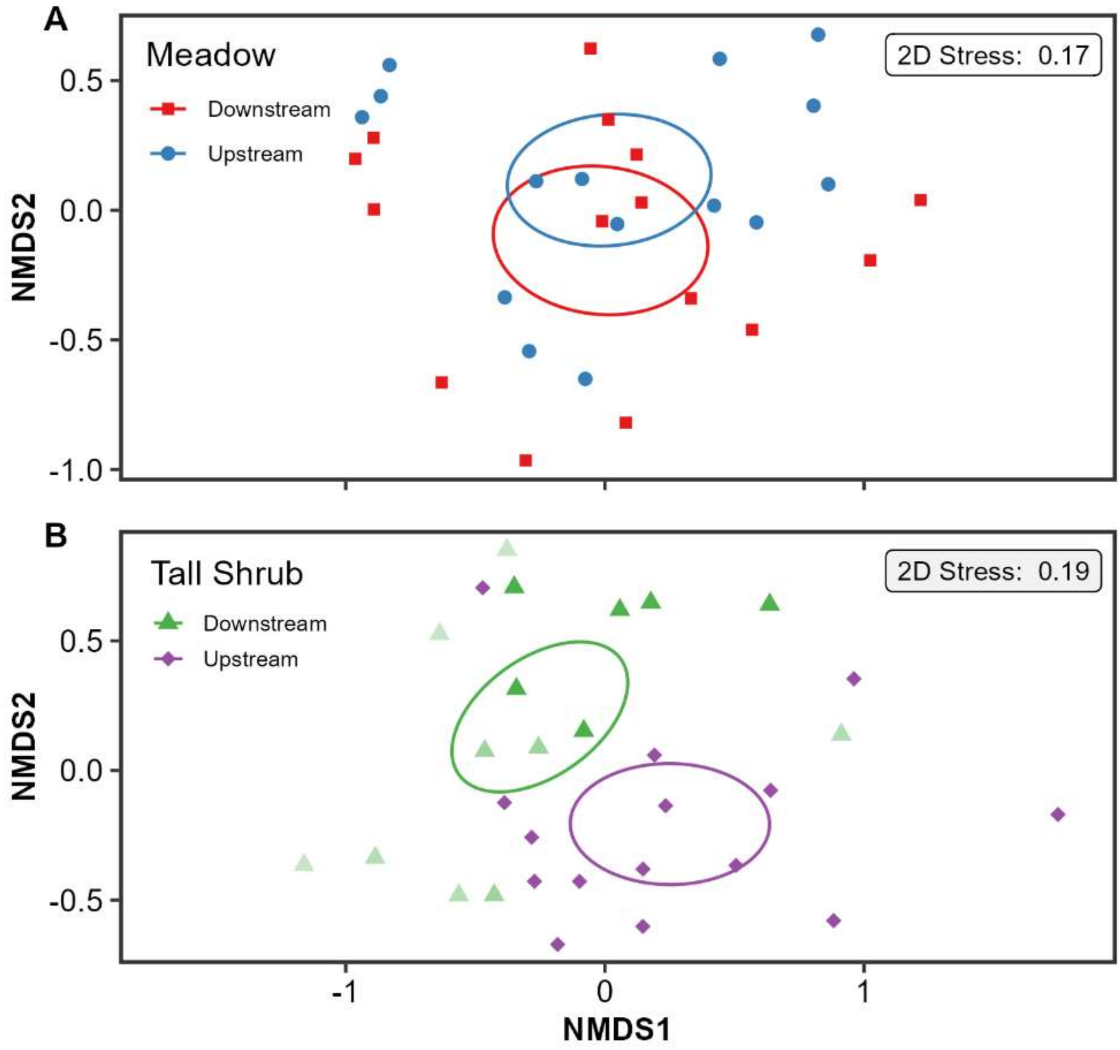

Figure 6 – Non-metric multidimensional scaling (NMDS) ordination plot of Bray-Curtis dissimilarities based on the abundances of the invertebrates species found. Ellipses show the 95% confidence interval of the mean. ***A****: The 30 replicates taken in the 5 meadow streams (stress value = 0.17, k = 2).* ***B****: The 30 replicates taken in the 5 tall shrub streams (stress value = 0.19, k=2). The tall shrub cover at the downstream station is represented by: high transparency = low shrub cover; low transparency = high shrub cover.*

3.4 Functional Composition

From the 33 total taxa, 28 taxa were assigned to the four functional traits and further used in the computation of community-weighted means. The partitioning of functional traits follows similar trends across all locations with small changes between up and downstream locations. The mean contribution of the collector functional trait was highest in all four locations with a mean contribution being 38.5% (± 19.1%) (Fig. 7). Grazer and predator functional traits follow with a mean contribution of 22.7% (± 14.2%) and 22.3% (± 18.6%) respectively. The shredder functional trait has the lowest mean contribution of 16.5% (± 13.0%).

Figure 7 - Stacked bar plot of percentage of functional feeding traits weighted means for the up-and downstream reaches of both tall shrub and meadow streams.

The NMDS ordination of functional composition in meadow and tall shrub streams, based on community-weighted means of functional traits, show overlap in mean confidence ellipses (Fig. 8). PERMANOVA results show differences in functional composition between up- and downstream meadow locations ($p = 0.048$, $F = 3.103$) (Appendix 9). The same analysis for tall shrub streams shows similar differences in functional composition between up- and downstream locations ($p = 0.030$, $F = 3.36$). As similar results were found in both meadow and tall shrub streams, no effect can be attributed to the presence of tall shrubs. NMDS ordinations for all data combined, including the position of each separate taxa can be found in Appendix 10.

