



NTNU – Trondheim
Norwegian University of
Science and Technology

Snow Depth Alteration and Vegetation Cover Effects on Invertebrate Communities in Headwater Streams.

Aina Mærk Aspaas

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Supervisor: Sigurd Einum, IBI

Co-supervisor: Zlatko Petrin, Norsk Institutt for Naturforskning
Annika Hofgaard, Norsk Institutt for Naturforskning

Norwegian University of Science and Technology
Department of Biology

Abstract

Climate change is expected to influence both snow cover and vegetation cover in the boreal zone. The length, duration and continuity of the snow cover during winter is expected to be altered, leading to increased occurrence of snow-free periods during early winter and spring, and delayed onset of snow cover in the autumn. Furthermore, the increasing temperature is expected to cause a shift in vegetation cover in alpine areas where the tundra vegetation may be replaced by encroaching shrub and forest vegetation. Both snow cover in the winter and vegetation cover in the riparian zone may have strong impacts on the abundance, diversity and composition of the benthic macroinvertebrate community through their effect on temperature and water chemistry. In this study, I examined the effects of vegetation cover and altered snow cover on the benthic macroinvertebrate community and the composition of functional feeding habits. I also examined if the effects of altered snow cover on benthic macroinvertebrate diversity and feeding habit composition differed between vegetation cover types. This was done by manipulating the continuity and depth of snow cover in the catchments of alpine headwater streams with three different vegetation cover types, forest, shrub and tundra, to affect soil temperature and water temperature. I then compared the macro invertebrate diversity and the composition of functional feeding habits in the manipulated streams with control streams with the same riparian vegetation. The diversity and abundance of macroinvertebrates generally decreased along a gradient of decreasing cover by tall woody vegetation in the riparian zone. Furthermore, the alterations in snow cover caused a reduction in abundance and diversity as well as a shift towards more opportunistic species in the manipulated streams. The examination of the combined effects of vegetation cover and snow depth manipulation revealed that the effect of snow depth reduction may be more severe in streams draining tundra than in streams draining forest. Additionally, streams draining shrub vegetation may be the least impacted, possibly reflecting a greater accumulation of snow in shrub vegetation compared to forest and tundra.

Sammendrag

De pågående klimaendringene forventes å påvirke snødekke og vegetasjonssammensetning i den boreale sonen. Tidsrommet, varigheten og kontinuiteten til snødekket om vinteren forventes å endres mot hyppigere forekomster av snøfrie perioder i løpet av tidlig vinter og vår, samt at snøen legger seg senere på høsten/vinteren. Videre forventes det at den økte temperaturen vil føre til en endring i vegetasjonssammensetningen i alpine områder, der en stigende tregrense vil kunne føre til at tundra-vegetasjon blir erstattet av busker og skogsvegetasjon. Både snødekke om vinteren og vegetasjonssammensetning i avrenningssonen kan påvirke utbredelsen, diversiteten og artssammensetningen av bentiske makroinvertebrater ved å påvirke temperaturen i og rundt bekken, samt vannkjemien i bekken. I dette studiet har jeg undersøkt hvilke effekter vegetasjonssammensetning og endret snødekke har på utbredelsen og diversiteten av bentiske makroinvertebrater, samt sammensetningen av ulike funksjonelle fôringsgrupper. Jeg har også undersøkt hvorvidt effektene av endret snødekke påvirker utbredelsen og diversiteten av bentiske makroinvertebrater, samt om sammensetningen av ulike funksjonelle fôringsgrupper varierte mellom ulike typer vegetasjonssammensetninger. Dette ble gjort ved å manipulere kontinuiteten og tykkelsen på snødekket i avrenningsområdet til små alpine bekker som rant gjennom tre ulike vegetasjonssammensetninger, skog, busker og tundra, for å påvirke temperaturen både i marken rundt bekken så vel som vanntemperaturen i selve bekken. Deretter sammenlignet jeg utbredelsen og diversiteten av bentiske makroinvertebrater, samt sammensetningen av ulike funksjonelle fôringsgrupper i de manipulererte bekkene med kontrollbekker med samme vegetasjonssammensetning i avrenningsområdet. Diversiteten og utbredelsen av makroinvertebrater sank langs en gradient av stadig mindre trær og busker i avrenningsområdet. Videre førte en endring i snødekket til at artsdiversiteten sank og artssammensetningen ble endret mot mer opportunistiske arter i de manipulererte bekkene. Undersøkelsen av de kombinerte effektene av vegetasjonssammensetning og endring i snødekke avslørte at effekten av en endring i snødekke antakelig vil være sterkest i bekker som renner gjennom områder med tundra-vegetasjon, mens effekten vil være noe svakere i skog. Videre viste det seg at bekker som renner gjennom buskvegetasjon antakelig vil være mindre påvirket av et endret snødekke, muligens på grunn av at buskvegetasjon er bedre til å akkumulere snø enn skog- og tundravegetasjon.

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1. Introduction

The boreal zone is characterized by distinct seasonal changes in temperature and precipitation. Climate change is predicted to affect the onset of the seasons, their termination and length, leading to an alteration in the timing, extent and duration of snow cover during winter (IPCC, 2007; Haei et al., 2010). Climate change may also affect vegetation cover in alpine areas, where the current tundra vegetation is expected to be replaced by encroaching shrub and forest vegetation (ACIA 2005; de Wit et al., 2013). Climate change is hence expected to greatly affect the distribution of species, both through direct and indirect mechanisms (Stenseth et al., 2002).

Persistent snow cover during winter reduces heat loss to the air and thus has a strong impact on soil and stream water temperatures (Stieglitz et al., 2003). An altered snow depth may hence influence benthic macroinvertebrate assemblages in headwater streams. For instance, the spring snowmelt is the dominating hydrological event in alpine headwater streams and has a major role in the influx of dissolved organic carbon (DOC) into the stream: The alteration of snow depth, by affecting soil temperatures, may have strong effects on soil biochemistry including microbial activity causing differences in the leaching of carbon, nitrogen and phosphorus (Haei et al., 2010; Kreyling et al., 2012). DOC concentrations in the stream water during the spring snowmelt are thus influenced by the soil temperature during the winter season, with lower soil temperatures potentially leading to higher concentrations of DOC in the stream water (Haei et al., 2010; Ågren et al., 2012). Alterations in water chemistry may have a major impact on the distribution of benthic macroinvertebrates (Herrmann et al., 1993; Courtney & Clements, 1998; Petrin, 2011).

A reduction in snow depth and the resulting poorer insulation during cold winter periods may also influence benthic macroinvertebrate distributions by increasing the probability of the formation of frazil ice and anchor ice in the stream. The formation of anchor ice on the substrate of the stream influences the flow conditions and may affect the temperature and the supply of oxygen to the substrate (Kerr et al., 2002). Previous studies have suggested that many freshwater invertebrates do not tolerate subzero temperatures and survive by overwintering in habitats that do not freeze (Irons et al., 1993). However, some invertebrate taxa such as Chironomidae and Empididae have been found to survive in frozen habitats (Olsson, 1981; Irons et al., 1993). Thus, if alteration of the snow depth causes extensive formation of anchor and frazil ice, possibly leading to parts of the stream bed freezing solid,

then changes in snow depth may have severe effects on the composition of benthic macroinvertebrate assemblages.

Previous studies have shown that benthic macroinvertebrate assemblages in headwater streams are strongly affected by both present and past land use in the riparian zone (Cummins & Klug, 1979; Harding et al., 1998). Most studies have focused on the degradation of forested streams along a gradient of increasing anthropogenic disturbance, e.g. agriculture and urbanization, and on the consequences of disturbance on biodiversity and ecological functioning (e.g. Allan, 2004; Compin & Cereghino, 2007). An altered vegetation cover may have different effects on invertebrate diversity, e.g. through changes in the energy sources of the stream, or through changes in the amount of snow accumulating in the riparian zone. The energy input in streams with a forested riparian zone is dominated by allochthonous detritus, such as leaf litter from the surrounding trees, because shading of the stream by riparian trees may limit autochthonous primary production (Wallace et al., 1997). However, in un-shaded, open-canopy streams autochthonous primary production, e.g. by benthic algae, is expected to be an important source of energy (DeLong & Brusven, 1998; Leberfinger & Bohman, 2010). The differences in the sources of energy between different land cover types may affect the diversity of macroinvertebrates in the streams. For instance, Wallace et al. (1997) found that invertebrate abundance decreased when leaf litter was excluded from forested streams, suggesting that lower input of detritus might also lead to lower richness. Also, a comparison between streams draining forested and mire catchments suggested that species richness tended to be higher in forested streams than in streams draining mires (Petrin et al., 2007). Furthermore, the vegetation in the riparian zone may significantly affect the depth of the snow cover, the length of the period with snow cover and its continuity. In tundra areas without tall woody vegetation, the snow cover may be considerably thinner than in forests and among shrub-dominated vegetation (Vajda et al., 2006). The vegetation cover may thus influence the formation of anchor ice in streams. Swanston (1991) suggested that unless insulated by snow before temperatures drop to low levels, open canopy streams may be more susceptible to the formation of anchor ice than forested streams under the same air temperature conditions.

Invertebrates are important for many ecological processes and are vital for the ecological functioning of headwater streams. For instance, aquatic insects contribute to the decomposition of organic matter and nutrient cycling, e.g. shredding invertebrates generate fine particulate organic matter, which makes nutrients in leaf litter from the riparian zone available to other organisms. Macroinvertebrates are an important food resource, but also play

an important role in the regulation of the abundance of their own prey (Covich et al., 1999). Since benthic macroinvertebrates show great diversity in form and habit and thus respond to environmental stress in many different ways, they comprise suitable organisms to study the effects of different ecological variables including climate change and land use (Dolédec et al., 1999). The taxonomic composition of macroinvertebrates has been widely used in assessments of river health, but may not suffice to distinguish between the effects of land use and natural spatial gradients (Dolédec et al., 2011). The composition of species traits appears to be more stable and shows less variability than taxonomic composition (Beche et al., 2006). In recent years, it has therefore become increasingly common to employ a combination of taxonomic and trait composition in ecological studies (Bonada et al., 2007; Petrin et al., 2007).

