



# **Influences of forests on invertebrate communities in Icelandic streams**

Gintarė Medelytė



**Faculty of Life- and Environmental  
Sciences  
University of Iceland  
2010**



# **Influences of forests on invertebrate communities in Icelandic streams**

Gintarė Medelytė

90 ECTS thesis submitted in partial fulfillment of a  
*Magister Scientiarum* degree in Biology

Advisors  
Jón S. Ólafsson  
Gísli Már Gíslason

External examiner  
Bjarni Kristófer Kristjánsson

Faculty of Life- and Environmental Sciences  
University of Iceland  
Reykjavik, May 2010

Influences of forests on invertebrate communities in Icelandic streams

90 ECTS thesis submitted in partial fulfillment of a *Magister Scientiarum* degree in Biology

Copyright © 2010 Gintarė Medelytė  
All rights reserved

Faculty of Life- and Environmental Sciences  
University of Iceland  
Askja - Sturlugata  
101, Reykjavík  
Iceland

Telephone: 525 4000

Bibliographic information:

Gintarė Medelytė, 2010, Influences of forests on invertebrate communities in Icelandic streams, Master's thesis, Faculty of Life- and Environmental Sciences, pp. 126.

Printing: Háskólaprent  
Reykjavík, Iceland, May 2010

# Abstract

Effects of forests on headwater stream invertebrate communities were studied in eastern and southern Iceland, which are two geologically different regions. The eastern research area is composed of solid basaltic rock with direct run-off streams. The streams drain treeless, birch and conifer forested catchments. The bedrock of the southern research area is porous hyaloclastite, and the streams are spring-fed. These streams drain two different types of catchments: barren land and birch forest.

The density and taxonomic richness were similar among direct run-off streams within all three catchment types. In winter, different proportions of some taxa were found between streams draining treeless land and forests. Invertebrate assemblages were similar between birch and conifer forest streams. In summer, invertebrate densities were higher in the streams that had the greatest proportion of birch woodlands in their catchments, highest values of riparian biomass and greater algal biomass.

In spring-fed streams, water temperature was the main factor explaining invertebrate densities and species composition, while presence of forest had no effect. Total densities and proportional abundances of taxa differed more between geographical locations than between catchment types. The younger bedrock influenced various habitat factors in the streams, such as availability of nutrients, water quality, temperature and primary productivity. Therefore, these factors were found to have a greater effect on invertebrate communities in Icelandic streams than forest presence or type.



# Útdráttur

Rannsókuð voru áhrif skógar á hryggleysingja í lækjum á tveimur svæðum á misgömlum berggrunni á Íslandi. Berggrunnur á rannsóknarsvæði á Héraði og Skriðdal á Austurlandi er ógengdræpt basalt með dragavötnum. Lækirnir runnu á vatnasviðum sem voru trjálausir, með birkiskógi og með barrskógi. Lækir í Landsveit á Suðurlandi runnum um berggrunn sem er hriplekt móberg og komu upp í lindum. Þeir runnu um skóglaus svæði og birkiskóg.

Þéttleiki og tegundafjölbreytileiki var svipaður í dragalækjum í öllum þremur gerðum vatnasviða. Á veturna voru hlutföll tegunda önnur í skógarlækjum en þeirra sem voru á berangri. Hryggleysingasamfélög voru svipuð í lækjum sem voru á vatnasvæðum vaxin birkiskógi og barrtrjám. Á sumrin var þéttleiki hryggleysingja meiri en á veturna og hæst í lækjum á vatnasviðum með birkiskóg, sem voru einnig með mestan plöntulífsmassa á bökkum lækjanna og mestan þörungalífsmassa.

Í lindalækjum var vatnshiti sá aðal þáttur sem útskýrði bestþéttleika hryggleysingja og tegundasamsetningu, en skógur á vatnasviði hafði engin tölfræðilega marktæk áhrif. Munur á heildarþéttleika og hlutfallslegum þéttleika tegunda og tegundahópa var meiri milli landsvæða en milli vatnasviðsgerða. Yngri berggrunnur hafði áhrif á ýmsa bússvæðaeiginleika í lækjunum, eins og magn næringarefna, vatnsgæði, hita og frumframleiðni. Þess vegna benda allt til að þessir þættir hafi meiri áhrif á hryggleysingasamfélög í íslenskum lækjum, en skóginn umhverfis.





*Dedication*

*In memory of Freysteinn Sigurðsson, geologist, who was instrumental in designing the ForStreams project and acted as a special advisor and mentor to the whole ForStreams research group throughout the first two years of the project. He passed away on December 29, 2008.*



# Table of Contents

<b>List of Figures .....</b>	<b>xiii</b>
<b>List of Tables.....</b>	<b>xvii</b>
<b>Abbreviations of taxa names .....</b>	<b>xix</b>
<b>Acknowledgements.....</b>	<b>xxi</b>
<b>1 Introduction .....</b>	<b>1</b>
1.1 Catchment forest and its multi-functional roles for stream invertebrates.....	1
1.1.1 Trophic effects of catchment vegetation.....	1
1.1.2 Physical and chemical effects of catchment vegetation.....	3
1.2 Features of Icelandic rivers and their catchments.....	5
1.2.1 Geology of Iceland.....	5
1.2.2 Origin of Icelandic invertebrate fauna .....	6
1.2.3 Catchment vegetation and river ecosystems in Iceland .....	6
1.2.4 Forestry history in Iceland .....	7
1.2.5 Previous researches on stream invertebrate communities in Iceland.....	7
1.3 Objectives and hypotheses of the study.....	8
<b>2 Materials and methods.....</b>	<b>9</b>
2.1 Research areas .....	9
2.1.1 The eastern research area .....	9
2.1.2 The southern research area .....	14
2.2 Field sampling .....	17
2.2.1 Physical and chemical variables .....	18
2.2.2 Riparian biomass.....	18
2.2.3 Autumn litterfall .....	19
2.2.4 Fish sampling.....	19
2.2.5 Invertebrate sampling .....	19
2.3 Laboratory procedures .....	20
2.3.1 Stream invertebrates .....	20
2.3.2 Primary production .....	23
2.3.3 Nutrient and elemental analysis.....	24
2.4 Numerical analyses.....	25
2.4.1 The eastern research area.....	26
2.4.2 The southern research area .....	26
2.4.3 Comparison of direct run-off and spring-fed streams.....	27
<b>3 Results.....</b>	<b>29</b>
3.1 Direct run-off streams in the eastern research area .....	29

3.1.1	Catchment composition .....	29
3.1.2	Physical and chemical characteristics of the streams .....	30
3.1.3	Catchment effect on stream ecology.....	35
3.1.4	Invertebrate community composition .....	37
3.1.5	Invertebrate assemblages in relation to stream ecology .....	52
3.1.6	Analysis of winter and summer seasons separately .....	54
3.2	Spring-fed streams in the southern research area .....	66
3.2.1	Catchment composition .....	66
3.2.2	Physical and chemical characteristics of the streams .....	66
3.2.3	Catchment effect on stream ecology.....	69
3.2.4	Invertebrate community composition .....	71
3.2.5	Invertebrate assemblages in relation to stream ecology .....	81
3.3	Comparison of direct run-off and spring-fed streams.....	83
3.3.1	Catchment composition .....	83
3.3.2	Invertebrate community composition .....	84
3.3.3	Invertebrate assemblages in relation to stream ecology .....	94
<b>4</b>	<b>Discussion .....</b>	<b>97</b>
4.1	Effect of catchment vegetation on stream ecology.....	97
4.2	Relation of stream invertebrate communities with catchment vegetation.....	99
4.2.1	Effect of catchment type on invertebrate densities and diversities in the streams .....	99
4.2.2	Effect of forest presence in the catchment on stream invertebrate assemblages .....	100
4.2.3	Effect of catchment type on invertebrate functional feeding groups in the streams .....	101
4.3	Effect of seasonality on stream invertebrate communities.....	104
4.4	Association of stream invertebrates with environmental variables .....	105
4.4.1	Direct run-off streams .....	105
4.4.2	Spring-fed streams .....	107
4.5	Comparisons of invertebrate communities between different geological areas .....	109
4.5.1	Differences in invertebrate communities between direct run-off and spring-fed streams.....	109
4.5.2	Factors, affecting the differences between direct run-off and spring-fed streams .....	110
	<b>Conclusions .....</b>	<b>111</b>
	<b>References .....</b>	<b>113</b>
	<b>Appendixes.....</b>	<b>123</b>

# List of Figures

Figure 2.1 The eastern research area with direct run-off streams and their catchments. ....	11
Figure 2.2 The eastern research area. Photographs of treeless, birch and conifer forested catchments. ....	12
Figure 2.3 The catchment composition of direct run-off streams in the eastern research area, based on the whole catchment area. ....	13
Figure 2.4 The catchment composition of direct run-off streams 400 metres upstream from each sampling station. ....	13
Figure 2.5 The southern research area with spring-fed streams and their catchments. ....	15
Figure 2.6 The southern research area. Photographs of barren and birch forested catchments. ....	16
Figure 2.7 The catchment composition of spring-fed streams in the southern research area, based on the whole catchment area. ....	17
Figure 2.8 Invertebrate sampling process. The streambed within the Surber sampler frame is being disturbed by hand for 30 seconds. ....	20
Figure 2.9 The head of chironomid Rheocricotopus (Rheocricotopus) effusus (Walker), mounted on a glass slide. ....	21
Figure 2.10 Stone, submersed in 96% ethanol to extract chlorophyll from the attached algae. ....	23
Figure 3.1 Cluster dendrogram of the similarity among catchment composition of direct run-off streams, using the Ward method, Euclidean distance. .	29
Figure 3.2 Cluster dendrogram of the similarity among composition of the catchment 400 metres upstream from the sampling station of each direct run-off stream, using the Ward method, Euclidean distance. ....	30
Figure 3.3 The substrate composition of direct run-off streams, based on averages for seven sampling occasions (November 2007, February 2008, May 2008, July 2008, October 2008, February 2009 and May 2009). ....	35
Figure 3.4 Ordination diagram of PCA based on ecological characteristics of the direct run-off streams during four sampling occasions. ....	37
Figure 3.5 Total invertebrate densities, number of taxa, Shannon diversity and evenness in direct run-off streams with different catchment types during five sampling occasions. ....	42

Figure 3.6 Functional feeding groups in direct run-off streams with different catchment types during four sampling occasions. Analysis, based on invertebrate densities. ....	45
Figure 3.7 Functional feeding groups in direct run-off streams with different catchment types during four sampling occasions. Analysis, based on invertebrate species presence/absence. ....	48
Figure 3.8 Ordination diagram of PCA, based on invertebrate densities in direct run-off streams during seven sampling occasions. ....	51
Figure 3.9 RDA ordination diagram based on invertebrate densities and environmental variables during five sampling occasions in direct run-off streams. ....	53
Figure 3.10 An ordination diagram of PCA, based on ecological characteristics of direct run-off streams in winter. ....	56
Figure 3.11 An ordination diagram of PCA, based on ecological characteristics of direct run-off streams in summer. ....	57
Figure 3.12 PCA ordination diagram based on invertebrate densities in direct run-off streams in winter. ....	59
Figure 3.13 PCA ordination diagram based on invertebrate densities in direct run-off streams in summer. ....	60
Figure 3.14 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in winter. ....	63
Figure 3.15 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in winter after fitting altitude as covariable. ....	64
Figure 3.16 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in summer. ....	65
Figure 3.17 Cluster dendrogram of the similarity among catchment composition of spring-fed streams, using the Ward method, Euclidean distance. ....	66
Figure 3.18 The substrate composition of spring-fed streams, based on averages for six sampling occasions (November 2007, February 2008, May 2008, July 2008, October 2008 and May 2009). ....	69
Figure 3.19 Ordination diagram of PCA based on ecological characteristics of the spring-fed streams during two sampling occasions. ....	71
Figure 3.20 Total invertebrate densities, number of taxa, Shannon diversity and evenness in spring-fed streams with different catchment types during two sampling occasions. ....	74
Figure 3.21 Functional feeding groups in spring-fed streams with different catchment types during two sampling occasions. Analysis, based on invertebrate densities. ....	76

Figure 3.22 Functional feeding groups in spring-fed streams with different catchment types during two sampling occasions. Analysis, based on invertebrate species presence/absence. ....	79
Figure 3.23 RDA ordination diagram based on invertebrate densities and environmental variables in spring-fed streams during two sampling occasions. ....	82
Figure 3.24 Cluster dendrogram of the similarity among catchment composition of direct run-off and spring-fed streams, using the Ward method, Euclidean distance. ....	83
Figure 3.25 Proportional abundances of stream invertebrate taxa, found in spring-fed and direct run-off streams during two sampling occasions. Since temperature was the main factor, determining invertebrate community structures in spring-fed streams (in the left side of the graph), they are grouped according to the temperature, not the catchment type. Direct run-off streams (in the right side of the graph) are grouped according to the catchment type. ....	85
Figure 3.26 Total invertebrate densities, number of taxa, Shannon diversity and evenness in November 2007 in spring-fed and direct-run-off streams with different catchment types. ....	88
Figure 3.27 Total invertebrate densities, number of taxa, Shannon diversity and evenness in July 2008 in spring-fed and direct-run-off streams with different catchment types. ....	89
Figure 3.28 Functional feeding groups in November 2007 in spring-fed and direct-run-off streams with different catchment types. Analysis, based on invertebrate densities. ....	90
Figure 3.29 Functional feeding groups in July 2008 in spring-fed and direct run-off streams with different catchment types. Analysis, based on invertebrate densities. ....	91
Figure 3.30 Functional feeding groups in November 2007 in spring-fed and direct-run-off streams with different catchment types. Analysis, based on invertebrate species presence/absence. ....	92
Figure 3.31 Functional feeding groups in July 2008 in spring-fed and direct run-off streams with different catchment types. Analysis, based on invertebrate species presence/absence. ....	93
Figure 3.32 RDA ordination diagram based on invertebrate densities and environmental variables in spring-fed and direct run-off streams during two sampling occasions. ....	95





# List of Tables

Table 2.1 Characteristics of direct run-off streams in the eastern research area. ....	10
Table 2.2 Characteristics of spring-fed streams in the southern research area. ....	14
Table 2.3 The functional feeding group of each taxa, found in direct run-off and spring-fed streams. ....	21
Table 2.4 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off streams. ....	27
Table 2.5 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off and spring-fed streams in November 2007. ...	28
Table 2.6 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off and spring-fed streams in July 2008. ....	28
Table 3.1 Physical and chemical parameters of direct run-off streams. Statistics across the sampling occasions are calculated. ....	33
Table 3.2 The presence of fish in direct run-off streams. ....	35
Table 3.3 Water quality and physical habitat loadings onto first four principal components of PCA analysis. ....	36
Table 3.4 Densities of invertebrate taxa (individuals per square metre) found in direct run-off streams. ....	39
Table 3.5 Catchment type and season effects on total invertebrate density, taxonomic richness, Shannon diversity and evenness in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. ....	43
Table 3.6 Catchment type and season effects on functional feeding groups in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. Analysis, based on invertebrate densities. ....	46
Table 3.7 Catchment type and season effects on functional feeding groups in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. Analysis, based on invertebrate species presence/absence. ....	49
Table 3.8 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables. ....	52

Table 3.9 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables within 400 metres upstream from the sampling station in each stream. ....	52
Table 3.10 Water quality and physical habitat loadings onto first four principal components of PCA analyses, done on winter and summer periods. ....	55
Table 3.11 Spearman's rank correlation coefficients between winter and summer species data PCA axes loadings and catchment composition variables. ....	61
Table 3.12 Spearman's rank correlation coefficients between winter and summer species data PCA axes loadings and catchment composition variables within 400 metres upstream from the sampling station of each stream. ....	61
Table 3.13 Physical and chemical parameters of spring-fed streams during November 2007 and July 2008. Algal biomass statistics is calculated across July 2008, October 2008 and May 2008. ....	68
Table 3.14 The presence of fish in spring-fed streams. ....	69
Table 3.15 Water quality and physical habitat loadings onto first four principal components of PCA analysis. ....	70
Table 3.16 Densities of invertebrate taxa (individuals per square metre) found in spring-fed streams in November 2007 and July 2008. ....	72
Table 3.17 Catchment type and season effects on total invertebrate density, taxonomic richness, Shannon diversity and evenness in spring-fed streams. Two-way repeated measure ANOVA tests. ....	75
Table 3.18 Catchment type and season effects on functional feeding groups in spring-fed streams. Two-way repeated measure ANOVA tests. Analysis, based on invertebrate densities. ....	77
Table 3.19 Catchment type and season effects on functional feeding groups in spring-fed streams. Two-way repeated measure ANOVA tests. Analysis, based on invertebrate species presence/absence. ....	80
Table 3.20 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables. ....	81

# Abbreviations of taxa names

Abbreviation	Taxa name
Acar	Acarina
Apat zon	<i>Apatania zonella</i>
Cap vid	<i>Capnia vidua</i>
Chaet	<i>Chaetocladius</i> spp.
Clad	Cladocera
Clin stag	<i>Clinocera stagnalis</i>
Cycl	Cyclopoidea (Copepoda)
Diam aber	<i>Diamesa aberrata</i>
Diam ber	<i>Diamesa bertrami</i>
Diam boh/zer	<i>Diamesa bohemani/zernyi</i>
Diam lat	<i>Diamesa latitarsis</i> group
Dicr	<i>Dicranota</i> sp.
Euk clar	<i>Eukiefferiella claripennis</i>
Euk min	<i>Eukiefferiella minor</i>
Harp	Harpacticoidea (Copepoda)
Hemer	Hemerodromiinae (Empididae)
Lim gris	<i>Limnephilus griseus</i>
Limnoph	<i>Limnophyes</i> sp.
Lymnaea	<i>Lymnaea</i> sp.
Macropel	<i>Macropelopia</i> sp.
Metriocn	<i>Metriocnemus</i> spp.
Microps	<i>Micropsectra</i> spp.
Musc	Muscidae
Olig	Oligochaeta
Orth frig	<i>Orthocladius frigidus</i>
Orth obl	<i>Orthocladius oblidens</i>
Ostrac	Ostracoda
Paraph	<i>Paraphaenocladius</i> spp.
Par kief	<i>Parochlus kiefferi</i>
Pot cing	<i>Potamophylax cingulatus</i>
Pro urs	<i>Prosimulium ursinum</i>
Ps bran	<i>Pseudodiamesa branickii</i>
Rheo eff	<i>Rheocricotopus effusus</i>
Sim vit	<i>Simulium vittatum</i>
Sim vern	<i>Simulium vernum</i>
Tardigr	Tardigrada
Thien gr	<i>Thienemannia gracilis</i>
Thienem	<i>Thienemanniella</i> sp.
Tipul	Tipulidae spp.



# Acknowledgements

My special gratitude goes to my supervisors, Jón S. Ólafsson and Gísli Már Gíslason, for their guidance and useful advises in this research. I also wish to thank to Bjarni D. Sigurðsson from Agricultural University of Iceland, who was the coordinator of this project, Sigurður Guðjónsson, a director of the Institute of Freshwater Fisheries and Hlynur Óskarsson from Agricultural University of Iceland. Thanks all of you for giving me an opportunity to be a part of ForStreams project.

I am indebted for the assistance and the company during field work to Helena M. Stefánsdóttir, Ragnhildur Þ. Magnúsdóttir, Karólína Einarsdóttir, Ameline Solen Mohéo, Gísli Már Gíslason, Bjarni D. Sigurðsson, Berglind Orradóttir, Leó A. Guðmundsson, Teitur Birgisson and my husband Reynir Svavarsson. I am very thankful to Jón S. Ólafsson, Gísli Már Gíslason, Ragnhildur Þ. Magnúsdóttir and Elísabet R. Hannesdóttir for the great help in identification of invertebrates. I would sincerely like to thank Jorge H. Fernández Toledano for his useful advices in statistical analysis, Daniel P. Govoni, who corrected the English grammar in my thesis, and the staff of the Institute of Freshwater Fisheries who were very helpful and friendly to me.

I am thankful to Baldur Jón Vigfússon and Arngrímur Thorlacius who ran chemical analysis, used in this research, Brynhildur Bjarnadóttir and Edda S. Oddsdóttir who measured the riparian biomass, Bjarni D. Sigurðsson and Robert Rosenberg, who mapped the catchment composition, Friðþjófur Árnason and Sigurður Guðjónsson, who did electrofishing, and Rakel Guðmundsdóttir and Helena M. Stefánsdóttir who helped with chlorophyll analysis. I am grateful to the librarian Guðrún Þórðardóttir for providing me always so quickly scientific articles that I really needed.

Numerous people from various universities and research institutes were included in the ForStreams project. I would like to thank for nice and friendly co-operation to Bjarni D. Sigurðsson, Hlynur Óskarsson, Berglind Orradóttir, Robert Rosenberg and Helena M. Stefánsdóttir from the Agricultural University of Iceland, Gísli M. Gíslason from University of Iceland, Jón S. Ólafsson and Sigurður Guðjónsson from the Institute of Freshwater Fisheries, Edda S. Oddsdóttir, Brynhildur Bjarnadóttir and Hreinn Óskarsson from the Iceland Forest Service, Guðmundur Halldórsson from the Soil Conservation Service, Franklín Georgsson from the Icelandic Food Research (MATÍS) and Nikolai Friberg from the Macaulay Institute in Aberdeen.

I am grateful to my family in Lithuania and in Iceland for their encouragement and support throughout my study time. And finally, special thanks to my husband Reynir for his unconditional love, great help and the patience during this arduous period.

This project was supported by grants from the Environmental and Energy Research Fund of Orkuveita Reykjavíkur (UOOR) which gave the core funding, Centre for Advanced Forest Research on Ecosystem Services (CAR-ES) – Nordic/Baltic project, Agricultural Productivity Fund (Framleiðnisjóður landbúnaðarins), Energy Research Fund of Landsvirkjun (Orkurannsóknasjóður Landsvirkjunar) and the Afforestation and Restoration Program Hekluskiógar.



# **1 Introduction**

Stream ecosystems are closely linked to their surrounding terrestrial environments. A stream is ruled by various geological, hydrological, climatic and riparian vegetation attributes. These attributes create various conditions within the stream, which provide different habitats for the organisms. The riparian vegetation is one of the most important factors that affects the structure and function of stream ecosystems (Cummins, 1974; Hynes, 1975; Vannote et al., 1980; Gregory et al., 1991).

A vast amount of studies have provided evidence that vegetation cover type within catchments may determine the community structure and productivity of stream invertebrates. In Denmark, invertebrate density and diversity were lower in streams within conifer forested catchments, than in streams running through deciduous beech forest (Friberg, 1997). In Japan, the proportions of stream invertebrate families differed between conifer forest and broad-leaved forest (Yoshimura and Maeto, 2006). The taxonomic composition of invertebrates was different between two streams in Portugal, where one stream was mainly surrounded by chestnut trees, and the other by more diverse deciduous vegetation (Abelho and Graca, 1996).

## **1.1 Catchment forest and its multi-functional roles for stream invertebrates**

### **1.1.1 Trophic effects of catchment vegetation**

The productivity of stream invertebrates is based on the food supply. Streams receive their energy from two sources: autochthonous material, which is provided by primary producers within the stream, and allochthonous material, which is derived from surrounding terrestrial vegetation. The proportions of autochthonous and allochthonous material in the stream vary depending on riparian vegetation composition, season, stream size and distance from the headwaters (Vannote et al., 1980; Richardson, 1994; Artmann et al., 2003).

#### **1.1.1.1 Allochthonous inputs**

Invertebrate communities in headwater streams within forested catchments are highly dependent on organic matter inputs from the riparian zone (Cummins, 1974; Vannote et al., 1980; Cummins et al., 1989). Riparian trees supply organic matter to the stream by shedding leaf litter, seeds, fruits and twigs. In the water, bacteria and fungi colonize this debris and make structural and biochemical changes, converting it to palatable state. Such nutrient rich plant material (coarse particulate organic matter; CPOM) is very important

food for shredders (Cummins et al., 1989). The densities of shredders have been shown to be significantly correlated with the quantity of CPOM in streams (Friberg, 1997). Shredders are the major link between riparian vegetation and stream invertebrate communities. They play a fundamental role in conversion of large plant litter pieces into smaller particles (fine particular organic matter; FPOM). The FPOM that shredders generate consists of smaller leaf fragments and, more significantly, of faecal pellets, which serve as a food source for collectors (Cummins, 1974; Cummins et al., 1989; Wotton et al., 1998; Malmqvist et al., 2001; Wotton and Malmqvist, 2001).

Various types of riparian vegetation provide different qualities and quantities of food for shredders. Litter decomposition rates in streams depend on water temperature and leaf chemistry, which varies among plant species (Cummins et al., 1989; Richardson et al., 2005; Swan and Palmer, 2006). For example, recalcitrant oak leaves are processed slowly, while high quality alder leaves are quickly consumed (Graça and Canhoto, 2006). Deciduous leaf litter is usually processed faster than coniferous (Friberg and Jacobsen, 1994; Collen et al., 2004). Some needles contain protective chemical compounds that reduce the use of the tissue by fungi or bacteria (Richardson et al., 2005).

According to some studies, conifer needles are nutritionally poor, and are commonly avoided by shredders (Whiles and Wallace, 1997). Some needles tend to have lower levels of nutritionally significant elements than deciduous litter (Richardson et al., 2005). Shredders were found more abundantly in the streams surrounded by deciduous forest, than in coniferous forest streams (Willacker et al., 2009). Sometimes retention of debris in streams is a more important factor than the species of the leaves. High retentiveness of detritus can result in higher densities of shredders. Therefore, streams with conifer forest within the catchment sometimes support greater shredder densities than streams running through deciduous forest (Murphy and Giller, 2000).

One additional product of significance supplied to streams by terrestrial vegetation is dissolved organic matter (DOM). It originates from the terrestrial decomposition processes or leaches from the debris submerged in the stream water. Dissolved organic carbon is then converted to FPOM by flocculation, which is a result of physical forces. Colonization by microbial communities also converts DOM into FPOM, which can then be eaten by stream invertebrate collectors (Cummins, 1974; Giller and Malmqvist, 1998).

#### 1.1.1.2 Primary production

Shading is an important effect that riparian forest has on streams (Sweeney, 1992; O'Driscoll et al., 2006; Von Schiller et al., 2007). Reduced light levels reaching the stream decrease photosynthetic activity and the rates of primary production. Algae, mosses and flowering plants are the main autotrophs in streams. Diatoms are a common food source for stream invertebrates (Berg, 1995), while mosses, flowering plants and macroalgae seem to be little used as a food source while they are alive (Cummins and Klug, 1979).

Light levels reaching the stream can strongly depend on riparian forest composition. For example, evergreen conifer forests can limit the light levels under the canopy year round. Deciduous and mixed forests can create the shade during summer, but only slightly modify light inputs after leaf fall (Gregory et al., 1991; Richardson, 2008). Algal biomass has been shown to be lower in naturally (Von Schiller et al., 2007) and artificially shaded streams



(Fuller et al., 1986). The composition of algae communities can depend on the degree of shading over the stream. Diatoms have been shown to dominate in shaded areas, whereas some taxa of macroalgae are more abundant in sunny places (Artmann et al., 2003).

Changes in stream primary production can have a great effect on invertebrate species composition and abundance. Unshaded streams with higher rates of algae production tend to have higher numbers of gathering collectors and scrapers. Densities of gathering collector mayfly species, which use algae as an important food source, were significantly reduced in an artificially shaded stream area (Fuller et al., 1986). Chironomid scraper communities were found to be positively correlated with algal biomass (Winterbourn et al., 1992). Algae as well can be a good additional food source for shredders. Some shredding species have been observed to eat algae in laboratory experiments (Friberg and Jacobsen, 1994; Franken et al., 2005).

### **1.1.2 Physical and chemical effects of catchment vegetation**

Invertebrate community structure and productivity are linked to physical and chemical factors of the streams. Physical factors include water temperature and velocity, channel width and substrate composition in the stream. Chemical factors include various water quality parameters and the amount of nutrients (Wallace and Eggert, 2009). All these effects can be significantly influenced by the presence of riparian forest.

#### **1.1.2.1 Temperature**

The temperature regimes are important for reproduction and growth of stream invertebrates. Surrounding forest can modify the microclimate around streams by reducing solar radiation, precipitation and wind speed. These changes regulate the thermal and moisture environments under canopies of trees and can influence diel and seasonal temperature regimes of the stream water (Moore et al., 2005).

The canopy of riparian forest can moderate the fluctuations of temperatures over the stream and in the stream water. Higher diel temperature fluctuations are more common in unshaded small streams, than in shaded ones. Riparian forests were the most effective in reducing daily maximum temperatures during the hottest days and in moderating the diel minimum temperatures on the coldest days below the canopy of the riparian forest in New Zealand (Meleason and Quinn, 2004). Smoother diel temperature variations can decrease summer mean temperatures of the stream water, influencing seasonal temperature regime (Moore et al., 2005).

Higher daily maximum and mean summer temperatures increase development rates of aquatic insects and result in smaller body size, which reduces fecundity (Allan, 1995; Richardson, 2008). Increased temperatures can even cause the mortality of stream invertebrates. For example, in a laboratory experiment, by Cox & Rutherford (2000), 50% mortality for some mayfly species occurred in 96 hours at a constant temperature of 24.2 °C and for snail species at 31 °C. In the native streams these two species were used to 15.7 °C summer maximum and 12.7 °C winter minimum temperature.

### 1.1.2.2 Other physical factors

Besides being a food source, twigs, branches and whole trunks can be an additional habitat for stream invertebrates. Woody debris serves as an important substrate for invertebrates in rivers with soft, fine sediments (Giller and Malmqvist, 1998). Many taxa are closely associated with wood. Many species of chironomids, caddisflies, blackflies, stoneflies, snails and beetles use wood for food, habitat, attachment and case building (Anderson et al., 1978; Gregory et al., 1991; Allan, 1995; Giller and Malmqvist, 1998; O'Driscoll et al., 2006). The presence of woody debris in streams increases the retention of deciduous and coniferous leaf litter, providing the food reservoir for invertebrates throughout the year. Shredder biomass was shown to be 300 times greater in detritus pools than in sandy and stony habitats (Dangles, 2002).

Riparian trees protect the stream bank from erosion by binding the soil with their roots and reducing the flow of fine sediments into the stream. Lower current velocities in the streams with forested catchments also decrease bank erosion. Water yielded to the stream can be reduced through evapotranspiration by riparian forest (Giller and Malmqvist, 1998).

Forest streams can be wider and shallower than the streams running through the treeless catchments. In Pennsylvania, the forest streams were found to be 2.5 times wider than the streams draining non-forested grassy meadows (Sweeney, 1992). In non-forested catchments the grass overgrows the edges of the stream narrowing the channel. At the same time discharge makes it deeper. The shade of the forest reduces the growth of the grass, keeping the stream wide and shallow. Wider streams provide larger surface area for stream invertebrates (Sweeney, 1992).

### 1.1.2.3 Water quality

Riparian vegetation cover can highly influence the stream water quality in different ways. A leaf's surface has the ability to collect ions from the atmosphere. These ions are washed by rain into the soil, groundwater and streams. Conifers have greater collecting abilities than other types of trees (Giller and Malmqvist, 1998). They can effectively collect acid components from the air and make stream water more acid. Studies have shown that water acidity in streams may depend on the proportion of conifer forest present in the catchment. Increased acidity can cause the absence of acid-sensitive invertebrate species and mobilise various ions, including toxic aluminium and manganese (Harriman and Morrison, 1982).

The type of streamside vegetation regulates the water chemistry by shedding debris directly into a stream and on the forest floor. Organic and inorganic compounds, released from debris, go into the stream or into groundwater, which later moves into the stream (Gregory et al., 1991; Sweeney, 1992). Before entering the stream, nutrient amounts in soil solution can be greatly reduced by riparian tree roots (Hynes, 1975; Broadmeadow and Nisbet, 2004). Since most of the water is in close contact with the soil in the catchment, the stream chemistry is closely related to the parent bedrock (Giller and Malmqvist, 1998).

## **1.2 Features of Icelandic rivers and their catchments**

### **1.2.1 Geology of Iceland**

Iceland is a North Atlantic island, located in the Atlantic Ocean at 63°23'N to 66°30'N. It is on the Mid-Atlantic Ridge where the North American and Eurasian plates are moving apart. Volcanically active rift zone extends from southwest to northeast Iceland. The crust there is pulled apart about 2 cm every year. The gash is gradually filled by rising magma and new crust is produced (Sæmundsson, 1979; Einarsson, 1994; Thordarson and Hoskuldsson, 2002).

Iceland is mainly built of basalts. They cover about 83% of the total surface area, whereas 8% are rhyolite lavas, 3% are andesite lavas and 6% are interbasaltic beds (tephra and sediment) (Einarsson, 1994). The formation of North Atlantic islands began 60 million years ago, when North American and Eurasian plates moved apart. This process was accompanied by massive volcanism in the early Atlantic Ocean. Iceland was built-up during the Tertiary and Quaternary periods, so the oldest rocks that occur lower than sea level are around 25 million years old. The oldest rocks exposed at the surface are around 14–16 million years old (Sæmundsson, 1979; Einarsson, 1994; Thordarson and Hoskuldsson, 2002).

Upper Tertiary formation basalts cover around half of the territory in Iceland. They are more than 3.3 million years old, and situated in eastern, western and northern parts of the country. The ages of the rocks increase with the distance from the volcanically-active spreading axis. The youngest rocks are postglacial lava fields and hyaloclastites from late Pleistocene formation. They are situated on the spreading axis and are less than 10 thousand years old (Jóhannesson and Sæmundsson, 1998; Thordarson and Hoskuldsson, 2002).

Geology within the catchment determines the origin of rivers. The bedrock, made of Tertiary basalts and Early Pleistocene lavas, is impermeable, since pores of lavas are filled with clay. The precipitation remains on the surface and the groundwater in such territories is limited. The streams there are direct run-off, originating in seepage from hollows and valley networks and mainly fed by precipitation. The youngest bedrocks, the Pleistocene basalt lavas, hyaloclastites and Holocene lavas are very porous. The precipitation percolates rapidly in these areas becoming groundwater. The water emerges at the surface in the form of springs and causing spring-fed streams. Therefore spring-fed rivers are very widespread in areas with young, porous bedrock (Einarsson, 1994).

Parent bedrock plays an important role in stream water chemistry. Terrestrial and aquatic ecosystems get some nutrients from the weathering of the bedrock. This process is especially important in the areas with younger bedrock. The mobility of various elements increases with the decreasing age of the catchment rocks. Old crystalline bedrock is relatively resistant and will release fewer chemicals through weathering. But the relative mobility of such elements like calcium and magnesium is less dependent on the age of rocks (Gíslason et al., 1996; Gíslason, 2008).

### **1.2.2 Origin of Icelandic invertebrate fauna**

The geographical position of Iceland determined the sparse flora and fauna within the country. In North Atlantic islands only few endemic species can be found. There is the theory, that North Atlantic islands lost almost all flora and fauna during Quaternary glaciations and were colonized by new species from northwest Europe in the end of the glacial periods (Coope, 1986; Sadler, 1999; Ægisdóttir and Þórhallsdóttir, 2004). The newest findings in Iceland have revealed that some freshwater inhabitants might have been living in subterranean waters before the glaciations began. Two recently discovered endemic subterranean amphipod species in Iceland suggest that there was a subglacial refugium during the Quaternary period. Amphipods could survive in groundwater flowing through the porous lava bedrock, build by active volcanism (Kristjánsson and Svavarsson, 2004; Svavarsson and Kristjánsson, 2006; Kristjánsson and Svavarsson, 2007).

It was observed, that North Atlantic insect fauna are dominated by Palaearctic species, mainly from Norway and Britain. Some species reached Iceland during the early Holocene. The transport of various insects could be supported by floating ice and freshwater (Coope, 1986; Sadler, 1999; Gíslason, 2005). In North Atlantic islands, continental crustacean freshwater species are found in higher numbers than freshwater insects. Crustaceans have diapausing eggs that can be transported on bird feathers or in stomachs (Gíslason, 2005).

The majority of insect species in North Atlantic islands could have been introduced by Norse colonists in the 9<sup>th</sup> century (Coope, 1986; Sadler, 1999). Before the invasion of humans, Iceland was more vegetated than it is today. Removal of woodland, overgrazing and soil erosion destroyed old habitats and created new ones. This may have changed the distribution of indigenous biota and enabled establishment of introduced species (Arnalds, 1987; Sadler, 1999).

### **1.2.3 Catchment vegetation and river ecosystems in Iceland**

Iceland is situated within the boreal/alpine vegetation zone. In boreal forest conifers dominate, but some areas can be permanently covered by birch forests (Sjörs, 1963, 1967). The lowland areas of Iceland, up to altitude 400 metres, belong to the boreal zone because territories there are covered by birch forest. They appear mostly along the coast, but in the southwest they can extend inland. In the east and north the birch woodlands spread within the valleys of the mountains, around big rivers, far from the coast (Steindórsson, 1964; Guðjónsson and Gíslason, 1998; Traustason and Snorrason, 2008).

Forests in Iceland are not widespread. They cover only about 1.5% of the total landscape. Vegetation consists mainly of woody shrubs, grasses and mosses, whose compositions vary depending on altitude and latitude (Steindórsson, 1964; Arnalds, 1987; Traustason and Snorrason, 2008). The rivers in Iceland are mainly characterized as alpine/arctic rivers. They typically originate in the arctic highlands and the vegetation around them is not high enough to shade the stream channel. Therefore, invertebrates in Icelandic streams are mainly dependent on primary production. Boreal forest rivers in Iceland resemble alpine/arctic rivers due to lack of birch woodlands (Petersen et al., 1995).