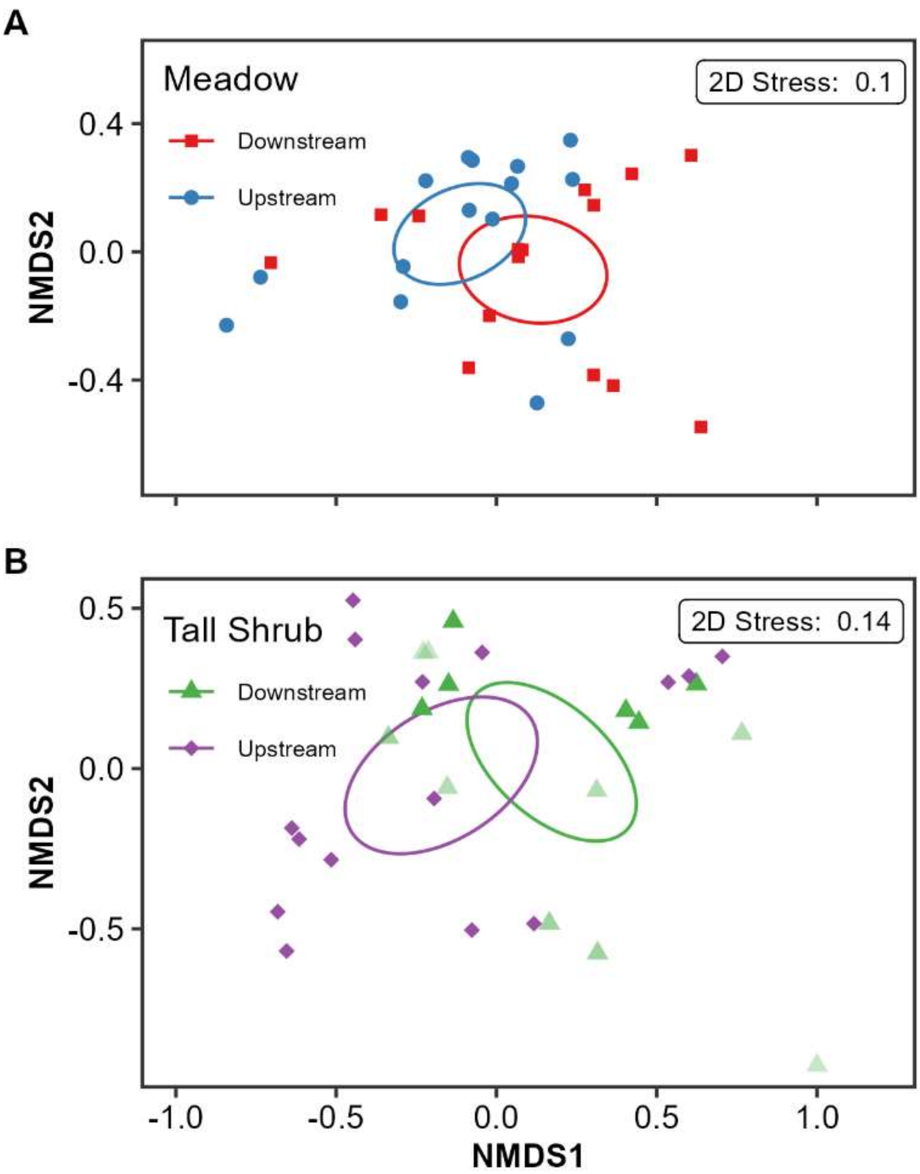

Figure 8 *- Non-metric multidimensional scaling (NMDS) ordination plot of Bray-Curtis dissimilarities based on the community weighted means of functional feeding groups of the invertebrates species found. Ellipses show the 95% confidence interval of the mean.* ***A****: The 30 replicates taken in the 5 meadow streams (stress value = 0.10, k = 2).* ***B****: The 30 replicates taken in the 5 tall shrub streams (stress value = 0.14, k=2). The tall shrub cover at the downstream station is represented by: high transparency = low shrub cover; low transparency = high shrub cover.*

3.5 Stable Isotope Analysis

The δ^{13}C values of invertebrates and resources were corrected for lipids. Invertebrate range of δ^{13}C values from -39.6 to 25.8 ‰ with a mean value of -31.5 ‰ (± 3.1) (Fig. 9). Values of δ^{15}N range from -1.4 to 4.8 ‰ with mean values of 1.1 ‰ (± 1.4). Both of the facultative grazing mayflies *Baetis rhodani* and *Ameletus inopinatus* and blackfly *Simuliidae spp.* show ^{13}C depletion in tall shrub streams compared to meadow streams. The δ^{13}C and δ^{15}N range of most of the invertebrates is broader in tall shrub downstream locations indicating a more diverse diet.

The crane fly *Dicranota spp.* shows higher δ^{15}N values compared to all other invertebrates confirming their trophic position and classification as predators.

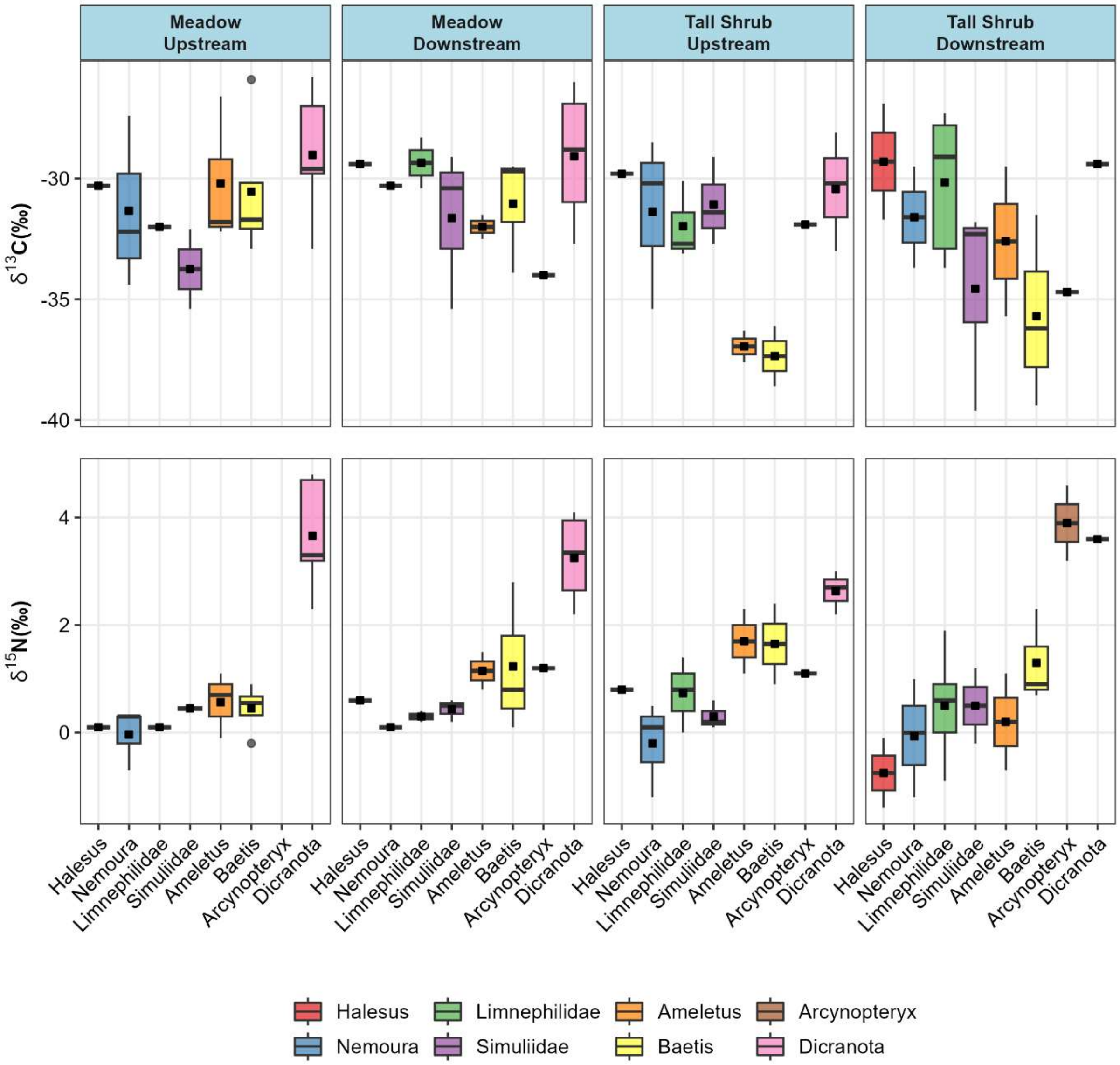

Figure 9 – Boxplots showing median, 25% and 75% quartiles, minimum- and maximum values, and outliers of invertebrate δ^{13}C and δ^{15}N values for different stream type and locations within stream. Mean values of δ^{13}C and δ^{15}N are represented by black squares. The eight taxa are presented in functional trait order; shredders, collectors, grazers, and predators. Invertebrate names have been simplified for visualization purposes: Halesus, Nemoura, Limnephilidae, Simuliidae and Dicranota are all "spp.". Ameletus = Ameletus inopinatus, Baetis = Baetis rhodani, and Arcynopteryx = Arcynopteryx compacta.