Most of the research that has been done on species composition and species traits linked to stream functioning and ecosystem health, entailed a comparison between forested areas and either wetland, agricultural or urban areas (Allan, 2004; Compin & Cereghino, 2007). Although watercourses in tundra have received some attention (Harvey et al., 1998; Blaen et al., 2014), there is a relative lack of such studies on catchments draining shrub and tundra in mountain areas. It is therefore intriguing to examine headwater streams draining alpine and subalpine mountain catchments. Furthermore, although the effects of climate change (Haei et al. 2010) and the effects of land use have been studied previously (Petrin et al., 2007; Dolédec et al., 2011), their combined effects need further scrutiny.

The aim of my study was to investigate how climate change entailing the increased occurrence of snow-free periods during winter, and how vegetation cover may influence macroinvertebrate assemblages and the composition of functional feeding groups in headwater streams. Specifically, I wanted to examine if the effects of an altered snow cover on benthic macroinvertebrate diversity and the composition of functional feeding groups differs between tundra, shrub and forested streams. If streams draining tundra resemble streams draining mires, and if streams draining catchments with shrub vegetation show an intermediate pattern between tundra and forest streams, then species diversity should decrease from forest to shrub to tundra streams. I hypothesized that if an increased number of snow-free periods cause extensive formation of anchor ice, possibly leading to the stream substrate freezing solid, then this should result in a decrease in diversity, favoring more frost tolerant taxa such as chironomids Olsson, 1981; (Irons et al., 1993). Given that species diversity is

expected to be higher in forested than in tundra streams and that the reduction in snow depth may cause a loss of biodiversity, I hypothesized that snow depth alteration and vegetation type may have opposing effects on invertebrate assemblages. I hypothesized that there would be a larger proportion of grazers in tundra sites, while the forested sites should have a larger proportion of shredders, reflecting differences in the availability of autochthonous and allochthonous energy sources (Sweeney, 1993).

2. Materials and methods

2.1 Study area

The study was conducted in sub-alpine to alpine headwater streams located near Kongsvoll Biological Station (N 62.30297, E 9.60543) in Dovrefjell, Central Norway (figure 1) in the period from August 2012 until June 2013, following a pilot study in 2011/2012. The streams are located in an area where mean winter (November – April) temperature was $-4,8^{\circ}\text{C}$ and mean total winter precipitation was 155 mm in the period from 1961 – 1990 (data obtained from Norwegian meteorological institute, Fokstugu meteorological station). The geology of the study area is dominated by calcareous bedrock causing the development of alkaline soils (Sæther et al., 1981). The study streams drained catchments with three types of vegetation cover: mountain birch forests characterized by *Betula tortuosa*, shrub vegetation dominated by *Salix* spp. and *Betula nana*, and tundra vegetation characterized by graminoids, mosses and lichens. The study sites comprised fishless first and second order streams where substrate particle size ranged from gravel to cobbles interspersed with patches of moss and fine sediment. Elevation of the sites ranged from 930-1200 m above mean sea level.

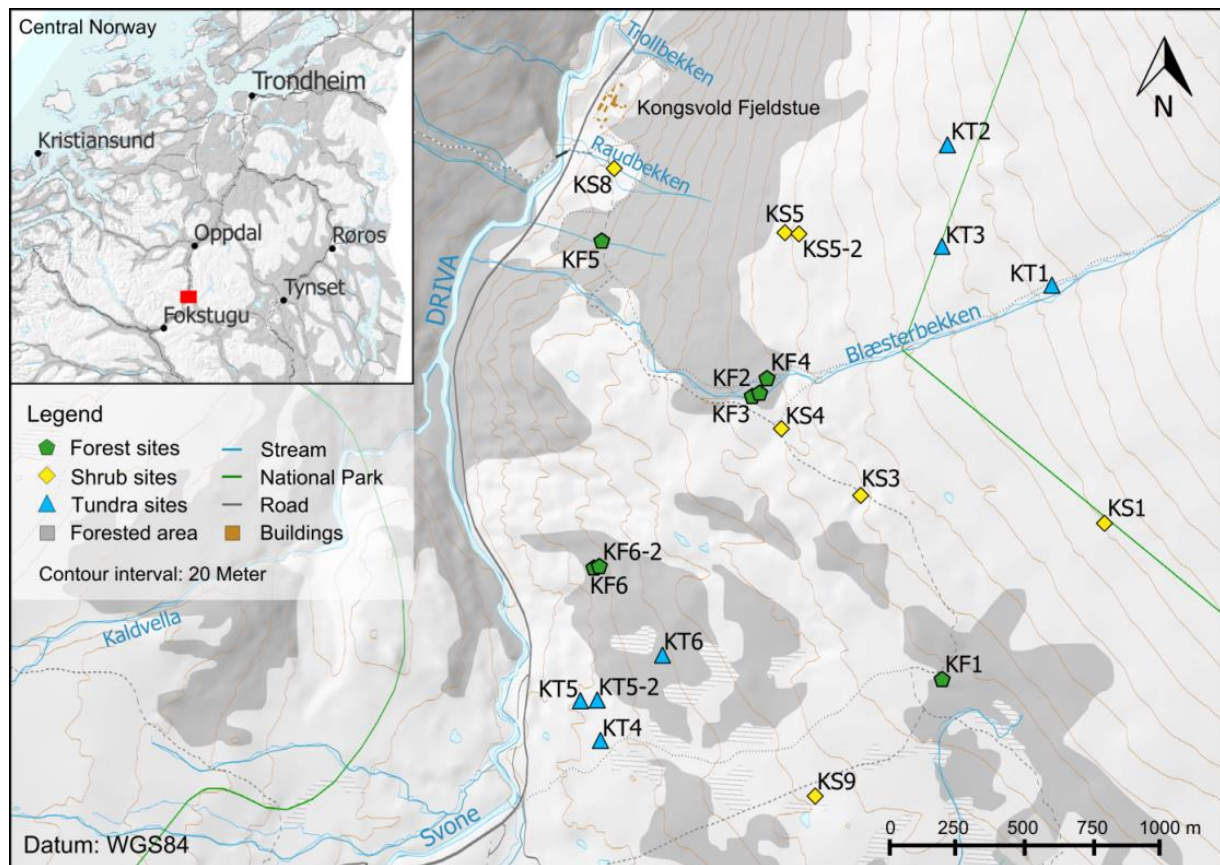


Figure 1. Map of the study area at Kongsvoll. Red square in inset map marks the location of the study area in Central Norway. Sites KT3 and KT1 were located inside Dovrefjell national park. The remaining study sites were located inside Knutshø protected area. Map designed by and reproduced with kind permission from Knut Andreas Eikland.

2.2 Study design

The study streams included six tundra, six shrub and six forest streams, eighteen streams in total (figure 1). At each of the study streams, an area of 100 m² (2.5 m * 20 m along each side of the stream) was delimited and marked. Three of the eighteen streams, one of each vegetation cover type, were selected for snow depth manipulation. Accessibility during winter was a significant criterion for the selection of the sites that were intended for the manipulation of the snow depth. In these three streams, one additional control site upstream from the plot that was subject to snow depth manipulation was established, giving a total of twenty-one sites. All land cover mapping and sampling was done within these experimental units.

2.3 Snow depth manipulation

Snow depth manipulation was done using shovels and brooms, removing as much of the snow cover as possible, but avoiding damage to the vegetation. Dates for manipulation were selected based on the weather forecast, and sites were manipulated when forecasts predicted

longer periods of temperatures below -10°C with no expected snowfall and little wind. A total of four manipulations were conducted: the first within days after the first snowfall in November 2012, and three more times during December 2012 and January and February 2013.

2.4 Vegetation mapping

Vegetation mapping was performed in August 2012 for the eighteen regular sites and in late August 2013 for the upstream control sites. Each site was mapped using five transects that were perpendicular to the stream; each transect was hence 5 m long. The mapping was conducted both on a coarse and on a fine scale. For the coarse scale mapping the vegetation was divided in four layers, tree layer, shrub layer, field layer and ground layer, and recorded for every meter along each transect. Ten vegetation and non-vegetation classes were used in total (Appendix 1). In addition, the average height of the tree- and shrub layer was recorded. For the fine scale mapping a modified point intercept method was used; placing points at 10 cm intervals along each transect and recording the vegetation and non-vegetation class that directly intercepted the point (first-hit approach). The amount of light entering the stream was recorded by a modified method for the measurement of the leaf area index (LAI) by calculations of the hemispherical area covered by vegetation and the local topography. I employed hemispherical photography using a digital camera with a fish-eye lens orientated towards the zenith and placed directly above the stream surface at five points along the stream (cf. Jonckheere et al., 2004). Images were processed with the software ImageJ (Abramoff et al., 2004). Threshold values were set manually creating binary black and white-pictures where the area covered by open sky was represented in white and the area covered by vegetation or by the local topography was represented in black. The modified index including topography was calculated using the definition of LAI in Chen et al. (1991). Since the method recorded not only the leaf area above the stream but also considered shading of the streams that was caused by the surrounding topography, I hereafter refer to the corresponding index as shade proportion index (SPI).

2.5 Abiotic factors

A thorough chemical analysis of water samples collected downstream of each site during the pilot study, including measurements of pH, alkalinity, and conductivity, the amount of calcium, total aluminum, monomeric organic aluminum, total monomeric aluminum, carbon, nitrate and phosphate, suggested a lack of conspicuous levels of calcium, aluminum, nitrate

and phosphate. Therefore, in the present study, only pH, alkalinity and dissolved/ total organic carbon (DOC/TOC) content were measured (Appendix 2). The analyses were done by an accredited laboratory (Trondheim Analytesenter). Three data loggers (HOBO Pendant[®] Temp/Light, 64K, Onset company) were placed at each site to measure soil temperature at a depth of 1 and 10 cm (approximately 1 m from the stream) and stream bottom temperature. The data loggers were placed at the sites in September 2012 and collected in September 2013, whereupon the data were downloaded to evaluate the effects of snow depth manipulations on soil temperature, stream water temperature and frost depth.