#### **1.2.4 Forestry history in Iceland**

Iceland's historic forest cover was much more extensive than it is now. Before human settlement in the late 9<sup>th</sup> century, about 25% of the land was covered by birch (*Betula pubescens*) forests and woodlands. At elevations of 300 to 400 metres, willows (*Salix* spp.) and other shrubs dominated (Sigurðsson, 1977; Arnalds, 1987). After the settlement, woodlands were cleared for farming purposes and the trees were cut and used for house construction and fuel. The woodlands had no chance to regenerate after the clear-cut because of uncontrolled farming. Sheep grazing was allowed all over the country. According to Kristinsson (1995), human activities were the factors that primarily caused deforestation in Iceland. Several natural catastrophes, such as cooler climate during the years 1500-1900, some volcanic eruptions, and floods along large glacier-fed rivers had less of an effect on deforestation and would never have caused such large changes.

Active afforestation in Iceland began just over one hundred years ago. Since then, native birch (*B. pubescens*) and some exotic conifer species have been planted (Pétursson, 1999). One of them is the Siberian larch (*Larix sibirica*), one of the dominating species, which has been planted in Hallormsstaðir (eastern Iceland). Today, forests and woodlands in Iceland cover only about 1.5% of the landscape. Birch forms natural forests, which cover 1.1% of that area. Planted broad-leaved, conifer and mixed forests and plantations cover only 0.4% of the total territory of Iceland (Traustason and Snorrason, 2008).

#### **1.2.5 Previous researches on stream invertebrate communities in Iceland**

Several studies on invertebrate communities were done in Iceland on big rivers and their tributaries of various origins (glacial, spring-fed and direct run-off) and bedrock ages in the catchments. It was observed, that geology, vegetation cover, topography and lakes in the river outlets, are the main factors that determine invertebrate community structure and productivity (Gíslason et al., 1998). Invertebrate communities in Icelandic rivers are dominated by Chironomidae (Gíslason et al., 2000; Ólafsson et al., 2000; Gíslason et al., 2001; Stefánsson, 2005; Stefánsson et al., 2006), but some rivers influenced by lakes can be dominated by Simuliidae (Gíslason et al., 1998; Gíslason et al., 1999).

Iceland has very heterogeneous geology with various ages of bedrocks. It was observed in previous studies, that the number of Chironomidae and Simuliidae adult taxa changed with the age of the bedrock in the stream catchments, being highest at youngest bedrock and decreasing with age (Ólafsson et al., 2002). Density and diversity of invertebrates tend to be highest in spring-fed and lake-fed river systems and much lower in the run-off systems (Gíslason et al., 1999).

The vegetation in the catchments of Icelandic streams is very scarce; forests are almost absent. Shrubs and grasses were the dominating vegetation in the catchments of the rivers studied previously. Despite this, some differences of invertebrate communities were found among the rivers and were associated with catchment vegetation cover. Rivers with better vegetated catchments had higher taxa richness and density than rivers draining less vegetated and barren areas (Gíslason et al., 1998; Gíslason et al., 1999; Ólafsson et al., 2002). Research aimed to determine the effect of forest type on headwater stream

communities has not been done in Iceland before. Such studies are very important because afforestation and revegetation activities in Iceland have been very active in recent decades and further increases in vegetation reclamation are anticipated.

### **1.3 Objectives and hypotheses of the study**

This study was part of a large, collaborative project in Iceland called ForStreams (SkógVatn in Icelandic). The objectives of this research were to assess: 1) what effect the presence and type of forest in the catchment has on invertebrate communities in headwater streams, 2) what effect forest has on invertebrate communities in the streams with different bedrock and run-off characteristics, and 3) the difference between invertebrate communities in the streams with different bedrock and run-off characteristics.

According to previous knowledge about Icelandic and foreign streams, the following hypotheses were made: 1) invertebrate communities will differ in the streams within treeless and within forested catchments due to different food resources, 2) invertebrate communities will differ between birch and conifer forest streams due to different quality of leaf litter, 3) shredding invertebrates will be more abundant in the streams within forested catchments compared to the streams within treeless catchments, due to higher input of leaf litter, 4) scraping invertebrates and gathering collectors will be more abundant in the streams within treeless catchments, comparing to the forest streams, because of higher primary production.

## 2 Materials and methods

### 2.1 Research areas

Two research areas were established within the eastern and southern Iceland, which are geologically different. The streams were chosen on the basis of forest type within their catchments: birch or conifer forests were selected and compared with the streams, running through the treeless catchments. Neither research area was influenced by agriculture. Although sheep grazing occurred, it was not of great enough intensity to significantly impact the streams.

#### 2.1.1 The eastern research area

The eastern research area was located in the municipality of Fljótsdalshérað, close to Egilsstaðir. Nine streams were selected in total, with three streams in each of the three catchment types: treeless land (AS1, AS2 and AS3), birch forest (AB1, AB2 and AB3) and conifer forest (AG1, AG2 and AG3) (Figures 2.1 and 2.2). Birch forests were dominated by a native birch species (*B. pubescens*), and the dominant species in conifer plantations was the exotic Siberian larch (*L. sibirica*). All streams were located within 20 km of each other. The streams originated from altitudes of 254–842 metres, and their sampling stations were established at 25–161 metres above sea level (Table 2.1).

The streams AS1 and AG1 were second order and all other streams were first order. The bedrock in the eastern research area is solid basaltic rock from the Tertiary period, not less than 3.1 million years old (Einarsson, 1994; Jóhannesson and Sæmundsson, 1998), and all streams were direct run-off.

The catchment sizes in the eastern research area ranged from 51 to 487 ha, with the exception of the AS1 catchment, which was very large, 2373 ha (Table 2.1). Gravel flats contributed 13–39% of the areas in the nine catchments and eroded land covered 4–21% of the territories there. The cover of heathland within the catchment of stream AB3 was only 1% of the territory; meanwhile in the other catchments it comprised 15–42%. The proportion of grassland was low, only 0–11%, except the catchment of the stream AB3, which had 25% grassland (Figure 2.3). Higher proportions of wetland (12–38%) covered the treeless catchments than the forested ones (7–20%).

The actual cover of birch within the birch forest catchments was only 14–36%. Some conifer forest (4%) even grew in the AB3 catchment. Catchments classified as conifer forest were covered with very small proportions of conifer plantations, only 2–10%. Birch forests also made a considerable contribution within these catchments (14–25%) (Figure 2.3).

The composition of the catchment 400 metres upstream the sampling station of each stream was drastically different from the composition of the catchment overall. These segments were highly forested with birch woodlands around the streams AB1, AB2 and AB3 (75–100% of the area) (Figure 2.4). The catchments of streams AG1, AG2 and AG3 were highly covered with conifer plantations (25–55%) 400 metres upstream their sampling stations. Streams AG2 and AG3 were still surrounded by considerable proportions of birch woodlands (40 and 64% respectively). Stream AG1 was surrounded by the smallest forested areas. Gravel flats, grassland and heathland together covered 70% of the territory within the 400 metres segment. Treeless catchments (AS1, AS2 and AS3) were similar to each other within the 400 metres upstream each sampling station and were mainly composed of grassland (13–62%), heathland (11–31%), gravel flats (20–28%) and eroded land (6–38%) (Figure 2.4).

*Table 2.1 Characteristics of direct run-off streams in the eastern research area.*

Stream	Catchment type	Stream order	Longitude	Latitude	Catchment size (ha)	Altitude at stream origin (m a.s.l.)	Altitude of sampling station (m a.s.l.)
AS1	Treeless	2	N 65° 09.247	W 14° 43.891	2373.5	657	161
AS2	Treeless	1	N 65° 01.261	W 14° 39.998	212.4	707	141
AS3	Treeless	1	N 65° 01.421	W 14° 39.995	101.6	726	143
AB1	Birch	1	N 65° 04.582	W 14° 48.126	461.2	608	91
AB2	Birch	1	N 65° 10.573	W 14° 28.999	464.6	730	97
AB3	Birch	1	N 65° 06.240	W 14° 43.020	210.0	445	61
AG1	Conifer	2	N 65° 04.173	W 14° 49.754	487.4	842	25
AG2	Conifer	1	N 65° 05.385	W 14° 45.260	50.7	563	58
AG3	Conifer	1	N 65° 05.126	W 14° 46.323	177.3	254	60



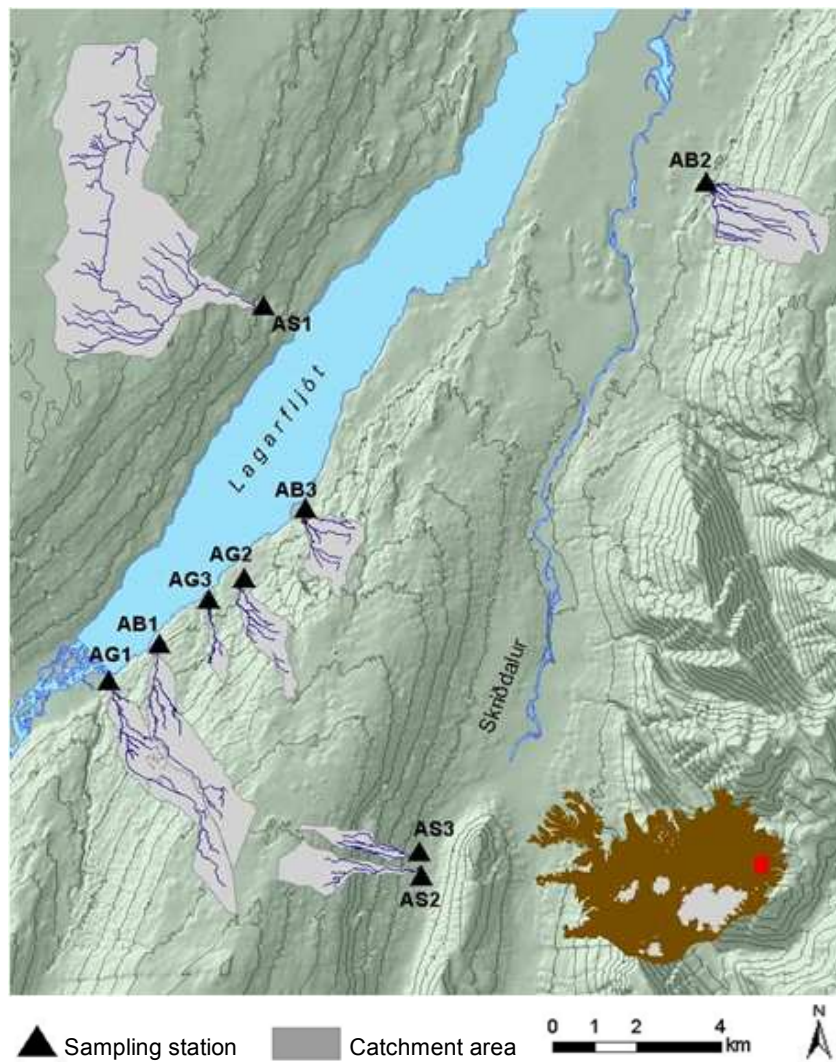


Figure 2.1 The eastern research area with direct run-off streams and their catchments. Letter A indicates that the streams are located in eastern Iceland; letters S, B and G indicate treeless land, birch forest and conifer forest respectively; numbers indicate the size of the catchments (1 – being the largest, 3 – being the smallest).



*Figure 2.2 The eastern research area. Photographs of treeless (a), birch (b) and conifer (c) forested catchments.*

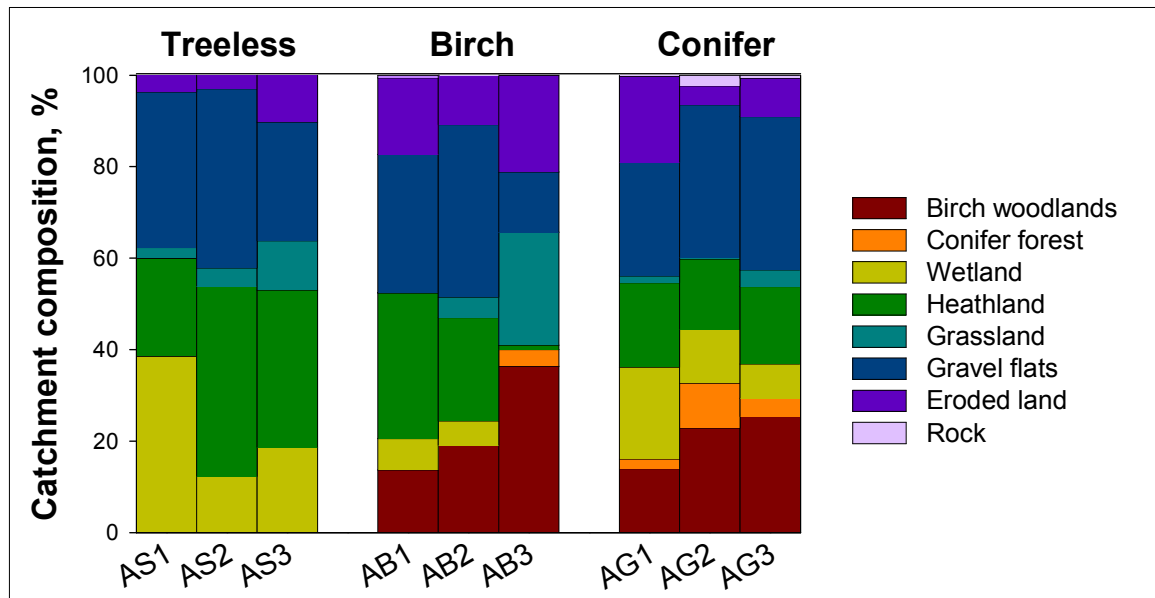


Figure 2.3 The catchment composition of direct run-off streams in the eastern research area, based on the whole catchment area.

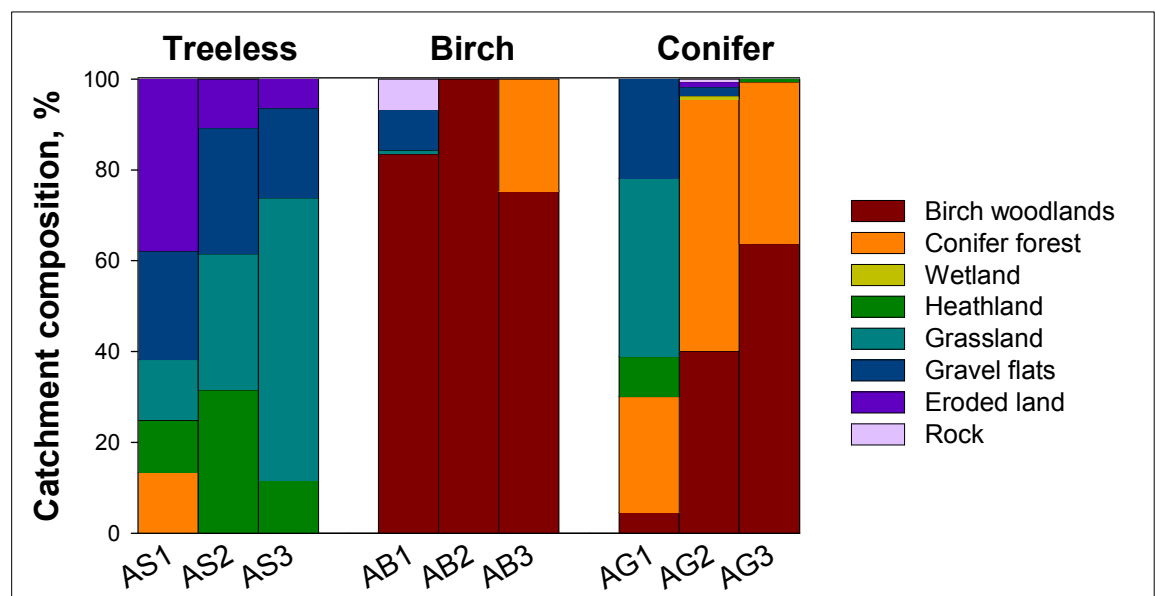


Figure 2.4 The catchment composition of direct run-off streams 400 metres upstream from each sampling station.

### 2.1.2 The southern research area

The southern research area was located in the foothills of the volcano Hekla in Rangárvellir. Eight streams running through two different types of catchments were studied: barren land (SS1, SS2, SS3 and SS4) and birch forest (SB1, SB2, SB3 and SB4) (Figures 2.5 and 2.6). The dominating species in birch woodlands was the native birch (*B. pubescens*).

All streams were first order and were located within 10 km of each other. They originated at 100–159 metres above sea level, and the sampling stations were established at altitudes of 88–139 metres (Table 2.2). The bedrock in this area is porous hyaloclastite. It is relatively young, not more than 10 thousand years old, from the Upper Pleistocene (Einarsson, 1994; Jóhannesson and Sæmundsson, 1998). All streams in this area were spring-fed.

The catchments in the southern research area were much smaller than in the east, they varied between 0.3 and 9.3 ha (Table 2.2). The characteristics of barren catchments were quite similar to each other, with cover of 58–95% of eroded land, 3–28% of gravel flats and 0–11% of grassland. The SS4 catchment was the only one among all eight catchments in which rock cover was 18% (Figure 2.7).

Two catchments, classified as birch forest (SB1 and SB2) were almost fully covered with birch woodlands (75 and 80% respectively). Half of the catchment area that stream SB3 run through was covered with birch forest and the other half was eroded. The SB4 catchment had only 7% birch woodland cover, and the remaining area was covered with gravel flats (Figure 2.7).

*Table 2.2 Characteristics of spring-fed streams in the southern research area.*

Stream	Catchment type	Stream order	Longitude	Latitude	Catchment size (ha)	Altitude at stream origin (m a.s.l.)	Altitude of sampling station (m a.s.l.)
SS1	Barren	1	N 63° 59.454	W 19° 54.510	5.3	142	121
SS2	Barren	1	N 63° 58.297	W 19° 59.368	9.3	100	90
SS3	Barren	1	N 63° 57.678	W 19° 57.833	0.8	125	114
SS4	Barren	1	N 63° 59.432	W 19° 54.506	0.3	136	121
SB1	Birch	1	N 63° 59.464	W 19° 58.017	2.0	100	92
SB2	Birch	1	N 63° 58.167	W 19° 59.496	1.3	100	88
SB3	Birch	1	N 64° 00.361	W 19° 53.456	2.9	159	137
SB4	Birch	1	N 64° 00.721	W 19° 53.217	2.9	152	139



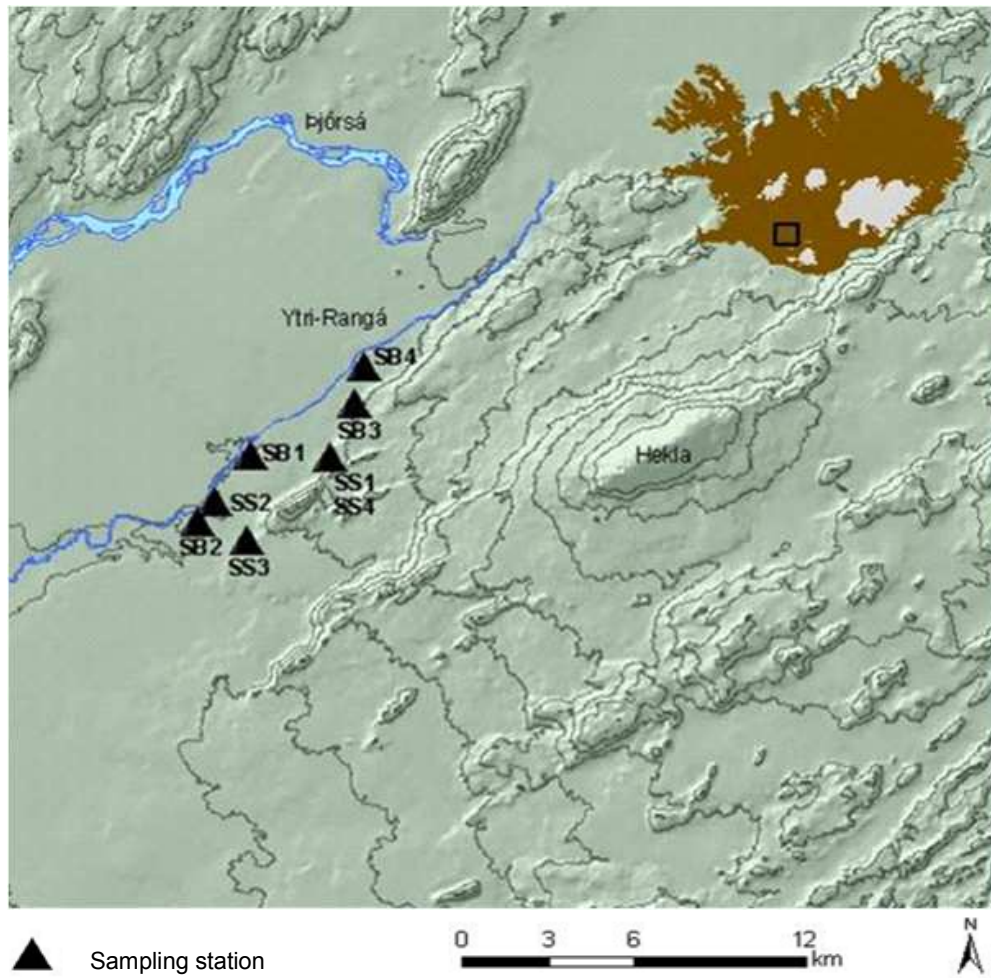


Figure 2.5 The southern research area with spring-fed streams and their catchments. Letter S indicates the location in southern Iceland; letters S and B indicate barren land and birch forest respectively; numbers indicate the size of the catchments (1 – being the largest, 4 – being the smallest).



*Figure 2.6 The southern research area. Photographs of barren (a) and birch forested (b) catchments.*

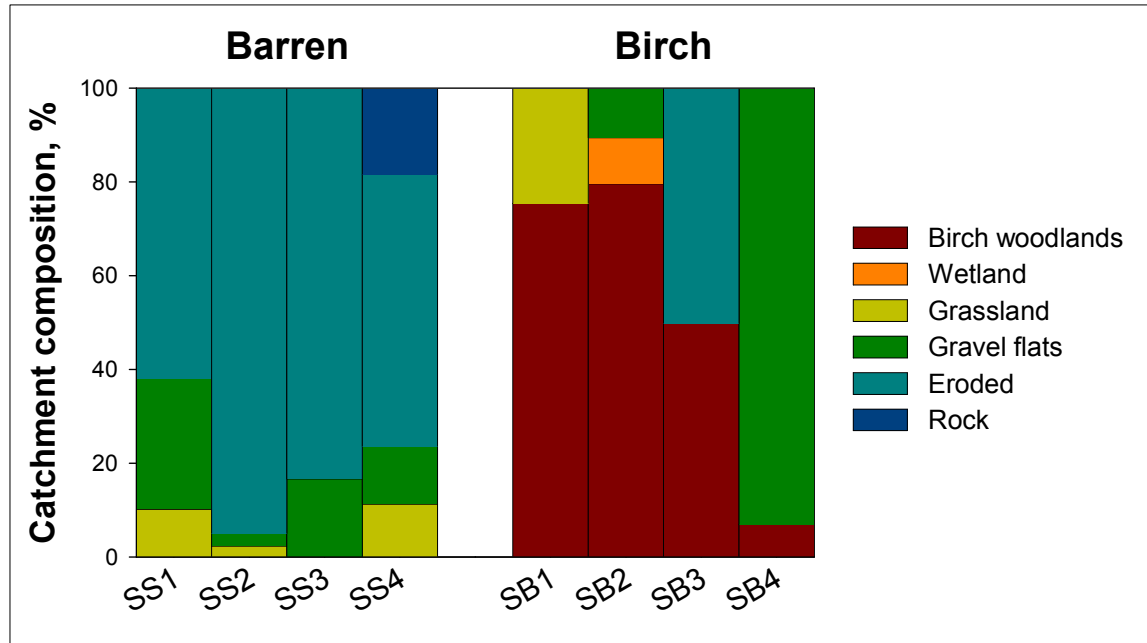


Figure 2.7 The catchment composition of spring-fed streams in the southern research area, based on the whole catchment area.

## 2.2 Field sampling

In the eastern research area, sampling was carried out seven times from November 2007 to May 2009. The sampling was confined to five time ranges: early winter (November 2007), late winter (February 2008 and 2009), spring (May 2008 and 2009), summer (July 2008) and autumn (October 2008). The samples collected and measurements taken are given in greater detail in Appendix 1.

In the southern research area, sampling was carried out six times from November 2007 to May 2009: early winter (November 2007), late winter (February 2008), spring (May 2008 and 2009), summer (July 2008) and autumn (September 2008). Due to a lack of time, only data from two sampling dates from the southern research area were used for analysis: November 2007 and July 2008. A list of samples collected and measurements taken are more thoroughly described in Appendix 2.

Before each sampling trip, tables with ten random sampling coordinates were made in MS Excel for each stream. The X coordinates were the points within a 20–50 metres reach from the sampling station in each stream. The Y coordinates were located along the width of the channel from the right margin to the left. Coordinates were expressed as a percentage, with 0% being the right margin and 100% being the left margin. In the field, a measuring tape was stretched along the stream to locate the X coordinate, and the Y coordinate was determined visually. Sampling commenced at the sampling station and proceeded upstream.

### **2.2.1 Physical and chemical variables**

During each field trip, water temperature, conductivity and pH were measured in each stream using a multiprobe sonde (YSI 600XLM, Yellow Springs Instrument Company). The width of each stream was measured at each sampling station by stretching a measuring tape across the stream.

Environmental variables, such as depth, current velocity, vegetation type of the stream bottom, as well as the substrate composition were determined at each sampling coordinate. The current velocity was measured with a flow tracker (SonTek/YSI ADV Series manufacturer). Percentage of substrate composition at each sampling coordinate within a 14x14 cm quadrat was estimated visually according to size of particles expressed in the Wentworth Scale: mud (silt and clay), sand (0.06–2 mm), gravel (2–4 mm), pebble (4–64 mm), cobble (6.4–25.6 cm) and boulder (>25.6 cm). The vegetation type and cover at each sampling coordinate within the 14x14 cm quadrat was estimated as a percentage of the following three categories: macroalgae, moss and macrophyte.

For algal biomass analysis, ten fist-sized stones were collected randomly from the stream bottom adjacent to each sampling coordinate. They were immediately wrapped in aluminium foil and placed in a dark cooling box. As soon as samples had been transported to the laboratory, they were stored in a freezer (-20 °C) until analysed.

Water samples for nutrient and elemental analysis were collected in 500 ml polyethylene bottles, which had been acid washed (7% HCl) and rinsed with deionised water. The bottles were kept in a cooling box, transported to the laboratory and kept in a freezer as well.

### **2.2.2 Riparian biomass**

In the eastern research area, the total riparian biomass within 400 metres of each sampling station was measured by summing biomass of tree layer, bush layer and ground vegetation. The trees were measured on 2–3 randomly-placed circular plots within forested catchments. The measured variables were stem diameter at heights of 0.5 and 1.3 metres and tree height. Some specific biomass functions were then used to estimate the total biomass at each catchment (Snorrason and Einarsson, 2006).

The dwarf bush layer was defined as the layer between 50 cm and 2 metres. Samples were collected at 1–2 plots within the catchments. They were later dried at 80 °C for 48 hours and weighed for biomass.

The ground vegetation was collected from 4–7 plots within each catchment using a 51x51 cm subplot. On each subplot all living plants <50 cm in height, all standing litter and all woody debris were collected. The samples were then later separated into different growth forms (such as grasses and woody debris) and then dried at 80 °C for 48 hours and weighed.



### **2.2.3 Autumn litterfall**

The fallen litter was collected in ten specially-installed litter traps (ten litres plastic buckets) in the banks of each stream. Five traps were dug into the ground in both sides of each stream approximately one metre from the channel margins. The first pair of traps was installed beside the sampling station of each stream. In the southern research area, the fifth pair of traps was installed at the origin of each stream since the streams were short. The fifth pair of traps in the eastern research area was installed about 200 metres from the sampling stations. The other pairs of litter traps were dug into the ground between the first and fifth pairs of traps, with similar spacing between all traps. The litter traps were emptied when the streams were sampled, (Appendixes 1 and 2). In the eastern research area, the litter traps were also emptied in August 2008 and November 2008.

To attain information about autumn litterfall, October 2008 and November 2008 samples were sorted into several categories (birch leaves, needles, grass litter, wood and other material), dried and massed. Then the mass of litterfall per stream meter was calculated. Complete details regarding litter transport in the streams can be obtained through Stefánsdóttir (2010).

### **2.2.4 Fish sampling**

All streams were electrofished once during the period of this study. In the rivers of the southern area, this was done in October 2007, and in the eastern area, it took place in August 2008. Stretches of the stream bottom upstream and downstream the sampling stations were sampled. All fish caught were anaesthetised. Each fish was identified to species; its length recorded and scale samples taken for age determination. After recovery, each fish was returned to its original location in the stream. This was done to have as minimal an effect on the stream biota as possible.

### **2.2.5 Invertebrate sampling**

The benthic invertebrate samples were collected with a mini Surber sampler (14x14 cm frame, 200 µm mesh size). Ten replicate samples were collected in each stream from the randomly chosen sampling coordinates. Within each coordinate, the streambed within the Surber sampler frame was disturbed gently by hand for 30 seconds (Figure 2.8). The disturbed sediment and organisms flowed downstream and were collected by the net bag of the Surber sampler. Each sample was rinsed from the net into a plastic jar. Later all samples were returned to laboratory and preserved with 75% ethanol.



*Figure 2.8 Invertebrate sampling process. The streambed within the Surber sampler frame is being disturbed by hand for 30 seconds.*

## **2.3 Laboratory procedures**

### **2.3.1 Stream invertebrates**

All invertebrates were sorted in the laboratory, identified to the lowest possible taxonomic level using 12–100 times magnification, and counted. Crustacea, Oligochaeta and Acarina were only identified to class, subclass or order. Members of the following taxa were identified to species or genus: Trichoptera, Plecoptera, Gastropoda, Coleoptera and Diptera. Members of the family Chironomidae were mounted on glass slides, using Hoyer's medium (Anderson, 1954). They were then identified according to mouth parts characteristics (Figure 2.9), antennae and body structures to species or genus level using 200–1000 times magnification. Identifications of invertebrates were based on Peterson (1977), Gíslason (1979), Cranston (1982), Wiederholm (1983), Schmid (1993) and Merritt and Cummins (1996). Subgeneric names of chironomids were defined more precisely according Hrafnisdóttir (2005).

Invertebrates were assigned to functional feeding groups (gathering collectors, filtering collectors, shredders, predators and gathering collectors scrapers) according to Merritt and Cummins (1996, 2006), Giller and Malmqvist (1998), Brönmark and Hansson (2005); Cummins et al. (2005). The list of taxa is given in Table 2.3.



Figure 2.9 The head of chironomid *Rheocricotopus* (*Rheocricotopus*) *effusus* (Walker), mounted on a glass slide.

Table 2.3 The functional feeding group of each taxa, found in direct run-off and spring-fed streams (gc stands for gathering collectors, fc stands for filtering collectors, sc stands for scrapers, sh stands for shredders and pr stands for predators).

Taxa	Feeding groups <sup>1</sup>	Reference
<i>Parochlus kiefferi</i>	gc, sc	Merritt and Cummins, 1996
<i>Macropelopia</i> sp.	pr	Merritt and Cummins, 1996
<i>Diamesa aberrata</i>	gc, sc	Merritt and Cummins, 1996
<i>Diamesa bertrami</i>	gc, sc	Merritt and Cummins, 1996
<i>Diamesa latitarsis</i> group	gc, sc	Merritt and Cummins, 1996
<i>Diamesa bertrami/latitarsis</i>	gc, sc	Merritt and Cummins, 1996
<i>Diamesa bohemani/zernyi</i>	gc, sc	Merritt and Cummins, 1996
<i>Diamesa</i> spp.	gc, sc	Merritt and Cummins, 1996
<i>Pseudodiamesa branickii</i>	gc, pr	Merritt and Cummins, 1996; pers. obs.
<i>Chaetocladius</i> spp.	gc	Merritt and Cummins, 1996
<i>Corynoneura</i> sp.	gc	Merritt and Cummins, 1996
<i>Cricotopus tibialis</i>	sh, gc	Merritt and Cummins, 1996
<i>Eukiefferiella claripennis</i>	gc, sc	Merritt and Cummins, 1996
<i>Eukiefferiella minor</i>	gc, sc	Merritt and Cummins, 1996
<i>Eukiefferiella</i> spp.	gc, sc	Merritt and Cummins, 1996
<i>Krenosmittia</i> sp.	gc	Merritt and Cummins, 1996
<i>Limnophyes</i> sp	gc	Merritt and Cummins, 1996
<i>Orthocladius frigidus</i>	gc	Merritt and Cummins, 1996
<i>Orthocladius oblidens</i>	gc	Merritt and Cummins, 1996
<i>Paraphaenocladius</i> spp.	gc	Merritt and Cummins, 1996
<i>Rheocricotopus effusus</i>	sh, gc	Merritt and Cummins, 1996
<i>Smittia</i> sp.	gc	Merritt and Cummins, 1996
<i>Thienemanniella</i> spp.	gc	Merritt and Cummins, 1996
<i>Metriocnemus</i> sp.	gc	Merritt and Cummins, 1996

*Continues*

Table 2.3 Continued

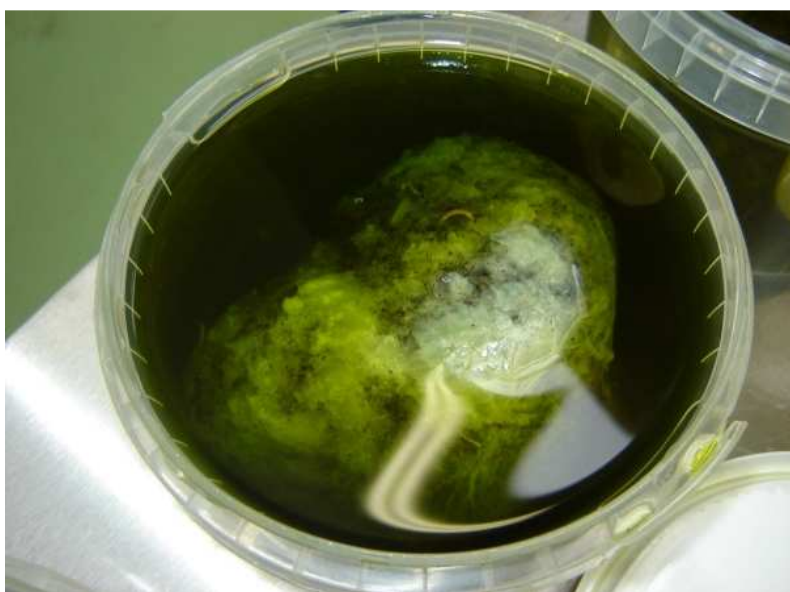
Taxa	Feeding groups <sup>1</sup>	Reference
<i>Micropsectra</i> spp.	gc	Merritt and Cummins, 1996
Thaumaleidae	sc	Merritt and Cummins, 1996
<i>Simulium vernalis</i>	fc	Merritt and Cummins, 1996
<i>Simulium vittatum</i>	fc	Merritt and Cummins, 1996
<i>Prosimulium ursinum</i>	fc	Merritt and Cummins, 1996
Simuliidae spp.	fc	Merritt and Cummins, 1996
Tipulidae sp. A - limoniinae	sh, gc, pr	Merritt and Cummins, 1996
Tipulidae sp. B - limoniinae	sh, gc, pr	Merritt and Cummins, 1996
Tipulidae sp. C - limoniinae	sh, gc, pr	Merritt and Cummins, 1996
Tipulidae sp. D - tipulinae	sh, pr	Giller and Malmqvist, 1998; Merritt and Cummins, 2006
<i>Dicranota</i> sp.	pr	Giller and Malmqvist, 1998; Merritt and Cummins, 2006
<i>Clinocera stagnalis</i>	pr	Merritt and Cummins, 1996
Hemerodromiinae (Empididae)	pr	Merritt and Cummins, 1996
Muscidae	pr	Merritt and Cummins, 1996
Ceratopogonidae	gc, pr	Merritt and Cummins, 1996
<i>Potamophylax cingulatus</i>	sh, sc	Giller and Malmqvist, 1998; Merritt and Cummins, 2006
<i>Limnephilus griseus</i>	sh, sc	Giller and Malmqvist, 1998; Merritt & Cummins, 2006
<i>Apatania zonella</i>	sh, sc	Gislason and Sigfússon, 1987; Giller and Malmqvist, 1998; Merritt and Cummins, 2006
<i>Capnia vidua</i>	sh	Merritt and Cummins, 1996
<i>Agabus</i> spp.	pr	Merritt and Cummins, 1996
Ostracoda	gc	Cummins, 2006
Cyclopoidea (Copepoda)	gc,sc	Brönmark and Hansson, 2005
Harpacticoidea (Copepoda)	gc,sc	Giller and Malmqvist, 1998; Brönmark and Hansson, 2005
Cladocera	fc	Brönmark and Hansson, 2005
Acarina	pr	Giller and Malmqvist, 1998; Cummins et al., 2005
Oligochaeta	gc	Giller and Malmqvist, 1998; Cummins et al., 2005
<i>Lymnaea</i> sp.	sc	Merritt and Cummins, 1996

<sup>1</sup>In this project, all taxa that can feed as shredders, gathering collectors and predators were classified as shredders. Taxa that can feed as shredders and scrapers were classified as shredders as well. Taxa that feed as gathering collectors and predators were classified as predators. The ones that can feed as scrapers and gathering collectors were classified as a separate group. *Pseudodiamesa branickii* (Nowicki) in Merritt and Cummins (1996) is classified as a gathering collector. Its gut contents, however, were observed to contain bodies of other chironomids, so in this study it is classified as a predator.