The resources δ^{13}C values range from -42.6 to -13.9 ‰ with a mean value of -30.3 ‰ (± 3.6), of which filamentous algae is most depleted in ^{13}C relative to biofilm (Fig. 10). Mean resource δ^{15}N is -1.6 ‰ (± 2.3), ranging from -9.1 to 7.6 ‰. The most negative mean δ^{15}N values are represented by birch whereas biofilm is mostly found to be enriched in ^{15}N. Similar patterns of δ^{13}C and δ^{15}N values are found across all stream types and locations.

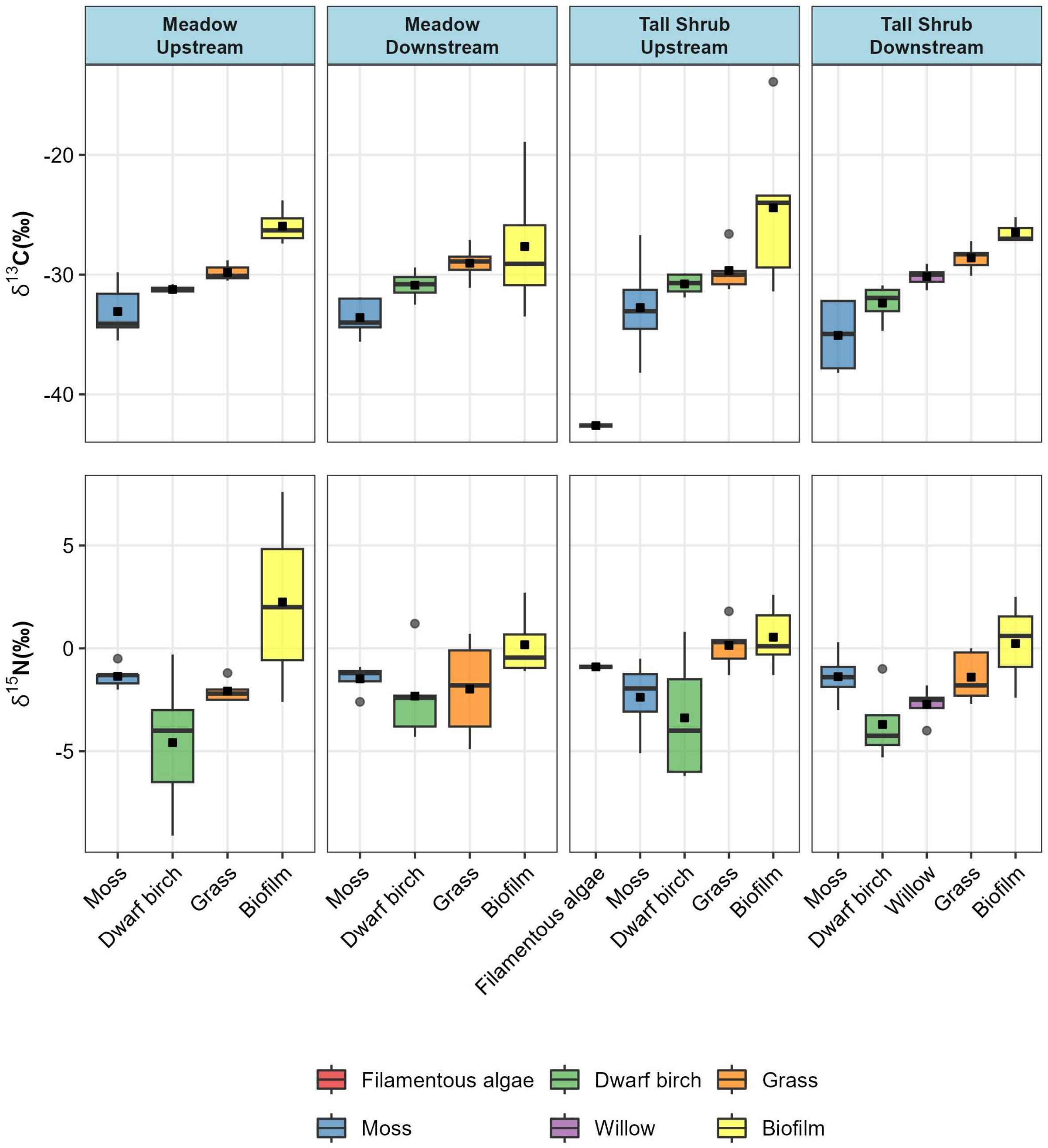

***Figure 10** – Boxplots showing median, 25% and 75% quartiles, minimum- and maximum values, and outliers of resource $\delta^{13}C$ and $\delta^{15}N$ values for different stream type and locations within stream. Mean values of $\delta^{13}C$ and $\delta^{15}N$ are represented by black squares. The different resources are presented in order of mean $\delta^{13}C$ values.*

No clear effects of location within the stream, or the presence of tall shrubs, are apparent in invertebrate isotope values $\delta^{13}C$ and $\delta^{15}N$ in both stream types (Fig. 11). A large number of invertebrates are very depleted in ^{13}C compared to the resources biofilm, willow, and grass. The low $\delta^{13}C$ values of some invertebrates indicate that filamentous algae and mosses may serve as a more important food source than the other resources as those similarly show ^{13}C depletion (Fig. 10). Further, low invertebrate $\delta^{13}C$ values may indicate the presence of another resource available in these streams, which I have not sampled.