2.6 Sampling and classification of benthic macro invertebrates

Sampling of benthic macro invertebrates was done using a 250 μ m Surber net (sampling area 0.09m², Educational Field Equipment UK Ltd, EFE & GB Nets), agitating the substrate to a depth of approximately 5 cm for 1 min. At each site, 8-10 samples were taken that were approximately 2 m apart from each other along the stream in the sampling plot. The first sampling was conducted in September 2012 prior to snow depth manipulation, and the second sampling was conducted in May 2013 a few days after snowmelt. One of the tundra streams dried out during summer 2012 and was therefore only sampled in May 2013. One of the shrub streams was still covered by snow in June 2013 and was therefore only sampled in September 2012. The samples were preserved in ethanol (approximately 75%) in the field and transported to the laboratory for sorting and classification of the macroinvertebrates.

For sorting I used a sieve with a mesh size of 250 μ m. When the sorting time of a sample exceeded 2 hours, the smallest size fraction (<1mm) was subsampled. After sorting, the invertebrates were classified and enumerated with the aid of a stereomicroscope (SZX2-ILLT, Olympus Corporation, Tokyo, Japan). All macroinvertebrates were classified to the lowest possible taxonomic level with the main focus on mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera) (EPT-taxa). EPT taxa were identified to species level except for the caddisfly genus *Oxyethira* sp. For which no suitable identification keys exist. Some non-EPT taxa could not be identified to species level, but were nevertheless identified to the lowest possible taxonomic level, including some beetle larvae (Coleoptera) and dipterans. The abundances of the different taxa were used in further analyses.

2.7 Analysis of functional traits

I have focused on the feeding habit of the macroinvertebrates, since this is one of the traits which can be used to link ecological structure to functioning (Petrin, 2011). Species traits

were not measured directly using the sampled material, but the macro invertebrates were classified according to information on species traits that was assembled from the literature. Only Ephemeroptera, Plecoptera, Trichoptera and Coleoptera were used in the analysis. I distinguished five different categories: piercers, collectors, scrapers, shredders and predators. Some species showed flexible feeding habits and were therefore classified in several categories (Appendix 3).

2.8 Statistical analyses

To analyse the effects of vegetation cover and snow depth manipulation, I used generalized linear models and linear mixed models with log-transformation of the response variable and site fitted as a random variable (Pinheiro & Bates, 2000; Bolker et al., 2009). Abundance, species density, individual based rarefied species richness and sample based rarefied species richness (Gotelli & Colwell, 2001) comprised the corresponding response variables. Feeding habit was analyzed with multinomial log-linear models (Venables & Ripley, 2002). For the analysis of the composition of invertebrate assemblages, I used similarity percentages for species' contributions (SIMPER), permutational multivariate analysis of variance (permutational MANOVA) and nonmetric multidimensional scaling (nmMDS) on Bray-Curtis similarities of square-root-transformed species abundance data (K. R. Clarke, 1993; Anderson, 2001; McArdle & Anderson, 2001). Statistical analyses were performed in R, version 3.0.3 (R Core Team, 2014), using the R packages lme4, nmls, rich, nnet and vegan (Venables & Ripley, 2002; Rossi, 2011; Oksanen et al., 2013; Pinheiro, 2013; Bates, 2014). All tests were performed at a probability level of 5 % for type I errors.

3. Results

I distinguished seventy-seven benthic macroinvertebrate taxa in total, with Diptera being the most diverse taxon. Furthermore, I found six mayfly (Ephemeroptera), fifteen stonefly (Plecoptera) and eleven caddisfly (Trichoptera) species.

3.1 Effects of vegetation cover on diversity and abundance

The degree of shading (shade proportion index, SPI) positively affected taxa richness: sample-based rarefied taxa richness (SB richness) increased by approximately 20 % from the lowest to the highest SPI levels (fig. 2a, table 1). However, vegetation type had no significant effect on SB richness, and I therefore removed vegetation type from the final model. Furthermore, SPI positively affected species density: the increase was greater at the tundra sites than at the shrub and forest sites (fig. 2c & d, table 1). Vegetation type and SPI did not affect individual-based rarefied taxa richness (IB richness).

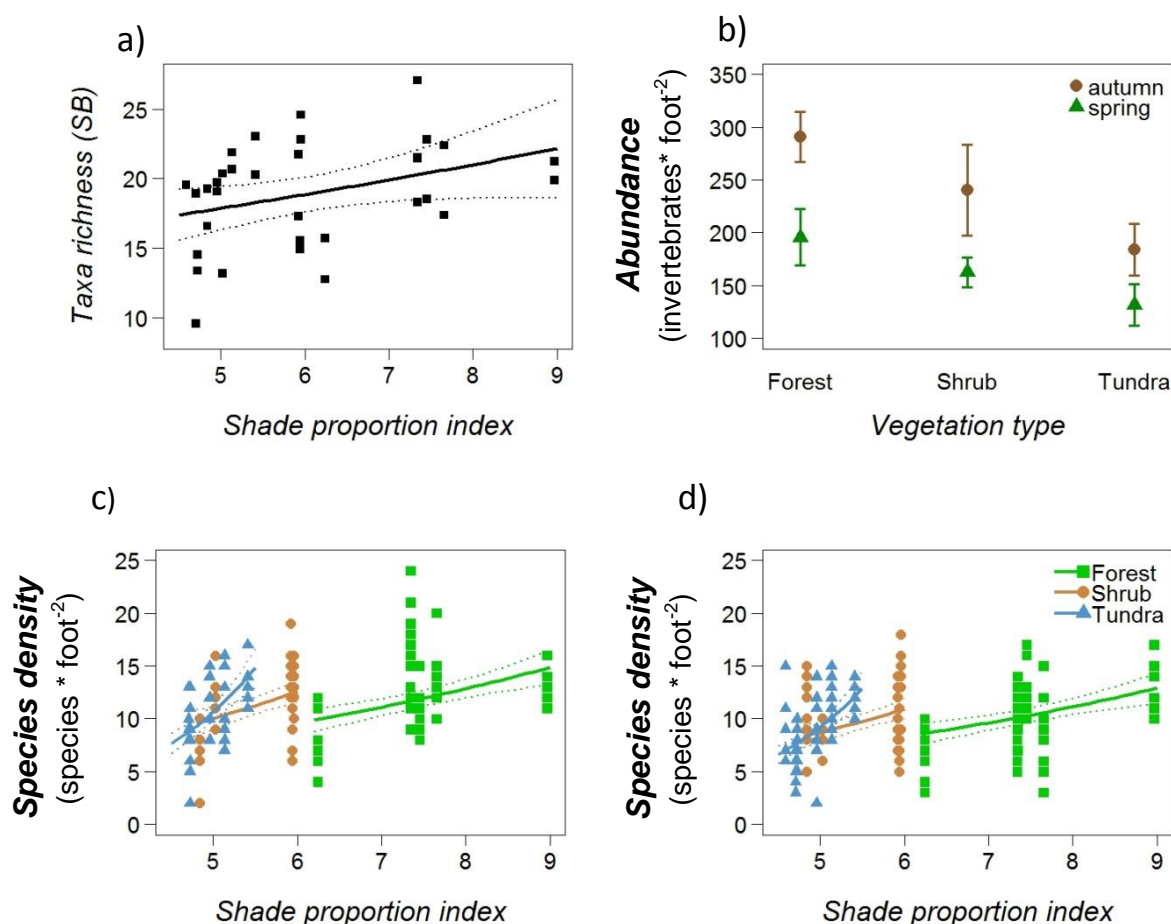


Figure 2 Effects of (a, c, d) shade proportion index (SPI) and (b) vegetation type on (a) sample based rarefied taxa richness, (b) abundance, (c) species density in autumn and (d) species density in spring .

Sample based rarefied taxa richness was standardized to 5 samples. (a, c, d) Dotted lines delimit 95 % confidence intervals; points represent raw data. (b) Dots represent mean values +/- standard error.

Species density was generally higher in autumn than in spring regardless of vegetation type, with the exception of shrub sites that showed no difference between seasons (fig.2c & d, table 1). Abundance was generally higher in autumn than in spring across vegetation types, although the difference between the seasons was greater at forest and shrub sites than at tundra sites (fig. 2b, table1).

Table 1. Effects of vegetation cover and season on abundance, species density and rarefied taxa richness. Snow depth manipulated sites were excluded from the dataset. *F*; conditional F statistic with numerator and denominator degrees of freedom.

Variable	Test statistic	p value
Abundance		
Season	$F_{1,303} = 12.6520$	< 0.001
Shade proportion index (SPI)	$F_{1,304} = 0.0032$	0.955
Vegetation type	$F_{2,305} = 6.2048$	0.002
SPI * vegetation type	$F_{2,301} = 4.5277$	0.012
Species density		
Season	$F_{1,303} = 19.5065$	< 0.001
Shade proportion index (SPI)	$F_{1,304} = 48.1215$	< 0.001
Vegetation type	$F_{2,305} = 6.3112$	0.002
SPI * vegetation type	$F_{2,301} = 10.6929$	< 0.001
Sample based rarefied taxa		
Season	$F_{1,30} = 2.8203$	0.103
Shade proportion index (SPI)	$F_{1,31} = 4.4047$	0.044

3.2 Effects of snow depth alteration on diversity and abundance

Snow depth manipulation affected the species density: From autumn (before the treatment) to spring (after the treatment), the decrease in species density was on average 3 species larger at the manipulated sites than at the up-stream control sites (fig. 3a, table 2). When comparing the manipulated sites with the inter-stream control sites (control sites in other streams), the difference was on average 2 species per sample (fig. 3a, table 3). Hence, the decrease in density was larger at the manipulated sites than at the control sites (fig.3a, tables 2 and 3). Furthermore, there was a significant treatment effect for abundance, which decreased more at the manipulated sites than at the inter-stream control sites (fig.3b, table 3). However, when

comparing the manipulated sites with the up-stream control sites, there was no significant effect of the treatment, as the decrease in abundance was of similar magnitude at the manipulated sites and at the up-stream controls sites (fig.3b, table 2).