### 2.3.2 Primary production

Algal biomass was estimated by measuring the amount of chlorophyll *a* from each sampled stone. A day before the analysis, the stones were allowed to thaw at room temperature for one hour, so the aluminium foil that covered them could be removed. Each stone was then placed in a clean plastic container and submersed in 96% ethanol to extract chlorophyll from the attached algae (Figure 2.10). They were left in the ethanol in a cool (6 °C) dark room for 24 hours.

Chlorophyll *a* concentration was measured by a Hach Lange DR5000 spectrophotometer (manufactured by Hach Company). The absorbance of each sample was measured at 665 and 750 nm wave lengths and repeated after acidification with 1N HCl to correct for pheophytins.



*Figure 2.10 Stone, submersed in 96% ethanol to extract chlorophyll from the attached algae.*

The stone surface area was estimated by wrapping each stone completely in aluminium foil, not leaving any overlap, and all excess foil was trimmed off. The foil was then removed from the stone and massed (Steinman et al., 2006). To estimate the surface area of the stone ( $A_r$ ), the following equation was used:

$$A_r = \left( \frac{A_k}{W_k} \right) \times W_r$$

$A_r$  – surface area of stone ( $\text{cm}^2$ ).

$A_k$  – known area of aluminium foil ( $\text{cm}^2$ ).

$W_k$  – mass of  $A_k$  area (g).

$W_r$  – mass of aluminium foil (g).

The surface area of each stone  $A_r$  was divided by two, assuming that only half the stone was exposed and therefore covered by periphyton. Chlorophyll  $a$  was calculated according to Lorenzen, (1967), using the extinction coefficient for 96% ethanol from Winternans & De Mots (1965).

$$\text{Chl } a = \frac{A * K * ((665_b - 750_b) - (665_a - 750_a)) * V}{S * l}$$

Chl  $a$  – concentration of chlorophyll  $a$  ( $\mu\text{g}/\text{cm}^2$ ).

$A$  – 11.99 absorption coefficient ( $\mu\text{g}/\text{cm}^2$ ) of chlorophyll  $a$ , derived from reciprocal of specific absorbance of chlorophyll  $a$  in 96% ethanol:  $83.4 \text{ l}/(\text{g} * \text{cm})$ .

$K$  – 2.43 factor of correction for acidification.

$665_b$  – absorbance at 665 nm before acidification.

$750_b$  – absorbance at 750 nm before acidification.

$665_a$  – absorbance at 665 nm after acidification.

$750_a$  – absorbance at 750 nm after acidification.

$V$  – volume of ethanol, used for extraction (ml).

$S$  – area of stone ( $\text{cm}^2$ ).

$l$  – length of path light through cuvette (cm).

### 2.3.3 Nutrient and elemental analysis

Each water sample was divided into three parts to make some special preparations before the analysis. Thirty bottles with the samples were unfrozen at once. One third of the sample from each bottle was taken for the first preparation. Then the bottles with the rest of the original water samples were frozen again until the other two preparations were finished. The first part of each unfiltered sample was put in a 50 ml acid washed (7% HCl) plastic (Polypropylene, Sarstedt) tube, acidified with 8 M  $\text{H}_2\text{SO}_4$  (2 ml/ 100 ml sample ratio) and kept in a cooler for total nitrogen and total phosphorus analysis later.

The second part of each sample was filtered through a  $0.45 \mu\text{m}$  microinjection syringe filter (hydrophilic teflon) into a 50 ml plastic tube (precleaned with 7% HCl). This portion of the sample was stored in a freezer until analysed. Then spectrophotometric methods using flow injection analysis (FIA) technique were applied for phosphate ( $\text{PO}_4^{3-}$ ), nitrate ( $\text{NO}_3^-$ ) and nitrite ( $\text{NO}_2^-$ ), ammonium ( $\text{NH}_4^+$ ) and chloride ( $\text{Cl}^-$ ) determination using FIALab 3500b system instrument. To increase the sensitivity and accuracy of the measurements, 10 cm cuvettes were used.

The phosphate concentration in the water was measured using the stannous chloride method (Tecator, 1983a). The nitrate concentration was determined by reducing it to nitrite with copperised cadmium (Tecator, 1983b). The ammonium concentration was measured by the salicylate method variation of the phenate method (Eaton et al., 1995), and chloride concentration was determined by mercuric thiocyanate and iron nitrate methods (Tecator, 1983c, 1983d). The total nitrogen (TN) and total phosphorus (TP) concentrations in the sample were obtained by applying simultaneous the digestion method, oxidizing all phosphorus and nitrogen into nitrate ( $\text{NO}_3^-$ ) and phosphate ( $\text{PO}_4^{3-}$ ) (Ladakis et al., 2003), and then by applying nitrate and phosphate determination methods.

Three reference samples, Rain 97, ION 915 and ION 96.3 (LGC Standards, Sweden) with declared values for all elements measured here, were analysed repeatedly along with the actual water samples in order to evaluate the accuracy of the measurements. Blank samples were also measured repeatedly to calculate limit of detection (LOD) for each analyte. Additionally, quality control samples RTC-QCI-028 no. 1, 2 and 3 were used for this purpose. No. 2 was used with TN and TP analyses.

The third part of each water sample was used for elemental analysis on calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), phosphorus (P), sulphur (S), silica (Si), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn) and aluminium (Al). The samples were measured by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES) using a Jobin-Yvon Ultima-2 instrument. Each sample was filtered through 0.45 µm microinjection syringe filter (hydrophilic teflon) and acidified by adding of 0.5 ml of concentrated nitric acid (Fluka Trace Select) to 50 ml of sample prior to analysis. The plastic tubes for the samples had previously been acid washed with concentrated HNO<sub>3</sub> and then deionised water.

Nine treatment blanks were produced from deionised water through the same pre-treatment procedure. LOD and limits of quantification (LOQ) were calculated for each element as three times the standard deviation of the measured concentrations of the treatment blank solutions. Two quality control samples, SPC-SW1 and SPC-SW2 (Spectrapure AS, Norway) with declared values for all elements measured here, were analysed along with the actual water samples in order to evaluate the accuracy of the measurements.

## 2.4 Numerical analyses

Various univariate and multivariate methods were applied to species and environmental data from the eastern research area, southern research area and to compare the data between both areas. Similarities in composition of the catchments among the streams were assessed by cluster analyses using Ward's method, which is based on the Euclidean distance measure of dissimilarity (Szekely and Rizzo, 2005).

Total invertebrate density, taxonomic richness, Shannon diversity index and evenness were calculated. The Shannon diversity index and evenness were chosen because they give equal weighting to rare species (Magurran, 2004). Proportions of functional feeding groups were calculated, based on invertebrate densities and species presence/absence data. Before any ANOVA tests were applied on density and diversity parameters, and proportions of functional feeding groups, data were checked for normality and following transformations were applied: positively skewed data was  $\log_{10}(x+1)$  or 4<sup>th</sup> power transformed, and some percentage data were arcsine transformed. When assumptions of normality and homogeneity were completely violated, rank transformations were applied (Quinn and Keough, 2002). The transformations are given in Tables 2.4, 2.5 and 2.6. For all ANOVA tests the significance was accepted at  $P < 0.05$  and pairwise multiple comparison was carried out using Tukey test.

Before applying any ordination method, detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) were first carried out to determine the length of gradient and to test the linearity of data (Lepš and Šmilauer, 2003). Since the

longest gradient never reached higher than 3.0, linear methods (redundancy analysis (RDA) and principal component analysis (PCA)) were therefore carried out rather than unimodal (canonical correspondence analysis (CCA) or correspondence analysis (CA)).

Species data were examined for normality and transformed by  $\log_{10}(x+1)$  before applying any ordination method. While applying RDA, manual selection was carried out on the environmental data to determine which variables explained a significant amount of variation ( $P=0.002$ , 499 Monte Carlo permutations). All statistical analyses were performed using, SigmaStat Version 3.1, SigmaPlot Version 9.01, R Version 2.7.1 and CANOCO Version 4.5.

#### **2.4.1 The eastern research area**

Principal component analyses were used to examine and define major environmental gradients among the streams and possible gradients in species data from direct run-off streams, located in the eastern research area. First the analysis was done with the data from all sampling occasions. To avoid seasonal influence, four more PCA analyses were made on environmental and species data for winter and summer separately. Environmental data were centred and standardised to a mean of zero and variance of one and then PCA was performed.

To test the differences among the seasons and catchment types, two-way ANOVA on repeated measures was used for density and diversity parameters, and functional feeding groups. Data from February 2008 and 2009 was not included in the analyses due to missing observations (Appendix 1). Data from May 2008 were excluded from the analyses of functional feeding groups because they had many outliers. A majority of the parameters violated the assumptions of normality and homogeneity of variance, so the corresponding transformations were applied (Table 2.4).

Spearman's rank correlations were used to test the associations of PCA axes loadings of species data and catchment composition. The analysis of similarities test (ANOSIM) was used to determine if there were significant differences in invertebrate assemblages among clusters of PCA made on winter and summer data separately. Significance level was accepted at  $P<0.05$ . Pairwise multiple comparisons were then carried out and Bonferroni adjusted significance level  $P<0.017$  was used (Quinn and Keough, 2002).

Redundancy analysis was conducted to determine how the taxonomic composition varied in relation to environmental variables. First the analysis was done with the data from all sampling occasions. To avoid seasonal influence, two more redundancy analyses were done on environmental and species data for winter and summer separately.

#### **2.4.2 The southern research area**

Two PCAs were run on environmental and species data from spring-fed streams in the southern research area. Environmental data were centred and standardized to a mean of zero and variance of one. Spearman's rank correlations were used to test the associations of PCA axes loadings of species data and catchment composition. Redundancy analysis



was made to determine how invertebrate community composition varied in relation to environmental variables.

To test the differences among the seasons and catchment types, a two-way ANOVA on repeated measures was used for density and diversity parameters and functional feeding groups. The proportion of filtering collectors, based on invertebrate species presence/absence, completely violated the normality assumption, and no transformations could help. So analysis was done on the raw data. No transformations were applied for other parameters, because none of them violated the assumptions of normality and homogeneity of variance.

### 2.4.3 Comparison of direct run-off and spring-fed streams

Two-way ANOVAs were done to compare density and diversity parameters, and functional feeding groups, between the streams, located in the eastern and southern research areas. The effect of seasonality was omitted by analysing data from November 2007 and July 2008 separately. Some parameters violated the assumptions of normality, so the corresponding transformations were applied (Tables 2.5 and 2.6). A PCA was used to examine possible gradients in species data, and an RDA was conducted to determine how the taxonomic composition varied in relation to environmental variables.

*Table 2.4 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off streams.*

Occasion	Parameter	Seasons used	Transformation
<b>2 way RM ANOVA for density and diversity parameters</b>	Total density	Nov'07, May'08,	$\log_{10}(x+1)$
	Taxa richness	July'08, Oct'08,	none
	Shannon index	May'09	4 <sup>th</sup> power
	Evenness		none
<b>2 way RM ANOVA for functional feeding groups, based on species densities</b>	%Gathering collectors	Nov'07, July'08,	arcsin
	%Gathering collectors scrapers	Oct'08, May'09	none
	%Filtering collectors		arcsin
	%Shredders		rank
	%Predators		none
<b>2 way RM ANOVA for functional feeding groups, based on species presence/absence</b>	%Gathering collectors	Nov'07, July'08,	none
	%Gathering collectors scrapers	Oct'08, May'09	none
	%Filtering collectors		arcsin
	%Shredders		none
	%Predators		none

*Table 2.5 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off and spring-fed streams in November 2007.*

<b>Occasion</b>	<b>Parameter</b>	<b>Seasons used</b>	<b>Transformation</b>
<b>2 way ANOVA for density and diversity parameters</b>	Total density	Nov '07, July '08	none
	Taxa richness		none
	Shannon index		none
	Evenness		none
<b>2 way ANOVA for functional feeding groups, based on species densities</b>	%Gathering collectors	Nov '07, July '08	none
	%Gathering collectors scrapers		none
	%Filtering collectors		arcsin
	%Shredders		arcsin
	%Predators		none
<b>2 way ANOVA for functional feeding groups, based on species presence/ absence</b>	%Gathering collectors	Nov '07, July '08	none
	%Gathering collectors scrapers		none
	%Filtering collectors		none
	%Shredders		none
	%Predators		none

*Table 2.6 Sampling dates and transformations of density and diversity parameters, and functional feeding groups in direct run-off and spring-fed streams in July 2008.*

<b>Occasion</b>	<b>Parameter</b>	<b>Seasons used</b>	<b>Transformation</b>
<b>2 way ANOVA for density and diversity parameters</b>	Total density	Nov '07, July '08	$\log_{10}(x+1)$
	Taxa richness		none
	Shannon index		none
	Evenness		4 <sup>th</sup> power
<b>2 way ANOVA for functional feeding groups, based on species densities</b>	%Gathering collectors	Nov '07, July '08	none
	%Gathering collectors scrapers		none
	%Filtering collectors		rank
	%Shredders		none
	%Predators		none
<b>2 way ANOVA for functional feeding groups, based on species presence/ absence</b>	%Gathering collectors	Nov '07, July '08	rank
	%Gathering collectors scrapers		none
	%Filtering collectors		none
	%Shredders		none
	%Predators		none

## 3 Results

### 3.1 Direct run-off streams in the eastern research area

#### 3.1.1 Catchment composition

Catchment compositions of the nine streams were divided into two clusters and an outlier using similarity analysis (Figure 3.1). The first cluster was composed of three treeless catchments (AS1, AS2, and AS3). These catchments consisted of higher proportions of heathland and wetland than all the other catchments (Figure 2.3). The other cluster included forested catchments (AG1, AG2, AG3 and AB1, AB2) (Figure 3.1), which had similar proportions of birch woodlands. The catchment AB3 was an outlier and did not fit with either cluster. It was covered with the highest percentage of birch woodland and grassland and had almost no heathland (Figure 2.3).

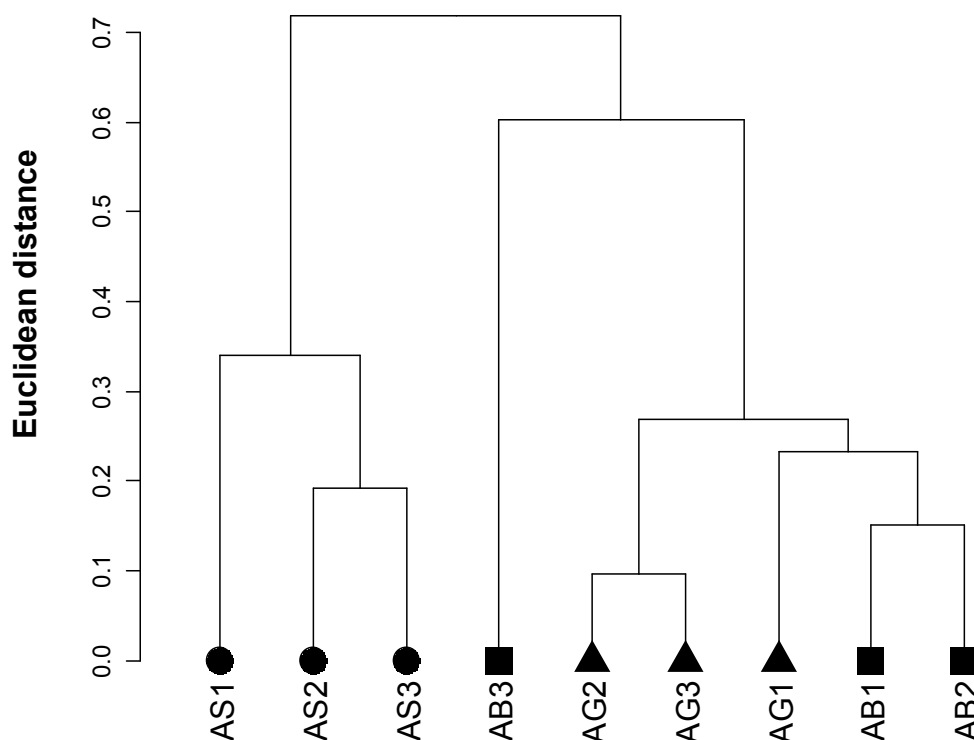


Figure 3.1 Cluster dendrogram of the similarity among catchment composition of direct run-off streams, using the Ward method, Euclidean distance. ● treeless catchments; ■ birch forested catchments; ▲ conifer forested catchments.

The similarity analysis divided the 400 metre catchment segments into two clusters (Figure 3.2). One cluster was made up of three birch forested catchments (AB1, AB2 and AB3) and two catchments, which were classified as conifer forested (AG2 and AG3). These five catchments were covered with the highest proportion of birch woodlands, which grew within the 400 metre catchment segment upstream from the sampling stations (Figure 2.4). The other cluster included the treeless catchments (AS1, AS2 and AS3) and one catchment classified as conifer forested (AG1) (Figure 3.2). These four catchments were covered with the highest proportion of heathland and gravel flats within the 400 metre segment from the sampling stations (Figure 2.4).

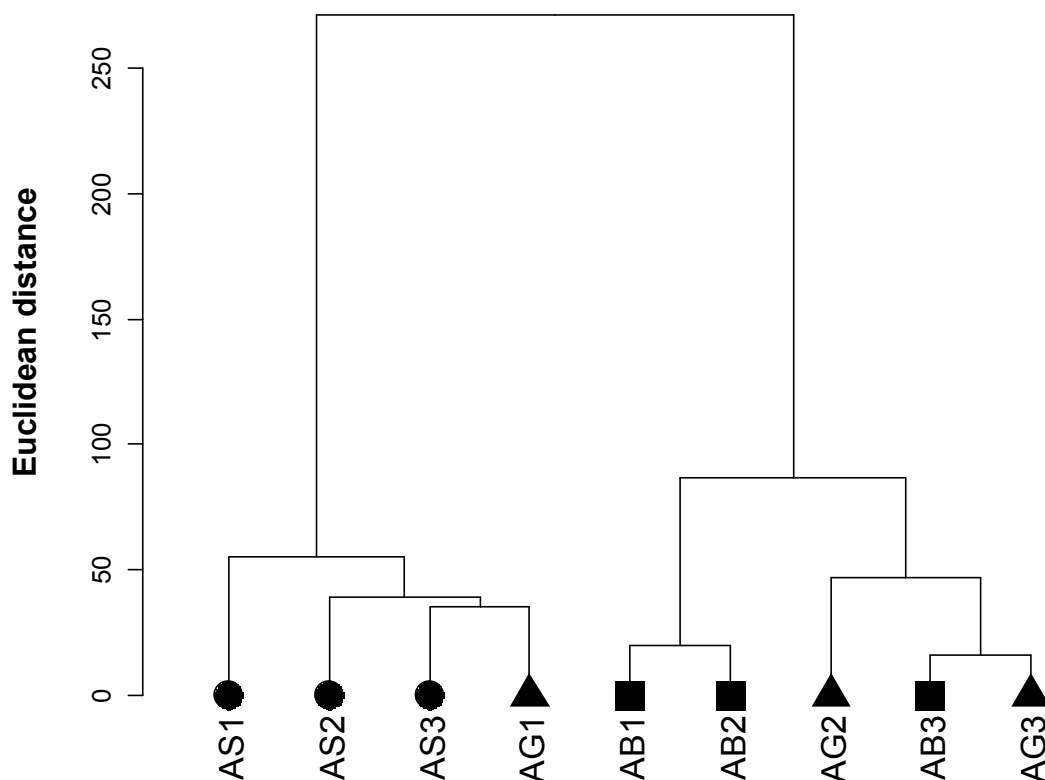


Figure 3.2 Cluster dendrogram of the similarity among composition of the catchment 400 metres upstream from the sampling station of each direct run-off stream, using the Ward method, Euclidean distance. ● treeless catchments; ■ birch forested catchments; ▲ conifer forested catchments.

### 3.1.2 Physical and chemical characteristics of the streams

Treeless catchments of the studied streams in eastern Iceland (AS1, AS2 and AS3) had relatively low total riparian biomass (0.29–0.86 kg m<sup>-2</sup>). Across the six forested catchments, total riparian biomass was highest around the streams AB3, AG2 and AG3 (10.36–13.57 kg m<sup>-2</sup>), meanwhile the rest of the forested catchments (AB1, AB2 and AG1) had approximately 2–5 times less riparian biomass (2.87–6.79 kg m<sup>-2</sup>) (Table 3.1). Autumn litterfall was highest in the streams AB1, AB3, AG2 and AG3 (41.24–49.57 g m<sup>-1</sup>), lower in AB2 and AG1 (18.52 and 28.61 g m<sup>-1</sup> respectively) and lowest in AS1, AS2 and AS3 (1–1.32 g m<sup>-1</sup>).

The difference between the altitudes of stream origin and the sampling station was used to roughly describe the gradient of the streams. The differences in altitude for the streams AB3 and AG3 were the smallest (384 and 194 metres respectively). The greatest altitudinal difference was in AG1 (817 metres) and AB2 (633 metres). The differences between altitudes in the other streams ranged from 496–583 metres (Table 3.1). Only three of the streams (AS2, AS3 and AG1) were accessible to fish (Table 3.2).

The substrate in the streams was dominated by boulders, cobbles and pebbles (77–91% of total stream bottom area) (Figure 3.3). AS1 and AG2 were the streams with the largest substrate particles. There, cobbles and boulders comprised 79% of bottom of each stream. The substrate of the stream AB3 was the finest, where cobbles and boulders together comprised only 31.6% of the bottom. The proportions of sand and gravel were slightly higher in this stream than in other streams, covering around 20.6% of the bottom. In the other streams sand and gravel covered around 5.7–15.7% of the bottom area (Figure 3.3).

The moss layer on the substrate of the streams was very scarce (Table 3.1). It was densest in stream AB3, with an average of 5% of the total bottom area across the sampling occasions. In all the other streams, moss covered only 0–3% of the bottom. The macroalgae layer was denser than the moss. In summer (May 2008 and 2009, and July 2008), maximum cover of macroalgae could reach 11–100% of total stream bottom area. In winter (November 2007, February 2008 and 2009, and October 2008), macroalgae was almost absent. The substrate of stream AG3 had the densest layer of macroalgae, with an average of 42.2% across the seasons. In all other streams, macroalgae covered around 2.2–19.7% of total stream bottom area.

A majority of the physical and chemical parameters varied across the streams and across the sampling occasions. All the descriptive statistics of these variables are given in Table 3.1. Water temperatures in the streams were highly variable across the seasons. They were lowest in November 2007 ( $-0.01$ – $1.64$  °C), and highest in July 2008 ( $7.19$ – $14.77$  °C). Some streams draining forested catchments (AB2, AB3, AG2 and AG3) exhibited lower seasonal temperature fluctuations. The lowest annual fluctuations were found in the densely-shaded stream AB3; they ranged from  $1.64$ – $7.19$  °C across the seasons.

The conductivity reached its peak during the winter (November 2007 and October 2008). It was as high as  $59$ – $145$   $\mu\text{S cm}^{-1}$  across nine studied streams during this season. In the summer (May 2008 and 2009, and July 2008), water conductivity was lower and ranged from  $34$ – $99$   $\mu\text{S cm}^{-1}$ . Stream AB3 exhibited the highest conductivity values during all seasons ( $99$ – $115$   $\mu\text{S cm}^{-1}$ ). In the other streams, conductivity varied from  $34$ – $94$   $\mu\text{S cm}^{-1}$ , with exception of stream AS1, where conductivity increased up to  $145$   $\mu\text{S cm}^{-1}$  in November 2007. The pH was slightly acidic or alkaline and ranged from  $6.36$ – $8.51$  during the five sampling occasions. In most of the streams, the pH values tended to be lower in summer (May 2008 and 2009, and July 2008).

Depth and velocity were highly correlated to each other ( $r_s=0.543$   $P<0.001$  Spearman rank correlation). Average velocity across the seasons was highest in the stream AB2 ( $0.66$   $\text{m s}^{-1}$ ) and smallest in the stream AG3 ( $0.13$   $\text{m s}^{-1}$ ). In all the other streams, average velocities ranged from  $0.32$ – $0.38$   $\text{m s}^{-1}$ . The seasonal variations in velocity were higher in AS1, AS3 and AB2. In these three streams, they peaked in May 2008 and 2009 due to snowmelt and in October 2008 due to heavy autumn rain.

The deepest streams were AS1, AB2 and AG1. Their average depths across the seasons were 17.44, 21.80 and 24.54 cm respectively. Mean depths of the other streams varied from 9.04 to 13.34 cm. The shallowest stream was AG3. The seasonal depth fluctuations were smallest there and varied from 8.00 to 10.20 cm.

Algal biomass in the streams was slightly higher in July 2008 and October 2008 ( $0.43\text{--}4.94\text{ }\mu\text{g cm}^{-2}$ ), than in May 2008 and 2009 ( $0.19\text{--}2.8\text{ }\mu\text{g cm}^{-2}$ ), except stream AB3 had exceptionally high algal biomass in May 2009 ( $5.86\text{ }\mu\text{g cm}^{-2}$ ). Stream AB3 in general was richest with algae. Average algal biomass there was  $3.85\text{ }\mu\text{g cm}^{-2}$  across the seasons. Slightly less rich were AS3, AG2 and AG3 ( $1.93\text{--}3.03\text{ }\mu\text{g cm}^{-2}$ ). Average algal biomass in all the rest of the streams varied from  $0.52$  to  $1.75\text{ }\mu\text{g cm}^{-2}$ .

A majority of concentration values of trace elements (iron, manganese, copper, zinc and aluminium), nitrate, ammonium, total phosphorus and total nitrogen were under the limits of detection, so they were excluded from the analyses. The concentration of calcium, magnesium, sodium, sulphur, silica, chlorine and phosphate in the streams was relatively low. Calcium, magnesium, sodium and sulphur levels were lowest in the summer (May 2008 and July 2008) and highest in the winter (November 2007, February 2008 and October 2008). The concentration of potassium did not vary a lot among seasons, but in most of the streams, it was highest during October 2008. Average concentrations of calcium and sodium were slightly higher in stream AB3 than in all the other streams and the concentration of sulphur in stream AB3 was around 2–3 times higher than in all the other streams.

Phosphate concentration was higher in November 2007 and October 2008, with the exception of stream AB3, where the phosphate level was highest in July 2008. The mean concentration of this nutrient in stream AB3 was around 1.5–3 times higher than in all other streams. Streams AG2, AG3 and AS2 also had increased levels of phosphate, around 1.5–2 times higher than in AS1, AS3, AB1, AB2 and AG1.

Silica level did not show any seasonal trend. In some streams, it was highest in summer, and in the other streams, it was highest in winter. The average concentration of this element did not vary much among streams either. In all streams, chlorine concentration exhibited the highest values in February 2008 and October 2008, and lowest in July 2008. The average concentration of chlorine was slightly higher in stream AB3 than all other streams. Seasonal fluctuations were lowest in stream AB3 as well.

Table 3.1 Physical and chemical parameters of direct run-off streams. Statistics across the sampling occasions are calculated. Due to lack of measurements (Appendix 1), temperature, conductivity, pH, depth, velocity, macroalgae and moss statistics is calculated across November 2007, May 2008, July 2008, October 2008 and May 2009. Algal biomass statistics is calculated across May 2008, July 2008, October 2008 and May 2009. Statistics of nutrients and elements is calculated across November 2007, February 2008, May 2008, July 2008 and October 2008. Altitude difference is calculated by subtracting the altitude of stream origin from the altitude of sampling station.

Stream	Statistics	Temperature (°C)	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Depth (cm)	Velocity ( $\text{m s}^{-1}$ )	Macroalgae (%)	Moss (%)	Algal biomass ( $\mu\text{g cm}^{-2}$ )	Ca ( $\text{mg l}^{-1}$ )	Mg ( $\text{mg l}^{-1}$ )	K ( $\text{mg l}^{-1}$ )	Na ( $\text{mg l}^{-1}$ )	S ( $\text{mg l}^{-1}$ )	Cl ( $\text{mg l}^{-1}$ )	Si ( $\text{mg l}^{-1}$ )	PO <sub>4</sub> <sup>2-</sup> ( $\text{mg l}^{-1}$ )	Total riparian biomass ( $\text{kg m}^{-2}$ )	Autumn litter-fall ( $\text{g m}^{-1}$ )	Altitude difference (m)
AS1	Mean	3.44	83.40	7.61	24.54	0.35	17.0	3.0	1.75	7.58	4.53	0.44	5.33	0.33	4.37	8.90	0.0055	0.29	1.00	496
	Minimum	-0.01	48.00	7.27	14.10	0.16	0.0	0.0	0.42	3.97	2.09	0.39	3.17	0.18	1.67	3.14	0.0032			
	Maximum	11.13	145.00	7.97	39.20	0.91	50.0	10.0	3.50	10.95	6.64	0.52	7.44	0.46	6.84	12.57	0.0095			
	Standard deviation	4.40	39.46	0.31	10.26	0.31	23.9	4.5	1.29	2.50	2.00	0.05	1.71	0.12	2.01	3.77	0.0031			
AS2	Mean	5.13	54.40	7.58	12.94	0.40	3.4	1.0	1.69	5.43	2.13	0.22	3.74	0.59	4.53	7.41	0.0081	0.56	1.23	566
	Minimum	0.04	39.00	7.31	8.80	0.23	0.0	0.0	1.11	3.78	1.43	0.17	3.02	0.29	1.43	4.25	0.0063			
	Maximum	13.20	74.00	7.89	19.80	0.67	12.0	5.0	3.33	7.04	2.80	0.28	4.76	0.88	7.65	8.93	0.0134			
	Standard deviation	4.95	15.53	0.23	4.86	0.20	5.3	2.2	1.09	1.45	0.60	0.05	0.73	0.26	2.84	1.94	0.0030			
AS3	Mean	5.68	60.40	7.33	13.34	0.44	12.2	0.0	2.18	5.88	2.55	0.28	3.98	0.40	4.33	8.43	0.0039	0.86	1.32	583
	Minimum	0.28	46.00	6.36	9.40	0.11	0.0	0.0	1.20	4.23	1.73	0.20	2.85	0.25	1.80	5.17	0.0032			
	Maximum	14.77	81.00	7.70	22.20	0.98	50.0	0.0	3.61	8.01	3.42	0.34	5.53	0.60	8.27	11.12	0.0067			
	Standard deviation	5.68	15.29	0.55	5.64	0.35	21.3	0.0	1.02	1.42	0.74	0.05	1.01	0.14	2.72	2.22	0.0016			
AB1	Mean	5.08	55.00	7.35	12.06	0.33	19.7	2.0	1.38	4.71	2.37	0.20	3.76	0.37	4.01	8.79	0.0055	6.79	41.24	517
	Minimum	0.13	43.00	6.97	7.90	0.12	1.0	0.0	1.20	3.36	1.59	0.16	3.07	0.24	1.83	7.39	0.0016			
	Maximum	12.63	78.00	7.73	14.70	0.61	51.0	10.0	1.79	6.43	3.32	0.23	4.49	0.46	6.05	10.44	0.0126			
	Standard deviation	5.24	15.15	0.27	2.73	0.19	19.1	4.5	0.28	1.23	0.68	0.03	0.62	0.09	1.50	1.20	0.0044			

*Continues*

Table 3.1 Continued

Stream	Statistics	Temperature (°C)	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Depth (cm)	Velocity ( $\text{m s}^{-1}$ )	Macroalgae (%)	Moss (%)	Algal biomass ( $\mu\text{g cm}^{-2}$ )	Ca ( $\text{mg l}^{-1}$ )	Mg ( $\text{mg l}^{-1}$ )	K ( $\text{mg l}^{-1}$ )	Na ( $\text{mg l}^{-1}$ )	S ( $\text{mg l}^{-1}$ )	Cl ( $\text{mg l}^{-1}$ )	Si ( $\text{mg l}^{-1}$ )	PO <sub>4</sub> <sup>2-</sup> ( $\text{mg l}^{-1}$ )	Total riparian biomass ( $\text{kg m}^{-2}$ )	Autumn litter-fall ( $\text{g m}^{-1}$ )	Altitude difference (m)
AB2	Mean	4.06	48.40	7.72	21.80	0.66	2.2	0.0	0.52	3.64	1.69	0.45	3.52	0.36	4.43	6.20	0.0055	2.87	18.52	633
	Minimum	0.16	40.00	7.31	14.40	0.31	0.0	0.0	0.20	1.86	1.13	0.35	2.71	0.26	1.85	-0.03	0.0032			
	Maximum	7.78	59.00	8.51	32.80	1.35	11.0	0.0	0.86	4.35	1.94	0.63	4.22	0.54	6.99	9.25	0.0067			
	Standard deviation	2.70	8.17	0.49	7.21	0.41	4.9	0.0	0.27	1.05	0.34	0.11	0.59	0.11	2.00	3.68	0.0015			
AB3	Mean	4.36	106.80	7.69	10.08	0.34	11.8	5.0	3.85	8.60	3.39	0.40	6.26	1.21	5.57	9.38	0.0171	10.36	49.40	384
	Minimum	1.64	99.00	7.22	7.20	0.21	0.0	0.0	2.64	4.85	2.89	0.34	5.78	1.10	4.52	2.10	0.0095			
	Maximum	7.19	115.00	8.00	14.60	0.56	28.0	20.0	5.86	11.32	4.19	0.55	6.80	1.46	6.65	12.71	0.0234			
	Standard deviation	2.10	7.01	0.30	2.90	0.17	13.0	8.7	1.46	2.35	0.51	0.08	0.41	0.15	0.88	4.16	0.0058			
AG1	Mean	4.30	52.40	7.38	17.44	0.38	7.5	0.0	0.89	4.73	2.31	0.20	3.81	0.33	3.82	7.32	0.0047	6.47	28.61	817
	Minimum	0.00	34.00	7.03	14.60	0.29	0.0	0.0	0.44	2.46	1.14	0.16	2.60	0.16	1.43	1.37	0.0032			
	Maximum	10.57	80.00	7.75	20.70	0.58	34.0	0.0	1.22	6.51	3.32	0.25	4.54	0.48	5.85	10.85	0.0067			
	Standard deviation	4.29	18.80	0.29	2.33	0.12	14.9	0.0	0.38	1.59	0.84	0.03	0.77	0.12	1.67	3.84	0.0017			
AG2	Mean	4.67	68.40	7.62	12.36	0.32	11.1	2.8	1.93	5.65	2.42	0.23	4.83	0.44	4.48	7.98	0.0078	13.57	42.34	505
	Minimum	0.56	60.00	6.91	7.00	0.20	0.0	0.0	0.49	4.39	2.15	0.20	4.39	0.33	2.99	2.46	0.0063			
	Maximum	7.98	79.00	8.34	16.70	0.46	54.0	12.0	4.21	6.82	2.90	0.26	5.20	0.52	5.71	9.89	0.0100			
	Standard deviation	2.80	8.02	0.52	3.71	0.11	24.0	5.2	1.62	0.92	0.31	0.02	0.36	0.08	1.05	3.11	0.0018			
AG3	Mean	5.11	59.40	7.38	9.04	0.13	42.2	0.0	3.03	5.32	2.43	0.21	3.89	0.38	3.98	8.26	0.0103	11.76	49.57	194
	Minimum	0.27	45.00	6.87	8.00	0.03	0.0	0.0	1.28	3.11	1.10	0.11	1.74	0.16	0.97	3.03	0.0032			
	Maximum	9.16	77.00	7.76	10.20	0.23	100.0	0.0	4.94	7.19	3.35	0.34	5.03	0.52	5.84	10.97	0.0284			
	Standard deviation	3.74	12.90	0.33	0.96	0.07	46.8	0.0	1.50	1.62	0.86	0.08	1.34	0.14	1.88	3.09	0.0103			



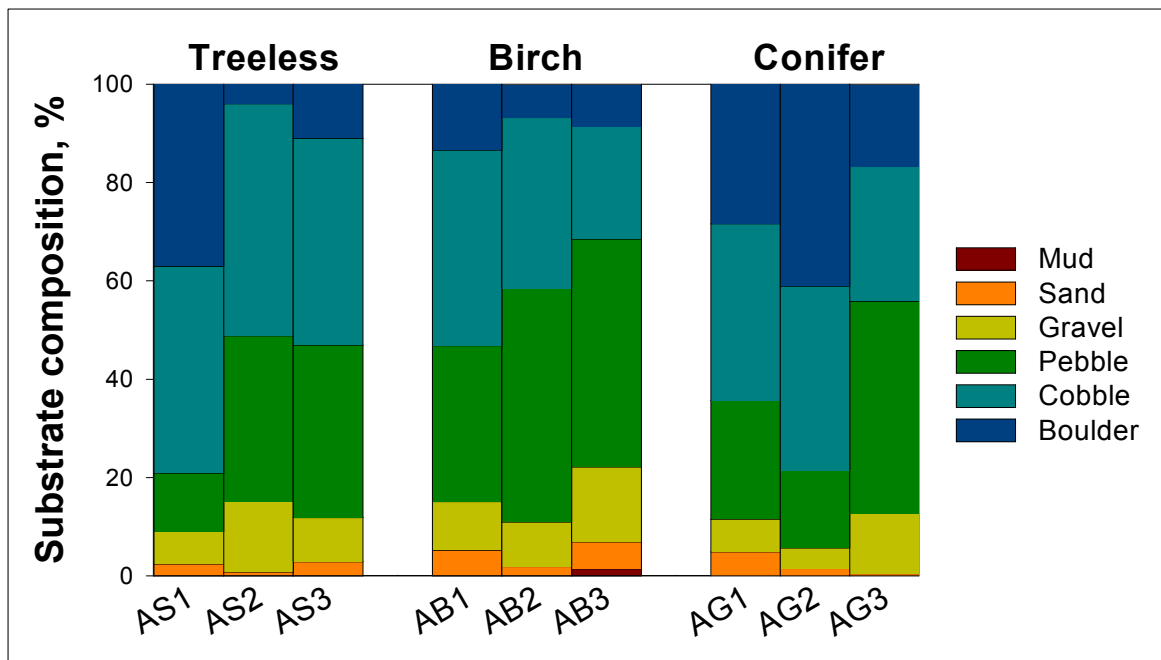


Figure 3.3 The substrate composition of direct run-off streams, based on averages for seven sampling occasions (November 2007, February 2008, May 2008, July 2008, October 2008, February 2009 and May 2009).