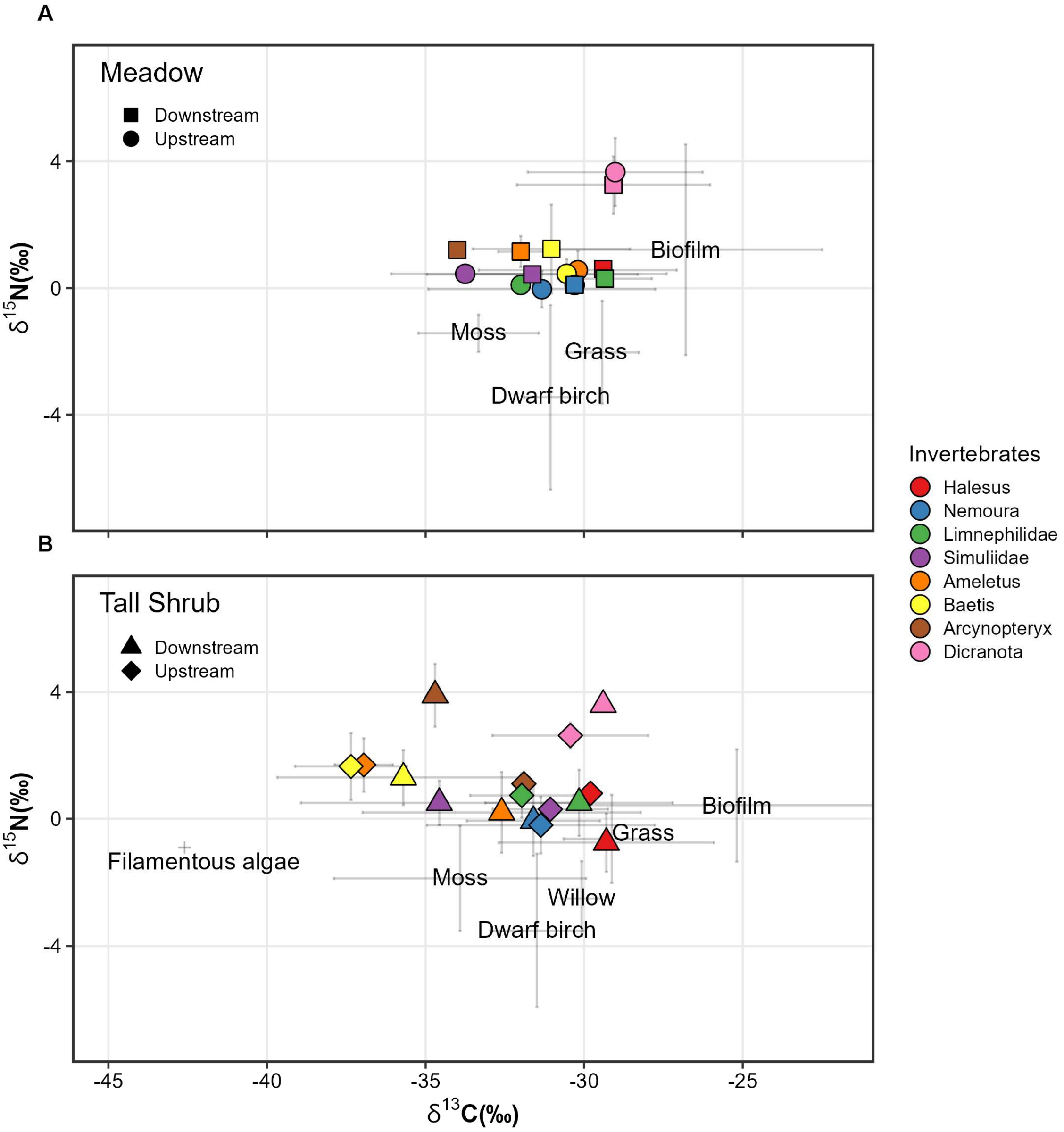

Figure 11 *– Invertebrates and resources mean δ^{13}C isotope and δ^{15}N isotope values, with their respective error bars for up- and downstream locations in meadow streams (**A**) and tall shrub streams (**B**). Invertebrate names have been simplified for visualization purposes: Halesus, Nemoura, Limnephilidae, Simuliidae and Dicranota are all "spp.". Ameletus = Ameletus inopinatus, Baetis = Baetis rhodani, and Arcynopteryx = Arcynopteryx compacta.*

4 Discussion

The results presented here provide insights into the Arctic tundra stream ecosystems and are meaningful given the projected expansion of tall shrubs into the Arctic. Terrestrial carbon, such as leaf litter, and shading by tall riparian vegetation have been recognized to be important for benthic invertebrate communities in headwater streams and to affect downstream processes (Hynes, 1970; Cummins & Klug, 1979; Vannote et al., 1980). For example, the input of terrestrial leaf litter to temperate streams is known to increase the abundance and diversity of benthic invertebrates, shift functional group composition, change diet, and support greater invertebrate populations at multiple trophic levels (Wallace et al., 1997; Giller & Malmqvist, 1998). Here, I will expand on how the proposed importance of allochthonous matter applies to the benthic invertebrate communities of Arctic tundra streams.

First, based on previous studies, I expected that the presence of tall shrubs would increase invertebrate abundance and diversity. Terrestrial leaf litter input into streams can increase food availability (Townsend, 1989; Wallace et al., 1997; Giller & Malmqvist, 1998) and contributes to sustaining a higher invertebrate abundance and diversity (Burdon et al., 2020). However, I found no effect of tall shrub presence on benthic invertebrate abundance and diversity. LeRoy et al. (2023) also did not find differences in invertebrate abundance and richness between open and closed canopy reaches in temperate mountain streams. They argued that the limited response of benthic invertebrate abundance and richness may be attributed to the small distance between the open and closed canopy reaches in their study, a factor that seems likely in my study as well. It is also possible that the anticipated positive effects of leaf litter were offset by the negative effects of shading, as shade reduces the production of periphyton and therefore decreases benthic invertebrate richness and abundance (Quinn et al., 1997). de Nadaï-Monoury et al. (2014) found similar periphyton abundance in closed compared to open canopy streams but observed greater benthic invertebrate diversity in open canopy streams. Hence, it is difficult to pinpoint a single factor that can explain the results that I found as the studies discussed above have diverse biotic and abiotic conditions. Differences in land use, riparian structure (Sandin & Johnson, 2004), or local physical and chemical variables associated with latitude (Culp et al., 2019) from temperate to Arctic catchments can determine the importance of riparian vegetation over smaller-scale drivers such as substrate and water chemistry. This may suggest that in Arctic tundra streams, factors other than tall shrubs in the riparian zone, that are further discussed below, may be responsible for determining benthic invertebrate abundance and diversity.

Second, I hypothesized a replacement of grazer taxa by shredder- and collector taxa, and as a consequence, a shift from grazer-dominated to shredder- and collector-dominated functional composition in the presence of tall shrubs. Although I found a shift in benthic invertebrate species composition in the presence of tall shrubs, there was no corresponding change in functional composition. Several facultative shredder taxa, including caddisflies (Limnephilidae *spp.*), stoneflies (*N. pictetii, A. sulcicollis, and* Leuctra *spp.*), and a cranefly (*Tipula spp.*), were indeed more closely associated with tall shrub presence. These findings are similar to the results of an experiment that demonstrated a higher abundance of shredding species (Limnephilidae *spp.* and Nemouridae *spp.*) in streams with greater litter input (Melody & Richardson, 2004). Furthermore, Estevez et al. (2019) reported the abundance of several shredding caddisflies and craneflies to be positively correlated with allochthonous resources. They also found that dominant grazing taxa like Baetidae decreased in abundance with increasing riparian cover. Similarly, I observed that grazer-collector *B. rhodani*, the most abundant species in my study, was more closely associated with tall shrub absence. These findings confirm the hypothesis that the presence of tall shrubs alters species composition.