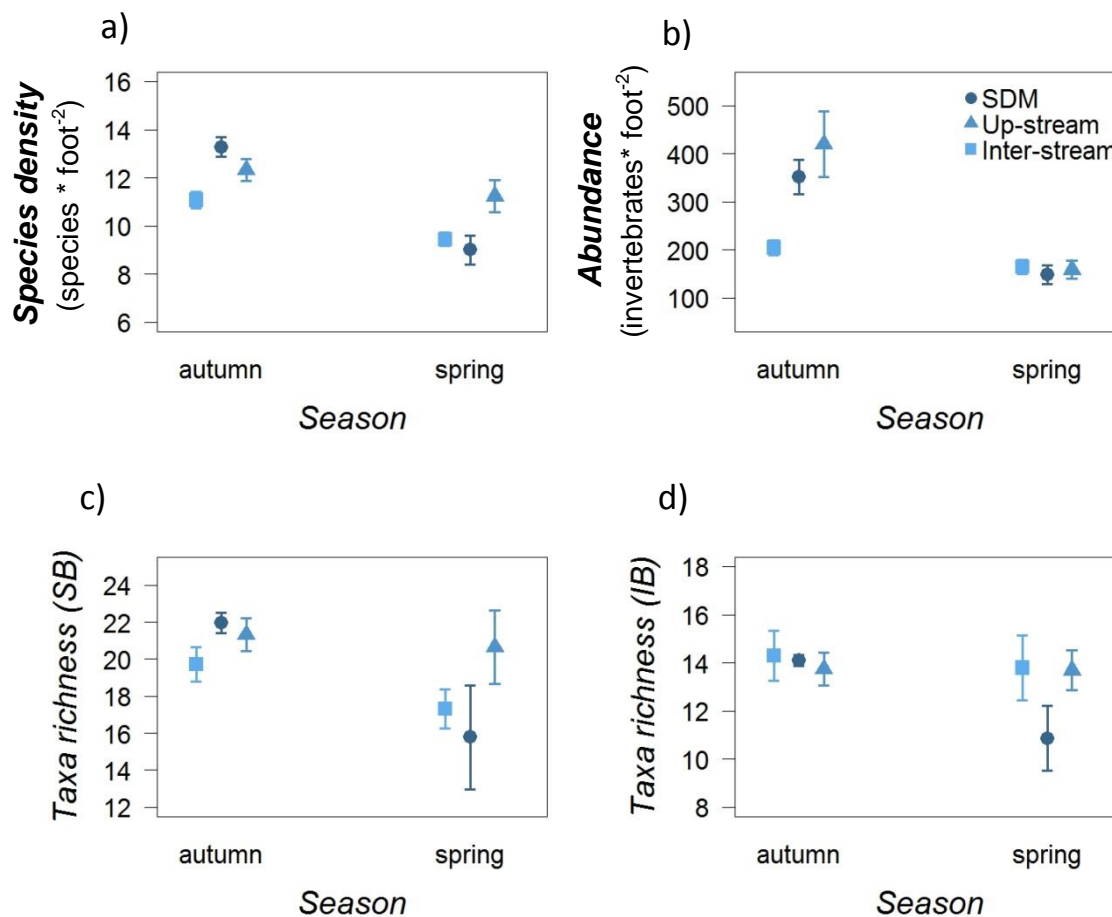


Fig. 3 The effects of snow depth manipulation on (a) species density, (b) abundance, (c) sample based rarefied taxa richness and (d) individual based rarefied taxa richness. Dots represent mean \pm 1 standard error.

There was no significant effect on SB richness ($p > 0.1$), probably due to large variation within manipulated sites and within up-stream control sites in spring (fig. 3c). IB richness was similar at manipulated and control sites in autumn. In spring there was a tendency towards lower richness at manipulated sites; however, the decrease was insignificant (fig. 3 d, table 2).

Table 2. Effects of vegetation cover, snow depth manipulation and season on abundance, species density and rarefied taxa richness. Comparison between manipulated sites and up-stream control sites. *F*; conditional F statistics with numerator and denominator degrees of freedom.

Variable	Test statistic	p value
Abundance		
Season	$F_{1,108} = 46.9221$	< 0.001
Light proportion index (LPI)	$F_{1,109} = 0.0092$	0.924
LPI * season	$F_{1,107} = 5.6750$	0.019
Species density		
Season	$F_{1,108} = 41.3418$	< 0.001
Vegetation type	$F_{1,106} = 35.1633$	< 0.001
Snow depth manipulation	$F_{1,109} = 2.2472$	0.137
Snow depth manipulation * season	$F_{1,107} = 16.0069$	< 0.001
Vegetation type * season	$F_{1,103} = 10.1198$	< 0.001
Individual based rarefied taxa richness		
Season	$F_{1,9} = 3.3061$	0.212
Snow depth manipulation	$F_{1,10} = 1.8446$	0.107
Snow depth manipulation * season	$F_{1,8} = 3.4573$	0.100

3.3 Combined effects of vegetation cover and snow depth alteration on diversity and abundance

Only tundra sites showed a difference in richness between the manipulated site compared to the inter-stream control sites in spring, with the manipulated site showing a lower richness than the controls (fig. 4a & c). When comparing the manipulated sites and the up-stream control sites, both IB richness and SB richness tended to be lower at the manipulated sites in spring, with the tundra site showing the greatest difference in IB richness and the forest and tundra site showing a greater difference in SB richness than the shrub site (fig. 4b & d).

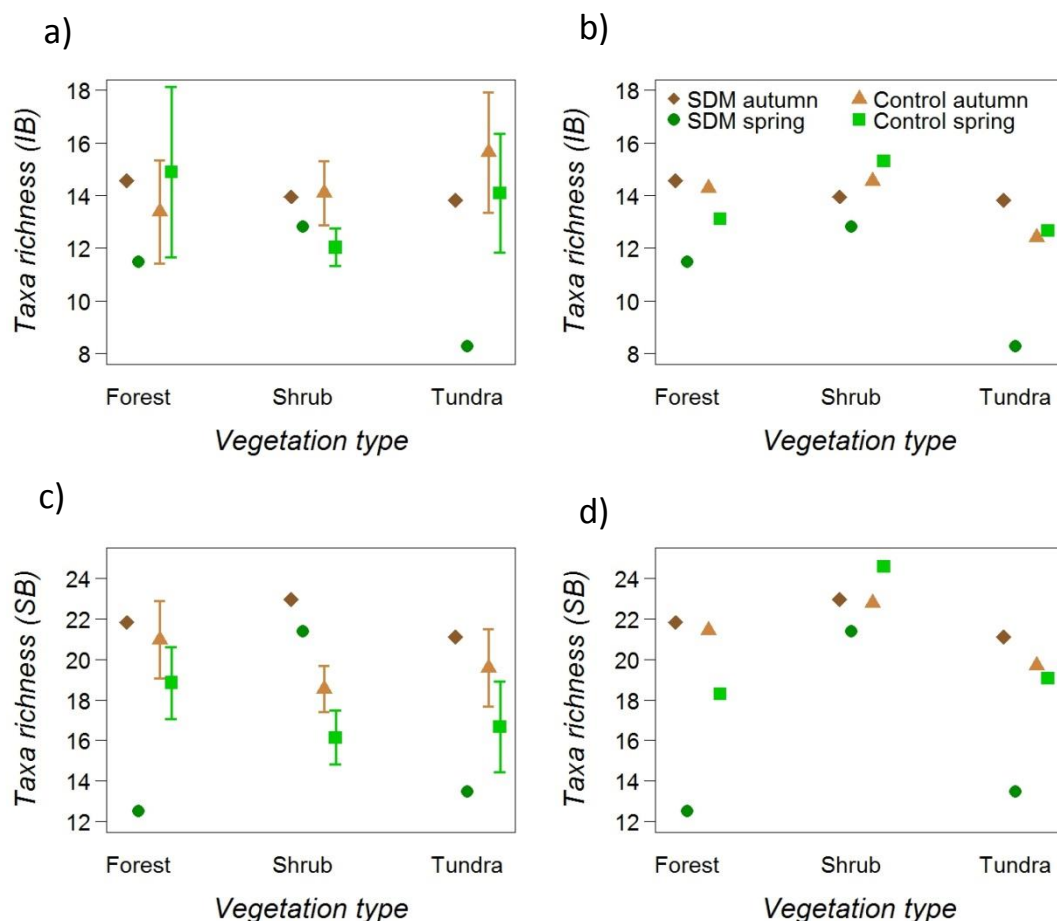


Fig. 4 Combined effects of vegetation type and snow depth manipulation on (a, b) individual based and (c, d) sample based rarefied taxa richness. (a, c) comparison between manipulated sites and inter-stream control sites. (b, d) comparison between manipulated sites and up-stream control sites. Sample based rarefied taxa richness was standardized to five samples. Individual based rarefied taxa richness was standardized to 171 individuals. Mean \pm standard error (not available for manipulated sites and up-stream control sites).

Species density decreased on average more at manipulated sites than at inter-stream control sites across vegetation types, with the greatest observed decrease at forest sites (fig. 5a & b, table 3). Furthermore, manipulated sites had generally higher species density than control sites in autumn, but generally lower species density in spring (fig. 5a). However, the manipulated shrub site had higher species density than the inter-stream control sites, but lower density than the up-stream control site in spring (fig. 5a & b, tables 2 & 3).