Table 3.2 The presence of fish in direct run-off streams.

	Arctic char ( <i>Salvelinus alpinus</i> )	Brown trout ( <i>Salmo trutta</i> )
AS1	-	-
AS2	-	+
AS3	-	+
AB1	-	-
AB2	-	-
AB3	-	-
AG1	+	+
AG2	-	-
AG3	-	-

### 3.1.3 Catchment effect on stream ecology

Physical and chemical environmental variables were analysed using principal component analysis. Only November 2007, May 2008, July 2008 and October 2008 data could be included in the analysis, because some observations were missing during other sampling occasions (Appendix 1). The first four axes of PCA explained 64.8% of the variance in environmental data. Variable loadings higher than 0.6, or lower than -0.6 were considered strong (Table 3.3).

Seasonal clustering was very distinctive in the ordination diagram (Figure 3.4). Principal component one (PC1) explained 26.6% of the variance and had the strongest loadings of chemical data: conductivity, calcium, magnesium, sodium, sulphur, phosphate and chlorine. PC1 separated summer seasons (July 2008 and May 2008), where the values of most chemical data were lowest, from winter seasons (November 2007 and October 2008), where those values were slightly higher. The concentrations of chemical data were much higher in stream AB3, than any other stream. So, all four sampling occasions of stream AB3 are distributed in one cluster, in the lower right part of ordination diagram (Figure 3.4).

Principal component two (PC2) explained 17% of the variance and had the strongest loadings of potassium, altitude, depth, stream velocity, total catchment area and total riparian biomass in the catchment (Table 3.3). Streams, running through treeless land (AS1, AS2 and AS3) were situated in the upper part of the ordination diagram because their sampling stations were located in higher altitudes. The catchments of these streams had lower amounts of riparian biomass, than streams within forested catchments (AB1, AB2, AB3, AG1, AG2, and AG3) (Figure 3.4).

*Table 3.3 Water quality and physical habitat loadings onto first four principal components of PCA analysis. Light shading indicates strong positive loadings (>0.6), dark shading indicates strong negative loadings (<-0.6).*

	PC1	PC2	PC3	PC4
Eigenvalues	0.26	0.17	0.12	0.10
Cumulative percentage of variance	26.2	43.3	54.8	64.8
Altitude	-0.07	0.65	0.21	-0.53
Temperature	-0.55	-0.04	0.13	0.00
Conductivity	0.84	0.06	0.35	-0.03
pH	0.41	0.11	-0.10	-0.33
Depth	-0.11	0.82	-0.32	0.35
Velocity	-0.08	0.69	-0.49	0.32
%Sand	0.09	0.24	-0.39	0.14
%Gravel	0.17	-0.12	-0.44	-0.27
%Pebble	0.20	-0.40	-0.49	-0.55
%Cobble	-0.32	0.32	0.46	-0.11
%Boulder	0.02	0.09	0.30	0.74
%Macroalgae	-0.49	-0.25	0.31	0.24
Calcium	0.88	0.05	0.30	-0.09
Magnesium	0.80	0.17	0.48	-0.06
Potassium	0.36	0.63	-0.21	-0.04
Sodium	0.93	-0.04	0.16	0.15
Sulphur	0.76	-0.17	-0.31	0.05
Phosphate	0.64	-0.28	0.00	0.00
Chlorine	0.64	0.26	-0.45	0.37
Total catchment area	0.11	0.68	0.46	-0.04
Total riparian biomass	0.23	-0.72	0.00	0.53

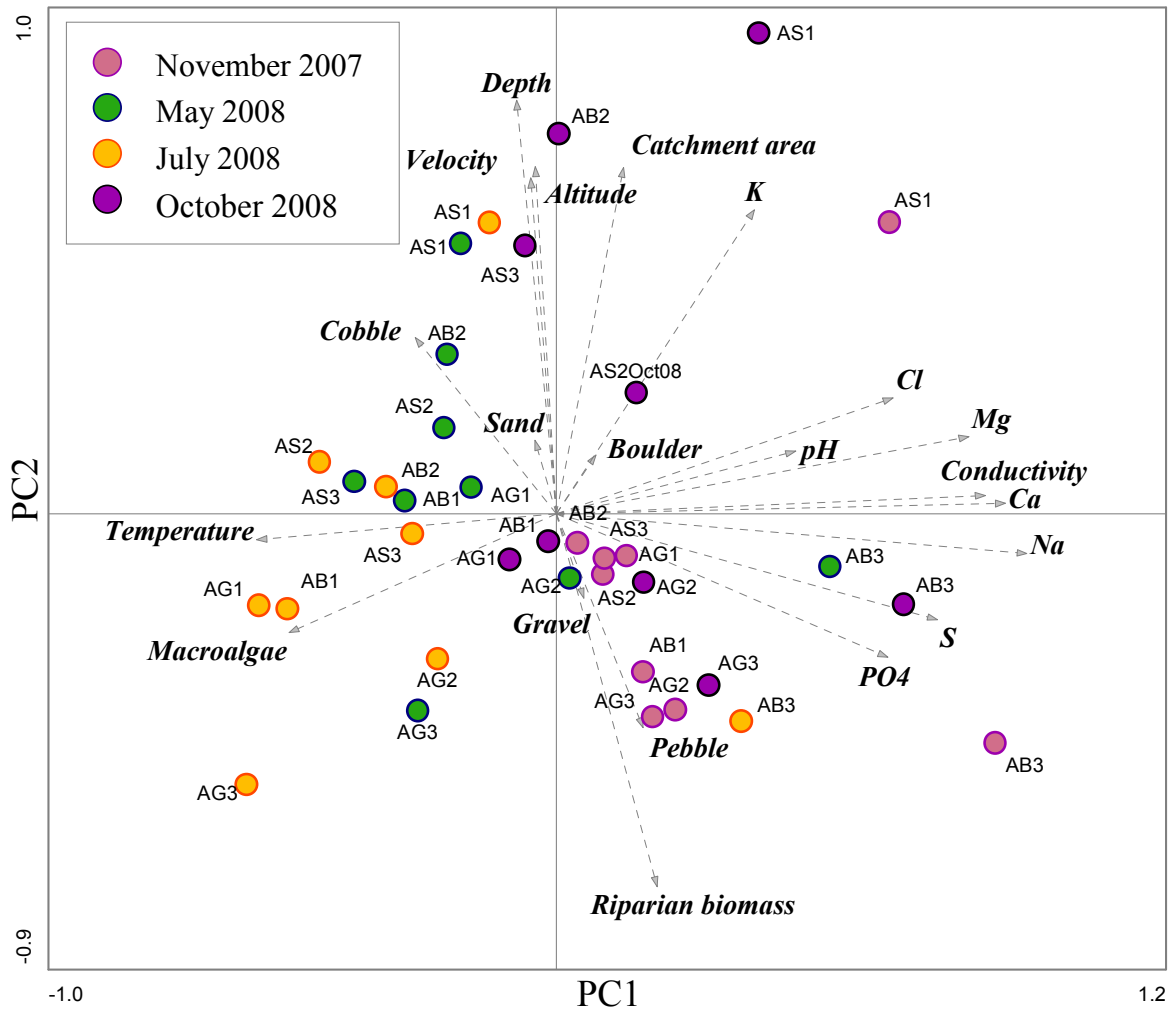


Figure 3.4 Ordination diagram of PCA based on ecological characteristics of the direct run-off streams during four sampling occasions.

### 3.1.4 Invertebrate community composition

A total of 45 invertebrate taxa were recorded in nine streams during seven sampling occasions (Table 3.4). Across the seven sampling occasions in the streams, invertebrate assemblages were dominated by Chironomidae (22–97% of total number of individuals), followed by Ostracoda (0–44%), Oligochaeta (0–36%), Simuliidae (0–25%), Acarina (0–17%) and Harpacticoidea (Copepoda) (0–14%). The other taxa, all making up 0–10% of the total number of individuals, included non-Chironomidae Diptera, Crustacea, Trichoptera, Plecoptera, Coleoptera, Gastropoda and Tardigrada.

The dominating species of Chironomidae in all streams were *Eukiefferiella claripennis* (Lundbeck), *Eukiefferiella minor* (Edwards), *Micropsectra* spp., *Thienemanniella* spp., *Orthocladius* (*Orthocladius*) *frigidus* (Zetterstedt), *Diamesa latitarsis* group (Goetghebuer), *Diamesa bertrami* (Edwards), *Diamesa bohemani/zernyi* (Goetghebuer/Edwards) and *R. (R.) effusus*. Smaller numbers were found of *P. branickii*, *Orthocladius* (*Orthocladius*) *oblidens* (Walker), *Krenosmittia* sp., *Chaetocladius* spp., *Parochlus kiefferi* (Garrett) and *Macropelopia* sp. Very few individuals were observed of *Limnophyes* sp.,

*Thienemannia gracilis* (Kieffer), *Paraphaenocladus* spp., *Metriocnemus* sp., *Pseudosmittia* sp., *Corynoneura* sp., *Smittia* sp. and *Cricotopus* (*Cricotopus*) *tibialis* (Meigen) (Table 3.4).

#### 3.1.4.1 Differences in density and diversity variables among catchment types and seasons

Stream AB3 was different from other streams by having exceptionally high numbers of *Simulium* (*Eusimulium*) *vernum* (Macquart), Ostracoda and Oligochaeta (Table 3.4). Total invertebrate densities there ranged from 1775 in May 2008 to 18969 individuals per square metre in October 2008. In other streams, total densities varied between 234 and 10000 individuals per square metre across seven sampling occasions. The fewest individuals lived in stream AG1 (from 133 in May 2008 to 1949 individuals per square metre in October 2008).

The number of taxa did not vary much among streams. Slightly more taxa lived in AB3 than in the other streams. Taxonomic richness in this stream ranged from 18 in May 2009 to 27 in October 2008. The most taxa-poor stream was AG1 (from 8 in May 2008 to 17 in July 2008). The other streams had from 9 to 30 different taxa across seven sampling occasions.

Total invertebrate density, taxonomic richness, Shannon diversity and evenness did not differ significantly among catchment types, but showed distinctive seasonal trends. Total invertebrate densities tended to be highest in streams running through birch forest and lower in streams running through treeless land and conifer forest (Figure 3.5). This disparity occurred because one stream draining birch forest, AB3, had exceptionally high densities of invertebrates than all other streams.

Seasonal variation of total invertebrate densities was statistically significant (Table 3.5). The densities in all streams were lowest in the spring (May 2008 and 2009), increased during the summer (July 2008) and reached a peak in the autumn (November 2007 and October 2008). Streams running through treeless land and birch forest showed high seasonal trends, while variations among the seasons were not as salient in streams running through conifer forest (Figure 3.5). However, the seasonal trend was only significant in streams draining treeless catchments. Total densities in October 2008 were significantly higher than in May 2008 and 2009. In November 2008 total invertebrate densities were significantly higher than in May 2008. In the streams draining conifer forest total invertebrate densities in October 2008 were significantly higher than in May 2008 (Table 3.5).

The other variable, taxonomic richness, was also highest in October 2008 for all types of catchments (Figure 3.5). During this season, streams draining treeless land were significantly richer in taxa than they were in other seasons. Streams with conifer forested catchments showed a similar pattern, but birch forest streams were not significantly different in taxonomic richness among the seasons (Table 3.5).

Table 3.4 Densities of invertebrate taxa (individuals per square metre) found in direct run-off streams. Averages are taken across five sampling occasions (November 2007, May 2008, July 2008, October 2008 and May 2009). SE stands for standard error.

	AS1		AS2		AS3		AB1		AB2		AB3		AG1		AG2		AG3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>CHIRONOMIDAE</b>																		
<b>Podonominae</b>																		
<i>Parochlus kiefferi</i> (Garrett)	0.0	0.0	2.0	2.0	6.1	4.9	1.0	1.0	2.0	2.0	1.9	1.9	1.0	1.0	1.0	1.0	0.0	0.0
<b>Tanypodinae</b>																		
<i>Macropelopia</i> sp.	4.1	4.1	0.0	0.0	5.1	5.1	0.0	0.0	3.1	2.0	1.0	1.0	0.0	0.0	2.7	2.7	6.8	6.8
<b>Diamesinae</b>																		
<i>Diamesa bertrami</i> (Edwards)	29.6	16.4	215.1	86.2	20.4	7.4	27.5	17.3	53.1	24.8	98.4	76.4	36.2	22.6	43.9	20.1	2.0	2.0
<i>Diamesa latitarsis</i> group (Goetghebuer)	61.1	48.5	98.6	53.1	5.1	4.0	18.0	8.4	15.3	6.2	419.7	342.3	29.1	18.4	28.2	19.4	1.0	1.0
<i>Diamesa bertrami/latitarsis</i> group (Edwards/ Goetghebuer)	29.3	26.8	100.3	88.9	6.1	1.9	12.2	7.0	16.1	6.0	157.6	147.3	4.4	3.3	15.5	8.6	2.0	2.0
<i>Diamesa bohemani/zernyi</i> (Goetghebuer/Edwards)	34.5	34.5	39.3	31.9	15.2	6.4	4.8	3.0	10.2	2.8	186.3	79.6	28.6	14.2	46.2	19.9	6.8	6.8
<i>Diamesa</i> spp.	1.0	1.0	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0
<i>Pseudodiamesa branickii</i> (Nowicki)	0.0	0.0	0.0	0.0	0.0	0.0	33.8	21.3	52.2	48.4	37.6	9.3	12.1	10.9	48.7	24.5	69.0	51.6
<b>Orthocladiinae</b>																		
<i>Chaetocladius</i> spp.	1.0	1.0	1.0	1.0	8.2	8.2	2.5	2.5	6.1	4.9	9.0	6.1	0.0	0.0	9.4	9.4	3.1	2.0
<i>Corynoneura</i> sp.	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	2.7	0.0	0.0
<i>Cricotopus (Cricotopus) tibialis</i> (Meigen)	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eukiefferiella claripennis</i> (Lundbeck)	686.1	371.5	97.3	40.1	90.8	38.4	944.2	507.6	576.6	442	806.9	426.0	238.4	132	502.1	182.4	569.7	147
<i>Eukiefferiella minor</i> (Edwards)	1176.8	744.1	654.6	339.1	285.4	102.1	325.5	161.7	201.5	155	445.1	180.5	77.4	52.6	219.6	108.9	146.8	34.7
<i>Eukiefferiella</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	5.0	0.0	0.0	0.0	0.0
<i>Krenosmittia</i> sp.	27.3	26.1	7.7	4.7	5.1	4.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1	4.0
<i>Limnophyes</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	2.7	9.2	9.2
<i>Metriocnemus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.6	8.6	0.0	0.0

Continues

Table 3.4 Continued

	AS1		AS2		AS3		AB1		AB2		AB3		AG1		AG2		AG3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Orthocladius (Orthocladius) frigidus</i> (Zetterstedt)	64.8	28.8	125.1	62.5	145.0	52.5	128.8	53.0	122.2	51.0	155.9	63.4	46.9	29.4	129.5	37.9	128.5	25.3
<i>Orthocladius (Orthocladius) oblidens</i> (Walker)	24.5	24.5	2.0	2.0	7.1	7.1	2.0	2.0	3.1	3.1	5.0	5.0	0.0	0.0	28.2	28.2	22.3	22.3
<i>Paraphaenocladus</i> spp.	0.0	0.0	1.0	1.0	2.0	2.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	8.2	8.2	0.0	0.0
<i>Pseudosmittia</i> sp.	7.1	7.1	0.0	0.0	2.0	2.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Rheocricotopus (Rheocricotopus) effusus</i> (Walker)	36.1	17.2	50.6	16.0	13.3	9.5	39.1	22.8	9.2	3.4	43.2	20.0	9.3	5.7	41.2	23.1	89.3	50.4
<i>Smittia</i> sp.	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Thienemannia gracilis</i> (Kieffer)	0.0	0.0	0.0	0.0	9.2	8.0	7.5	7.5	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	0.0	0.0
<i>Thienemanniella</i> spp.	64.8	55.3	146.3	65.7	114.9	75.3	153.2	36.3	95.9	50.3	413.7	219.3	43.7	21.7	387.4	261.8	613.5	310
<i>Orthoclaudiinae</i> spp.	22.4	11.0	17.2	9.0	24.2	12.1	30.3	16.5	21.6	8.7	8.2	3.5	7.6	2.3	19.9	11.3	12.0	4.1
<b>Tanytarsini</b>																		
<i>Micropsectra</i> spp.	470.2	427.5	224.5	127.0	185.7	87.3	347.7	309.9	185.2	118	666.6	372.3	34.7	22.1	508.2	184.9	673.1	140
Chironomidae spp.	11.2	1.0	24.5	4.9	38.8	9.2	24.9	11.8	38.9	18.3	35.1	14.5	25.6	12.7	34.0	11.1	47.8	6.2
<b>NON-CHIRONOMIDAE</b>																		
<b>DIPTERA</b>																		
Thaumatelidae	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	0.0	0.0	15.0	15.0	0.0	0.0	1.0	1.0	0.0	0.0
<i>Simulium (Eusimulium) venum</i> (Macquart)	4.1	4.1	18.4	8.9	18.4	10.0	21.4	13.1	4.1	3.0	1457.1	941.2	0.0	0.0	231.6	155.1	169.4	115
<i>Simulium (Psilozia) vittatum</i> (Zetterstedt)	106.1	96.2	8.2	5.9	0.0	0.0	0.0	0.0	11.2	11.2	11.2	10.0	0.0	0.0	2.0	1.2	3.1	2.0
<i>Prosimulium (Prosimulium) ursinum</i> (Edwards)	12.2	11.0	3.1	3.1	0.0	0.0	3.1	2.0	1.0	1.0	5.1	4.0	1.0	1.0	1.0	1.0	3.1	2.0
Simuliidae spp.	0.0	0.0	3.1	3.1	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0
Tipulidae sp. A - limoniinae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	4.1	0.0	0.0	2.0	2.0	0.0	0.0
Tipulidae sp. B - limoniinae	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0
<i>Dicranota</i> sp.	11.2	4.7	5.1	3.2	9.2	3.4	7.1	7.1	5.1	4.0	77.6	23.8	1.0	1.0	14.3	4.9	6.1	3.0
<i>Clinocera stagnalis</i> (Haliday)	21.4	16.6	2.0	2.0	1.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0	1.1	1.1	0.0	0.0	1.0	1.0
Hemerodromiinae (Empididae)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0	1.0	1.0	0.0	0.0	1.0	1.0	12.2	7.5

Continues

Table 3.4 Continued

	AS1		AS2		AS3		AB1		AB2		AB3		AG1		AG2		AG3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Muscidae spp.	2.0	2.0	4.1	4.1	2.0	1.2	0.0	0.0	3.1	3.1	2.0	2.0	1.0	1.0	2.0	2.0	0.0	0.0
Ceratopodgonidae spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0
Diptera spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>TRICHOPTERA</b>																		
<i>Potamophylax cingulatus</i> (Stephens)	6.1	4.9	2.0	1.2	5.1	4.0	4.1	1.9	8.2	7.0	39.8	27.7	0.0	0.0	17.3	12.0	8.2	8.2
<b>PLECOPTERA</b>																		
<i>Capnia vidua</i> (Klapalek)	0.0	0.0	0.0	0.0	0.0	0.0	25.5	19.4	15.3	14.1	54.1	35.9	0.0	0.0	21.4	13.1	1.0	1.0
<b>COLEOPTERA</b>																		
<i>Agabus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<b>CRUSTACEA</b>																		
Ostracoda	424.5	281.5	454.1	388.8	383.7	224.6	170.4	119.7	230.6	88.3	3143.9	1291	50.2	41.9	392.9	263.3	458.2	126
Cyclopoidea (Copepoda)	80.6	75.6	22.4	21.2	18.4	14.7	8.2	4.1	5.1	1.6	37.8	22.6	2.0	2.0	17.3	14.9	20.4	13.0
Harpacticoidea (Copepoda )	61.2	56.2	152.0	147.0	39.8	24.7	45.9	44.7	11.2	4.7	18.4	6.6	6.7	5.5	26.5	20.7	145.9	93.9
Cladocera	87.8	87.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	4.1	4.1	0.0	0.0
<b>GASTROPODA</b>																		
<i>Lymnaea</i> sp.	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>ACARINA</b>																		
<b>OLIGOCHAETA</b>	76.5	53.1	167.3	74.3	168.4	58.2	60.2	9.9	75.5	20.9	100.0	25.1	28.3	12.1	34.7	11.3	216.3	106
<b>TARDIGRADA</b>	219.4	139.0	393.9	237.8	393.9	177.0	88.8	42.0	164.3	75.9	1183.7	262.7	57.4	40.0	240.8	118.7	480.6	257
	6.1	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	6.1	0.0	0.0	0.0	0.0	4.1	4.1

Shannon diversity and evenness did not vary much across catchment types and seasons (Figure 3.5). Shannon diversity in conifer forest streams was significantly higher in October 2008 than in November 2007. The evenness was significantly higher in May 2009 than in November 2007 taking into account all catchments together. Tukey post-hoc comparisons, however, revealed no difference in seasonal variation within each catchment separately (Table 3.5).

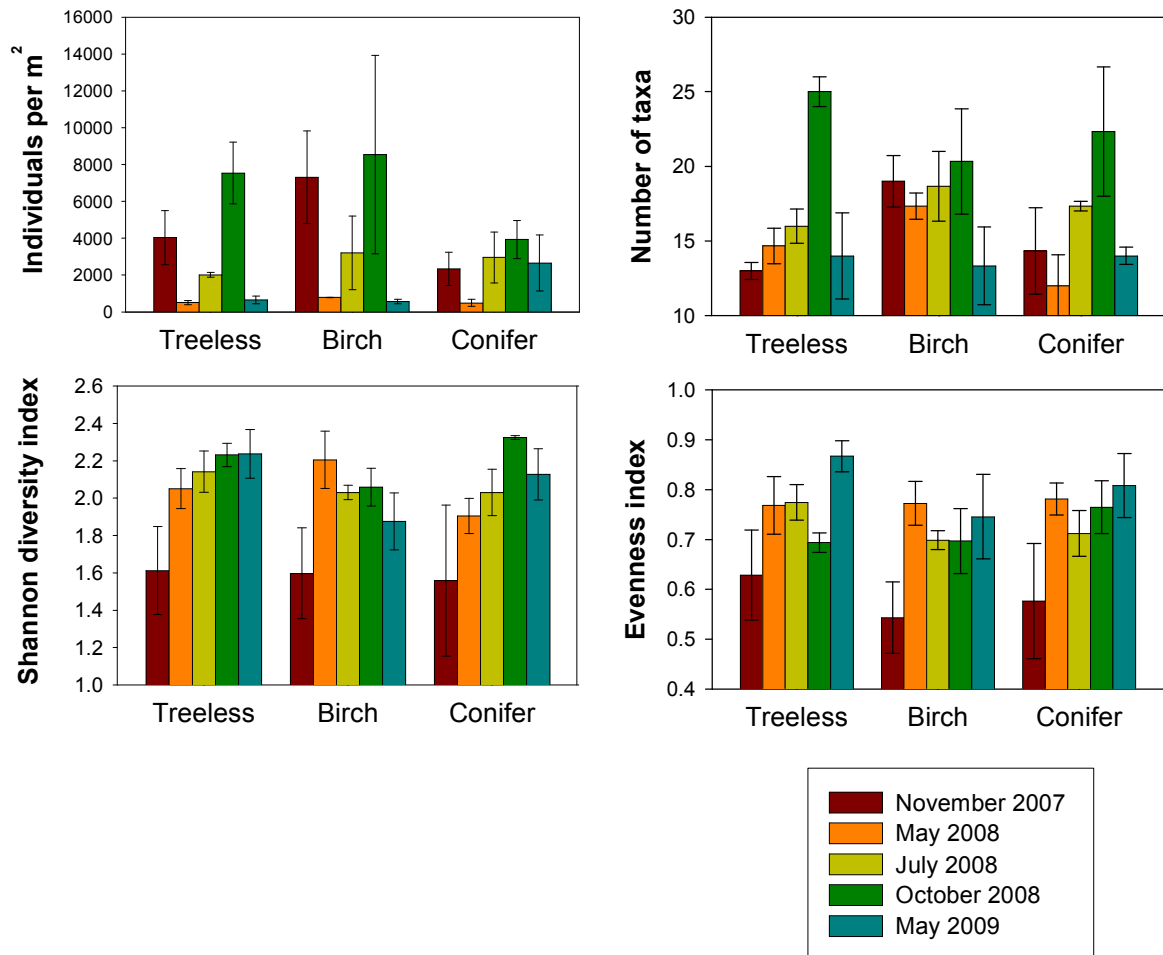


Figure 3.5 Total invertebrate densities, number of taxa, Shannon diversity and evenness in direct run-off streams with different catchment types during five sampling occasions.



Table 3.5 Catchment type and season effects on total invertebrate density, taxonomic richness, Shannon diversity and evenness in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom. Bold values indicate the significant difference at  $P < 0.05$ .

ANOVA		df	F	P	Tukey post-hoc			
					Comparisons among seasons	Season within treeless	Season within birch	Season within conifer
Density	<b>Between subjects</b>							
	Catchment	2	0.268	0.774	Oct'08>May'08	Oct'08>May'08		Oct'08>May'08
	Error	6			Oct'08>May'09	Oct'08>May'09		
	<b>Within subjects</b>				Nov'07>May'08	Nov'07>May'08		
	Season	4	11.832	<b>&lt;0.001</b>	Nov'07>May'09			
	Season X Catchment	8	1.060	0.422	July'08>May'08			
	Error	24						
Taxa richness	<b>Between subjects</b>							
	Catchment	2	0.728	0.728	Oct'08>May'08	Oct'08>May'08		Oct'08>May'08
	Error	6			Oct'08>May'09	Oct'08>May'09		Oct'08>May'09
	<b>Within subjects</b>				Oct'08>Nov'07	Oct'08>Nov'07		Oct'08>Nov'07
	Season	4	11.738	<b>&lt;0.001</b>	Oct'08>July'08	Oct'08>July'08		
	Season X Catchment	8	0.166	0.166				
	Error	24						
Shannon diversity	<b>Between subjects</b>							
	Catchment	2	1.525	0.291	Oct'08>Nov'07			Oct'08>Nov'07
	Error	6						
	<b>Within subjects</b>							
	Season	4	4.989	<b>0.005</b>				
	Season X Catchment	8	1.229	0.325				
	Error	24						
Evenness	<b>Between subjects</b>							
	Catchment	2	1.418	0.313	May'09>Nov'07			
	Error	6						
	<b>Within subjects</b>							
	Season	4	5.494	<b>0.003</b>				
	Season X Catchment	8	0.304	0.957				
	Error	24						

#### 3.1.4.2 Differences in functional feeding groups among catchment types and seasons. Analysis, based on invertebrate densities

Gathering collectors and gathering collectors scrapers were the largest functional feeding groups in direct run-off streams. They comprised 6–90% and 5–93% respectively of total invertebrate communities across seven sampling occasions. The proportions of gathering collectors were lowest in the largest streams (AS1, AB1 and AG1), higher in the smaller streams (AS2, AB2 and AG2) and highest in the smallest streams (AS3, AB3 and AG3). Gathering collectors scrapers showed the opposite trend. Their percentages were highest in AS1, AB1 and AG1, lower in AS2, AB2 and AG2, and lowest in AS3, AB3 and AG3.

The other three functional feeding groups were found in smaller proportions: predators (0–19%), filtering collectors (0–25%) and shredders (0–13% of total community across the seven sampling occasions). Three streams had much higher proportions of filtering collectors than the other streams: AB3 (0.6–25%), AG2 (0.2–20%), AG3 (0–14% of total community across the seven sampling occasions). In all other streams, the communities of filtering collectors were not as abundant and comprised only 0–10% of the community across the seven sampling occasions.

None of the five functional feeding groups showed significant variation among catchment types, but some of them varied significantly among season. The proportion of gathering collectors was smallest in November 2007 in all types of catchments (Figure 3.6). Taking into account all catchment types, the percentage of gathering collectors was significantly smaller in November 2007 than in July 2008, October 2008 and May 2009. However, only in conifer forest was the proportion of gathering collectors significantly higher in July 2008 than in November 2007 (Table 3.6).

Gathering collectors scrapers showed the completely opposite trend. The percentage of this functional feeding group was higher in November 2007 than in July 2008, October 2008 and May 2009 (Figure 3.6) and the differences were statistically significant. However, taking into account each catchment separately, proportion of gathering collectors scrapers was significantly different between November 2007 and July 2008 only in conifer forest (Table 3.6).

In the streams draining birch and conifer forests, proportions of filtering collectors were very high in November 2007 and October 2008 (Figure 3.6). It was because during these two seasons, proportions of filtering collectors were few times higher the streams AB3, AG2 and AG3 than in other streams. The seasonal differences were statistically significant only in conifer forest. The proportions of filtering collectors in November 2007 were significantly higher than in July 2008 and May 2009 (Table 3.6).

Shredders were the least abundant functional feeding group. In streams running through treeless land and conifer forest, shredder proportions were highest in July 2008 and May 2009 (Figure 3.6). The seasonal differences were not statistically significant (Table 3.6). Predators comprised smaller proportions of the community in November 2007 than during all other seasons (Figure 3.6). In the streams draining treeless catchments the proportions of predators were significantly different between November 2007 and July 2008 (Table 3.6).

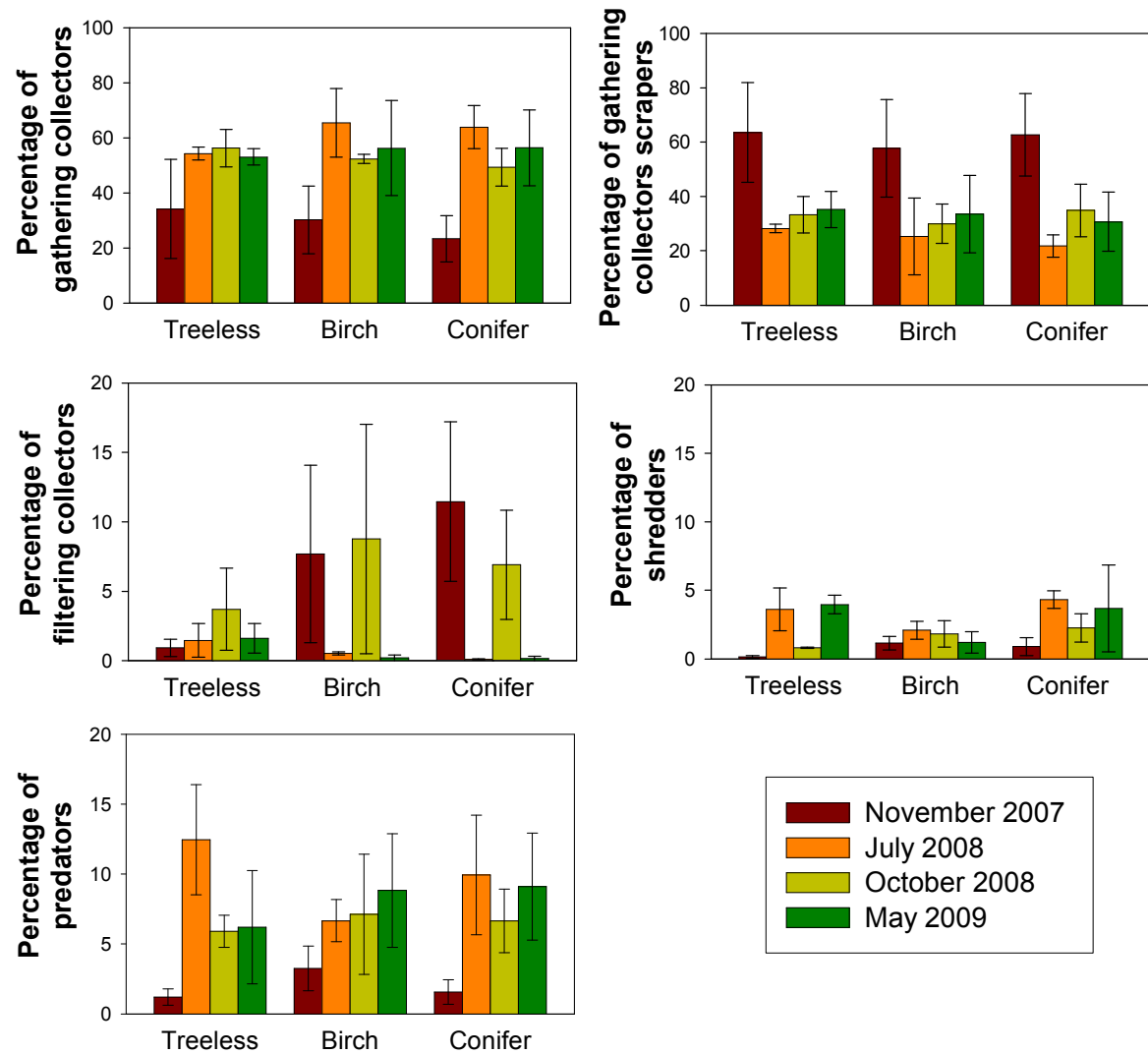


Figure 3.6 Functional feeding groups in direct run-off streams with different catchment types during four sampling occasions. Analysis, based on invertebrate densities.

Table 3.6 Catchment type and season effects on functional feeding groups in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. Analysis, based on invertebrate densities. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom. Bold values indicate the significant difference at  $P < 0.05$ .

ANOVA		df	F	P	Tukey post-hoc			
					Comparisons among seasons	Season within treeless	Season within birch	Season within conifer
Gathering collectors	<b>Between subjects</b>							
	Catchment	2	0.055	0.947	July'08>Nov'07			July'08>Nov'07
	Error	6			May'09>Nov'07			
	<b>Within subjects</b>				Oct'08>Nov'07			
	Season	3	6.706	<b>0.003</b>				
	Season X Catchment	6	0.253	0.952				
		Error	18					
Gathering collectors scrapers	<b>Between subjects</b>							
	Catchment	2	0.052	0.950	Nov'07>July'08			Nov'07>July'08
	Error	6			Nov'07>Oct'08			
	<b>Within subjects</b>				Nov'07>May'09			
	Season	3	7.210	<b>0.002</b>				
	Season X Catchment	6	0.059	0.999				
		Error	18					
Filtering collectors	<b>Between subjects</b>							
	Catchment	2	0.114	0.894				Nov'07>May'09
	Error	6						Nov'07>July'08
	<b>Within subjects</b>							
	Season	3	4.433	<b>0.017</b>				
	Season X Catchment	6	1.238	0.333				
		Error	18					
Shredders	<b>Between subjects</b>							
	Catchment	2	1.793	0.245				
	Error	6						
	<b>Within subjects</b>							
	Season	3	2.968	0.060				
	Season X Catchment	6	0.967	0.475				
		Error	18					
Predators	<b>Between subjects</b>							
	Catchment	2	0.010	0.990	July'08>Nov'07	July'08>Nov'07		
	Error	6						
	<b>Within subjects</b>							
	Season	3	4.368	<b>0.018</b>				
	Season X Catchment	6	0.584	0.739				
		Error	18					

#### 3.1.4.3 Differences in functional feeding groups among catchment types and seasons. Analysis, based on invertebrate species presence/absence

In direct run-off streams, gathering collectors and gathering collectors scrapers were the functional feeding groups richest in species. Taxa comprised 18–50% and 25–55% respectively of total number of species across seven sampling occasions. The other three functional feeding groups were found in smaller proportions: predators (0–33%), filtering collectors (0–20%) and shredders (0–20% of total community across the seven sampling occasions).

None of the functional feeding groups varied significantly among catchment types (Table 3.7). Gathering collectors and filtering collectors did not show any seasonal trends (Figure 3.7). Proportions of shredders were higher in July 2008 and October 2008, lower in November 2007 and May 2009. The differences were not statistically significant (Table 3.7). The proportions of gathering collectors scrapers were higher in May 2009, than in July 2008 and October 2008 (Figure 3.7), and the differences were statistically significant (Table 3.7). Percentage of predators varied significantly among seasons. Proportions in October 2008 were significantly higher than in May 2009 (Table 3.7).