While the benthic invertebrate species composition is different in streams with tall shrub presence, my study contradicts the common finding that the presence of tall riparian vegetation shifts the functional composition of benthic invertebrate communities. I expected a lower relative abundance of the grazer, and a higher relative abundance of the shredder functional group in the presence of tall shrubs (Houghton et al., 2023). I also expected that collector relative abundance would increase in response to increased shredder relative abundance as a result of shredder-collector facilitation (Heard & Richardson, 1995; Jonsson and Malmqvist, 2005). Since I did not detect a change in the proportion of shredders versus grazers in the presence of tall shrubs, it is unsurprising that the collector functional group did not increase in relative abundance either. Johnson and Almlöf (2016) also found no difference in the proportion of grazers versus shredders and collectors between open- and closed canopy streams in Northern Sweden.

The observed lack of response in invertebrate diversity, abundance, and functional composition indicates that although allochthonous organic matter from tall shrubs enters the stream, the invertebrate communities in those streams are not necessarily affected by the presence of tall shrubs. This observation, however, may be complicated by the chosen sampling time in which I sampled benthic invertebrates. My initial sampling time was postponed due to regulations of the Varanger National Park. During fieldwork, in the first week of July, I observed adult mayflies and empty caddisfly cases along the streams, indicating that the community of benthic invertebrates present in the stream was not complete during my sampling. Despite this potential limitation, the results from stable isotope analysis provide some insight into the findings presented above. I hypothesized that invertebrates in the presence of tall shrubs would exhibit δ^{13}C values reflecting those of tall shrub leaf litter, indicating a relatively large reliance on that resource. Interestingly, in all streams, the leaf litter was not reflected in the isotope values of many of the benthic invertebrate consumers. Benthic invertebrate isotope values were more depleted in ^{13}C than expected. While there is indication of an increased feeding range for several invertebrate species in the presence of tall shrubs, this does not appear to be the result of increased feeding on leaf litter. Rather, invertebrate δ^{13}C values indicate the integration of resources depleted in ^{13}C, whereas leaf litter is more enriched in ^{13}C. In my study, moss and filamentous algae have δ^{13}C values that can explain those of the consumers, but other unsampled low ^{13}C sources could help explain the patterns identified here.

Submerged moss is typically considered a substrate for periphyton growth and a suitable habitat for several invertebrate species, but, due to its low nutritional value, not a dietary resource itself (Cummins & Klug, 1979; Giller & Malmqvist, 1998). Nevertheless, mosses may have been eaten by some of the species I studied, as this resource is equally depleted in ^{13}C as some of the invertebrates. Previous research has shown a range of importance regarding moss consumption by benthic invertebrates, with moss avoidance commonly observed when other food sources are abundant (Suren & Winterbourn, 1991; Junger & Planas, 1994). In high-altitude streams benthic invertebrates feed primarily on autochthonous periphyton, however, they may prefer moss as a secondary carbon source over other recalcitrant sources of allochthonous carbon that require long microbial conditioning (Labed-Veydert et al., 2021). Similarly, moss has been found to be a primary food source for grazing invertebrates in low-productivity and nutrient-limited temperate headwaters (McWilliam-Hughes et al., 2009). This suggests that in the low availability of nutritional resources, invertebrates can actively feed on mosses.

The invertebrates that have similar δ^{13}C values as moss may also be feeding on the most ^{13}C depleted resource filamentous algae in combination with resources such as willow leaf litter and periphyton. Friberg and Jacobsen (1994) reported shredder caddisflies favouring filamentous algae together with nutritious alder leaf litter over other resources. Another study found grazing caddisflies to selectively feed on filamentous algae when it covered over 25% of the stream surface in late spring and early summer (Feminella & Resh, 1991). I observed filamentous algae in only two streams of which only one had a substantial cover of filamentous algae. In addition, periphyton and willow leaf litter were both present in these streams. It is unusual that in the presence of more nutritious food sources, moss or filamentous algae would be favoured by invertebrates. Perhaps the availability of willow leaf litter was not large enough to show changes in the stable isotope composition of consumers, or invertebrates in these Arctic streams have mouthparts adapted to feed more on moss and filamentous algae. A more extensive sampling of invertebrates will be necessary to increase the clarity of these results. Further, feeding experiments may address the possible trade-offs faced by the invertebrates.

Alternatively, invertebrates can be feeding on methane-oxidizing bacteria, although this resource has not been sampled in this study. Especially the grazer-collector mayflies *B. rhodani* and *A. inopinatus* show unusually low δ^{13}C values, which can indicate their reliance on a methane pathway in the stream food web (Kohzu et al*.,* 2004). This carbon source is made available by bacteria oxidizing the methane lost from the sediment (Stanley et al., 2016) and these bacteria may enter the benthic invertebrate food chain by being eaten by grazers (Kohzu et al., 2004). Trimmer et al. (2009) found grazing caddisflies with isotope values depleted in ^{13}C to have assimilated 30% of their carbon of methane origin. Similarly, another study in streams with methane input found that grazing caddisflies were depleted in ^{13}C relative to their putative food source, periphyton (Sampson et al. 2019). My results indicate that methane may play a significant role in the carbon flow of Arctic tundra stream food webs. Although methane production in oxygenated stream riffles is uncommon, methane may derive from upstream methane pools or may be present in groundwater fed streams (Stanley et al., 2016).

This study aimed to investigate whether terrestrial carbon derived from tall shrubs affects Arctic stream ecosystem functioning. My results challenge the commonly regarded importance of terrestrial input to stream ecosystems, as I find no indication that tall shrubs change diversity and abundance of invertebrates in small Arctic streams. Moreover, despite a shift in the species composition in the presence of tall shrubs, the overall functional composition of the benthic communities remains similar. The observed shift in species composition in the presence of tall shrubs is more likely attributed to changes in abiotic factors than from leaf litter. This is supported by the finding that even in an abundance of terrestrial leaf litter, the invertebrate diet appears to be dominated by other resources, indicating that the energy pathway in Arctic tundra streams is different than what is expected based on information from temperate and boreal streams. The autochthonous pathways present in my studied streams appear sufficient to sustain the invertebrate community. Additionally, the invertebrates may simply not have developed adaptations to feed on the leaf litter from the willow shrubs. As leaf litter decomposition is usually initiated by microorganisms (Graça & Canhoto, 2006; Swan et al., 2021), and microbially-mediated leaf processing is lower at higher latitude (Irons et al., 1994; Tiegs et al., 2019), it might be that leaf litter in Arctic tundra streams is less accessible for invertebrates (Graça, 2001).

My results also indicate that using the functional groups classification based on temperate streams can have several shortcomings in studying Arctic tundra streams. The use of functional traits can be a powerful tool to assess food webs and ecosystem functioning, however, the accuracy of these feeding trait-based approaches has been questioned (Hamilton et al., 2020). They have been criticized because they may neglect the local conditions and habitat that can influence a species' diet (Zah et al., 2001; Dangles, 2002; Collins et al., 2015). For example, invertebrates classified as predators can feed on algae in their first larval stages, and, generalist species may specialize in only one resource if the availability of other resources is limited (Dangles, 2002). These issues can be tackled by integrating a variety of biological traits, such as reproductive traits and body size, as discussed by Usseglio-Polatera et al. (2001). Acquiring more in-depth knowledge of the invertebrate traits in understudied areas like the Arctic tundra, will likely improve the way we analyse functional diversity and composition.