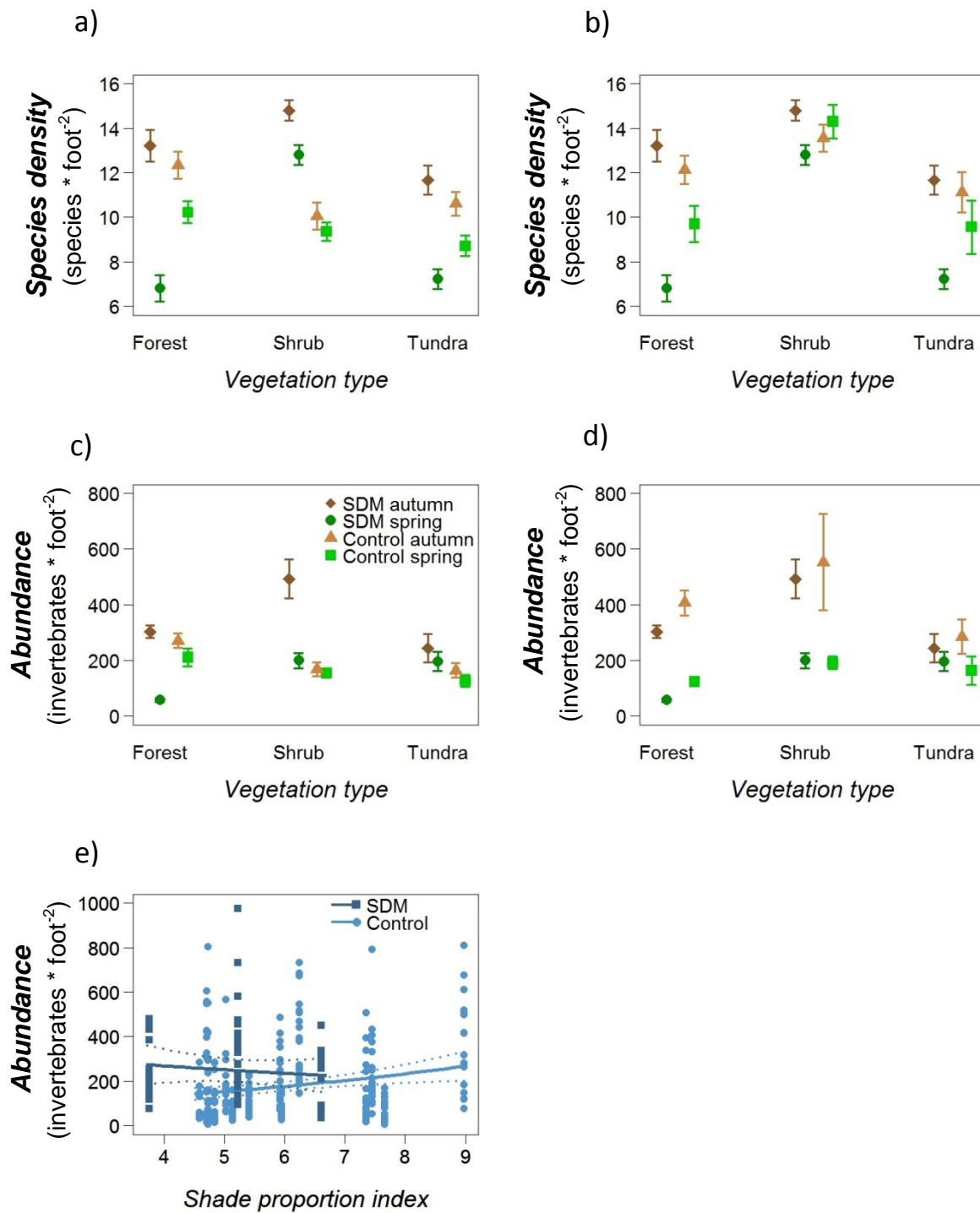


Fig. 5. Combined effects of vegetation type and snow depth manipulation on (a, b) species density and (c, d) abundance. (a, c) comparison between manipulated sites and inter-stream control sites. (b, d) comparison between manipulated sites and up-stream control sites. Mean \pm standard error. (e) Combined effects of shade proportion index (SPI) and snow depth manipulation on abundance in manipulated sites compared to inter-stream control sites. Dotted lines delimit 95 % confidence interval, points represent raw data.

The interaction between snow depth manipulation and vegetation cover had no significant effect on abundance when comparing the manipulated sites and the up-stream control sites (fig. 5d). However, there was a significant interaction effect between reduced snow cover and SPI with abundance increasing slightly at inter-stream control sites, but decreasing at manipulated sites with increasing SPI (fig. 5e, table 3). Furthermore, there was a marginally insignificant interaction effect between season, manipulation and vegetation type with abundance decreasing more at manipulated sites than at inter-stream control sites in forest and shrub, but not in tundra streams from autumn to spring (fig. 5c, table 3).

Table 3. Effects of vegetation cover, snow depth manipulation and season on abundance and species density. Comparison between manipulated sites and inter-stream control sites. *F*; conditional *F* statistics with numerator and denominator degrees of freedom.

Variable	Test statistic	<i>p</i> value
Abundance (model with LPI)		
Snow depth manipulation (SDM)	$F_{1,309} = 7.0495$	0.008
Light proportion index (LPI)	$F_{1,308} = 7.5989$	0.006
Season	$F_{1,307} = 12.1364$	< 0.001
SDM * LPI	$F_{1,306} = 4.1739$	0.042
SDM * season	$F_{1,305} = 7.7868$	0.006
LPI * season	$F_{1,304} = 4.2159$	0.041
Abundance (model with vegetation type)		
SDM	$F_{1,12} = 1.3335$	0.271
Vegetation type	$F_{2,12} = 0.6817$	0.524
Season	$F_{1,294} = 29.6736$	< 0.001
Vegetation type * SDM	$F_{2,12} = 0.7251$	0.504
SDM * season	$F_{1,294} = 6.9443$	0.009
Vegetation type * season	$F_{2,294} = 9.4808$	< 0.001
SDM * Vegetation type * season	$F_{2,294} = 3.0022$	0.051
Species density (model with LPI)		
Snow depth manipulation	$F_{1,309} = 3.1532$	0.077
Light proportion index (LPI)	$F_{1,308} = 34.2891$	< 0.001
Season	$F_{1,307} = 34.5993$	< 0.001
Snow depth manipulation * LPI	$F_{1,306} = 3.7657$	0.053
Snow depth manipulation * season	$F_{1,305} = 6.3358$	0.012
Species density (model with vegetation type)		
Snow depth manipulation	$F_{1,14} = 0.3861$	0.544
Vegetation type	$F_{2,14} = 0.5835$	0.571
Season	$F_{1,296} = 40.5239$	< 0.001
Vegetation type * snow depth manipulation	$F_{2,296} = 3.8430$	0.023
Snow depth manipulation * season	$F_{1,296} = 8.9098$	0.003

3.3 Combined effects of vegetation cover and snow depth alteration on functional feeding habits

There was a significant interaction effect of SPI, season and snow depth manipulation on feeding habit (fig. 6, table 4). The number of collectors was generally higher in autumn than in spring. At the manipulated sites collectors almost disappeared in spring, while at the up-stream control sites there was only a slight change between the seasons (fig.6, table 4). Furthermore, the number of collectors decreased while the number of shredders increased with increasing SPI at both manipulated and control sites in autumn (fig. 5a & c, table 4). This was also true for the up-stream control sites in spring (fig. 6b). However, there was no change in feeding habits with increasing SPI at the manipulated sites in spring (fig.6d). There was a slight increase in scrapers at the manipulated sites with increasing SPI in autumn (fig. 6c). Furthermore, the up-stream control sites showed no significant change in autumn but a slight decrease in scrapers with increasing SPI in spring (fig. 6a&b). Piercers were only present at the manipulated forest site and at tundra inter-stream control sites in autumn (fig. 6 c & e). The piercers disappeared after manipulation of the snow cover (fig. 6d). However, piercers also disappeared from the control sites in spring (fig. 6f).

Table 4. Effects of vegetation cover, snow depth manipulation and season on feeding habit. *LR*; log-likelihood ratio statistic. All p-values <0.001.

Variable	F value
Feeding habit (manipulated vs. inter-stream control)	
Season	<i>LR</i> = 104.09296
Light proportion index (LPI)	<i>LR</i> = 125.20873
SDM	<i>LR</i> = 34.77878
SDM * LPI	<i>LR</i> = 484.13037
LPI * season	<i>LR</i> = 554.50184
SDM * season	<i>LR</i> = 266.70009
SDM * LPI * season	<i>LR</i> = 552.11259
Feeding habit (manipulated vs. up-stream control)	
Season	<i>LR</i> = 127.653
LPI	<i>LR</i> = 866.059
SDM	<i>LR</i> = 208.906
SDM * LPI	<i>LR</i> = 33.156
LPI * season	<i>LR</i> = 199.920
SDM * season	<i>LR</i> = 26.001
SDM * LPI * season	<i>LR</i> = 25.579