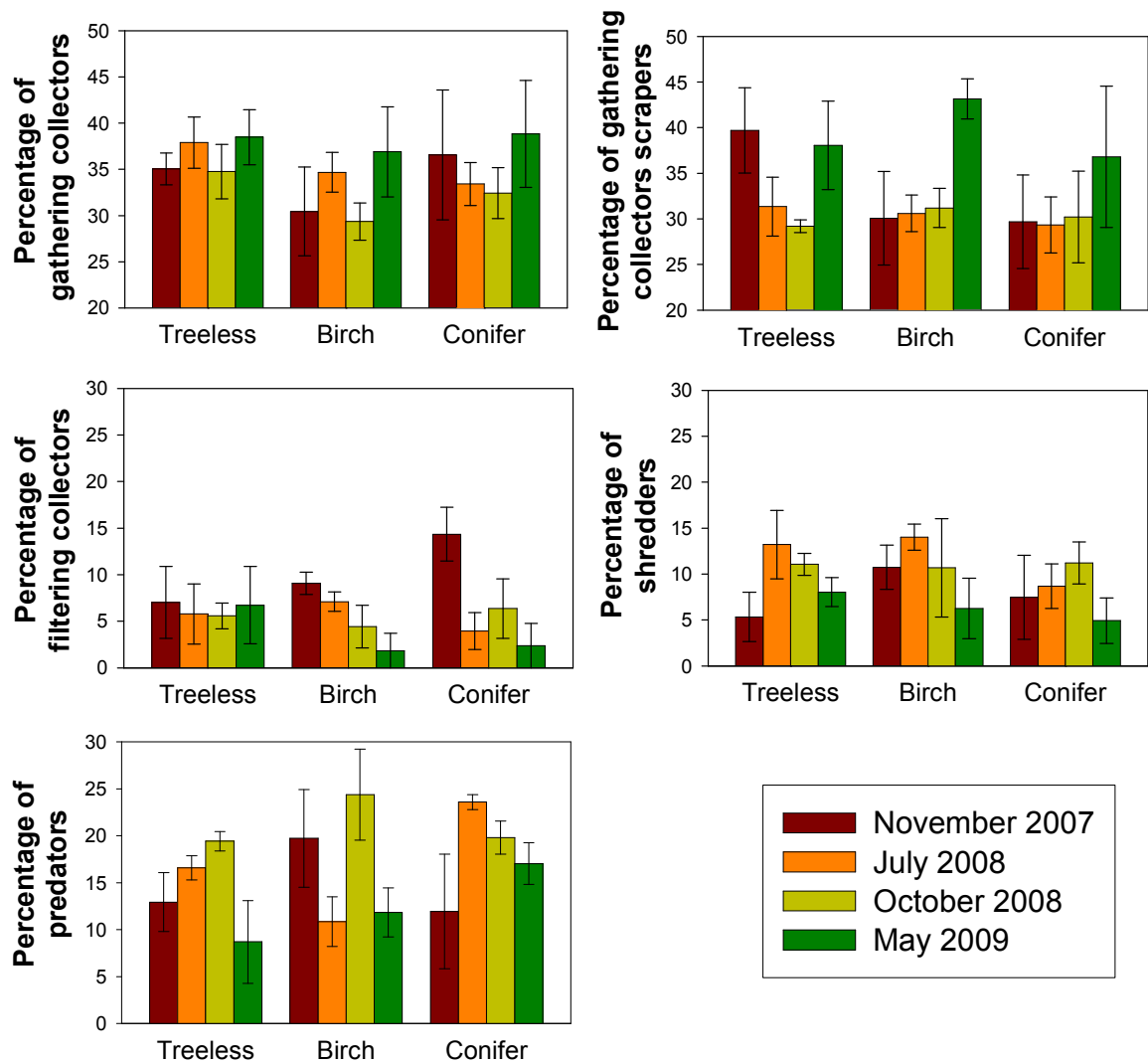


Figure 3.7 Functional feeding groups in direct run-off streams with different catchment types during four sampling occasions. Analysis, based on invertebrate species presence/absence.

Table 3.7 Catchment type and season effects on functional feeding groups in direct run-off streams. Two-way repeated measure ANOVA tests and post-hoc Tukey comparisons. Analysis, based on invertebrate species presence/absence. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom. Bold values indicate the significant difference at  $P < 0.05$ .

	ANOVA	df	F	P	Tukey post-hoc
					Comparisons among seasons
Gathering collectors	<b>Between subjects</b>				
	Catchment	2	1.384	0.320	
	Error	6			
	<b>Within subjects</b>				
	Season	3	1.119	0.368	
	Season X Catchment	6	0.196	0.974	
	Error	18			
Gathering collectors scrapers	<b>Between subjects</b>				
	Catchment	2	0.335	0.728	May'09>Oct'08
	Error	6			May'09>July'08
	<b>Within subjects</b>				
	Season	3	3.836	<b>0.028</b>	
	Season X Catchment	6	0.834	0.559	
	Error	18			
Filtering collectors	<b>Between subjects</b>				
	Catchment	2	0.010	0.990	
	Error	6			
	<b>Within subjects</b>				
	Season	3	2.571	0.086	
	Season X Catchment	6	0.886	0.525	
	Error	18			
Shredders	<b>Between subjects</b>				
	Catchment	2	2.470	0.165	
	Error	6			
	<b>Within subjects</b>				
	Season	3	1.941	0.159	
	Season X Catchment	6	0.673	0.673	
	Error	18			
Predators	<b>Between subjects</b>				
	Catchment	2	1.155	0.376	Oct'08>May'09
	Error	6			
	<b>Within subjects</b>				
	Season	3	3.466	<b>0.038</b>	
	Season X Catchment	6	1.986	0.121	
	Error	18			

#### 3.1.4.4 Invertebrate assemblages

Principal component analysis performed on invertebrate densities from seven sampling occasions yielded four principal components, which explained 76.6% of the variance in invertebrate community structure. The first two principal components accounted for most of the variation in species composition (43.5 and 16.4% respectively). The summer seasons (May 2008, May 2009 and July 2008) were mostly located in the left upper part of ordination diagram, whereas the winter seasons (November 2007, October 2008, February 2008 and February 2009) were located at the right lower part of diagram (Figure 3.8).

Samples from May 2008 and May 2009 cluster together indicating similarity of both sampling occasions and low densities of Ostracoda, Oligochaeta, *Micropsectra* spp., *S. vernum*, *E. claripennis* and some others. Some samples from November 2007, February 2008 and February 2009 form the other cluster indicating the low numbers of *Thienemanniella* spp., Acarina, *Diamesa* species and *R. (R.) effusus*. In July 2008, densities of *E. claripennis*, *E. minor*, *S. vernum* and *Micropsectra* spp. were low in the streams. The densities of *Thienemanniella* spp. were highest in July 2008. Two outliers, streams AG3 and AB3 in May 2009, had the high numbers of *Thienemanniella* spp. too (Figure 3.8).

Samples from October 2008 were the most spread in the diagram. Many species were abundant during this season: *Micropsectra* spp., Ostracoda, Harpacticoidea (Copepoda), *D. bohemani/zernyi*. Some rare species, such as Empididae, *Dicranota* sp., Cyclopoidea (Copepoda), *Potamophylax cingulatus* (Stephens) and *Capnia vidua* (Klapalek) were slightly more abundant in October 2008 than during other seasons. *S. vernum* was the most abundant in the streams AB3, AG2 and AG3 in winter: November 2007, October 2008, February 2000 and 2009. *E. minor* was the most abundant in November 2007 and slightly less in October 2008. PCA revealed very clear seasonal trends of invertebrate community composition but no clustering by catchment type (Figure 3.8).

Principal component one was highly correlated with whole catchment composition (Table 3.8). Birch woodlands, conifer forest and grassland were positively correlated with PC1. Wetland and heathland were negatively correlated with PC1. Principal component one separated some samples of stream AB3 from all the other samples (Figure 3.8). However, principal components one and two were not correlated with the percentage of forest within 400 metres catchment upstream from the sampling station in each stream (Table 3.9).



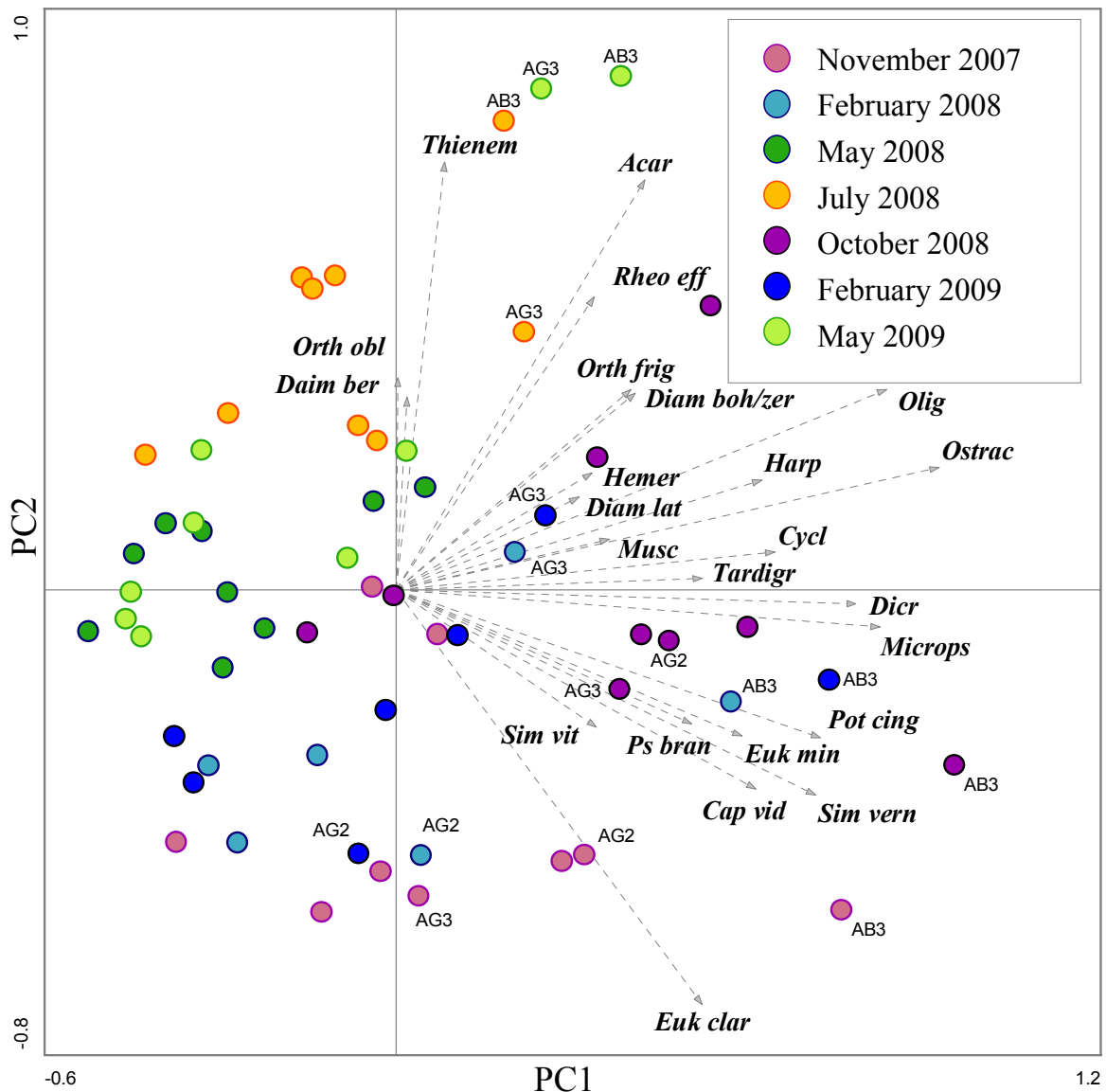


Figure 3.8 Ordination diagram of PCA, based on invertebrate densities in direct run-off streams during seven sampling occasions. Species that were found in less than seven samples across the streams and sampling occasions were omitted. For explanation on abbreviations for the taxa see a table at page XIX.

Table 3.8 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables. Light shading indicates positive correlation, dark shading indicates negative correlation. Bold values indicate a significant correlation at  $P < 0.05$ .

	PC1		PC2	
	$r_s$	P	$r_s$	P
<b>Birch woodlands</b>	0.427	<b>0</b>	-0.084	0.528
<b>Conifer forest</b>	0.332	<b>0.011</b>	-0.085	0.525
<b>Wetland</b>	-0.349	<b>0.007</b>	0.045	0.737
<b>Heathland</b>	-0.375	<b>0.004</b>	0.158	0.235
<b>Grassland</b>	0.367	<b>0.005</b>	0.251	0.058
<b>Gravel flats</b>	-0.074	0.580	0.100	0.456
<b>Eroded land</b>	-0.016	0.902	-0.152	0.255
<b>Rock</b>	-0.064	0.634	-0.180	0.174

Table 3.9 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables within 400 metres upstream from the sampling station in each stream. Shading indicates negative correlation. Bold values indicate a significant correlation at  $P < 0.05$ .

	PC1		PC2	
	$r_s$	P	$r_s$	P
<b>Birch woodlands</b>	0.107	0.423	-0.189	0.155
<b>Conifer forest</b>	0.210	0.113	-0.100	0.452
<b>Wetland</b>	0.074	0.578	-0.134	0.313
<b>Heathland</b>	-0.169	0.204	0.275	0.037
<b>Grassland</b>	-0.415	<b>0.001</b>	0.113	0.395
<b>Gravel flats</b>	-0.418	<b>0.001</b>	0.058	0.666
<b>Eroded land</b>	-0.027	0.841	0.146	0.273
<b>Rock</b>	-0.126	0.346	-0.232	0.080

### 3.1.5 Invertebrate assemblages in relation to stream ecology

Temperature, sulphur, silica, total riparian biomass, altitude and substrate composition (the proportions of sand, gravel and cobble) were the most important variables, explaining community composition in streams according to RDA. The amount of variability explained (sum of all canonical eigenvalues) was 58.5%. The first canonical axis explained 31% of total variance of species data and the second axis explained 11.5% of the variance.

Sulphur concentrations and substrate composition were the most important variables explaining the variation of invertebrate assemblages on axis one (Figure 3.9). In stream AB3 sulphur concentrations were much higher than in other streams and the bottom of this stream was characterised by having fine substrate with less boulders and cobbles (Figure 3.3). The concentrations of sulphur and proportions of gravel and sand were positively associated with such taxa as Ostracoda, Oligochaeta, *E. minor*, *Micropsectra*, *S. verum* and some rare taxa (*Dicranota* sp., *P. cingulatus* and *C. vidua*). These taxa were most

abundant in AB3. Total riparian biomass was also an important variable on axis one. *Micropectra* spp., *C. vidua* and *P. cingulatus* were positively associated with this variable and the most widespread in stream AB3 (Figure 3.9).

Water temperature was strongly correlated with RDA axis two. Higher water temperatures influenced higher numbers of *Thienemanniella* spp., *O. (O.) oblakens* and *R. (R.) effusus* (Figure 3.9). These species were the most abundant in July 2008, when the temperatures were highest. Silica was an important variable on axis two as well. It indicated low levels of this nutrient in July 2008.

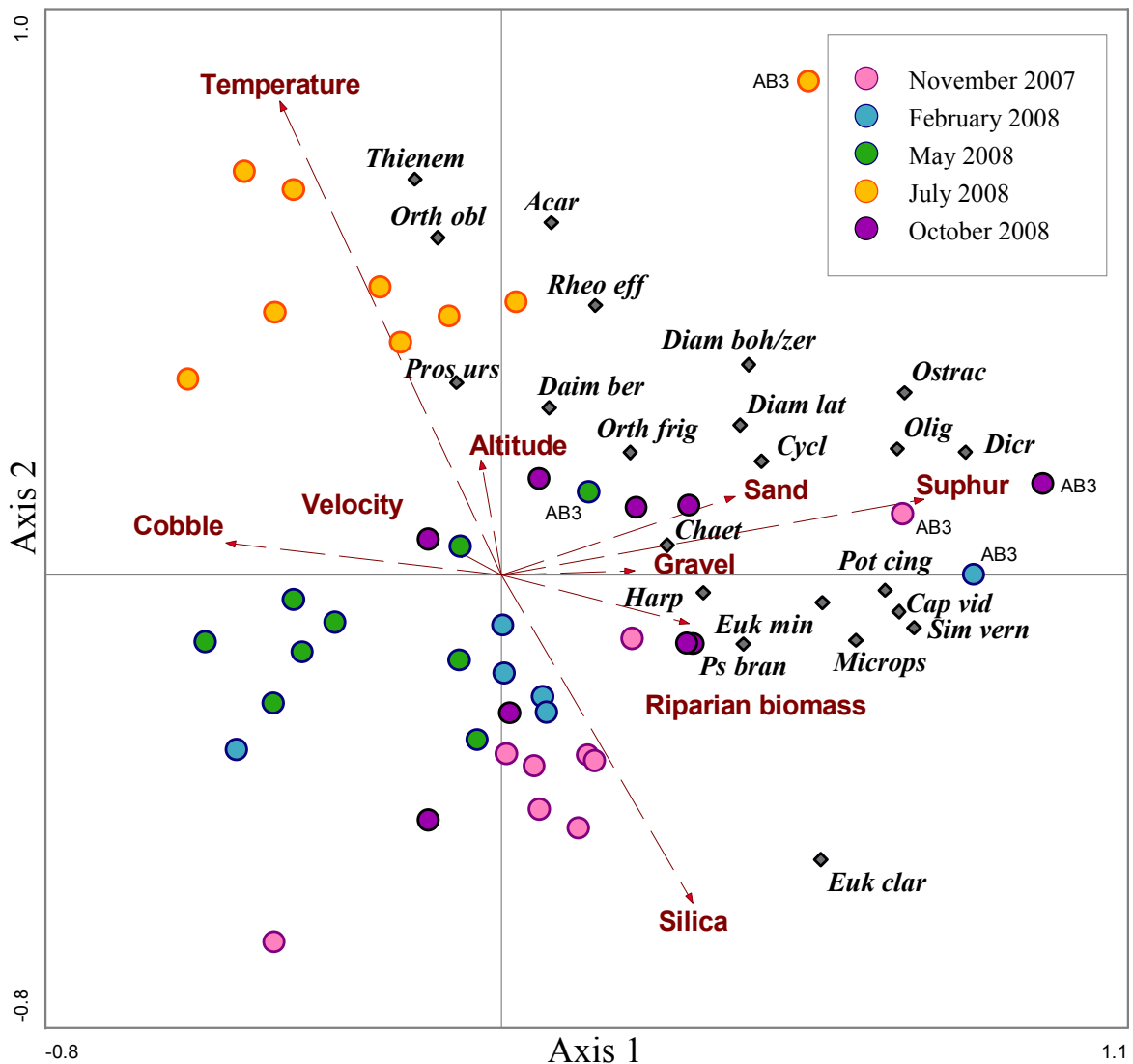


Figure 3.9 RDA ordination diagram based on invertebrate densities and environmental variables during five sampling occasions in direct run-off streams. Species that were found in less than five samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

### **3.1.6 Analysis of winter and summer seasons separately**

#### **3.1.6.1 Catchment effect on stream ecology during winter and summer**

Ordination methods clearly separated winter seasons (November 2007, February 2008 and October 2008) and summer seasons (May 2008, May 2009 and July 2008) into two clusters (Figures 3.4 and 3.8). To omit the effect of seasonality, the ordination methods were applied on the data from winter and summer seasons separately.

Environmental variables from November 2007, February 2008 and October 2008 were involved in PCA of the winter seasons. February 2009 was not included in this analysis because of the lack of some measurements (Appendix 1). PCA of the summer seasons included environmental data from May 2008 and July 2008. May 2009 lacked some measurements (Appendix 1) and was omitted from the analysis. The first four principal components of PCA on winter and summer seasons explained 70.2 and 72% of variance respectively. The first principal components of both analyses had strong loadings on variables, highlighted in Table 3.10.

The ordination diagram of winter seasons did not show any clustering by catchment type (Figure 3.10). The samples taken from conifer forest streams were close to each other. The samples taken from the streams running through the treeless land and birch woodlands were more spread in the ordination diagram. The samples of the stream AB3 formed a separate cluster on the right side of the diagram (Figure 3.10).

No separation by catchment type was seen in ordination diagram of the summer seasons. Samples from stream AB3 were located farther away from the other samples (Figure 3.11). Such separation of stream AB3 in the summer and winter ordination diagrams is determined by higher concentrations of chemicals in this stream than in the other streams.

Table 3.10 Water quality and physical habitat loadings onto first four principal components of PCA analyses, done on winter and summer periods. Light shading indicates strong positive loadings (>0.6), dark shading indicates strong negative loadings (<-0.6).

	Winter				Summer			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Eigenvalues	0.25	0.19	0.17	0.09	0.27	0.18	0.15	0.12
Cumulative percentage variance	25.4	43.8	61	70.2	27.3	45.5	60.2	72
Altitude	0.06	0.06	0.62	0.57	-0.34	-0.34	0.54	0.30
Temperature	0.19	0.84	-0.12	0.03	-0.13	0.44	0.60	0.24
Conductivity	0.87	-0.10	0.31	-0.08	0.88	-0.01	0.40	-0.08
pH	0.08	-0.24	0.02	0.20	0.11	-0.64	-0.29	0.38
Depth	-	-	-	-	-0.44	-0.75	-0.22	-0.19
Velocity	-0.18	0.78	0.34	0.26	-0.05	-0.60	-0.63	0.28
Width	-	-	-	-	-0.52	-0.53	0.15	-0.52
Algal biomass	-	-	-	-	0.77	0.39	0.27	-0.16
%Sand	0.28	0.68	-0.29	0.00	-0.45	-0.09	0.43	-0.38
%Gravel	0.48	0.17	-0.59	0.22	-0.32	-0.30	0.09	-0.10
%Pebble	0.00	-0.35	-0.55	0.62	0.13	0.19	0.12	0.60
%Cobble	-0.44	0.10	0.41	-0.61	-0.14	-0.10	0.41	0.28
%Boulder	0.24	-0.05	0.48	-0.02	0.16	0.06	-0.55	-0.68
%Macroalgae	-	-	-	-	0.00	0.56	0.13	-0.59
Calcium	0.94	-0.22	0.06	-0.08	0.66	-0.36	0.36	-0.08
Magnesium	0.74	-0.38	0.46	-0.14	0.69	-0.35	0.45	-0.32
Potassium	0.39	0.57	0.35	0.38	0.15	-0.65	0.47	0.05
Sodium	0.96	-0.06	0.00	-0.19	0.88	-0.27	0.15	-0.10
Sulphur	0.70	0.34	-0.42	0.11	0.88	-0.22	0.01	0.16
Phosphate	0.42	-0.19	-0.23	-0.06	0.83	-0.26	-0.08	0.25
Chlorine	0.13	0.84	-0.10	-0.10	0.56	-0.54	-0.51	-0.22
Silica	0.71	-0.36	-0.15	0.15	-	-	-	-
Aluminium	0.38	0.58	0.18	-0.39	-	-	-	-
Total catchment area	0.29	-0.13	0.89	0.03	-0.30	-0.54	0.53	-0.50
Total riparian biomass	0.20	-0.07	-0.67	-0.52	0.60	0.45	-0.35	-0.34

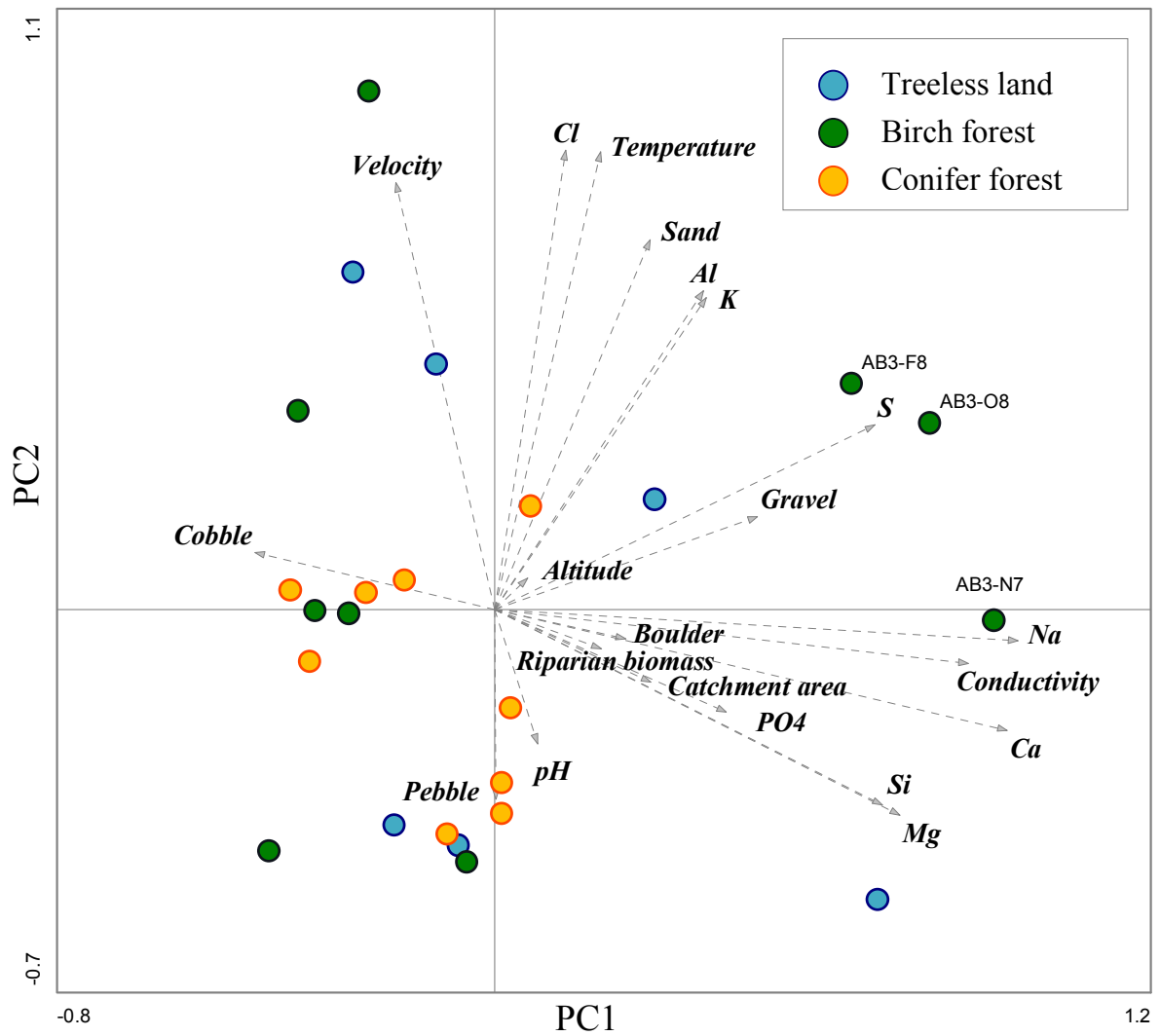


Figure 3.10 An ordination diagram of PCA, based on ecological characteristics of direct run-off streams in winter (N7 stands for November 2007, F8 stands for February 2008 and O8 stands for October 2008).

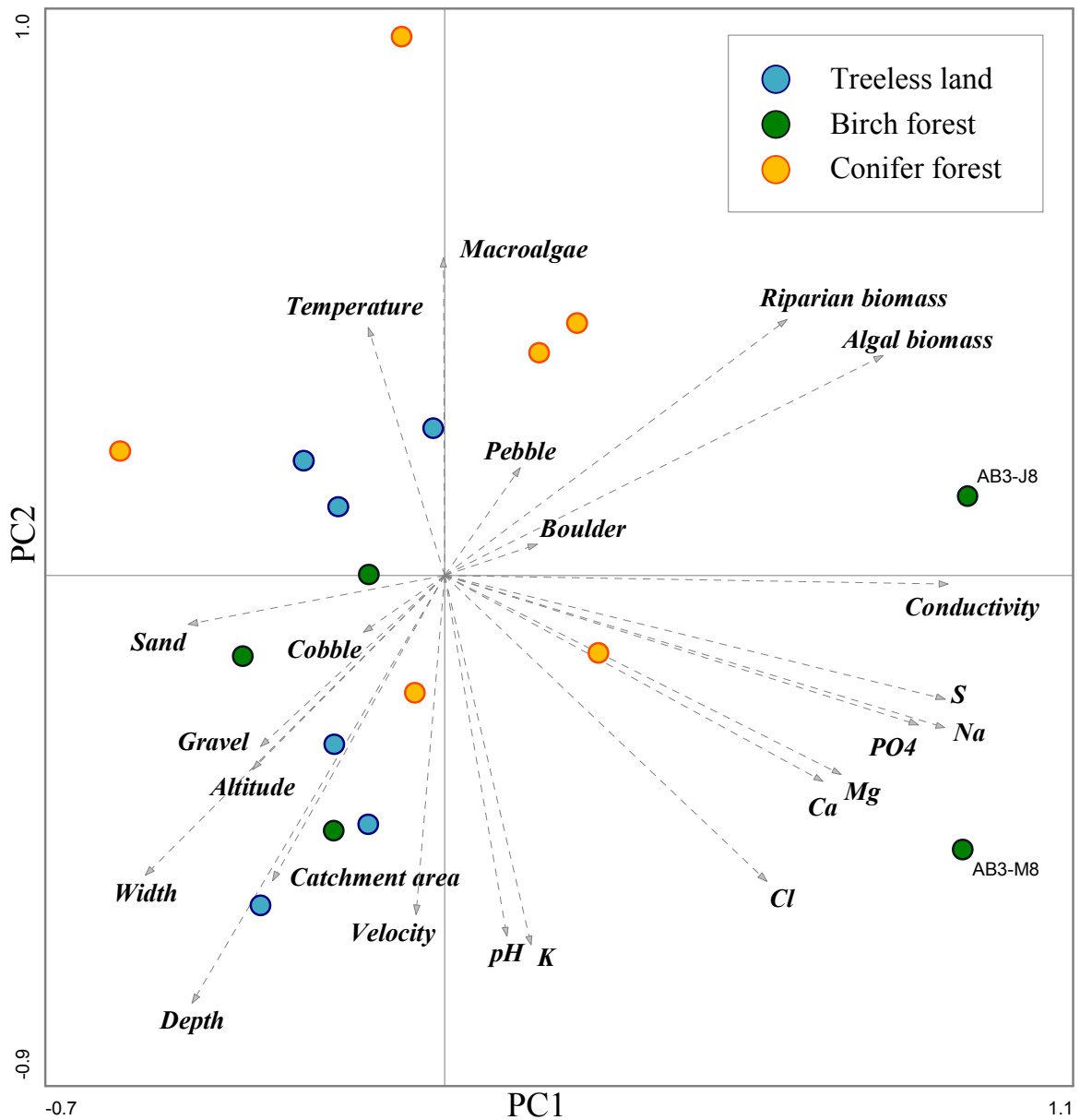


Figure 3.11 An ordination diagram of PCA, based on ecological characteristics of direct run-off streams in summer (M8 stands for May 2008 and J8 stands for July 2008).

### 3.1.6.2 Invertebrate assemblages in winter and summer

The first four principal components of the PCA performed on species data from winter seasons explained 80.8% of the variation. Some separation of samples, in terms of catchment type, was distinctive in the diagram (Figure 3.12). PC1 explained 47.9% of the variation and separated an outlier, AB3, from all the streams. PC2 explained 15.1% of the variation and separated streams with forested catchments (AB1, AB2, AB3, AG1, AG2 and AG3) from the streams with treeless catchments (AS1, AS2 and AS3) (Figure 3.12).

The samples taken from two birch forest streams (AB1 and AB2) were located in the left part of the diagram. The samples taken from conifer forest streams (AG1, AG2 and AG3) were more spread, with AG1 being situated near AB1 and AB2 (Figure 3.12). The samples from stream AB3, which is always an outlier in this study, appeared to cluster in the lower right corner of the diagram. The distribution of samples in the ordination diagram resembles the clusters of catchment composition dendrogram (Figure 3.1).

Species such as *D. bertrami* were more abundant in the streams running through the treeless land. Few other species (*S. venum*, *P. branickii* and *E. claripennis*) were more abundant in the streams within forested catchments. *C. vidua* was not found in the streams draining the treeless catchments. A majority of taxa were most abundant in stream AB3. Both principal components of winter invertebrate data were highly correlated with catchment variables (Table 3.11). PC2 was also highly correlated with catchment composition 400 metres upstream from the sampling station in each stream (Table 3.12).

Three clusters were compared by analysis of similarities. The first cluster was made of samples from stream AB3, the second cluster included the samples from the streams with forested catchments (AB1, AB2, AG1, AG2 and AG3), and the third cluster included the samples taken from streams with treeless catchments (AS1, AS2 and AS3). Significant differences in invertebrate assemblages were indicated between clusters by an ANOSIM test ( $R=0.213$   $P=0.019$ ). However, pairwise tests indicated no significant differences occurred between the pairs of clusters, using adjusted significance levels  $P=0.017$  (AB3 vs. Forested:  $R=0.207$   $P=0.056$ ; Treeless vs. AB3:  $R=0.429$   $P=0.029$ ). Forested vs. Treeless were on the border of being significant ( $R=0.216$   $P=0.017$ ).

The other PCA done on summer seasons grouped the streams according to proportion of the forests in the catchment. The first four principal components explained 80.3% of the variation, with the first two components contributing 48.5% and 14.5% of variance in species data. The samples from the streams AB3, AG2 and AG3 were situated in the right side of the ordination diagram and were widely spread from each other. Samples from all other streams were situated in the left side of the ordination diagram and were located close to each other (Figure 3.13).

Many taxa were more abundant in streams AB3, AG2 and AG3 than in all other streams. *Diamesa* spp., *O. (O.) frigidus*, *P. branickii*, *Chaetocladius* spp., *Thienemanniella* spp., *Dicranota* sp., *S. venum*, Ostracoda and Oligochaeta were the most abundant in AB3. *E. claripennis*, *O. (O.) frigidus*, *O. (O.) oblidens*, *Thienemanniella* spp. and *Micropsectra* spp. were the most abundant in AG2 and AG3.

Principal components one and two were not strongly correlated with catchment variables (Table 3.11). PC1 was still positively correlated with birch woodlands. Streams AB3, AG2



and AG3 were positively associated with PC1 (Figure 3.13). Birch woodlands covered the highest proportion of catchments for these three streams (Figure 2.3). However, PC1 was not correlated with proportions of birch woodlands or conifer forest in the first 400 metres of the catchment (Table 3.12). Invertebrate communities in both clusters were compared with ANOSIM test: first cluster (AS1, AS2, AS3, AB1, AB2 and AG1) and second cluster (AB3, AG2 and AG3). ANOSIM indicated no difference between invertebrate assemblages in these clusters ( $R=0.138$ ,  $P=0.062$ ).