As of now, in the studied Arctic streams, autochthonous sources appear more important in sustaining benthic invertebrate communities than tall shrubs, however, species may be affected by a change in abiotic factors caused by tall shrub presence. As ecosystems in the low Arctic tundra change to more closely resemble boreal systems, the supply of allochthonous matter to streams will likely increase. However, warmer temperatures associated with these changes could equally promote the existing autochthonous pathways by increasing periphyton production. While the current input of leaf litter is not causing profound changes to benthic invertebrate communities, it remains a resource available for utilization by some species. Some of the species found in this study are also found in boreal and temperate ecosystems but differences in life history, including size and phenology, may drive variability between boreal and Arctic invertebrate populations. In addition, the physical barriers between boreal and tundra ecosystems might currently limit the movement of species capable of exploiting willow leaf litter. Over time, species from lower latitudes may overcome the dispersal barriers and establish themselves in Arctic tundra streams. Consequently, current species may gradually be replaced by those consuming more leaf litter, thereby increasing its role in the stream food web, shifting ecosystem metabolism to net heterotrophic, and affecting resources and metabolism downstream. Overall, ongoing climate change makes it challenging to predict the responses of

Arctic tundra catchments to shrubs and forest expansion. Nonetheless, my study reveals a limited response of benthic invertebrate community structure and function to the presence of tall shrubs in Arctic streams.

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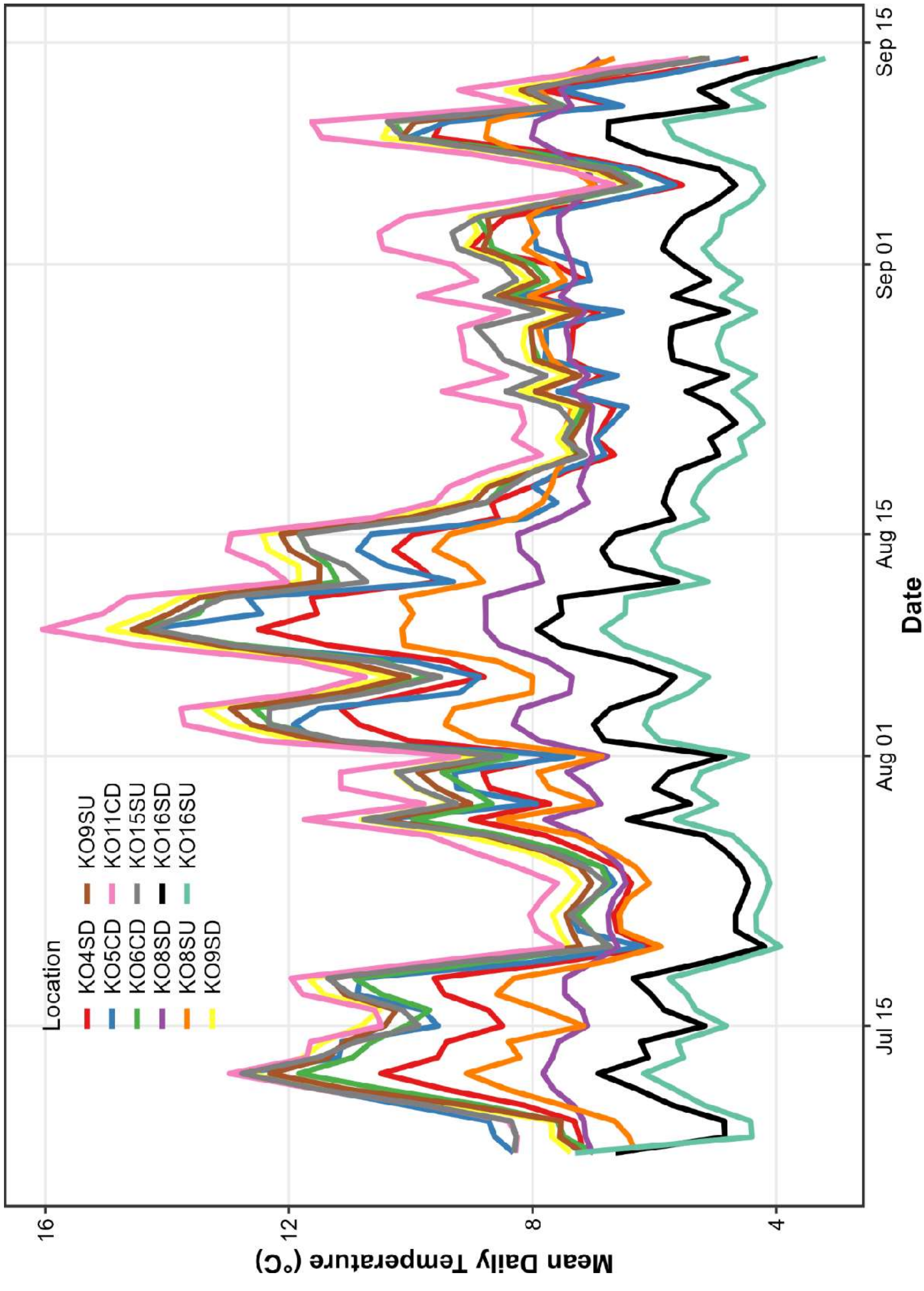
Appendix

Appendix 1 – The characteristics of the twenty study locations in the ten streams.

Sample ID	Stream	Type	Location	Date	Longitude (E)	Latitude (N)	Elevation (m)	HOBO ID	Shrub Cover (%)	Green algae (%)	Moss (%)	Boulders (%)	Cobbles (%)	Pebbles (%)	Sand (%)
KO_4_S_D	4	Tall Shrub	Downstream	02-07	30.008152	70.325145	311	20834703	21	50	0	5	45	50	0
KO_4_S_U	4	Tall Shrub	Upstream	02-07	30.011289	70.326055	315	-	0	30	0	20	30	40	0
KO_5_C_D	5	Meadow	Downstream	01-07	30.008343	70.321287	213	21478714	0	0	50	30	10	60	0
KO_5_C_U	5	Meadow	Upstream	01-07	30.006849	70.321701	213	-	0	0	0	20	30	50	0
KO_6_C_D	6	Meadow	Downstream	01-07	30.009355	70.320210	241	20834698	0	0	30	60	20	10	0
KO_6_C_U	6	Meadow	Upstream	01-07	30.006383	70.320196	247	-	0	0	0	20	10	0	60
KO_8_S_D	8	Tall Shrub	Downstream	02-07	30.056421	70.315541	304	21478708	49	0	80	50	25	25	0
KO_8_S_U	8	Tall Shrub	Upstream	02-07	30.052086	70.317312	280	21478696	0	5	5	50	25	25	0
KO_9_S_D	9	Tall Shrub	Downstream	01-07	30.068446	70.312779	220	20834709	100	0	0	0	0	10	90
KO_9_S_U	9	Tall Shrub	Upstream	01-07	30.060889	70.312777	223	-	0	0	25	10	30	30	30
KO_11_C_D	11	Meadow	Downstream	01-07	30.084909	70.312507	211	21478686	0	0	50	60	20	20	0
KO_11_C_U	11	Meadow	Upstream	01-07	30.088642	70.313376	188	-	0	0	20	60	25	15	0
KO_13_C_D	13	Meadow	Downstream	06-07	30.105300	70.306323	148	-	0	0	5	5	40	40	15
KO_13_C_U	13	Meadow	Upstream	06-07	30.104056	70.306743	149	-	0	0	5	30	40	30	0
KO_15_S_D	15	Tall Shrub	Downstream	06-07	30.167348	70.293992	140	21478687	15	0	0	0	40	40	0
KO_15_S_U	15	Tall Shrub	Upstream	06-07	30.154057	70.295058	137	21478704	0	0	0	5	15	40	40
KO_16_S_D	16	Tall Shrub	Downstream	07-07	30.182956	70.291156	75	21478707	27	0	0	0	35	35	30
KO_16_S_U	16	Tall Shrub	Upstream	07-07	30.179974	70.289601	75	20834714	0	0	10	5	40	35	10
KO_17_C_D	17	Meadow	Downstream	07-07	30.185874	70.291207	76	-	0	0	5	0	20	60	20
KO_17_C_U	17	Meadow	Upstream	07-07	30.188057	70.289172	83	-	0	5	5	0	5	60	35