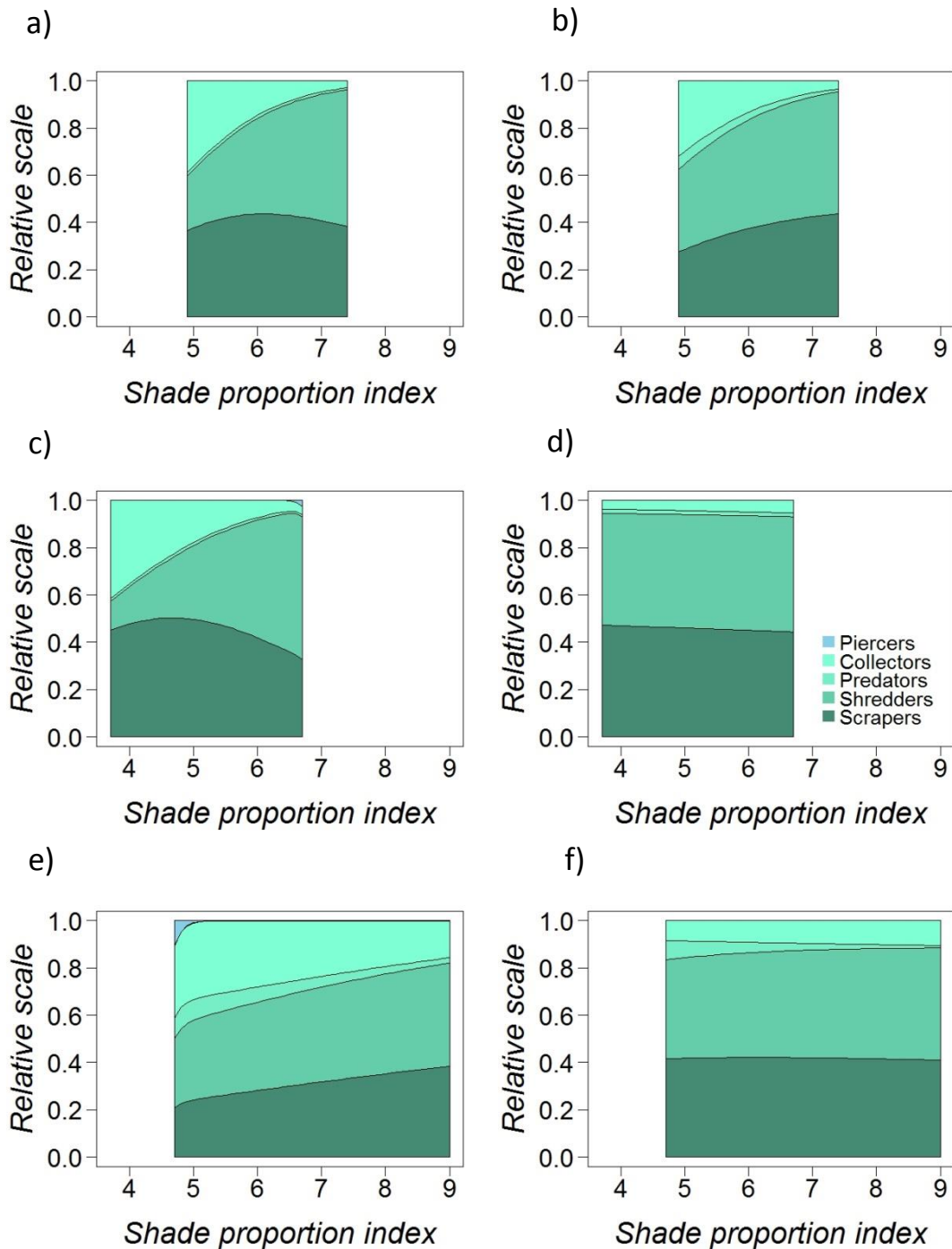


Fig. 6 Combined effects of shade proportion index (SPI) and snow depth manipulation on feeding habit (relative numbers) in (a) up-stream control sites in autumn, (b) up-stream control sites in spring, (c) snow depth manipulated sites in autumn, (d) snow depth manipulated sites in spring, (e) inter-stream control sites in autumn and (f) inter-stream control sites in spring. Plotting area limited according to the appropriate range of SPI values for the different sites.

3.4 Combined effects of vegetation cover and snow depth alteration on species composition

The effects of stream identity (site) and the interaction between stream identity and season were more important determinants of macroinvertebrate assemblages than vegetation type and snow depth manipulation (table 5). Thus, variation among streams explained a larger proportion of the compositional differences than vegetation type, or whether or not snow depth was manipulated. The results also suggested considerable variation that was explained by other factors than those considered in my study. However, for the manipulated forest and tundra sites there was a tendency towards the presence of different assemblages between seasons (fig. 7 a & b).

Table 5. Permutational MANOVA on Bray-Curtis distances for the macroinvertebrate assemblages. Comparison between manipulated sites and inter-stream control sites.

Source	d.f.	SS	MS	F	r^2	P
Snow depth manipulation (SDM)	1	2.255	2.2553	18.2876	0.02846	<0.001
Vegetation type	2	2.637	1.3183	10.6900	0.03328	<0.001
Season	1	3.267	3.2673	26.4939	0.04124	<0.001
Site	14	22.272	1.5908	12.8998	0.28109	<0.001
SDM * season	1	1.256	1.2561	10.1859	0.01585	<0.001
Vegetation type * season	2	1.772	0.8858	7.1825	0.02236	<0.001
Site * season	12	10.752	0.8960	7.2653	0.13570	<0.001
Residuals	284	35.023	0.1233		0.44203	
Total	317	79.233			1	

When comparing up-stream and manipulated sites after aggregating the dataset to one value per season*site combination, there was a clear trend towards separation between the manipulated sites and the up-stream control sites in spring, whereas there was no difference between manipulated and control sites within each vegetation type in autumn (fig. 7c & d). Furthermore, the change was largest for forest sites, and smaller for shrub and tundra sites (fig. 7d).

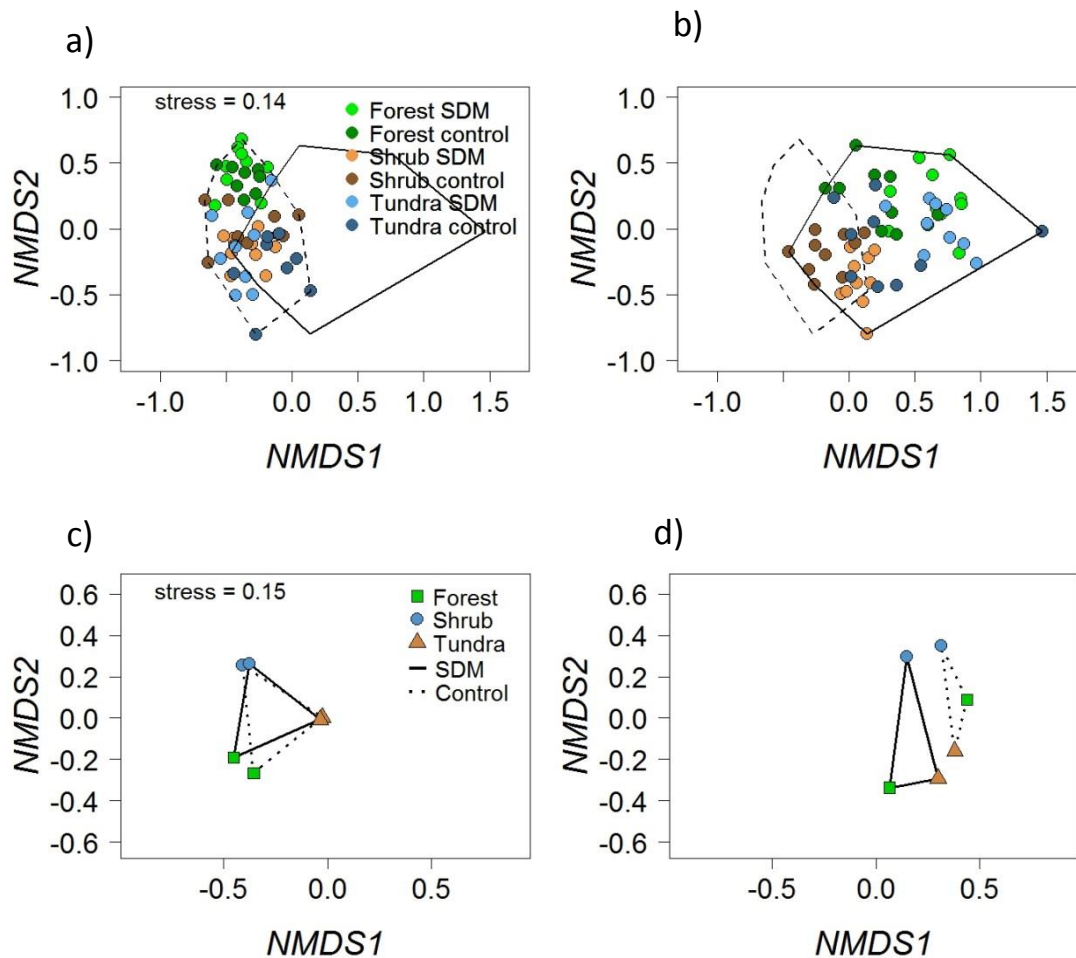


Fig. 7. Non-metric multidimensional scaling (nmMDS) plot of snow depth manipulated (SDM) sites and up-stream control sites in (a) autumn and (b) spring with non-aggregated data (8-10 points per site*season – combination). Dashed line delimits the autumn samples, solid line delimits the spring samples. Four dimensional solution, only the first two dimensions are plotted. (c, d) nmMDS – plot of snow depth manipulated sites and up-stream control sites with aggregated data (one point per site*season - combination). (c) autumn, (d) spring. Two dimensional solution.

Differential distribution of non-biting midges (Chironomidae) and Oligochaeta played a significant role in explaining the compositional differences between the different vegetation types and between the manipulated and the control sites. Additionally, the differences between the shrub sites and the tundra sites were also driven by differences in the abundance of the stonefly *Nemurella pictetii*, the mayfly *Baetis rhodani* and blackflies (Simuliidae). Furthermore, the stoneflies *N. pictetii* and *Leuctra nigra* differed in abundance both between forest and shrub sites, as well as between forest and tundra sites. *B. rhodani* was most prominent at the tundra sites, whereas *N. pictetii* was more prominent at shrub than at tundra sites. Both *N. pictetii* and *L. nigra* were more prominent at forest than at shrub sites (Table 6).

Table 6. Species contributions (SIMPER) to dissimilarities of benthic macroinvertebrate assemblages between the different vegetation types. Vegetation type refers to the vegetation type at which the respective taxon was more abundant. D, Diptera; P, Plecoptera; E, Ephemeroptera.