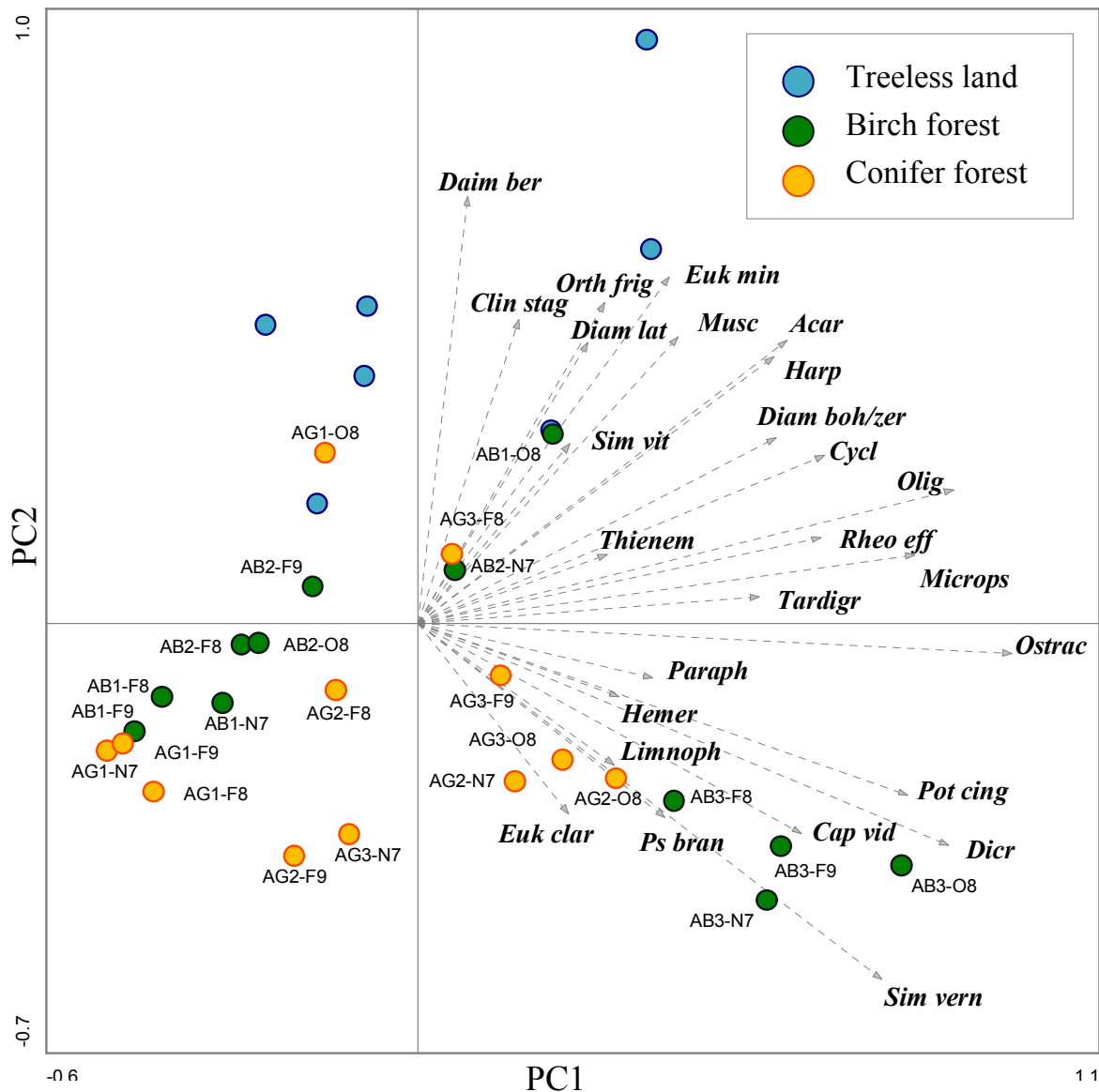


Figure 3.12 PCA ordination diagram based on invertebrate densities in direct run-off streams in winter (N7 stands for November 2007, F8 stands for February 2008, O8 stands for October 2008 and F9 stands for February 2009). Species that were found in less than five samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

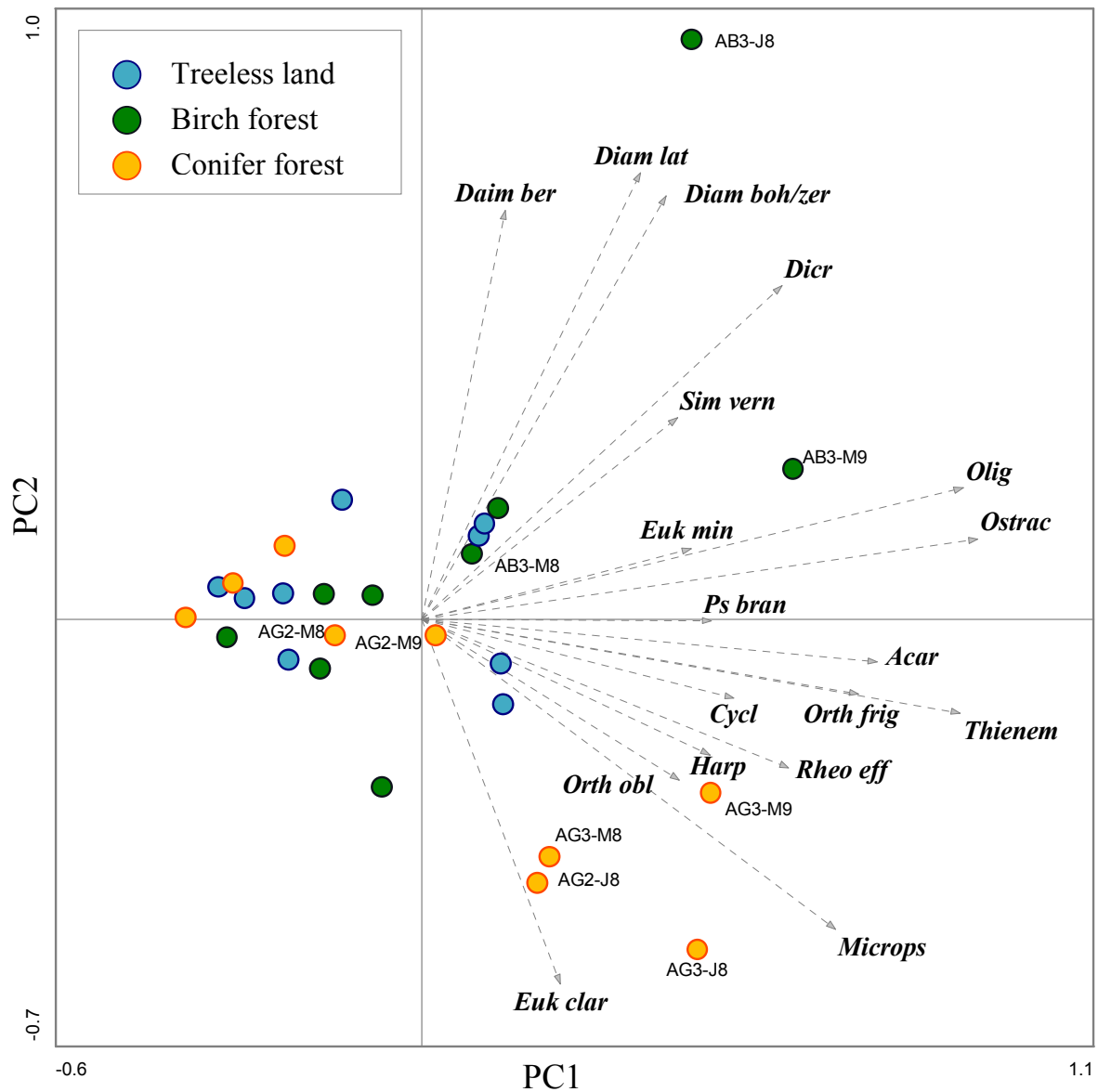


Figure 3.13 PCA ordination diagram based on invertebrate densities in direct run-off streams in summer (M8 stands for May 2008, J8 stands for July 2008 and M9 stands for May 2009). Species that were found in less than five samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

Table 3.11 Spearman's rank correlation coefficients between winter and summer species data PCA axes loadings and catchment composition variables. Light shading indicates positive correlation, dark shading indicates negative correlation. Bold values indicate a significant correlation at  $P < 0.05$ .

	Winter				Summer			
	PC1		PC2		PC1		PC2	
	$r_s$	P	$r_s$	P	$r_s$	P	$r_s$	P
<b>Birch woodlands</b>	0.383	<b>0.034</b>	-0.773	<b>0</b>	0.500	<b>0.008</b>	-0.08	0.686
<b>Conifer forest</b>	0.306	0.094	-0.616	<b>0</b>	0.361	0.064	-0.23	0.256
<b>Wetland</b>	-0.32	0.084	0.456	<b>0.01</b>	-0.448	<b>0.019</b>	-0.05	0.797
<b>Heathland</b>	-0.372	<b>0.039</b>	0.769	<b>0</b>	-0.357	0.067	0.044	0.825
<b>Grassland</b>	0.491	<b>0.005</b>	-0.004	0.984	0.363	0.063	0.418	<b>0.03</b>
<b>Gravel flats</b>	-0.081	0.662	0.527	<b>0.002</b>	-0.055	0.783	-0.2	0.316
<b>Eroded land</b>	-0.084	0.649	-0.492	<b>0.005</b>	0.000	0.999	0.271	0.17
<b>Rock</b>	-0.279	0.127	-0.339	0.062	0.089	0.657	-0.58	<b>0.002</b>

Table 3.12 Spearman's rank correlation coefficients between winter and summer species data PCA axes loadings and catchment composition variables within 400 metres upstream from the sampling station of each stream. Light shading indicates positive correlation, dark shading indicates negative correlation. Bold values indicate a significant correlation at  $P < 0.05$ .

	Winter				Summer			
	PC1		PC2		PC1		PC2	
	$r_s$	P	$r_s$	P	$r_s$	P	$r_s$	P
<b>Birch woodlands</b>	-0.053	0.776	-0.378	<b>0.036</b>	0.208	0.294	-0.088	0.659
<b>Conifer forest</b>	0.141	0.447	-0.547	<b>0.002</b>	0.255	0.198	-0.264	0.181
<b>Wetland</b>	0.065	0.728	-0.301	0.099	0.091	0.648	-0.257	0.193
<b>Heathland</b>	-0.060	0.747	0.594	<b>0</b>	-0.211	0.288	0.105	0.599
<b>Grassland</b>	-0.349	0.054	0.527	<b>0.002</b>	-0.488	<b>0.010</b>	0.199	0.316
<b>Gravel flats</b>	-0.304	0.096	0.542	<b>0.002</b>	-0.534	<b>0.004</b>	0.174	0.382
<b>Eroded land</b>	0.180	0.330	0.530	<b>0.002</b>	-0.167	0.401	0.059	0.769
<b>Rock</b>	-0.206	0.264	-0.171	0.354	-0.091	0.648	-0.323	0.099

### 3.1.6.3 The relation of stream ecology with invertebrate assemblages during winter and summer

In winter, invertebrate community composition in the streams was explained by altitude, velocity, sulphur concentrations and temperature according to RDA (Figure 3.14). The amount of variability explained (sum of all canonical eigenvalues) was 50.2%. The first canonical axis explained 31.8% of total variance of species data and the second axis explained 10.4% of the variance.

Temperature and sulphur concentration were important variables on axis one. Oligochaeta, Ostracoda, Cyclopoidea (Copepoda), *R. (R.) effusus*, *D. bohemani/zernyi* and *Micropsectra* spp. were positively associated with higher temperatures during winter (Figure 3.14). In October 2008 water temperatures in the streams were warmer than in November 2007 and February 2008. The above aforementioned species were most abundant in October 2008, so the samples taken in October 2008 are located mostly in the right side of ordination diagram and showed positive associations with temperature. The concentration of sulphur was positively correlated with such taxa as Ostracoda, *S. vernum*, *P. cingulatus* and *Dicranota* sp. That corresponds to stream AB3, where the densities of these taxa were higher and concentrations of sulphur were greater than in the other streams.

Altitude was also an important factor explaining invertebrate community composition in the winter. It was strongly positively correlated with RDA axis two. This axis divided the streams into two groups. The streams draining treeless land (AS1, AS2 and AS3) were clustered in the upper part of the ordination diagram because their sampling stations were situated at higher altitudes than the sampling stations of forest streams (AB1, AB2, AB3, AG1, AG2 and AG3).

Current velocity was correlated with altitude. The sampling stations of streams AS1, AS2, AS3, AB1 and AB2 were located at higher altitudes than the sampling stations of other streams. Seasonal current velocity fluctuations were the highest there. After fitting altitude as a covariable, current velocity became one of the most important variables affecting invertebrate communities in the streams. A few dominating taxa of chironomids (*E. minor*, *E. claripennis* and *D. latitarsis* group) were strongly negatively associated with this variable (Figure 3.15).

Streams draining treeless catchments were not clustered together anymore after fitting altitude as a covariable (Figure 3.15), but they did not overlap with forest streams either. Samples from stream AB3 still formed a separate cluster, and other samples from forest streams were still clustered together.

Algal biomass, total riparian biomass, concentration of sulphur and chlorine were the most important variables, explaining community composition in the summer (Figure 3.16). The amount of variability explained (sum of all canonical eigenvalues) was 61.2%. The first canonical axis explained 35% of total variance of species data and the second axis explained 15.5% of the variance.

The most important variable on axis one was algal biomass. Algae rich streams (AB3, AG2 and AG3) were situated on the right side of the ordination diagram, indicating that majority of the invertebrate taxa were most abundant in these three streams (Figure 3.16). Total riparian biomass was positively associated with *Micropsectra* spp., *E. claripennis*, *Thienemanniella* spp. and *O. (O.) oblidens*. These species were the most abundant in streams AG2 and AG3 where riparian biomass was highest. A couple of species in these two streams, such as *Thienemanniella* spp., *R. (R.) effusus*, *O. (O.) oblidens* and *P. branickii* were negatively correlated with lower values of chlorine in July 2008. Sulphur concentration also played an important role in explaining invertebrate community composition in winter. Sulphur concentrations were the highest in stream AB3, where *Diamesa* spp., *S. vernum* and *P. cingulatus* were the most abundant (Figure 3.16).

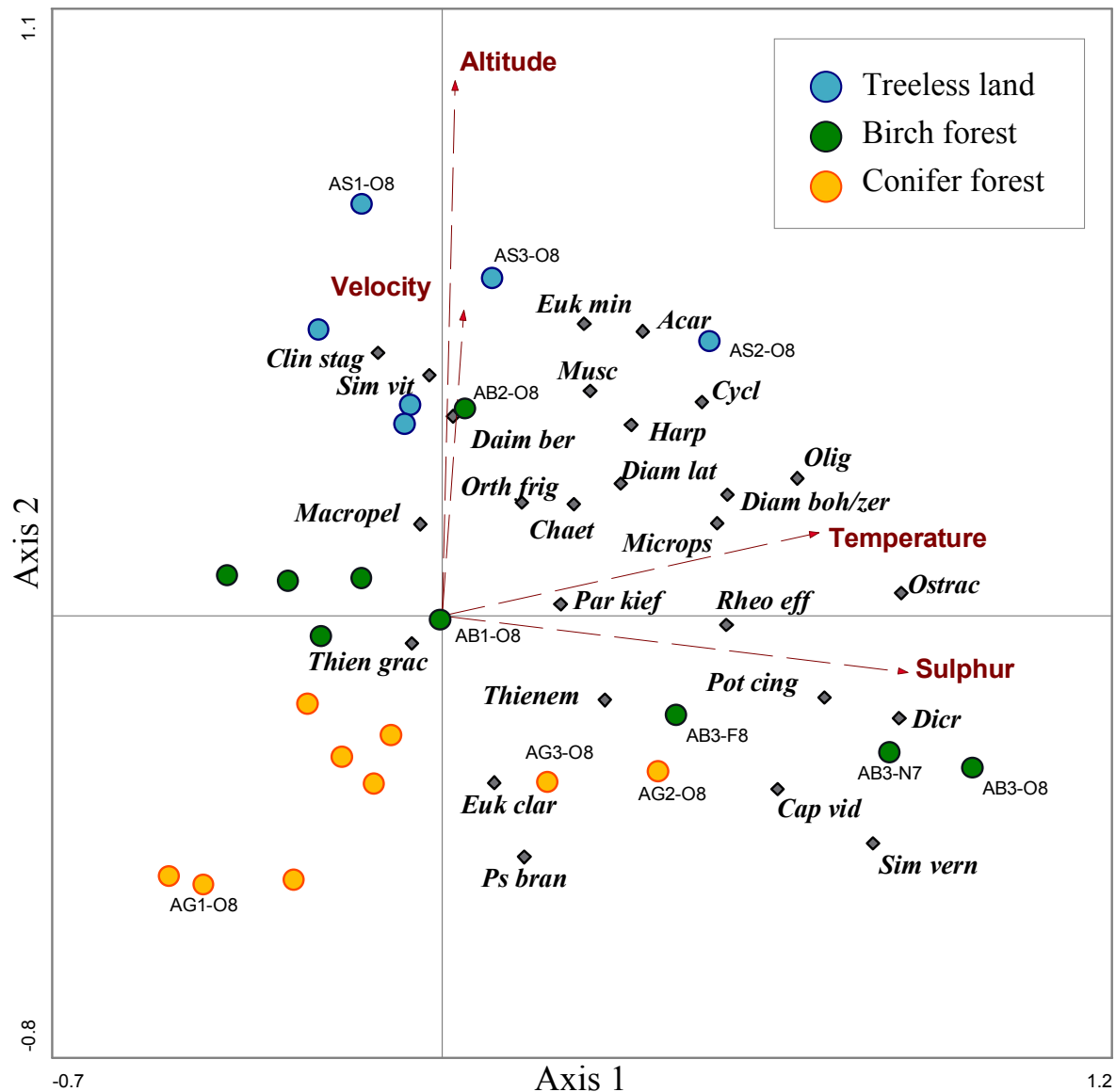


Figure 3.14 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in winter (N7 stands for November 2007, F8 stands for February 2008 and O8 stands for October 2008). Species that were found in less than five samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

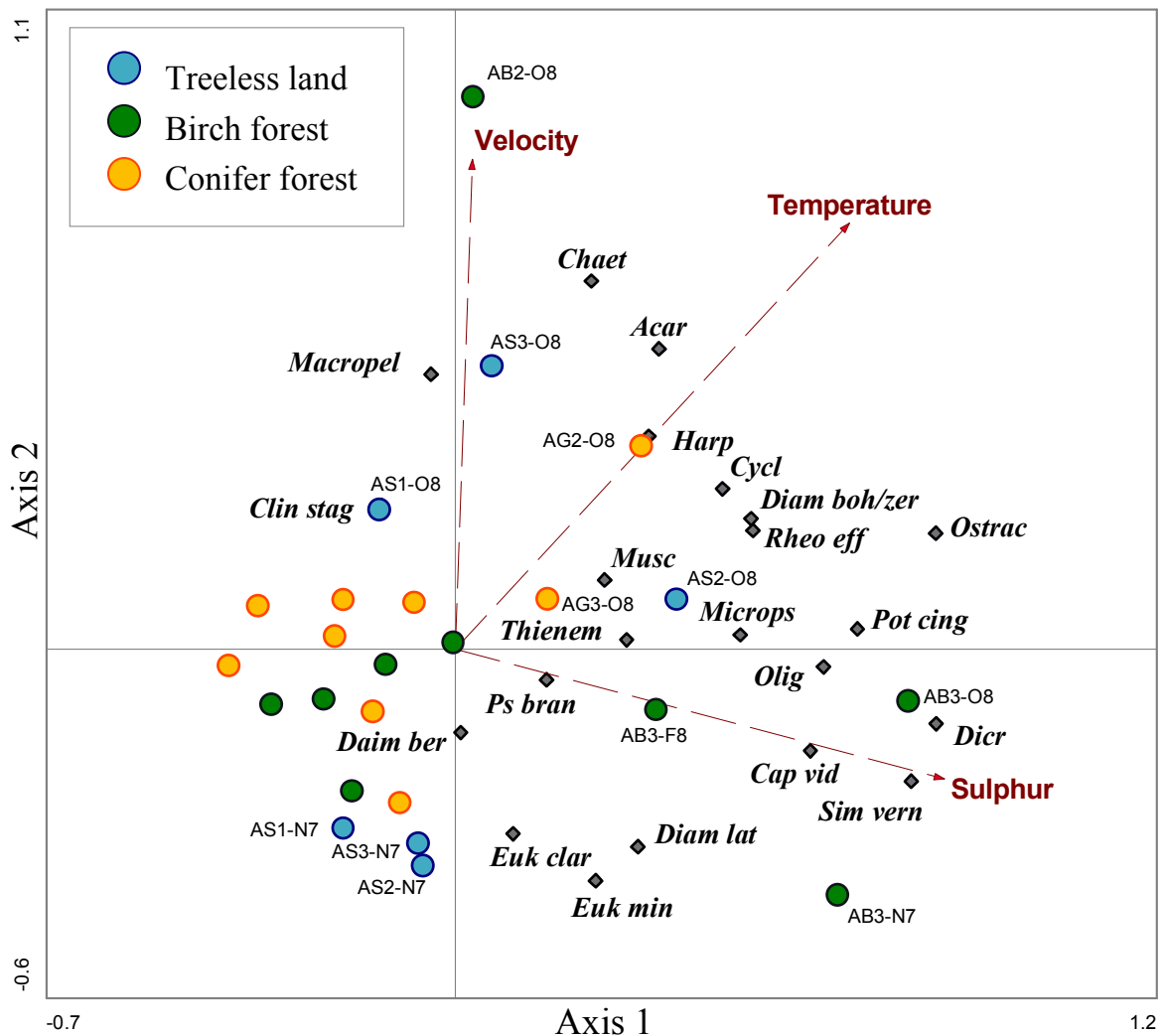


Figure 3.15 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in winter after fitting altitude as covariable (N7 stands for November 2007, F8 stands for February 2008 and O8 stands for October 2008). Species that were found in less than five samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

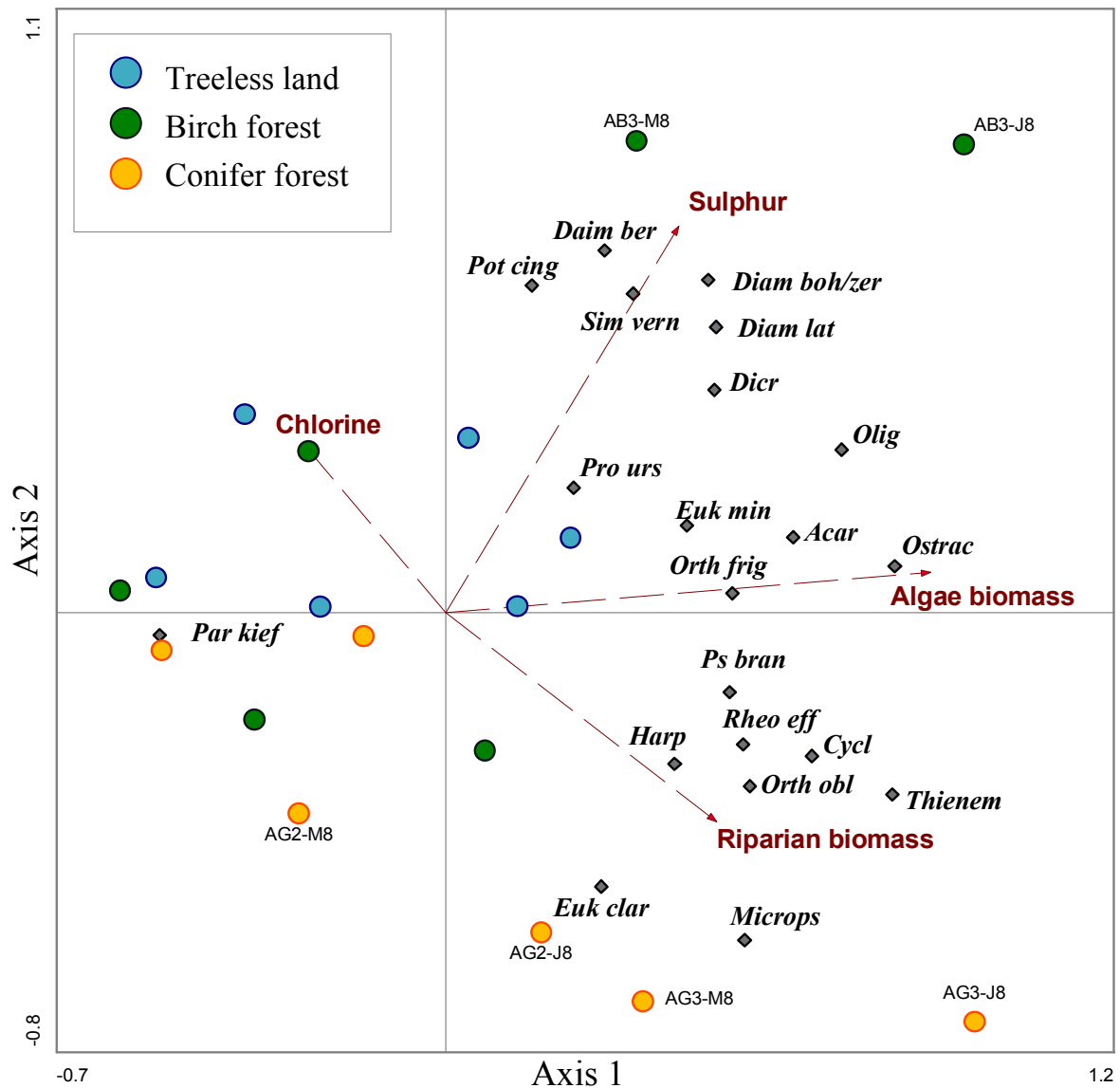


Figure 3.16 RDA ordination diagram based on invertebrate densities and environmental variables in direct run-off streams in summer (M8 stands for May 2008 and J8 stands for July 2008). Species that were found in less than four samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.

## 3.2 Spring-fed streams in the southern research area

### 3.2.1 Catchment composition

Similarity analysis divided the catchments of the southern research area into two clusters and an outlier (Figure 3.17). The first cluster consisted of four barren catchments (SS1, SS2, SS3 and SS4), which were mainly composed of eroded land (Figure 2.7). The other cluster included three forested catchments (SB1, SB2 and SB3) highly covered with birch woodlands. Catchment SB4 was an outlier because it was mainly covered with gravel flats and only small areas around the stream were covered with birch woodlands.

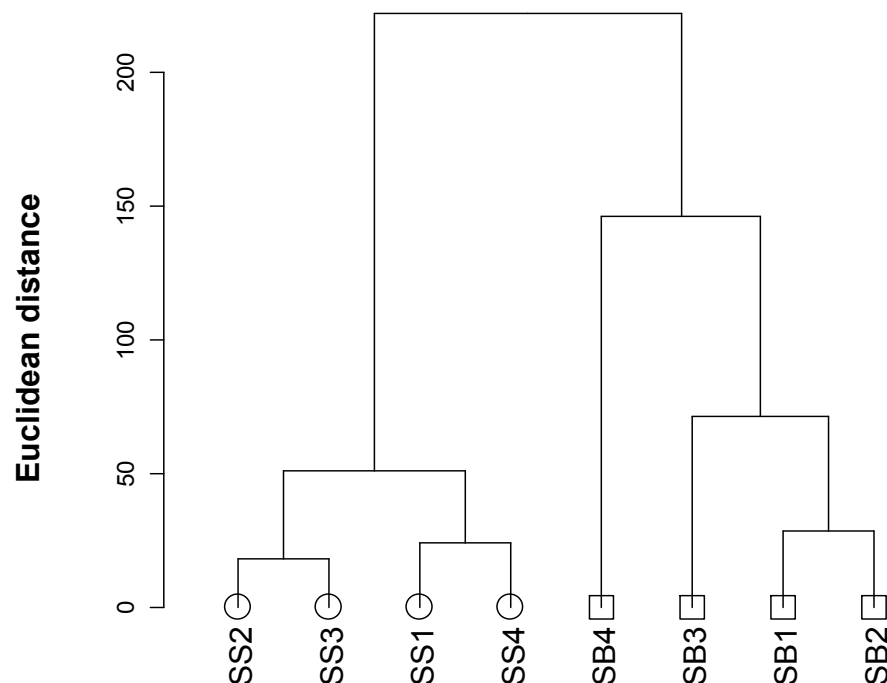


Figure 3.17 Cluster dendrogram of the similarity among catchment composition of spring-fed streams, using the Ward method, Euclidean distance. ○ barren catchments; □ birch forested catchments.

### 3.2.2 Physical and chemical characteristics of the streams

Substrate composition was very different in the bottoms of the eight studied streams. The substrate was coarsest in the stream SS3. Fifty-eight percent of the bottom there was covered by cobbles and boulders. The substrate was finest in the streams SB2 and SB4. The bottom of SB4 was really boggy, comprised only of sand and mud. The dominating substrate particles in stream SB2 were sand (54%) and gravel (23%). The bottoms of streams SS1, SS2, SS4, SB1 and SB3 were similar to each other and were dominated by gravel and pebble (68–94%) (Figure 3.18).



Water temperature in spring-fed streams ranged from 2.57 to 5.95 °C in November 2007. In July 2008 it increased only slightly up to 2.97–7.31 °C. Streams SS1, SS3, SS4 and SB3 were colder than the other ones. Their temperatures varied from 2.57 to 3.47 °C during both sampling occasions. The temperatures in warmer streams (SS2, SB1, SB2 and SB4) ranged between 3.34 and 7.31 °C. All the physical and chemical variables, describing the streams, are given in Table 3.13.

Higher pH values were observed in the streams in November 2007, ranging from 8.02 to 9.41. In July 2008 they were a little bit lower (7.40–8.45). Colder streams (SS1, SS3, SS4 and SB3) exhibited higher pH values (7.90–9.41 across both seasons). pH values in warmer streams (SS2, SB1, SB2 and SB4) were slightly lower and ranged from 7.40 to 8.33 across both seasons.

The conductivities in colder streams (SS1, SS3, SS4 and SB3) were relatively high and ranged from 183 to 227  $\mu\text{S cm}^{-1}$  across the two seasons. In some of the warmer streams (SS2, SB1 and SB4), they were lower (137–163  $\mu\text{S cm}^{-1}$ ). Stream SB2 had exceptionally high conductivities: 256  $\mu\text{S cm}^{-1}$  in November 2007 and 258  $\mu\text{S cm}^{-1}$  in July 2008. Calcium and magnesium concentrations in this stream were around 1.5–2 times higher than in all other streams. The calcium concentration in colder streams (SS1, SS3, SS4 and SB3) were higher than in some warmer ones (SS2, SB1 and SB4). Magnesium concentration did not differ a lot between these two groups of streams.

The potassium and sodium concentrations were higher in colder streams (SS1, SS3, SS4 and SB3) than in warmer ones (SS2, SB1, SB2 and SB4). The sulphur level was generally lower in warmer streams. Exceptionally low sulphur concentrations were found in streams SS1 and SB2 in July 2008. In stream SB2 in November 2007 sulphur concentration was much higher than in the other warm streams.

The silica level was generally higher in warmer streams (SS2, SB1, SB2 and SB4) than in colder ones (SS1, SS3, SS4 and SB3). Total nitrogen and nitrate concentration did not vary a lot. Phosphate level was higher in warmer streams than in colder ones, while total phosphorus concentrations did not vary a lot. In stream SS4, the total phosphorus level was exceptionally high, 2–3 times higher than in the other streams during both seasons. None of the mentioned nutrients and elements showed distinctive trends between the two seasons. A majority of the concentration values of trace elements (iron, manganese, copper, zinc and aluminium) and ammonium were under the limits of detection, so they were excluded from the analyses.

The depth of some streams was slightly greater in November 2007 than in July 2008, but velocities did not show any seasonal trend. The warmer streams (SS2, SB1, SB2 and SB4) were generally wider than the colder ones (SS1, SS3, SS4 and SB3). In July 2008 the surfaces of warmer streams (SS2, SB1, SB2 and SB4) were densely covered with macroalgae (3.5–8.7% of total surface area), meanwhile in colder streams (SS1, SS3, SS4 and SB3) macroalgae was almost non-existent. Algal biomass (chlorophyll *a*) also showed the tendency to be higher in warmer streams. The streams SS1, SB1 and SB2 were the richest in moss (1–12.5% of total bottom surface area). The differences between altitudes in the origin and sampling station were relatively low, 11–22 metres in colder streams. In warmer streams they were even lower, 8–13 metres. Fish were present in three warmer streams (SS2, SB1 and SB2) (Table 3.14).

Table 3.13 Physical and chemical parameters of spring-fed streams during November 2007 and July 2008. Algal biomass statistics is calculated across July 2008, October 2008 and May 2008 (SE stands for standard error). Altitude difference is calculated by subtracting the altitude of stream origin from the altitude of sampling station.

Stream	Season	Temperature (°C)	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Depth (cm)	Velocity ( $\text{m s}^{-1}$ )	Width (m)	Macroalgae (%)	Moss (%)	Ca ( $\text{mg l}^{-1}$ )	Mg ( $\text{mg l}^{-1}$ )	K ( $\text{mg l}^{-1}$ )	Na ( $\text{mg l}^{-1}$ )	S ( $\text{mg l}^{-1}$ )	Si ( $\text{mg l}^{-1}$ )	Cl ( $\text{mg l}^{-1}$ )	Al ( $\text{mg l}^{-1}$ )	$\text{NO}_3^-$ ( $\text{mg l}^{-1}$ )	Total N ( $\text{mg l}^{-1}$ )	$\text{PO}_4^{2-}$ ( $\text{mg l}^{-1}$ )	Total P ( $\text{mg l}^{-1}$ )	Algal biomass (mean (SE)) ( $\mu\text{g cm}^{-2}$ )	Altitude difference (m)
SS1	Nov'07	2.57	219	8.88	18.5	0.34	0.97	0	0	12.39	3.43	1.67	25.17	6.90	8.03	14.82	0.03	0.27	0.06	0.17	0.06	10.66	21
	July'08	3.06	227	7.90	13.1	0.32	0.95	0	10	10.68	3.35	1.81	26.56	0.04	7.09	0.06	7.74	0.21	0.05	0.17	0.06	(0.40)	
SS2	Nov'07	5.95	137	8.33	16	0.38	1.10	1.1	0	6.08	2.69	0.74	10.98	1.26	13.91	8.75	0.02	0.21	0.05	0.13	0.07	24.79	10
	July'08	7.31	156	7.88	9.4	0.19	1.00	80	0	8.58	3.79	1.20	17.20	2.35	13.84	13.81	0.01	0.01	0.04	0.18	0.08	(11.41)	
SS3	Nov'07	3.31	220	8.67	13.65	0.24	0.55	0	0.6	10.66	4.44	1.37	25.88	6.09	8.82	13.98	0.03	0.30	0.06	0.18	0.08	4.75	11
	July'08	3.47	222	8.10	13.8	0.49	0.61	10	0	10.40	4.29	1.37	26.19	6.09	8.68	14.33	0.02	0.30	0.06	0.17	0.06	(0.41)	
SS4	Nov'07	2.8	217	8.94	6.7	0.05	0.20	0	0.5	11.84	3.31	1.71	24.81	6.48	7.64	14.73	0.03	0.20	0.07	0.14	0.06	8.20	15
	July'08	2.93	226	7.90	6.3	0.03	0.16	0	0	9.68	2.71	1.33	19.87	5.52	7.68	11.65	0.02	0.16	0.14	0.15	0.27	(2.69)	
SB1	Nov'07	5.27	150	8.04	7.5	0.39	1.80	0	12.5	6.36	3.18	1.24	19.47	2.92	11.20	8.79	0.02	0.32	0.08	0.26	0.10	13.48	8
	July'08	5.75	163	7.51	7.1	0.25	1.90	3.5	11	6.93	3.08	1.36	21.95	3.47	11.14	9.29	0.02	0.28	0.07	0.25	0.09	(2.73)	
SB2	Nov'07	3.34	256	8.02	17.6	0.18	0.55	0	10.5	15.78	6.64	1.53	24.05	7.36	11.64	13.82	0.02	0.32	0.06	0.21	0.08		12
	July'08	5.27	258	7.68	18.5	0.11	0.50	17	1	16.66	6.85	1.54	24.93	0.05	7.98	0.07	11.47	0.15	0.05	0.18	0.06		
SB3	Nov'07	3.06	183	9.41	14.7	0.40	0.55	0	0.5	5.53	1.38	1.49	28.36	7.15	9.88	12.41	0.02	0.15	0.07	0.18	0.07	8.98	22
	July'08	3.23	184	8.45	8.5	0.41	0.43	1	0	5.86	1.24	1.57	28.57	7.20	9.71	13.01	0.02	0.15	0.01	0.22	0.08	(1.17)	
SB4	Nov'07	5.09	145	8.31	15.8	0.07	1.15	0	0	6.30	2.94	1.31	20.09	2.81	10.49	8.27	0.01	0.44	0.12	0.25	0.15		13
	July'08	5.25	162	7.40	10.8	0.05	0.85	87.5	0	7.32	3.30	1.43	21.38	3.32	11.34	8.92	0.02	0.34	0.09	0.25	0.09		

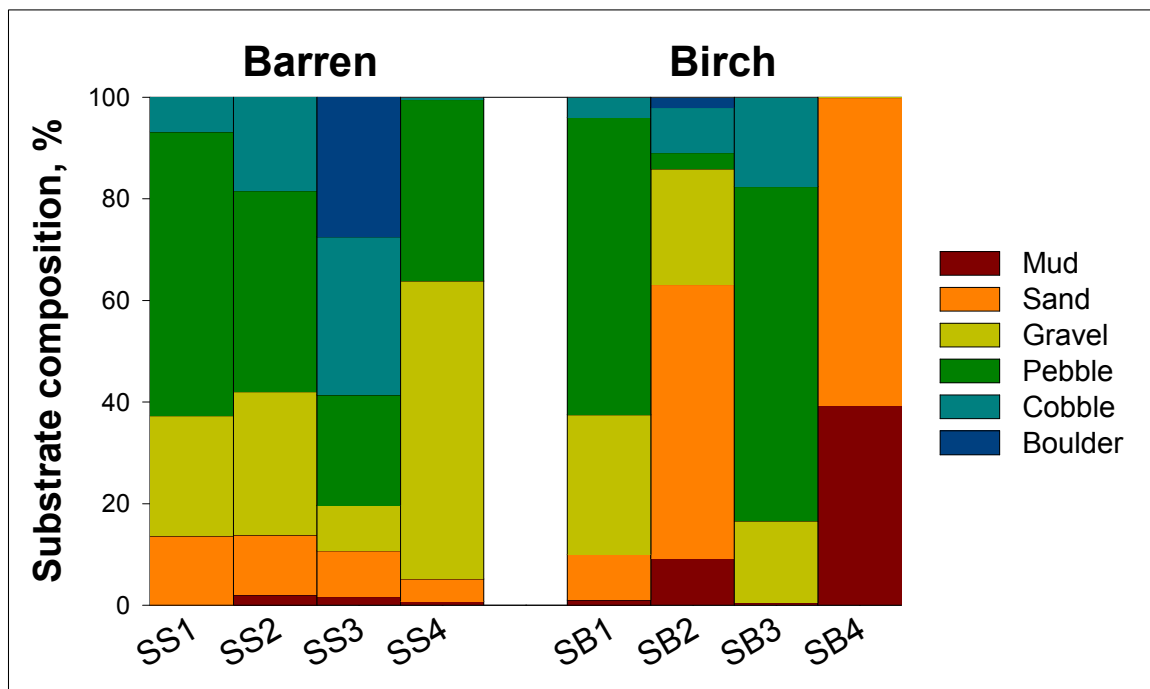


Figure 3.18 The substrate composition of spring-fed streams, based on averages for six sampling occasions (November 2007, February 2008, May 2008, July 2008, October 2008 and May 2009).

Table 3.14 The presence of fish in spring-fed streams.

	Arctic char ( <i>Salvelinus alpinus</i> )	Brown trout ( <i>Salmo trutta</i> )
SS1	-	-
SS2	+	+
SS3	-	-
SS4	-	-
SB1	+	+
SB2	+	+
SB3	-	-
SB4	-	-

### 3.2.3 Catchment effect on stream ecology

A principal component analysis, done on environmental data created four principal components, which explained 68.6% of the variance. Variable loadings, that were higher than 0.6, or lower than -0.6, were considered as strong. PC1 explained 30.1% of the variance and had the strongest loadings of temperature, conductivity, stream width, calcium, potassium, sodium, sulphur, silica, aluminium and chlorine (Table 3.15).