Appendix 2 *– Mean daily stream temperature in degrees Celsius (°C) from 07-07-2023 – 14-09-2023. Data was collected using HOBO temperature loggers at 11 locations within streams.*



Appendix 3 – Classification of taxa to a ten-point system of the functional groups shredder, collector, grazer and predator. The darkness of the red colour reflects the amount of points of a functional group assigned to the species. Note: Invertebrate species that could not be assigned to the functional groups have been excluded from this table.

TAXA	Shredder	Collector	Grazer	Predator
Tipula salicetorum	10	0	0	0
Halesus radiatus	7	0	1	2
Halesus tessellatus	7	0	1	2
Nemoura spp.	7	3	0	0
Protenemura spp.	5	2	3	0
Limnephilidae *spp.*	4	2	3	1
Nemurella pictetii	4	4	2	0
Amphinemura sulcicollis	3	4	3	0
Leuctra fusca	3	4	3	0
Leuctra spp.	3	4	3	0
Ephemerella aroni	1	5	4	0
Isoperla obscura	1	1	1	7
Ameletus inopinatus	0	5	5	0
Apatania dalecarlica	0	2	8	0
Apatania stigmatella	0	2	8	0
Apatania zonella	0	2	8	0
Arcynopteryx compacta	0	0	2	8
Baetis rhodani	0	5	5	0
Dicranota spp.	0	0	0	10
Diura nanseni	0	0	0	10
Hemerodromia spp.	0	0	0	10
Holocentropus dubius	0	1	0	9
Holocentropus picicornis	0	1	0	9
Pedicia spp.	0	0	0	10
Pediciidae *spp.*	0	0	0	10
Plectrocnemia conspersa	0	1	0	9
Rhyacophila nubila	0	0	0	10
Simuliidae *spp.*	0	10	0	0

Appendix 4 – Summary of Analysis of Variance testing for effects of stream type (meadow and tall shrub) in downstream locations, and location (upstream and downstream) in tall shrub streams on abundance and four measures of diversity.

	Type				**Location**			
Response	NumDF	DenDF	F	P	NumDF	DenDF	F	P
Abundance	1	28	0.192	0.664	1	28	0.056	0.814
Richness	1	28	5.202	0.030	1	28	0.751	0.394
Shannon's diversity	1	27	2.453	0.129	1	26	0.475	0.497
Evenness	1	27	0.291	0.594	1	26	0.055	0.816
Functional Dispersion	1	28	4.154	0.051	1	28	0.215	0.646

Appendix 5 — Summary of mixed effects model analyses testing for effects of stream type (meadow and tall shrub) and location (upstream and downstream) on three measures of algal standing biomass with a random stream replicate term (random intercept).

Green Algae

Random effects	Variance	SD	ICC	
Stream	0.477	0.691	0.238	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	0.108	0.751
Location	1	89	0.707	0.403

Diatoms

Random effects	Variance	SD	ICC	
Stream	0.239	0.246	0.183	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	0.001	0.977
Location	1	89	1.855	0.177

Cyanobacteria

Random effects	Variance	SD	ICC	
Stream	0.012	0.107	0.288	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	0.527	0.488
Location	1	89	0.739	0.392

Appendix 6 — *Summary of mixed effects model analyses testing for effects of stream type (meadow and tall shrub) and location (upstream and downstream) on abundance and four measures of diversity with a random stream replicate term (random intercept).*

Log (Abundance + 1)

Random effects	Variance	SD	ICC	
Stream	0.387	0.622	0.385	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	0.127	0.73
Location	1	49	0.391	0.53

Richness

Random effects	Variance	SD	ICC	
Stream	1.058	1.029	0.248	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	3.230	0.11
Location	1	49	0.632	0.43

Shannon's Diversity

Random effects	Variance	SD	ICC	
Stream	0.082	0.287	0.413	
Fixed effects	NumDF	DenDF	F	P
Type	1	8.012	2.336	0.17
Location	1	47.157	2.627	0.11

Evenness

Random effects	Variance	SD	ICC	
Stream	0.022	0.148	0.441	
Fixed effects	NumDF	DenDF	F	P
Type	1	7.885	0.606	0.46
Location	1	47.028	2.562	0.12

Functional Dispersion

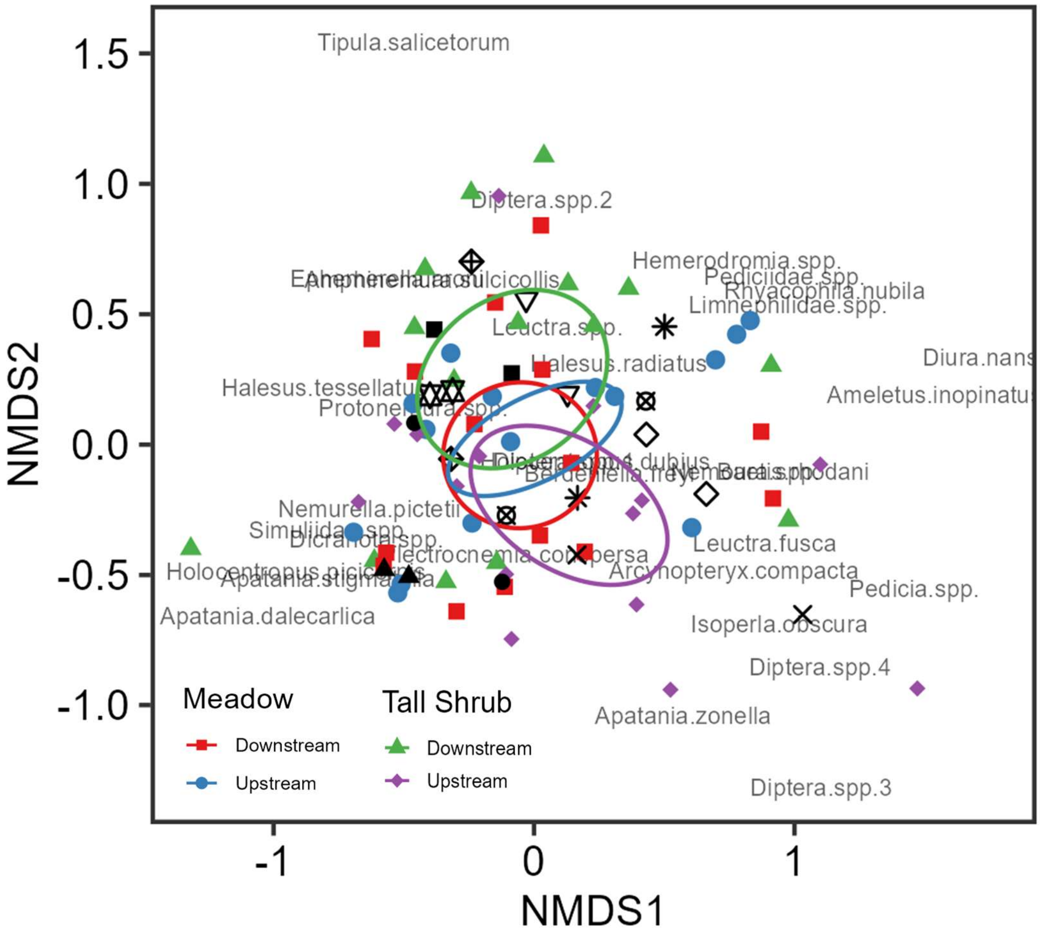
Random effects	Variance	SD	ICC	
Stream	1.412	1.188	0.406	
Fixed effects	NumDF	DenDF	F	P
Type	1	8	2.923	0.13
Location	1	49	1.120	0.30