Taxon	Species contribution (%)	Vegetation type
Shrub vs. Tundra		
Chironomidae (D)	40.03	Shrub
Oligochaeta	12.04	Shrub
<i>Nemurella pictetii</i> (P)	10.04	Shrub
Simuliidae (D)	5.18	Shrub
<i>Baetis rhodani</i> (E)	4.56	Tundra
Forest vs. Tundra		
Chironomidae (D)	38.39	Forest
Oligochaeta	13.49	Forest
<i>Nemurella pictetii</i> (P)	13.37	Forest
<i>Leuctra nigra</i> (P)	5.67	Forest
Forest vs. Shrub		
Chironomidae (D)	35.68	Forest
<i>Nemurella pictetii</i> (P)	15.95	Forest
Oligochaeta	12.54	Forest
<i>Leuctra nigra</i> (P)	6.65	Forest

When comparing the manipulated sites with inter-stream control sites, I found that the difference was driven by different distributions of Chironomidae and Oligochaeta, the stoneflies *N. pictetii* and *Nemoura cinarea*, and the mayfly *B. rhodani*, all of which were more abundant at the control sites than at the manipulated sites. The Chironomidae and Oligochaeta were also responsible for the difference between the manipulated sites and the up-stream control sites, together with blackflies, *N. pictetii* and *B. rhodani*. With the exception of *B. rhodani*, which were more abundant at the manipulated sites, all taxa were most abundant at the up-stream control sites (table 7).

Table 7. Species contributions (SIMPER) to dissimilarities of benthic macroinvertebrate assemblages between the snow depth manipulated sites and the up-stream and inter-stream control sites. Treatment refers to the treatment type at which the respective taxon is more abundant. USC = Up-stream control, ISC = Inter-stream control, SDM = Snow depth manipulated. D, Diptera; P, Plecoptera; E, Ephemeroptera.

Taxon	Species contribution (%)	Treatment
Up-stream control vs. SDM		
Chironomidae (D)	28.88	USC
<i>Nemurella pictetii</i> (P)	18.28	USC
Oligochaeta	12.97	USC
<i>Baetis rhodani</i> (E)	8.1	SDM
Simuliidae (D)	6.6	USC
Inter-stream control vs. SDM		
Chironomidae (D)	27,5	ISC
<i>Nemurella pictetii</i> (P)	9,7	ISC
Oligochaeta	9,6	ISC
<i>Baetis rhodani</i> (E)	4,1	ISC
<i>Nemoura cinarea</i> (P)	10,8	ISC

4. Discussion

The results suggested generally decreasing abundance and diversity along a gradient with decreasing cover by tall woody vegetation in the riparian zone. At sites with reduced snow depth, diversity also decreased. However, the decrease in diversity was largest at the tundra site, whereas I measured only a small decrease at the shrub site. Snow depth manipulation also shifted the species composition towards the predominance by the relatively opportunistic *B. rhodani*, whereas the abundance of the shredding stoneflies *N. pictetii* and *N. cinerea* in addition to further taxa decreased. Also, following snow depth manipulation macro invertebrates feeding on fine particulate organic matter were replaced by those feeding on coarse particulate organic matter and periphyton. In summary, the effects of reduced snow cover were largest at the least diverse site, the most marginal site.

4.1 Study design

My study design entailed a gradient from forested to tundra streams. Vegetation type was well replicated yielding valuable information on among site variation along the whole vegetation cover gradient. Also, my study design considered the combined effects of snow depth manipulation and vegetation cover. In addition, I studied all sites during two seasons, before and after manipulation of the snow depth. Last, my study design included two levels of control: I compared the sites where I reduced snow depth both with unmanipulated up-stream control sites and with different streams that were not subject to snow depth manipulation. However, logistical constraints disallowed for replicating snow depth manipulation for each vegetation cover type, and I therefore had to use information about within site variation at the manipulated sites and among-site variation between unmanipulated sites to assess the biological significance of the combined effects of vegetation cover and snow depth manipulation (Hurlbert, 1984; Oksanen, 2001). Also, it is important to point out that the reductions in snow depth were only temporary, whereas the differences in vegetation cover remained permanent, suggesting that the strengths of the effects of the two different variables were not directly comparable. Despite the limitations in my study design, I am confident that the multiple levels of control and extensive information on natural variation among sites allowed for an informed assessment of the biological significance of both vegetation cover and snow depth manipulation.

4.2 Effects of vegetation cover and reduced snow depth

The decrease in diversity and abundance with decreasing shading and thus lower input of leaf detritus was in agreement with previous studies (Melody & Richardson, 2004; Wallace et al., 1997). Open canopy streams are traditionally thought of as depending on autochthonous energy deriving from primary production e.g. by benthic algae because unshaded streams are more exposed to sunlight and receive less allochthonous detritus (Sweeney, 1993; Allan, 2004). However, in the study period autochthonous production was generally low across all study streams (Eikland, unpublished), which may indicate that the decreasing input of litter with decreasing shading may not be compensated for by increasing autochthonous primary production in the study streams (e.g. by benthic algae; Hagen et al., 2010). Hence, fewer resources may be available in streams with lower SPI leading to a reduction in benthic macroinvertebrate abundance, species density and SB richness (Fisher & Likens, 1973; Mann, 1988; Wallace et al., 1997). However, when standardizing to a given number of individuals by using IB richness, I found no significant effect of vegetation cover suggesting that the study streams were very patchy and consisted of many small micro habitats inhabited by different macroinvertebrate assemblages (Gotelli & Colwell, 2001). Furthermore, the reduction in SB richness and species density but not in IB richness indicates that the observed loss in diversity is driven by decrease in abundance.

As expected, the decrease in species density, SB richness and IB richness was greater at manipulated sites than at both up-stream and inter-stream control sites. This indicates that a reduction in snow cover may have severe effects on macroinvertebrate communities as it may increase the extinction probability of species (Oswood et al., 1991; Irons et al., 1993). Abundance was similar at all sites (manipulated, up-stream control and inter-stream control sites) in spring. However, in autumn the abundance was much greater at the manipulated sites than at the inter-stream control sites. Yet, the effect of snow depth manipulation on abundance was insignificant when comparing manipulated sites with up-stream control sites. Hence, there was no noticeable effect of the manipulation on abundance. This indicates that the abundance of the species that survived the manipulation increased following the disappearance of possibly frost intolerant species (Olsson, 1981). The manipulated sites and inter-stream control sites were overlapping in both species density and SB richness, but not in IB richness. Both up-stream and inter-stream sites had similar IB richness, while manipulated sites were clearly characterized by lower IB richness. Species density and SB richness disregard the number of individuals taking only samples into account. However, IB richness

accounts for the number of individuals, so any pattern in IB richness is not explained by differences in abundance (Gotelli & Colwell, 2001). This implies that for a fixed number of individuals the number of species was lower at the manipulated sites than at the control sites. The variance in SB richness between manipulated sites was much larger in spring than in autumn and larger than the variation within up-stream control sites and within inter-stream control sites. This indicates that the snow depth manipulation might have caused different responses at the three manipulated sites, which is further supported by examining the combined effects of snow cover reduction and vegetation type (Vajda et al., 2006).

Some of the effects of snow cover reduction were only visible when comparing the manipulated sites with the up-stream control sites suggesting that the effects might be masked by the great variation between different streams (Meyer et al., 2007; Clarke et al., 2008). However, there were strong indications that the interaction between snow cover reduction and vegetation had a significant effect on IB richness in tundra leading to fewer species at tundra sites after manipulation even when compared with inter-stream control sites. A possible explanation for this is that open streams are more exposed to cold temperatures during winter due to a thinner snow cover and hence, a poorer insulation possibly leading to the extinction of freeze intolerant species (Olsson, 1981; Irons et al., 1993; Vajda et al., 2006). Furthermore, there appeared to be a significant effect on SB richness, with a slightly greater decrease at manipulated forest sites than at manipulated tundra sites both when comparing with up-stream control sites and with inter-stream control sites. There seemed to be little effect of the interaction between treatment, vegetation type and season on the diversity in shrub streams. A possible explanation for the weaker trends found at the manipulated shrub site compared to the forest and tundra sites is that the manipulated tundra and forest sites bottom froze during the winter with minimum in-stream temperatures dropping to -8.3°C and -3.5°C , respectively (Appendix 4). Macroinvertebrates are generally not adapted to freezing and tend to survive by retreating to microhabitats that do not freeze (Olsson, 1981; Sinclair et al., 2003). This might explain why reduced snow cover with subsequent bottom freezing at the tundra and forest sites led to such strong impacts on the invertebrate diversity (Hoffsten, 2003). The effect seemed to be stronger at the tundra than at the forest site, which could be explained by the lower temperature at the tundra stream (Vajda et al., 2006). Furthermore, the tundra site had 140 days with sub-zero water temperatures, while the forest site had 122 days of sub-zero water temperatures (Appendix 4). The shrub site and the up-stream control sites did not bottom freeze (min. in-stream temp. $\sim 0^{\circ}\text{C}$). There are several possible explanations

for this difference in minimum temperature between the manipulated sites. Firstly, shrubs tend to accumulate snow better than tundra and forest vegetation (Vajda et al., 2006). This may have led to shorter periods from the onset of the manipulation to wind covering the sites with snow again in shrub compared to forest and tundra catchments. Furthermore, forest vegetation may accumulate snow better than tundra vegetation, causing slightly shorter snow-free periods after manipulation in forest than in tundra sites (Vajda et al., 2006). Another aspect is that a lot of snow accumulated under the shrubs and was therefore difficult to remove without damaging the vegetation; hence there may have been snow left under shrubby vegetation at the shrub stream after manipulation.

When looking at the species contributions to dissimilarities of the macroinvertebrate assemblages between the different vegetation types, it appeared that the stonefly *N. pictetii* had its highest abundance in forest sites, and was more abundant in shrub than in tundra sites. In addition, the stonefly *L. nigra* was also more abundant in forest than in shrub and tundra sites, which is in agreement with the expectation of higher shredder abundance in forest than in tundra streams with shrub catchments being intermediate (Wallace et al., 1997). The analysis of feeding habits brings further support to this since the number of shredders was higher at sites with more shading and hence greater canopy cover and consequently greater inputs of allochthonous detritus (Wallace et al., 1997; Melody & Richardson, 2004; Compin & Cereghino, 2007). Furthermore, the mayfly *B. rhodani* was the only taxon which had higher abundance in tundra than in shrub and forest streams. *B. rhodani* can be characterized as an opportunistic species giving further support to the prevalence of more opportunistic species at tundra sites compared to shrub and forest sites (Brittain, 1982; Winemiller & Rose, 1992; Petrin, 2011).