In the ordination diagram, there was no clustering by catchment type. The groups of samples, from barren land and birch forest streams, overlap each other (Figure 3.19). PC1 separated the streams into two groups. In the left side of ordination diagram, samples taken from streams SS1, SS3, SS4 and SB3 were clustered. These four streams were characterised by lower temperatures, higher conductivities, slightly higher concentrations of calcium, potassium, sodium, sulphur and chlorine. The right side of ordination diagram contained streams SS2, SB1, SB2 and SB4. Temperatures and silica concentrations were higher in these streams (Figure 3.19).

*Table 3.15 Water quality and physical habitat loadings onto first four principal components of PCA analysis. Light shading indicates strong positive loadings (>0.6), dark shading indicates strong negative loadings (<-0.6).*

	PC1	PC2	PC3	PC4
Eigenvalues	0.30	0.16	0.13	0.10
Cumulative percentage of variance	30.1	45.8	58.6	68.6
Altitude	-0.31	-0.27	-0.70	-0.55
Temperature	0.92	0.13	0.25	0.05
Conductivity	-0.90	-0.12	0.23	0.22
pH	-0.55	0.30	-0.33	-0.13
Depth	-0.17	-0.07	0.38	-0.50
Velocity	-0.05	0.65	0.12	-0.18
Stream width	0.72	-0.06	0.26	-0.05
%Mud	0.37	-0.60	-0.25	-0.45
%Sand	0.06	-0.61	0.36	-0.33
%Gravel	-0.12	0.07	-0.18	0.82
%Pebble	0.21	0.71	-0.20	0.11
%Cobble	-0.33	0.48	0.11	-0.41
%Boulder	-0.44	-0.04	0.40	-0.15
%Macroalgae	0.40	0.04	0.18	-0.33
%Moss	0.22	-0.22	0.45	0.50
Calcium	-0.66	-0.20	0.57	0.23
Magnesium	-0.23	-0.31	0.86	0.13
Potassium	-0.75	-0.16	-0.14	-0.14
Sodium	-0.79	-0.01	-0.17	-0.28
Sulphur	-0.94	0.05	-0.08	-0.02
Silica	0.79	0.24	0.42	-0.00
Aluminium	-0.84	-0.12	0.39	0.00
Chlorine	-0.82	0.40	0.19	0.00
Nitrate	0.00	-0.79	0.22	-0.27
Total nitrogen	0.12	-0.75	-0.38	0.30
Phosphate	0.42	-0.47	0.05	-0.22
Total phosphorus	0.12	-0.43	-0.49	0.42
Total catchment area	0.59	0.54	0.17	-0.20

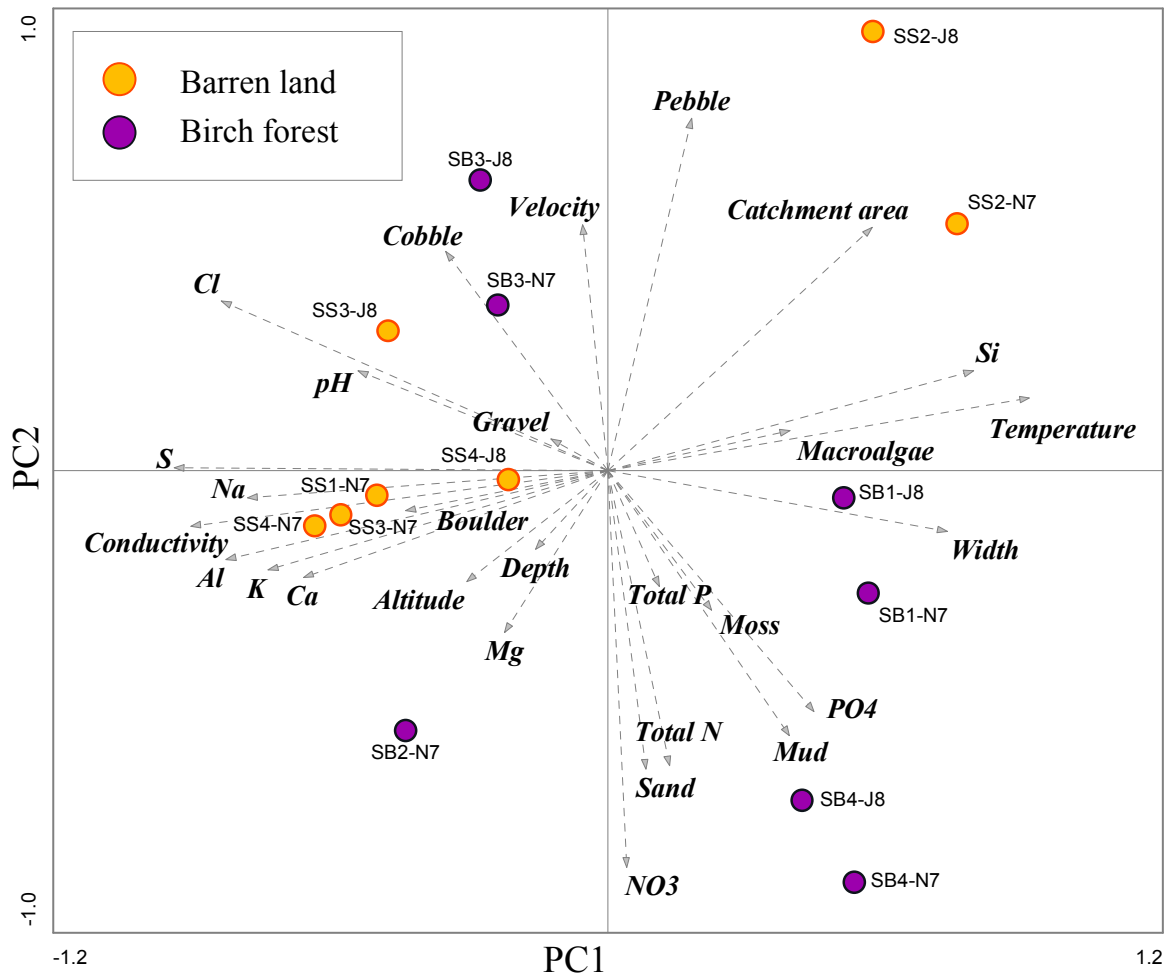


Figure 3.19 Ordination diagram of PCA based on ecological characteristics of the spring-fed streams during two sampling occasions (N7 stands for November 2007 and J8 stands for July 2008).

### 3.2.4 Invertebrate community composition

Thirty nine invertebrate taxa were identified in the southern research area from eight streams in November 2007 and six streams in July 2008 (Table 3.16). The most widespread taxa were: Chironomidae (3–96% of total number of individuals), followed by Ostracoda (0.1–91.7%), Oligochaeta (1–22%) and Harpacticoidea (Copepoda) (0–24%). Other groups were Trichoptera, Plecoptera, Coleoptera, Acarina, Gastropoda, Crustacea, *Hydra* spp., Tardigrada and various taxa of non-Chironomidae Diptera. All together these taxa made 3.5–28.5% of total individuals.

The dominating species of Chironomidae were *E. minor* and *O. (O.) frigidus*. Chironomid *O. (O.) frigidus* was much more abundant in stream SB4 than any other stream. Less abundant in the streams were *D. bohemani/zernyi*, *Diamesa aberrata* (Lundbeck), *D. latitarsis* group, *Micropsectra* spp. and *Thienemanniella* spp. The smallest amounts were found of *D. bertrami*, *R. (R.) effusus*, *O. (O.) oblidens*, *Chaetocladius* spp., *Macropelopia* sp. and *E. claripennis*. Very few individuals appeared of *Limnophyes* sp. and *Metriocnemus* sp. (Table 3.16).

Table 3.16 Densities of invertebrate taxa (individuals per square metre) found in spring-fed streams in November 2007 and July 2008.

	SS1		SS2		SS3		SS4		SB1		SB2		SB3		SB4	
	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08
<b>CHIRONOMIDAE</b>																
<b>Tanypodinae</b>																
<i>Macropelopia</i> sp.	0.0	–	178.1	510.7	0.0	0.0	0.0	0.0	0.0	0.0	203.6	–	0.0	0.0	224.5	1011.2
<b>Diaesinae</b>																
<i>Diaesa aberrata</i> (Lundbeck)	0.0	–	0.0	0.0	50.0	359.2	257.1	11699.0	0.0	232.7	0.0	–	0.0	2832.1	0.0	0.0
<i>Diaesa bertrami</i> (Edwards)	460.7	–	0.0	0.0	165.8	614.3	20.4	88.8	0.0	707.7	0.0	–	191.8	2021.4	0.0	0.0
<i>Diaesa latitarsis</i> group (Goetghebuer)	1401.0	–	0.0	0.0	642.9	1130.1	172.4	1161.7	15.3	0.0	0.0	–	508.2	2850.0	0.0	0.0
<i>Diaesa bertrami/latitarsis</i> group (Edwards/Goetghebuer)	1050.0	–	29.1	0.0	37.8	112.8	10.2	0.0	139.3	0.0	0.0	–	758.2	469.9	0.0	0.0
<i>Diaesa bohmani/zernyi</i> (Goetghebuer/Edwards)	84.2	–	396.4	7977.0	74.0	50.0	10.2	1983.2	0.0	2023.0	22.4	–	74.5	76.0	107.1	14881.1
<i>Diaesa</i> spp.	0.0	–	5.1	57.1	40.8	20.4	0.0	0.0	0.0	10.2	0.0	–	0.0	10.2	0.0	20.4
<b>Orthoclaadiinae</b>																
<i>Chaetocladius</i> spp.	30.6	–	380.6	178.6	185.2	0.0	0.0	178.1	0.0	1097.4	0.0	–	10.2	244.4	0.0	0.0
<i>Corynoneura</i> sp.	0.0	–	0.0	178.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0
<i>Eukiefferiella claripennis</i> (Lundbeck)	15.3	–	0.0	0.0	392.9	150.5	5.1	0.0	123.5	0.0	0.0	–	852.6	0.0	5.1	0.0
<i>Eukiefferiella minor</i> (Edwards)	9070.9	–	11500.0	21273.5	3275.5	2176.5	2109.2	4654.6	24709.2	42440.3	857.7	–	1684.2	5106.6	10.2	48.5
<i>Limnophyes</i> sp.	0.0	–	0.0	178.6	0.0	0.0	20.4	0.0	0.0	376.5	0.0	–	78.6	0.0	5.1	0.0
<i>Metriocnemus</i> sp.	0.0	–	0.0	0.0	0.0	60.2	5.1	62.8	0.0	0.0	0.0	–	58.7	96.4	10.2	0.0
<i>Orthocladus (Orthocladus) frigidus</i> (Zetterstedt)	208.7	–	421.4	4305.1	858.2	214.3	130.1	999.0	5339.8	6183.2	4161.2	–	124.0	718.4	91.8	87847.4
<i>Orthocladus (Orthocladus) oblidens</i> (Walker)	0.0	–	112.8	2439.3	5.1	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	876.5
<i>Rheocricotopus (Rheocricotopus) effusus</i> (Walker)	0.0	–	0.0	1808.2	0.0	0.0	0.0	0.0	0.0	1620.4	156.6	–	0.0	0.0	0.0	0.0
<i>Thienemanniella</i> spp.	5.1	–	0.0	9746.9	0.0	0.0	0.0	0.0	139.3	1230.6	70.4	–	0.0	0.0	5.1	0.0
Orthoclaadiinae spp.	0.0	–	598.5	3183.7	10.2	70.4	0.0	103.6	319.9	128.1	554.6	–	52.0	127.0	0.0	7911.2
<b>Tanytarsini</b>																
<i>Microsestra</i> spp.	0.0	–	6981.6	3080.1	0.0	0.0	0.0	0.0	2512.2	416.8	2367.9	–	0.0	0.0	489.8	2037.2
Chironomidae spp.	35.7	–	0.0	86.7	5.1	0.0	20.4	51.0	0.0	256.1	101.0	–	10.2	20.4	81.6	32.1
<b>NON-CHIRONOMIDAE DIPTERA</b>																
Thaumetelidae	0.0	–	0.0	0.0	16.8	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0
<i>Simulium (Eusimulium) venum</i> (Macquart)	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	1290.8	0.0	755.1	–	0.0	0.0	0.0	0.0
<i>Simulium (Psilozia) vittatum</i> (Zetterstedt)	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	40.8	0.0	270.4	–	0.0	0.0	0.0	0.0
Simuliidae spp.	0.0	–	0.0	505.1	0.0	0.0	0.0	0.0	0.0	244.9	5.1	–	0.0	0.0	0.0	0.0

Continues

Table 3.16 Continued

	SS1		SS2		SS3		SS4		SB1		SB2		SB3		SB4	
	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08	Nov '07	July '08
Tipulidae sp. A – limoniinae	66.3	–	45.4	0.0	0.0	0.0	5.1	0.0	25.5	0.0	25.5	–	5.1	0.0	5.1	0.0
Tipulidae sp. C - limoniinae	0.0	–	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	5.1	0.0
Tipulidae sp. D - tipulinae	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0	0.0	–	0.0	0.0	0.0	0.0
Tipulidae spp.	0.0	–	0.0	0.0	0.0	10.2	0.0	10.2	0.0	213.3	0.0	–	0.0	0.0	0.0	42.3
<i>Dicranota</i> sp.	188.8	–	991.8	1882.1	66.3	30.6	71.4	30.6	1010.2	813.8	1209.2	–	81.6	40.8	71.4	139.3
<i>Clinocera stagnalis</i> (Haliday)	10.2	–	118.9	937.2	10.2	0.0	0.0	0.0	173.5	10.2	86.7	–	0.0	0.0	25.5	219.4
Hemerodromiinae (Empididae)	0.0	–	102.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.5	–	0.0	0.0	96.9	52.6
Muscidae spp.	0.0	–	67.9	259.7	0.0	0.0	0.0	0.0	0.0	20.4	0.0	–	0.0	0.0	0.0	0.0
Diptera spp.	0.0	–	5.6	0.0	0.0	10.2	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	5.1	0.0
<b>TRICHOPTERA</b>																
<i>Potamophylax cingulatus</i> (Stephens)	0.0	–	5.6	0.0	0.0	0.0	0.0	0.0	76.5	38.8	5.1	–	25.5	0.0	0.0	0.0
<i>Apatania zonella</i> (Zetterstedt)	102.0	–	5.6	35.7	0.0	10.2	15.3	0.0	15.3	38.8	40.8	–	15.3	0.0	10.2	0.0
<i>Limnephilus griseus</i> (Linnaeus)	5.1	–	0.0	0.0	5.1	0.0	5.1	0.0	20.4	49.0	40.8	–	30.6	0.0	30.6	0.0
Trichoptera spp.	0.0	–	0.0	0.0	0.0	10.2	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	80.6
<b>PLECOPTERA</b>																
<i>Capnia vidua</i> (Klapalek)	35.7	–	532.7	3882.1	25.5	40.8	61.2	91.8	494.9	748.5	107.1	–	367.3	193.9	81.6	209.7
<b>CRUSTACEA</b>																
Ostracoda	66.3	–	3622.4	66918.4	10.2	0.0	5.1	0.0	7747.4	17734.7	3280.6	–	5.1	10.2	27500.0	41821.4
Cyclopoidea (Copepoda)	5.1	–	5.6	1041.8	0.0	0.0	0.0	0.0	0.0	0.0	20.4	–	0.0	0.0	153.1	599.0
Harpacticoida (Copepoda )	0.0	–	56.6	15040.8	0.0	10.2	0.0	102.0	178.1	5385.2	6045.9	–	0.0	51.0	15.3	1787.8
Cladocera	0.0	–	51.0	374.0	0.0	0.0	0.0	0.0	0.0	0.0	250.0	–	0.0	0.0	0.0	32.1
<b>GASTROPODA</b>																
<i>Lymnaea</i> sp.	0.0	–	11.2	48.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	64.8
<b>HYDROZOA</b>																
<i>Hydra</i> spp.	0.0	–	0.0	28.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0
<b>ACARINA</b>																
OLIGOCHAETA	51.0	–	481.6	5065.8	10.2	30.6	56.1	81.6	1524.5	3845.4	153.1	–	30.6	30.6	40.8	796.4
TARDIGRADA	1760.2	–	2993.4	40914.3	127.6	71.4	193.9	857.1	3698.0	24428.6	3612.2	–	45.9	295.9	908.2	16444.4
	0.0	–	0.0	66.8	0.0	0.0	0.0	0.0	0.0	471.9	0.0	–	0.0	0.0	0.0	96.9

### 3.2.4.1 Differences in density and diversity variables among catchment types and seasons

In the southern research area, density and diversity did not vary significantly between the two seasons and did not show any significant differences between catchment types (Table 3.17). Although they were not significant, all variables still had some distinctive trends. Total invertebrate densities were higher in July 2008 than in November 2007. Invertebrate densities were higher in birch forest streams than in the streams, running through the barren land (Figure 3.20). The standard errors were very high in July 2008. It was because the densities were extremely high in one stream draining barren land (SS2) and in two streams draining birch woodlands (SB1 and SB4). But total invertebrate densities in streams SS3, SS4 and SB3 increased very slightly in July 2008.

The number of taxa in July 2008 was a little bit lower than in November 2007. Birch forest streams were slightly richer in taxa than the streams running through the barren land (Figure 3.20). Shannon diversity and evenness were greater in July 2008 than in November 2007. In the streams surrounded by birch woodlands, these parameters tended to be lower than in streams, running through barren land (Figure 3.20).

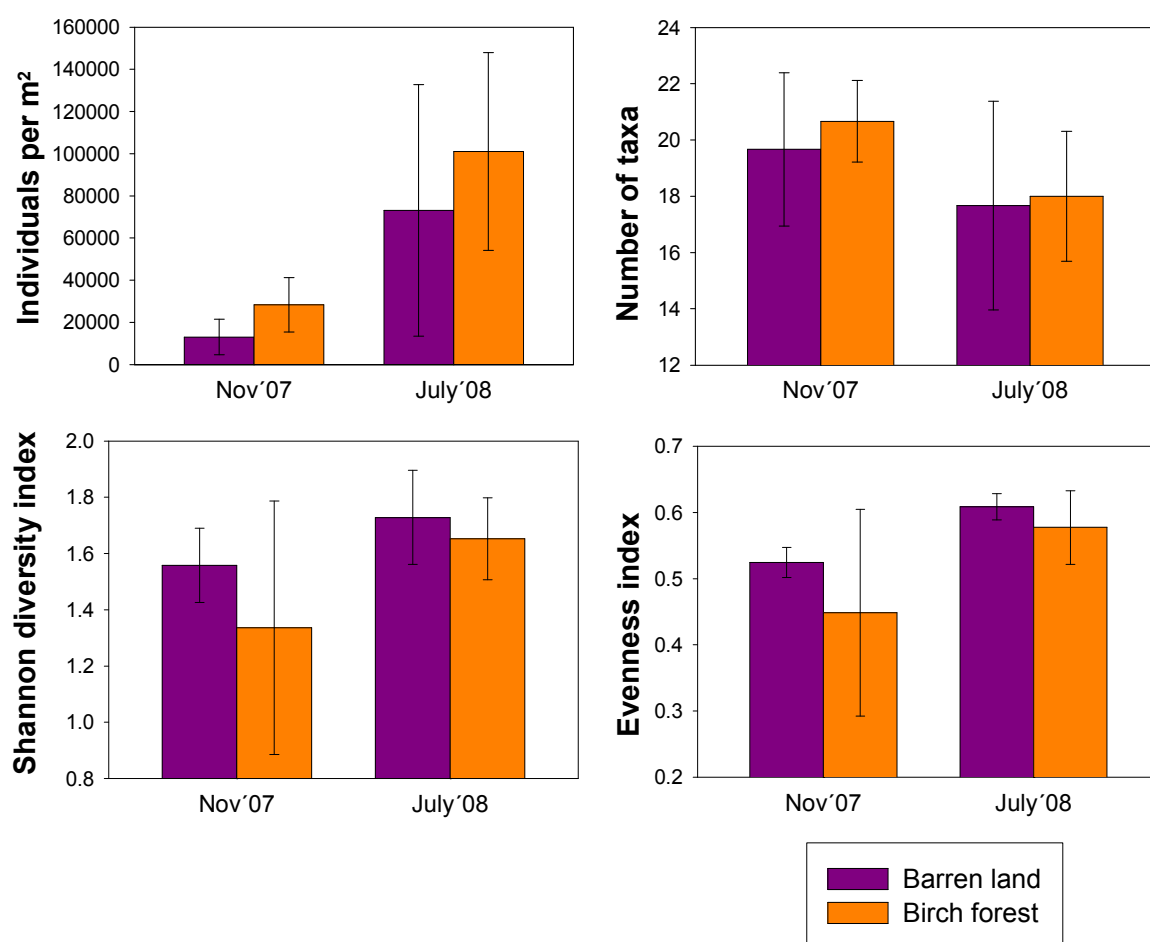


Figure 3.20 Total invertebrate densities, number of taxa, Shannon diversity and evenness in spring-fed streams with different catchment types during two sampling occasions.



Table 3.17 Catchment type and season effects on total invertebrate density, taxonomic richness, Shannon diversity and evenness in spring-fed streams. Two-way repeated measure ANOVA tests. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom.

	ANOVA	df	F	P
Density	<b>Between subjects</b>			
	Catchment	1	0.240	0.650
	Error	4		
	<b>Within subjects</b>			
	Season	1	4.166	0.111
	Season X Catchment	1	0.038	0.854
	Error	4		
Taxa richness	<b>Between subjects</b>			
	Catchment	1	0.034	0.063
	Error	4		
	<b>Within subjects</b>			
	Season	1	4.900	0.091
	Season X Catchment	1	0.100	0.768
	Error	4		
Shannon diversity	<b>Between subjects</b>			
	Catchment	1	0.202	0.676
	Error	4		
	<b>Within subjects</b>			
	Season	1	2.340	0.201
	Season X Catchment	1	0.210	0.671
	Error	4		
Evenness	<b>Between subjects</b>			
	Catchment	1	0.247	0.645
	Error	4		
	<b>Within subjects</b>			
	Season	1	4.335	0.105
	Season X Catchment	1	0.191	0.685
	Error	4		

#### 3.2.4.2 Differences in functional feeding groups among catchment types and seasons. Analysis, based on invertebrate densities

The two largest functional feeding groups in spring-fed streams were gathering collectors (6.5–97% of total invertebrate community) and gathering collectors scrapers (1–91%). All other groups were less abundant. Predators comprised 0.5–7% of total community, shredders 0.2–9% and filtering collectors only 0–5%. None of the functional feeding groups varied significantly between catchment types, and the predators were the only group that varied significantly between two seasons (Table 3.18).

The percentages of gathering collectors were lower in streams draining barren land than in streams draining birch forest. Gathering collectors scrapers showed an opposite tendency. Their proportions were higher in the streams within barren land and lower in the birch

forest streams (Figure 3.21). Such differences were found because the proportional abundances of gathering collectors were higher in warmer streams (SS2, SB1 and SB2). In colder streams (SS3, SS4 and SB3), gathering collectors scrapers were more abundant.

The proportion of predators was higher in streams running through barren land than in birch forest streams. The proportions were higher in November 2007 and July 2008 (Figure 3.21), and the differences were statistically significant (Table 3.18). The percentages of filtering collectors and shredders did not show any distinctive seasonal trend or any trend between the two catchment types (Figure 3.21).

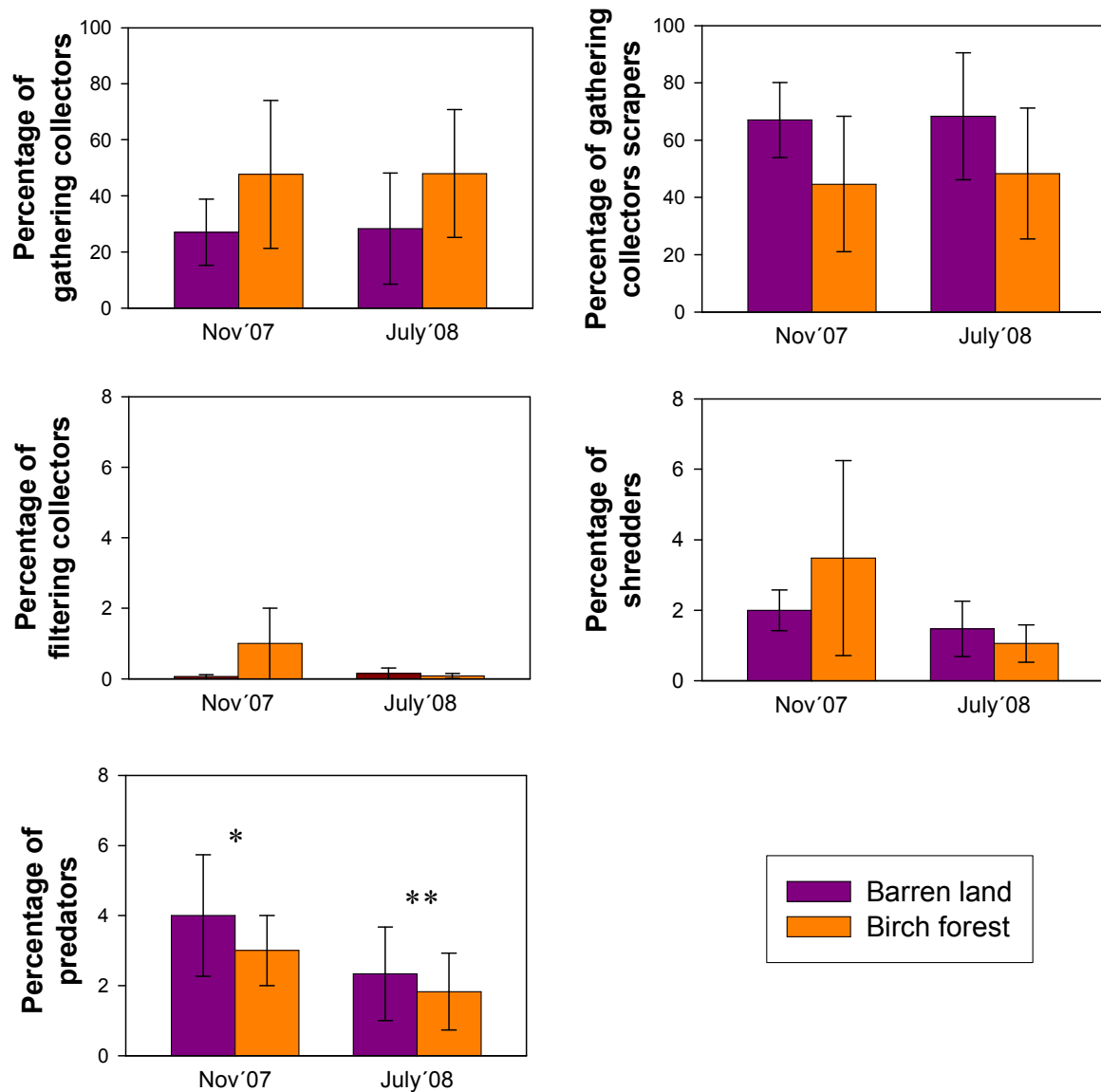


Figure 3.21 Functional feeding groups in spring-fed streams with different catchment types during two sampling occasions. Analysis, based on invertebrate densities. \* and \*\* indicate significant difference between the seasons ( $P < 0.05$ , two way RM ANOVA).

Table 3.18 Catchment type and season effects on functional feeding groups in spring-fed streams. Two-way repeated measure ANOVA tests. Analysis, based on invertebrate densities. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom. Bold value indicates the significant difference at  $P < 0.05$ .

	ANOVA	df	F	P
Gathering collectors	<b>Between subjects</b>			
	Catchment	1	0.485	0.524
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.020	0.895
	Season X Catchment	1	0.004	0.951
Gathering collectors scrapers	<b>Between subjects</b>			
	Catchment	1	0.521	0.510
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.227	0.659
	Season X Catchment	1	0.077	0.796
Filtering collectors	<b>Between subjects</b>			
	Catchment	1	0.595	0.484
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.749	0.436
	Season X Catchment	1	1.205	0.334
Shredders	<b>Between subjects</b>			
	Catchment	1	0.245	0.647
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.765	0.431
	Season X Catchment	1	0.527	0.508
Predators	<b>Between subjects</b>			
	Catchment	1	0.088	0.781
	Error	4		
	<b>Within subjects</b>			
	Season	1	8.269	<b>0.045</b>
	Season X Catchment	1	0.689	0.453
	Error	4		

#### 3.2.4.3 Differences in functional feeding groups among catchment types and seasons. Analysis, based on invertebrate species presence/absence

The majority of taxa in spring-fed streams were gathering collectors (21–39% of total number of taxa) and gathering collectors scrapers (21–50%). All other groups were less abundant. Predators comprised 12–31% of total number of taxa, shredders 6–32% and filtering collectors, only 0–10.5%.

None of the functional feeding groups varied significantly between catchment types (Table 3.19). Proportions of gathering collectors and gathering collectors scrapers were higher in the streams running through barren land than in birch forest streams (Figure 3.22). Such differences were related to the water temperature. In colder streams (SS3, SS4 and SB3) proportions of gathering collectors and gathering collectors scrapers were higher than in warmer streams (SS2, SB1 and SB2). The proportions of shredders were higher in birch forest streams (Figure 3.22). Such differences were also related to stream water temperature. More species of shredders lived in warmer streams (SS2, SB1 and SB2) than in colder ones (SS3, SS4 and SB3).

Proportions of gathering collectors were slightly higher in July 2008, than in November 2007 (Figure 3.22), but the differences were not statistically significant (Table 3.19). Proportions of gathering collectors scrapers were significantly higher in July 2008 than in November 2007 (Table 3.19). Proportions of shredders were significantly higher in November 2007 than in July 2008 as well (Table 3.19). Tukey post-hoc revealed that differences between two seasons were also significant in birch forest streams. Percentages of filtering collectors varied very slightly between two seasons and catchment types. Proportions of predators did not show clear trends between catchment types or seasons (Figure 3.22).

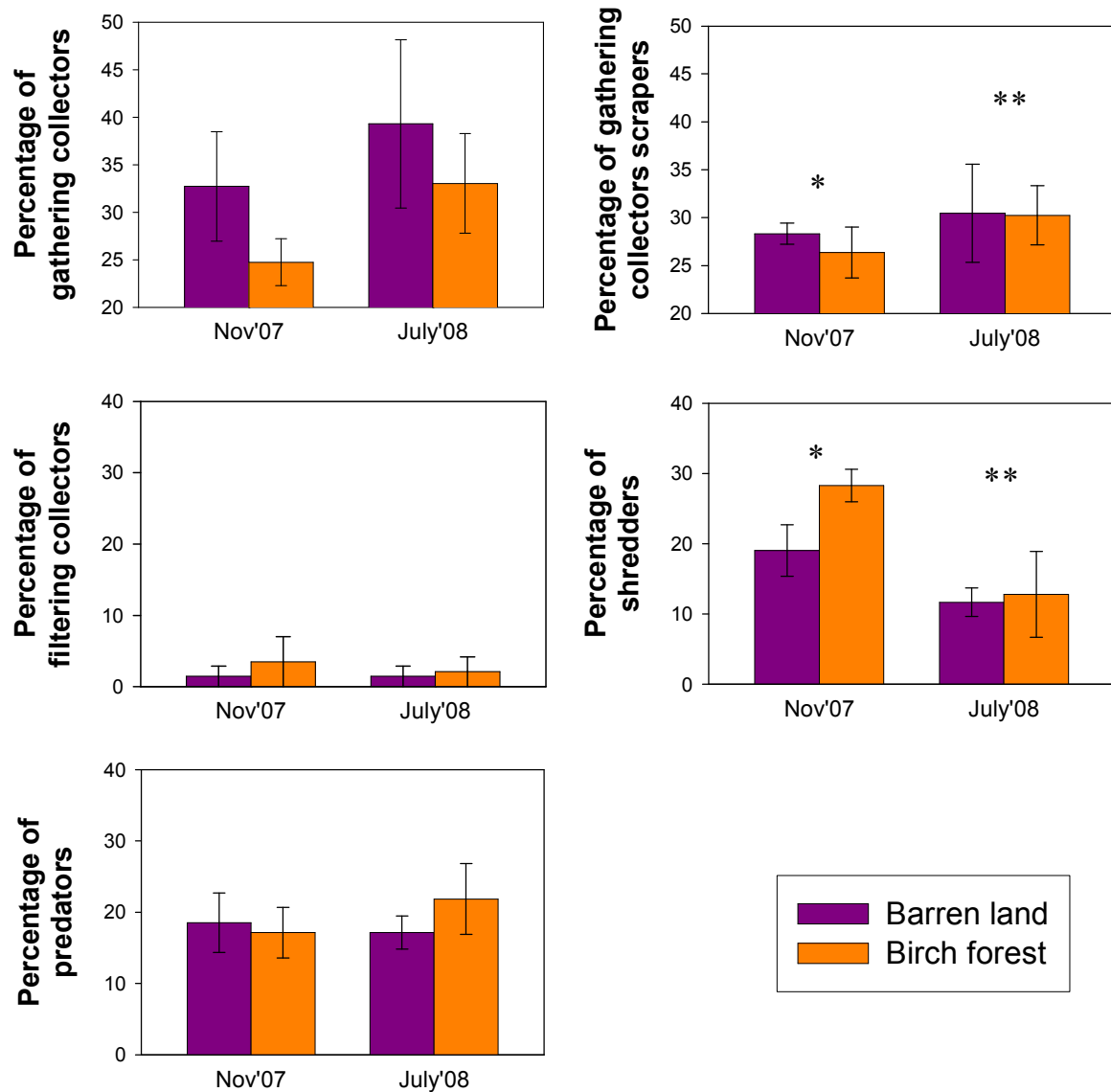


Figure 3.22 Functional feeding groups in spring-fed streams with different catchment types during two sampling occasions. Analysis, based on invertebrate species presence/ absence. \* and \*\* indicate significant difference between the seasons ( $P < 0.05$ , two way RM ANOVA).

Table 3.19 Catchment type and season effects on functional feeding groups in spring-fed streams. Two-way repeated measure ANOVA tests. Analysis, based on invertebrate species presence/absence. *F* is a variance ratio, *P* is a probability, *df* are degrees of freedom. Bold values indicate the significant difference at  $P < 0.05$ .

	ANOVA	df	F	P
Gathering collectors	<b>Between subjects</b>			
	Catchment	1	0.128	0.738
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.706	0.448
	Season X Catchment	1	0.060	0.819
Gathering collectors scrapers	<b>Between subjects</b>			
	Catchment	1	0.749	0.436
	Error	4		
	<b>Within subjects</b>			
	Season	1	11.712	<b>0.027</b>
	Season X Catchment	1	0.157	0.712
Filtering collectors	<b>Between subjects</b>			
	Catchment	1	0.409	0.557
	Error	4		
	<b>Within subjects</b>			
	Season	1	0.0848	0.785
	Season X Catchment	1	0.0848	0.785
Shredders	<b>Between subjects</b>			
	Catchment	1	1.536	0.283
	Error	4		
	<b>Within subjects</b>			
	Season	1	10.371	<b>0.032</b>
	Season X Catchment	1	1.319	0.315
Predators	<b>Between subjects</b>			
	Catchment	1	0.0993	0.768
	Error	4		
	<b>Within subjects</b>			
	Season	1	1.349	0.310
	Season X Catchment	1	4.426	0.103
	Error	4		

### 3.2.4.4 Invertebrate assemblages

The first four components of the PCA done on species density data explained 85.4% of the variance. Principal components one and two accounted for 57 and 15% of the variance respectively. The distributions of samples in PCA and RDA ordination diagrams were very similar, therefore only the RDA diagram is given here. In the diagram, there was no clustering by season or catchment type (Figure 3.23). PC1 divided the streams into two groups. The colder streams (SS1, SS3, SS4 and SB3) formed a cluster and were situated in the left part of the ordination diagram. The warmer streams (SS2, SB1, SB2 and SB4) formed another cluster. They were located in the right part of diagram and were spread farther from each other.

*D. aberrata*, *D. bertrami*, *D. latitarsis* group and *E. claripennis* were more abundant in colder streams (SS1, SS3, SS4 and SB3), while in the warmer streams (SS2, SB1, SB2 and SB4) they were almost absent. Harpacticoidea (Copepoda), Ostracoda, Acarina, *Micropsectra* spp., *Thienemanniella* spp., *R. (R.) effusus*, *O. (O.) oblidens* and *Macropelelopia* sp. were highly abundant in warmer streams, and were absent or very few individuals were found in colder streams (Figure 3.23).

The other taxa, such as Oligochaeta, *O. (O.) frigidus*, *E. minor*, *Chaetocladius* spp. and *D. bohemani/zernyi* were found in all the streams, but in the warmer ones (SS2, SB1, SB2 and SB4), they were more abundant. None of the first two principal components were correlated with catchment variables (Table 3.20), indicating that invertebrate community structure had nothing in common with the composition of the streams' catchments.

Table 3.20 Spearman's rank correlation coefficients between species data PCA axes loadings and catchment composition variables.