Appendix 7 *— Summary of Permutational Analysis of Variance testing for effects of stream and location (upstream and downstream) in meadow and tall shrub streams on Bray-Curtis distance matrices of species composition.*

Species Composition

Meadow Streams	NumDF	DenDF	R^2	F	P
Stream	4	24	0.457	5.308	0.001
Location	1	24	0.026	1.184	0.306
Tall Shrub Streams	**NumDF**	**DenDF**	**R^2**	**F**	**P**
Stream	4	24	0.384	4.316	0.001
Location	1	24	0.058	2.549	0.010

Appendix 8 *— Non-metric multidimensional scaling (NMDS) ordination plot of Bray-Curtis dissimilarities based on the abundances of the invertebrates species found. The 60 replicates taken in all 10 streams (stress value = 0.22, k = 3).Points are labelled according to the station at which they were taken (Meadow: downstream = red squares, upstream = blue circles; Tall shrub: downstream = green pyramids, upstream = purple diamonds). Black points represent centroids for every station and its shape indicates the stream.*

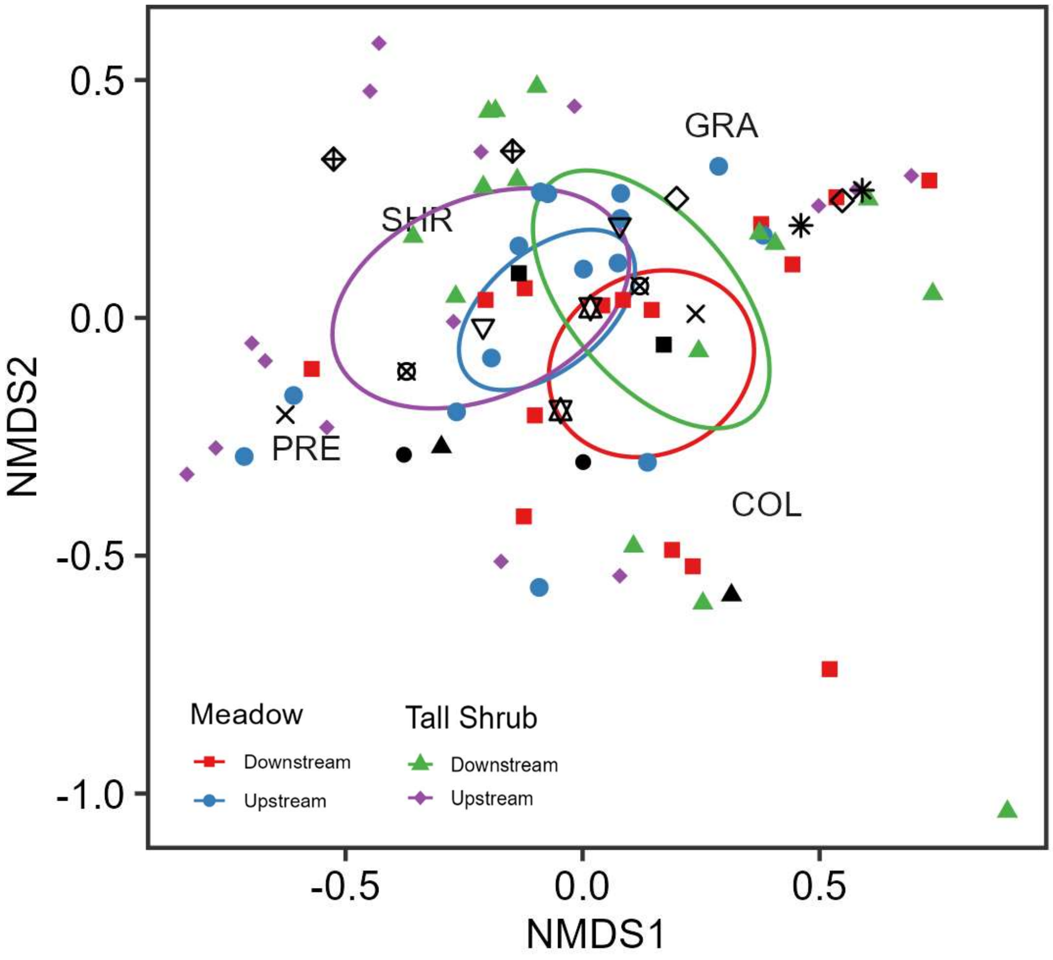


Appendix 9 — Summary of Permutational Analysis of Variance testing for effects of stream and location (upstream and downstream) in meadow and tall shrub streams on Bray-Curtis distance matrices of functional composition.

Functional Composition

Meadow Streams	NumDF	DenDF	R^2	F	P
Stream	4	24	0.327	3.290	0.005
Location	1	24	0.077	3.103	0.048
Shrub Streams	**NumDF**	**DenDF**	**R^2**	**F**	**P**
Stream	4	24	0.415	4.852	0.001
Location	1	24	0.072	3.356	0.030

Appendix 10 — Non-metric multidimensional scaling (NMDS) ordination plot of Bray-Curtis dissimilarities based on the community weighted means of functional feeding groups (SHR = Shredder; COL = Collector; GRA = Grazer; PRE = Predator) of the invertebrates species found. The 60 replicates taken in all 10 streams (stress value = 0.15, k = 2). Points are labelled according to the station at which they were taken (Meadow: downstream = red squares, upstream = blue circles; Tall shrub: downstream = green pyramids, upstream = purple diamonds). Black points represent centroids for every station and its shape indicates the stream.



to the Sea