4.3 Future perspectives

Fluvial ecosystems are important for the delivery of ecosystem services relying, amongst others, on their capacity for water cleansing and hence for the provision of accessible drinking water (Gleick & Palaniappan, 2010; Vörösmarty et al., 2010). Benthic macroinvertebrates include organisms that are functionally of central importance in mediating a range of ecosystem-level ecological processes that contribute to water cleansing (Wallace & Webster, 1996; Doleddec et al., 1999). The consequences of changes in vegetation cover and snow depth alteration for the diversity, abundance and composition of macroinvertebrates should

therefore be of great importance. The present study suggests potentially large effects of climate change and vegetation cover change for aquatic biodiversity and possibly also ecological functioning.

Climate change is expected to lead to the expansion of the tree line resulting in the replacement of tundra vegetation with shrubs and forests (de Wit et al., 2014). Given that species diversity is indeed higher in forested streams than in tundra streams and that the reduction in snow depth may cause a loss of biodiversity (Hoffsten, 2003), the snow depth alteration and the change in vegetation appear to have opposing effects on the invertebrate assemblages. If the effects are similar in strength, they may neutralize each other. However, the study design disallowed for the exact measurement of effect sizes. Large variation between streams made it statistically difficult to detect any effect of snow depth manipulation when testing the manipulated sites versus the inter-stream control sites. Furthermore, the inter-stream control sites sometimes showed trends which were different from the up-stream control sites (e.g. the effect of snow depth manipulation on abundance), suggesting that further factors may have contributed to the difference between manipulated sites and inter-stream control sites. However, given the difference in the response between the up-stream controls and the manipulated sites, I cannot exclude the possibility that there might be much greater effects of alteration in snow cover that will only be detectable if the experiment is repeated on a larger scale and for a longer duration (cf. Kreyling et al., 2012) or with more replicates per treatment combination. Hence, further studies are required in order to determine the relative effect sizes of vegetation cover change and climate change and to measure the absolute net effects. Future studies should also involve manipulation of snow cover over a longer period (several years).

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Appendix

Appendix 1: Classes used for vegetation mapping.

Class	Class description
be	<i>Betula nana</i>
B	<i>Betula tortuosa</i>
sa	<i>Salix</i> spp.
ju	<i>Juniperus communis</i>
Woody	deciduous and evergreen dwarf shrubs
nonWoody	Non woody plants
Wa	water
mo	mosses (including <i>Sphagnum</i> spp.)
nonVeg	stone, bare ground, litter
li	lichens

Appendix 2: Chemistry data from the water analysis. No water samples were taken at site KT2 in autumn because the streambed was dry and at site KS3 in spring since the site was still covered by large amounts of snow. The variation in pH, alkalinity and carbon was biologically insignificant. Snow depth manipulated sites in italics, up-stream control sites labeled by '-2' (e.g. KF6-2).

Site	Autumn			Spring		
	pH	alkalinity	Carbon	pH	alkalinity	Carbon
KF1	7.55	0.379	1.4	7.26	0.373	2.9
KF2	7.59	0.443	1.0	7.17	0.205	1.8
KF3	7.18	0.428	1.0	7.09	0.304	2.0
KF4	7.60	0.441	1.0	7.14	0.206	1.9
KF5	7.71	0.837	3.2	7.61	0.643	4.4
<i>KF6</i>	7.54	0.541	2.8	7.07	0.279	5.7
<i>KF6-2</i>	7.43	0.502	3.1	7.11	0.266	5.4
KS1	7.49	0.348	1.8	7.20	0.272	3.7
KS3	7.45	0.390	2.2	NA	NA	NA
KS4	7.30	0.357	2.1	7.03	0.254	4.1
<i>KS5</i>	7.79	0.843	1.5	7.62	0.641	3.2
<i>KS5-2</i>	7.39	0.396	2.7	7.62	0.633	3.0
KS8	7.72	0.905	2.7	7.62	0.669	4.2
KS9	7.85	1.047	1.6	7.45	0.495	4.4
KT1	7.66	0.441	0.8	7.17	0.200	1.6
KT2	NA	NA	NA	7.35	0.450	3.4
KT3	7.76	0.795	1.1	7.59	0.633	3.8
KT4	7.94	1.274	2.3	7.47	0.645	3.8
<i>KT5</i>	7.99	1.179	2.1	7.71	0.743	3.8
<i>KT5-2</i>	7.84	1.140	2.4	7.64	0.750	3.8
KT6	7.65	0.542	2.2	7.16	0.225	5.2

Appendix 3: Functional feeding habits of the taxa. C, collector; Sc, scraper; Sh, shredder; P, predator; Pi, piercer, NA, information not available. Some species have been classified into multiple feeding habit categories. Feeding habits were classified according to Hansen (1987), Nilsson & Holmen (1995), Elliott (2006), Cummins et al. (2008), Petrin (2011) and Waringer & Graf (2011).

Taxon	Feeding habit
Mayflies (Ephemeroptera)	
<i>Acentrella lapponica</i>	C
<i>Baetis rhodani</i>	C/Sc
<i>Baetis bundyae</i>	C/Sc
<i>Baetis subalpinus</i>	C/Sc
<i>Baetis muticus/niger/digitatus</i>	C/Sc
<i>Ameletus alpinus</i>	C/Sc
Stoneflies (Plecoptera)	
<i>Arcynopteryx compacta</i>	C/P
<i>Diura bicaudata</i>	Sc/P
<i>Diura nanseni</i>	Sc/P
<i>Isoperla difformis</i>	C/P
<i>Brachyptera risi</i>	Sc
<i>Capnopsis schilleri</i>	Sh
<i>Capnia atra</i>	Sh
<i>Capnia bifrons</i>	Sh
<i>Leuctra nigra</i>	C/Sh
<i>Leuctra digitata</i>	C/Sh
<i>Leuctra hippopus</i>	C/Sh
<i>Nemurella pictetii</i>	Sc/Sh
<i>Nemoura cinerea</i>	Sc/Sh
<i>Amphinemura sulcicollis</i>	C/Sc/Sh
<i>Protonemura meyeri</i>	Sh

Appendix 3 (Continued)

Species	Feeding habit
Beetles (Coleoptera)	
<i>Helophorus flavipes</i> (adult)	Sh
<i>Helophorus</i> sp.	Sh
<i>Agabus guttatus</i>	P
<i>Agabus guttatus</i> (adult)	P
<i>Agabus congener</i> (adult)	P
<i>Hydroporus</i> cf. <i>striola</i>	P
<i>Hydroporus striola</i> (adult)	P
<i>Hydroporus memnonius</i> (adult)	P
<i>Hydroporus nigrita</i> (adult)	P
<i>Elmis aenea</i> (adult)	Sc
<i>Limnebius truncatellus</i>	NA
Caddisflies (Trichoptera)	
<i>Oxyethira</i> sp.	Pi
<i>Rhyacophila nubila</i>	P
<i>Philopotamus montanus</i>	C
<i>Plectrocnemia conspersa</i>	P
<i>Apatania muliebris</i>	Sc/C
<i>Apatania hispida</i>	Sc/C
<i>Ecclisopteryx dalecarlica</i>	Sc/C/Sh
<i>Potamophylax nigricornis</i>	Sh/P
<i>Potamophylax cingulatus</i>	Sh/P
<i>Chaetopteryx villosa</i>	Sh/P
<i>Limnephilus coenosus</i>	Sh/P/Gr

Appendix 4 Temperature data measured at soil depths 1cm and 10cm and at the stream bottom (Water). Min., minimum temperature; days < 0, number of days with subzero temperatures; mean < 0, mean temperature during the days with subzero temperature.

Site	Soil depth 1 cm			Soil depth 10 cm			Water		
	Min.	days < 0	mean < 0	Min.	days < 0	mean < 0	Min.	days < 0	mean < 0
KF1	-0,7	133	-0,4	-0,5	126	-0,3	-0,8	56	-0,2
KF2	-0,8	112	-0,4	-0,5	71	-0,2	-1,5	24	-0,4
KF3	-0,2	80	-0,1	-0,2	87	-0,1	0,2	0	NA
KF4	-0,7	135	-0,4	-0,4	84	-0,2	0,1	0	NA
KF5	-1,1	131	-0,5	-0,4	105	-0,2	0,1	0	NA
KF6	-13,9	150	-3,2	-10,6	148	-2,5	-3,5	122	-1,1
KF6-2	-0,9	138	-0,4	-0,5	137	-0,2	-0,1	2	-0,1
KS1	-1,8	133	-0,8	-1,3	131	-0,7	-0,2	18	-0,1
KS3	0,1	0	NA	0,1	0	NA	-0,6	10	-0,4
KS4	0,1	0	NA	0,1	0	NA	0,2	0	NA
KS5	-8,7	133	-2,3	-7,2	139	-1,8	0,2	0	NA
KS5-2	-0,5	137	-0,2	-0,1	40	-0,1	0,1	0	NA
KS8	-2,7	143	-0,9	-0,9	113	-0,4	0,1	0	NA
KS9	-1,9	136	-0,8	-1,0	115	-0,5	0,2	0	NA
KT1	-1,1	144	-0,5	-0,9	151	-0,4	-0,1	5	-0,1
KT2	1,2	0	NA	-2,0	148	-0,9	-0,3	38	-0,2
KT3	-0,2	81	-0,1	-0,1	19	-0,1	0,2	0	NA
KT4	-1,5	169	-0,6	-0,9	137	-0,4	0,0	3	0,0
KT5	-17,8	178	-4,5	-15,3	158	-4,3	-8,3	140	-2,7
KT5-2	-4,0	150	-1,8	-3,5	158	-1,4	0,4	0	NA
KT6	-4,7	171	1,5	-1,3	141	-0,6	0,2	0	NA