	PC1		PC2	
	$r_s$	P	$r_s$	P
<b>Birch woodlands</b>	0.266	0.348	0.214	0.453
<b>Conifer forest</b>	0.241	0.399	0.31	0.271
<b>Wetland</b>	0.327	0.244	-0.398	0.152
<b>Heathland</b>	-0.013	0.952	0.395	0.157
<b>Grassland</b>	-0.278	0.324	-0.373	0.184
<b>Gravel flats</b>	-0.203	0.472	-0.152	0.594
<b>Eroded land</b>	-0.02	0.902	-0.15	0.255
<b>Rock</b>	-0.06	0.634	-0.18	0.174

### 3.2.5 Invertebrate assemblages in relation to stream ecology

Four variables were the most important predictors of invertebrate assemblages according to RDA: water temperature, moss, mud and sand. The amount of variability explained (sum of all canonical eigenvalues) was 79.9% and the first two axes explained 55 and 11.7% of the variance respectively.

Water temperature was the most important variable in explaining the variation of invertebrate assemblages on axis one (Figure 3.23). It was positively associated with

Harpacticoidea (Copepoda), Ostracoda, Acarina, Oligochaeta, *Micropsectra* spp., *Thienemanniella* spp., *R. (R.) effusus*, *O. (O.) oblidens*, *D. bohemani/zernyi*, *Macropelopia* sp. and many rare taxa. Increased water temperature corresponded to streams SS2, SB1, SB2 and SB4, where the densities of mentioned taxa were the greatest.

Percentage cover of moss was associated with such species as *S. vernum*, *P. cingulatus* and *Limnophyes* sp. Mud and sand were positively correlated with RDA axis two (Figure 3.23). They were related to stream SB4, whose bottom substrate was very different than all other streams, mainly made of sand and mud. This stream was notable for extremely low densities of *E. minor* and high proportions of Ostracoda.

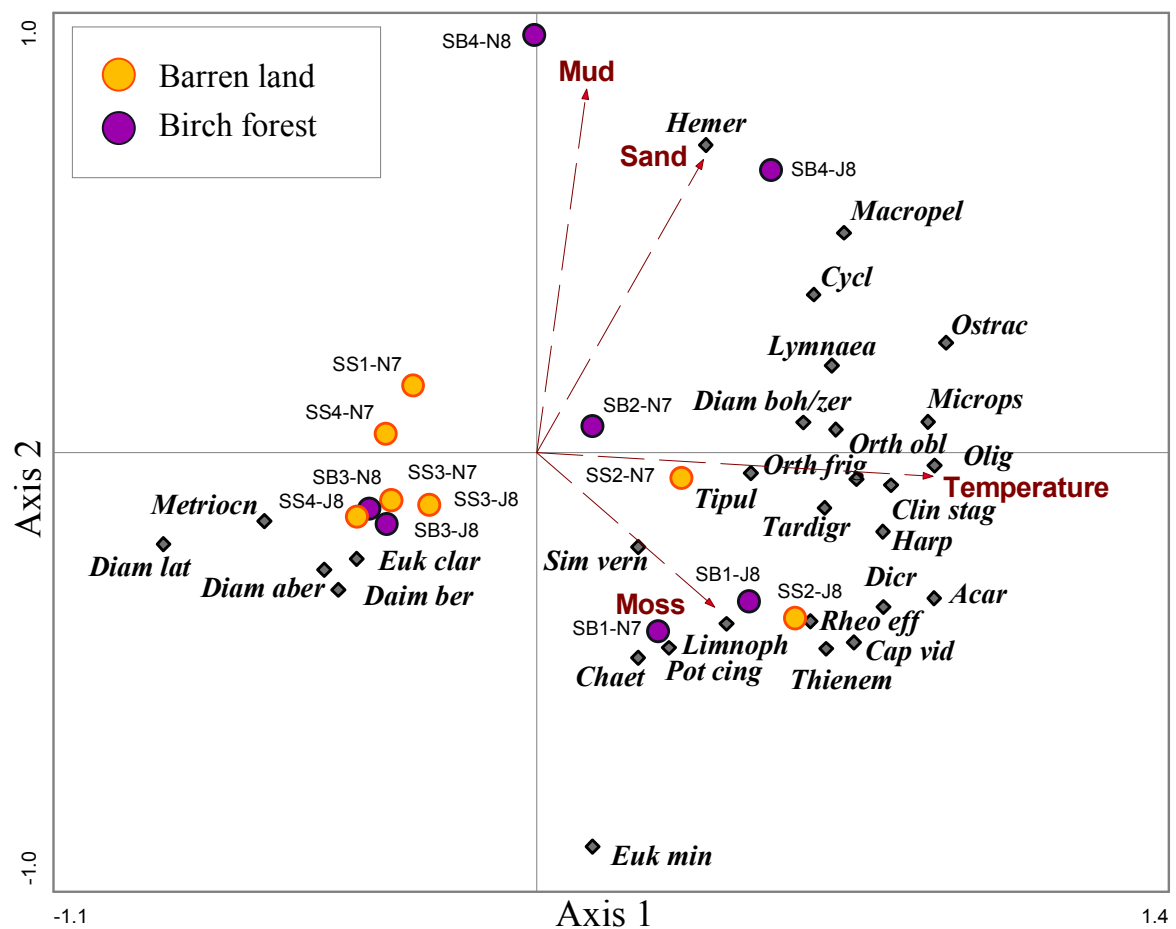


Figure 3.23 RDA ordination diagram based on invertebrate densities and environmental variables in spring-fed streams during two sampling occasions (N7 stands for November 2007, J8 stands for July 2008). Species that were found in less than two samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.



### 3.3 Comparison of direct run-off and spring-fed streams

#### 3.3.1 Catchment composition

Similarity analysis divided the catchments of spring-fed and direct run-off streams into three clusters and an outlier (Figure 3.24). The first cluster grouped four treeless catchments that were located in the southern research area (SS1, SS2, SS3 and SS4). These catchments were mainly covered by eroded land. Other cluster included three forested catchments from the south (SB1, SB2 and SB3) and one from the east (AB3). Birch woodlands covered the greater territories of these catchments, comparing to the other forested catchments (Figures 2.3 and 2.7). The third cluster included the catchments from the eastern research area (AB1, AB2, AS1, AS2 and AS3) (Figure 3.24). The largest territories of these catchments were covered by heathland and gravel flats (Figures 2.3 and 2.7). One catchment located in the south, SB4, was an outlier. It was classified as birch forested, but it was mainly covered by gravel flats (Figure 2.7). Only a small area of this catchment around the stream was covered by birch woodlands.

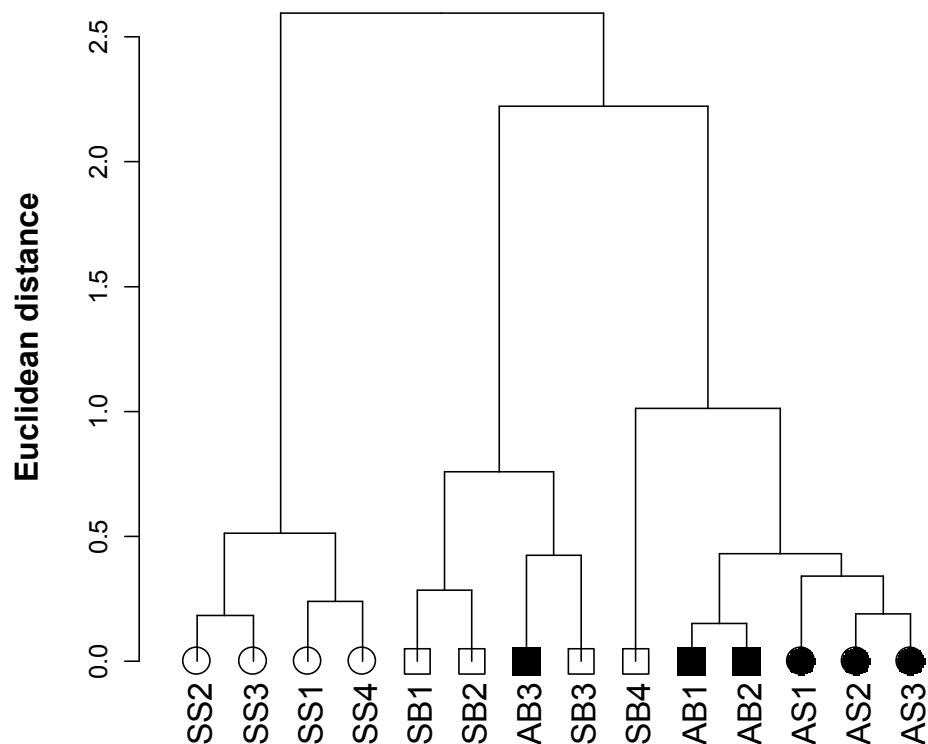


Figure 3.24 Cluster dendrogram of the similarity among catchment composition of direct run-off and spring-fed streams, using the Ward method, Euclidean distance. ○ treeless catchments of spring-fed streams; □ birch forested catchments of spring-fed streams; ● treeless catchments of direct run-off streams; ■ birch forested catchments of direct run-off streams.

### 3.3.2 Invertebrate community composition

Species of stream invertebrates in the eastern and southern research areas were more or less the same, they were just found in different proportions (Figure 3.25). The most dominant taxon in spring-fed and direct run-off streams was Chironomidae, followed with Ostracoda, Oligochaeta, Harpacticoidea (Copepoda) and Acarina. Several species of Chironomidae dominated in both types of streams: *E. minor*, *Thienemanniella* spp., *Micropsectra* spp., *O. (O.) frigidus*, *D. bohemani/zernyi*, *D. latitarsis* group, *D. bertrami* (Tables 3.4 and 3.16).

The main difference in chironomid communities between direct run-off and spring-fed streams were the densities of species *E. claripennis* and *D. aberrata*. In direct run-off streams *E. claripennis* was the most dominant species of Chironomidae, while in spring-fed streams it was found in small proportions. *D. aberrata* (Lundbeck) was one of the most dominant species of Chironomidae in colder spring-fed streams, while in direct run-off streams it was not found.

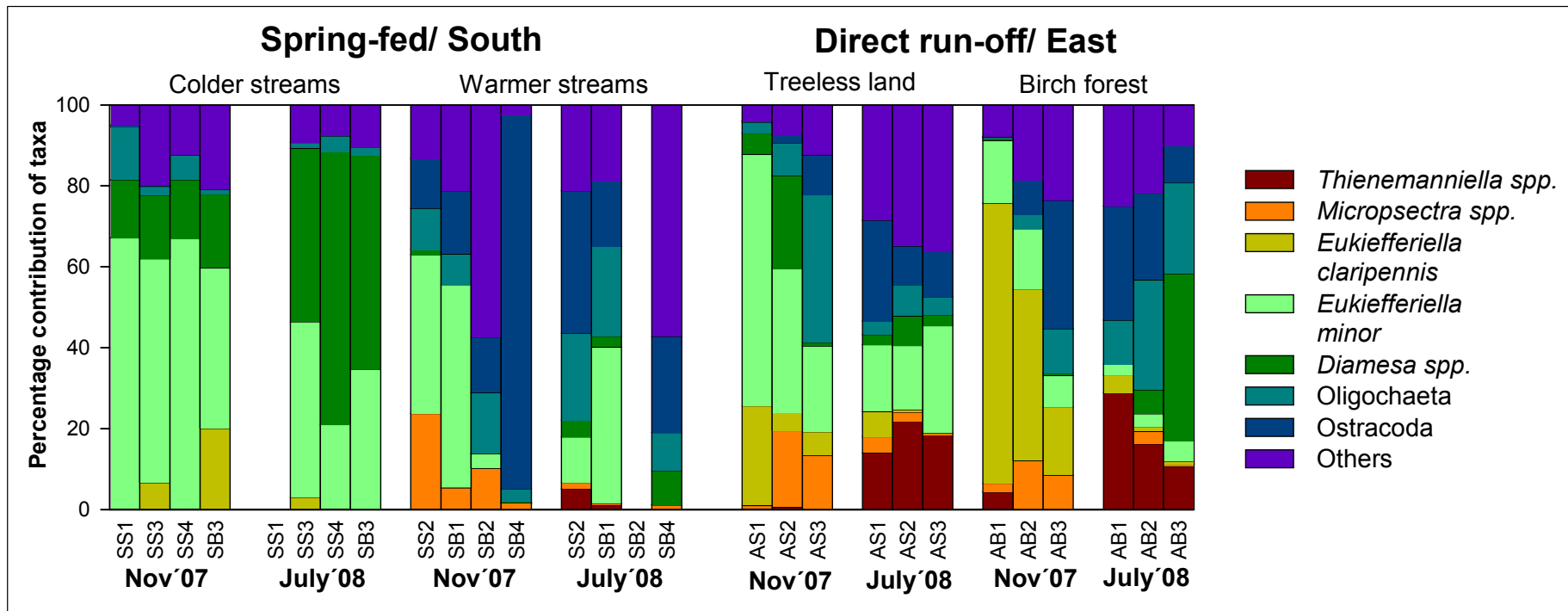


Figure 3.25 Proportional abundances of stream invertebrate taxa, found in spring-fed and direct run-off streams during two sampling occasions. Since temperature was the main factor, determining invertebrate community structures in spring-fed streams (in the left side of the graph), they are grouped according to the temperature, not the catchment type. Direct run-off streams (in the right side of the graph) are grouped according to the catchment type.

### 3.3.2.1 Differences in density and diversity variables among research areas and catchment types

Density and diversity parameters were highly variable across the eastern and southern research areas. Total invertebrate densities in spring-fed streams were higher than in direct run-off streams (Figures 3.26 and 3.27). In November 2007 the difference was not statistically significant (two-way ANOVA  $F_{8,1}=3.618$   $P=0.094$ ), but in July 2008 it was highly significant (two-way ANOVA  $F_{8,1}=17.732$   $P=0.003$ ).

In July 2008 the number of taxa was quite similar in both research areas (Figure 3.27) (two-way ANOVA  $F_{8,1}=0.039$   $P=0.849$ ). It differed significantly between direct run-off and spring-fed streams in November 2007 (two-way ANOVA  $F_{8,1}=6.259$   $P=0.037$ ). Numbers of taxa were significantly higher in streams draining treeless catchments in the southern research area than in streams draining treeless catchments in the east (Figure 3.26).

Shannon diversity and evenness did not vary significantly between direct run-off and spring-fed streams in November 2007 (two-way ANOVA  $F_{8,1}=0.302$   $P=0.598$  and  $F_{8,1}=1.049$   $P=0.336$  respectively). In July 2008, both these variables were higher in the streams running through the treeless land in the east, than in the south (two-way ANOVA  $F_{8,1}=9.614$   $P=0.015$  and  $F_{8,1}=16.808$   $P=0.003$  respectively) (Figures 3.26 and 3.27).

### 3.3.2.2 Differences in functional feeding groups among research areas and catchment types. Analysis, based on invertebrate densities

The proportions of each functional feeding group did not differ a lot between the streams located in the eastern and southern research areas. The two dominant functional feeding groups, gathering collectors and gathering collectors scrapers, did not show any distinctive trends between direct run-off and spring-fed streams in November 2007 (Figure 3.28) (two-way ANOVA for gathering collectors  $F_{8,1}=0.081$   $P=0.784$ , and for gathering collectors scrapers  $F_{8,1}=0.064$   $P=0.807$ ).

In July 2008 the proportions of gathering collectors were higher in direct run-off streams. Proportions of gathering collectors scrapers showed an opposite trend. They were lower in direct run-off than spring-fed streams in July 2008 (Figure 3.29). The proportions of both functional feeding groups did not vary significantly between the research areas (two-way ANOVA for gathering collectors  $F_{8,1}=1.763$   $P=0.221$ , and for gathering collectors scrapers  $F_{8,1}=3.310$   $P=0.106$ ).

The percentage of filtering collectors was greater in direct run-off streams during both seasons, even though the differences were not statistically significant (two-way ANOVA in November 2007  $F_{8,1}=2.989$   $P=0.122$ , and July 2008  $F_{8,1}=5.051$   $P=0.055$ ). The proportions of shredders in November 2007 were higher in spring-fed streams, but in July 2008 it was vice versa (Figures 3.28 and 3.29). Neither difference was statistically significant (two-way ANOVA in November 2007  $F_{8,1}=3.635$   $P=0.093$ , and July 2008  $F_{8,1}=2.171$   $P=0.179$ ). In November 2007 the proportion of predators did not show any clear trend between east and south (Figure 3.28) (two-way ANOVA  $F_{8,1}=1.096$   $P=0.326$ ). In July 2008, significantly

higher proportions of predators were found in direct run-off streams, than in spring-fed streams running through treeless land (Figure 3.29) (two-way ANOVA,  $F_{8,1}=10.868$   $P=0.011$ ).

### 3.3.2.3 Differences in functional feeding groups among research areas and catchment types. Analysis, based on invertebrate species presence/absence

The proportions of gathering collectors did not differ much between the streams located in eastern and southern research areas in November 2007 (Figure 3.30) (two-way ANOVA  $F_{8,1}=3.430$   $P=0.101$ ). The proportions of gathering collectors scrapers were higher in direct run-off streams than in spring-fed streams (Figure 3.30), but the differences were not statistically significant (two-way ANOVA  $F_{8,1}=0.0113$   $P=1.719$ ). In July 2008 proportions of gathering collectors were slightly lower in spring-fed streams than direct run-off streams (two-way ANOVA  $F_{8,1}=2.064$   $P=0.189$ ). Percentages of gathering collectors scrapers were higher in spring-fed streams (Figure 3.31), but the differences were not statistically significant (two-way ANOVA  $F_{8,1}=0.979$   $P=0.351$ ).

Proportions of filtering collectors were higher in direct run-off streams, comparing to spring-fed streams (Figures 3.30 and 3.31), the differences, though, were not statistically significant (two-way ANOVA for November 2007  $F_{8,1}=4.011$   $P=0.080$ , and for July 2008  $F_{8,1}=5.129$   $P=0.053$ ). Proportions of predators did not show any trends between two different geological areas (Figures 3.30 and 3.31) (two-way ANOVA for November 2007  $F_{8,1}=0.136$   $P=0.722$ , and for July 2008  $F_{8,1}=3.610$   $P=0.094$ ).

Shredders were the only functional feeding group that differed significantly between direct run-off and spring-fed streams. In November 2007 percentages of shredders were higher in spring-fed streams within both catchment types, comparing to direct run-off streams (Figure 3.30) (two-way ANOVA  $F_{8,1}=30.700$   $P<0.001$ ). In July 2008, no differences between east and south were found (Figure 3.31) (two-way ANOVA  $F_{8,1}=0.005$   $P=0.945$ ).

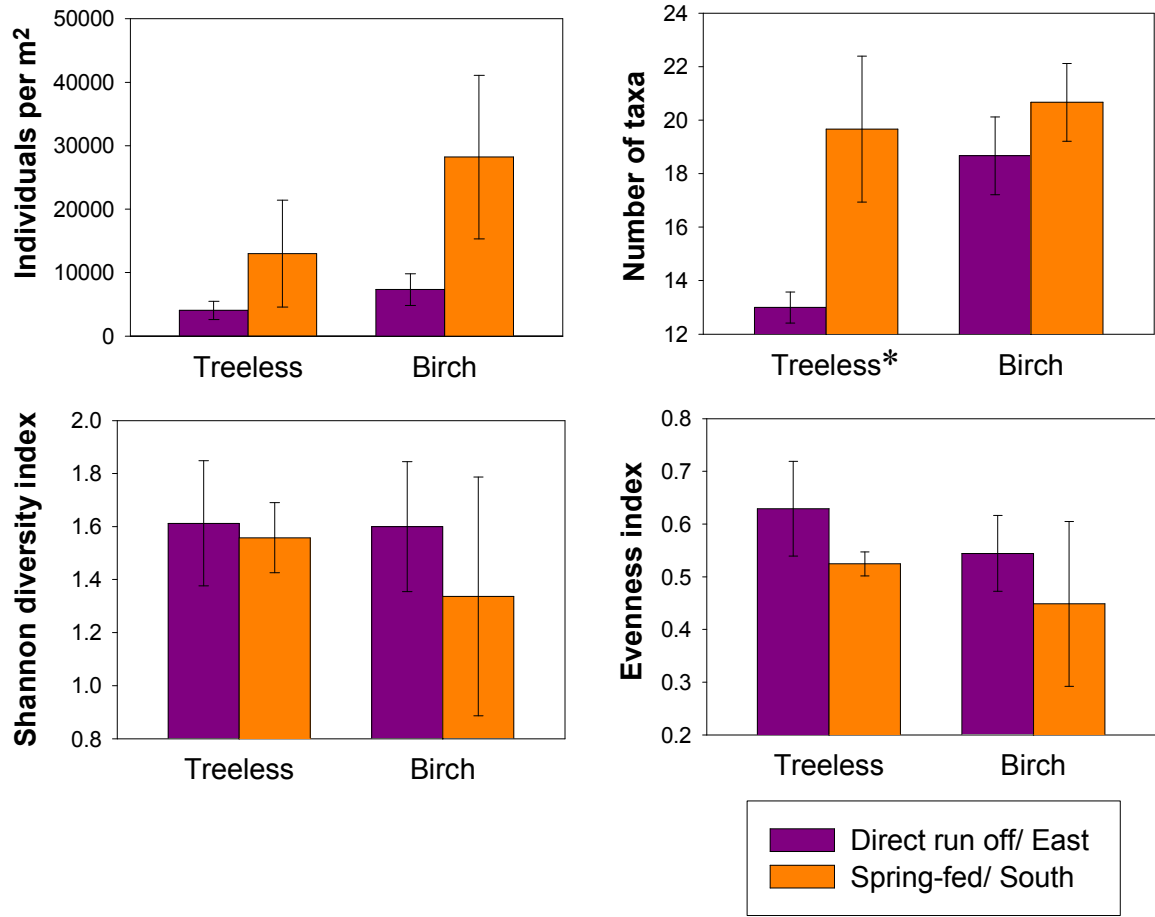


Figure 3.26 Total invertebrate densities, number of taxa, Shannon diversity and evenness in November 2007 in spring-fed and direct-run-off streams with different catchment types. \* indices significant difference between research areas ( $P < 0.05$ , two way ANOVA).

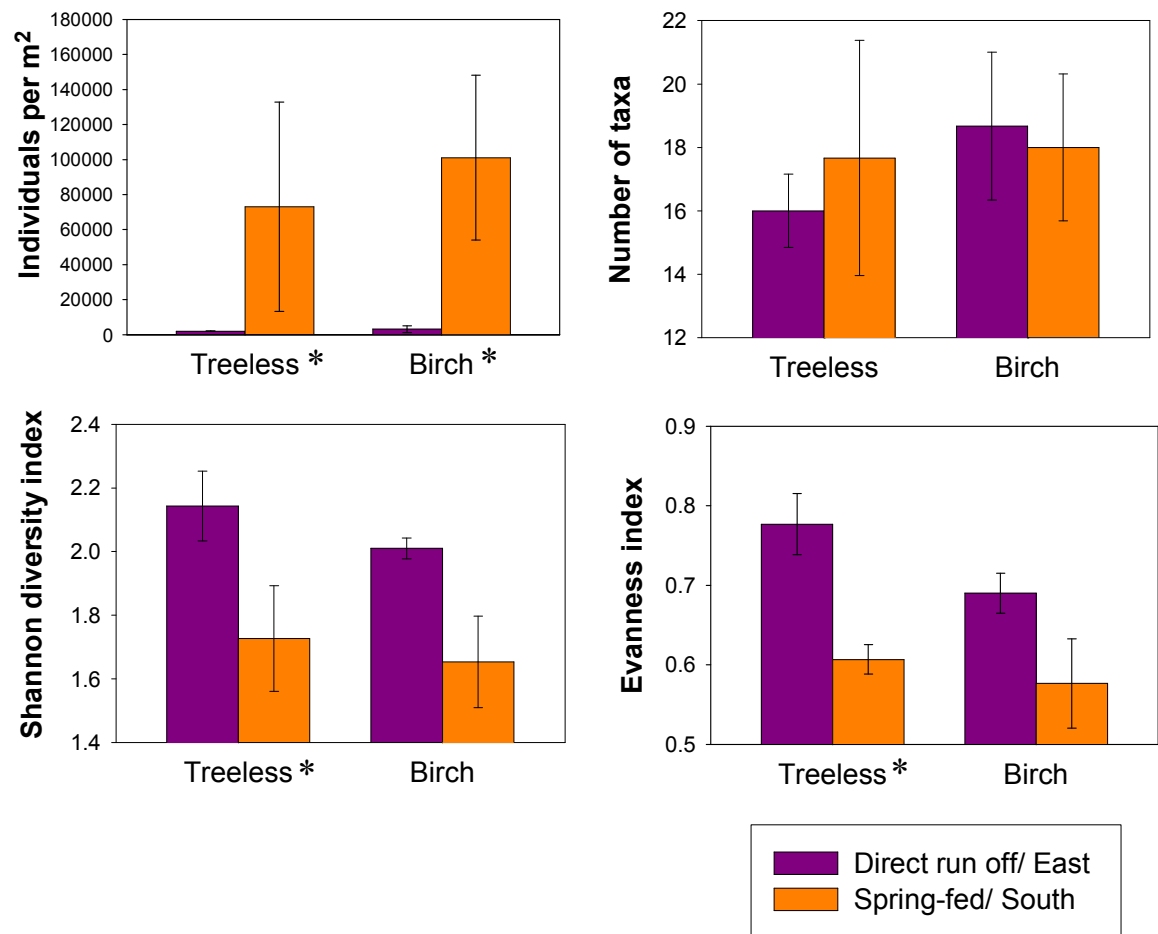


Figure 3.27 Total invertebrate densities, number of taxa, Shannon diversity and evenness in July 2008 in spring-fed and direct-run-off streams with different catchment types. \* indices significant difference between research areas ( $P < 0.05$ , two way ANOVA).

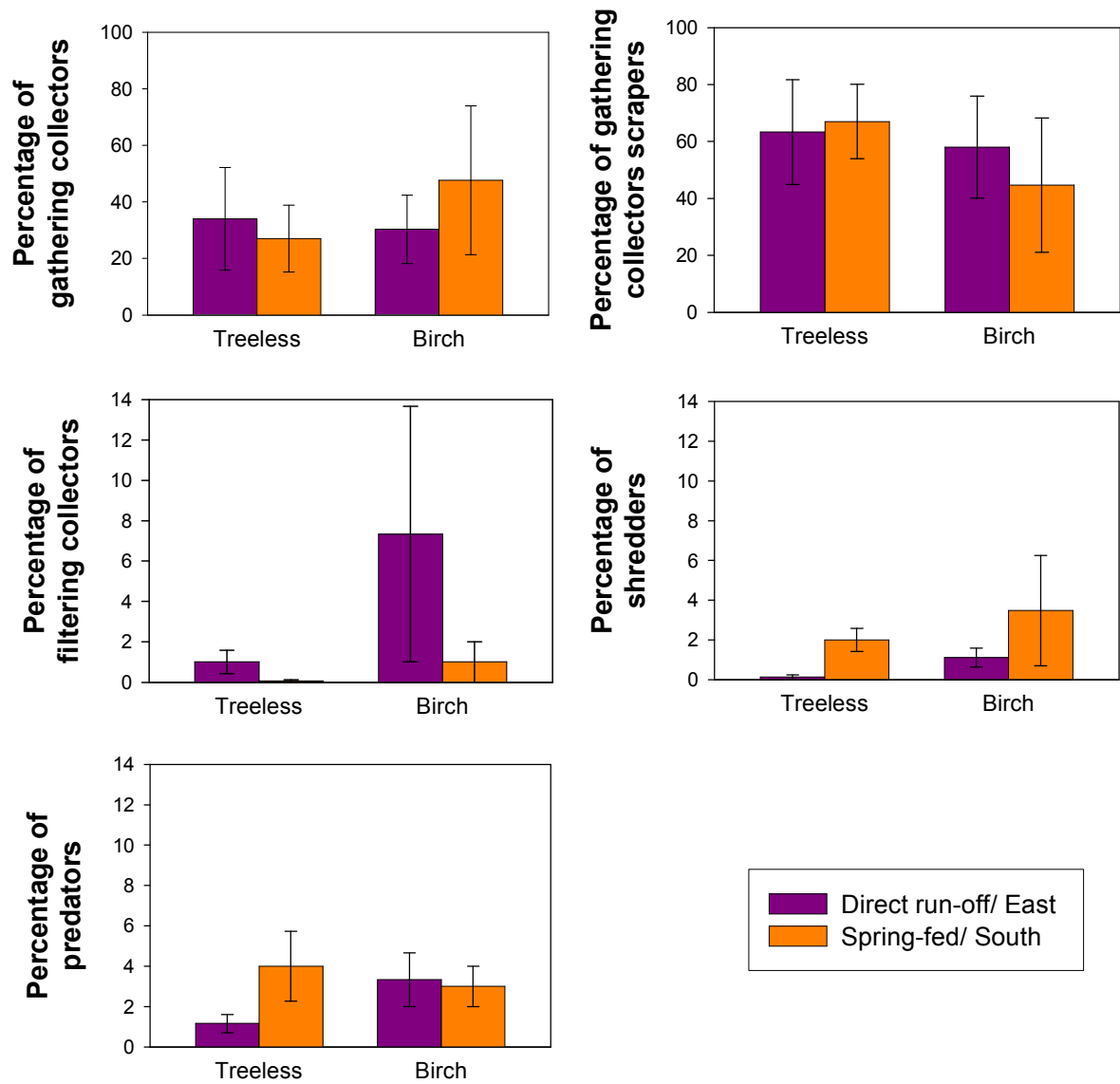


Figure 3.28 Functional feeding groups in November 2007 in spring-fed and direct-run-off streams with different catchment types. Analysis, based on invertebrate densities.



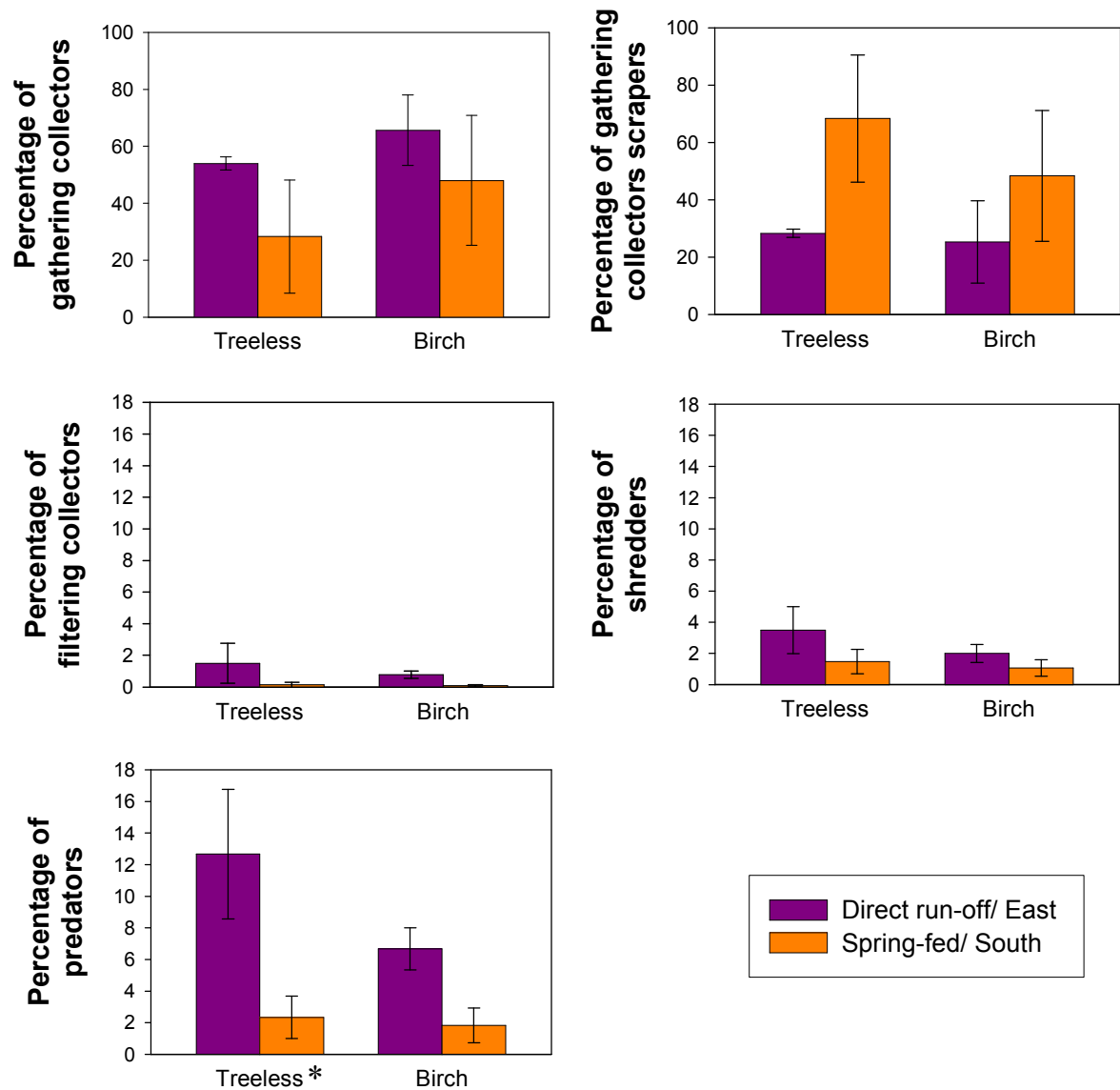


Figure 3.29 Functional feeding groups in July 2008 in spring-fed and direct run-off streams with different catchment types. Analysis, based on invertebrate densities. \* indices significant difference between the research areas ( $P < 0.05$ , two way ANOVA).

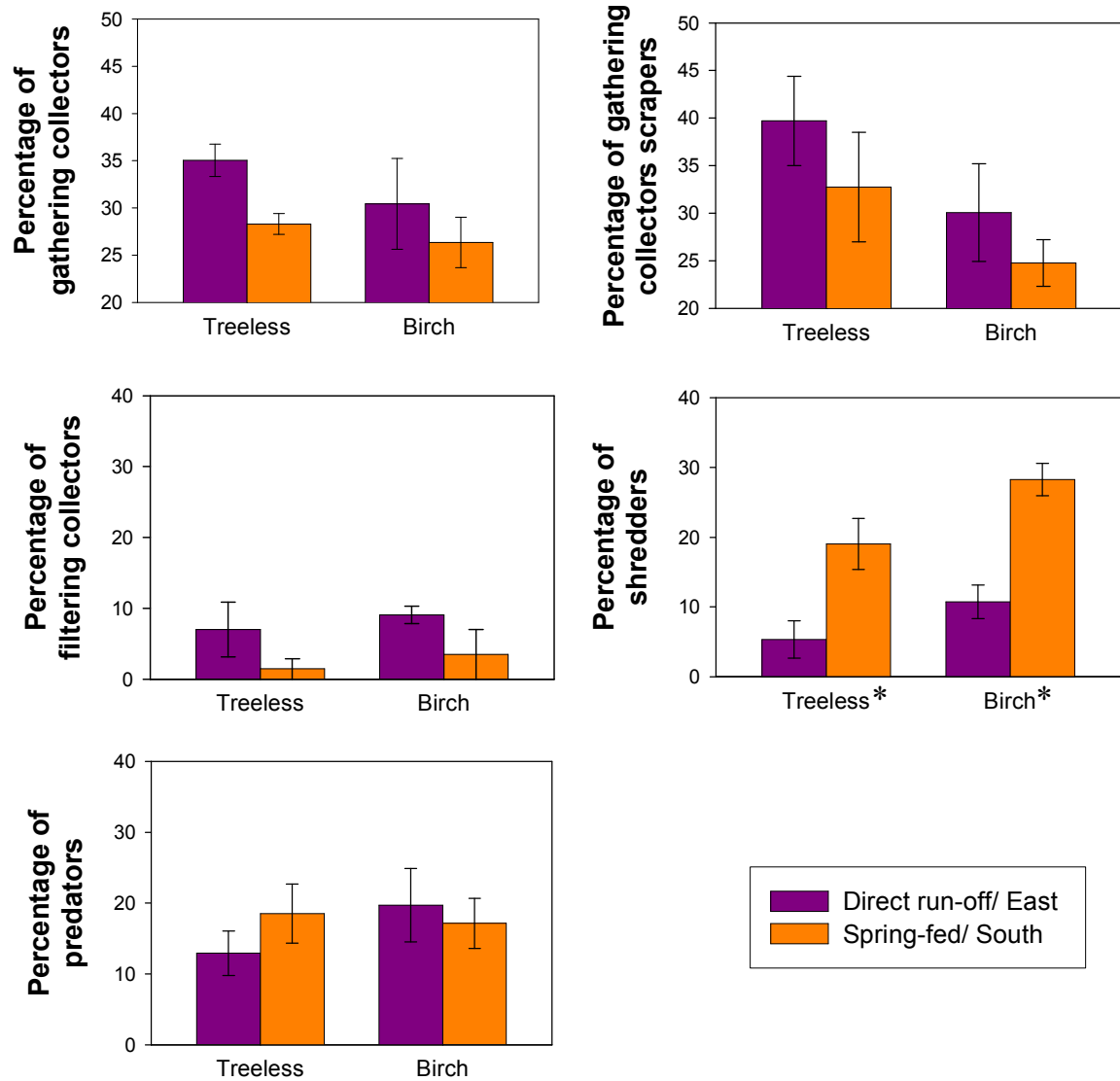


Figure 3.30 Functional feeding groups in November 2007 in spring-fed and direct-run-off streams with different catchment types. Analysis, based on invertebrate species presence/absence. \* indices significant difference between the research areas ( $P < 0.05$ , two way ANOVA).

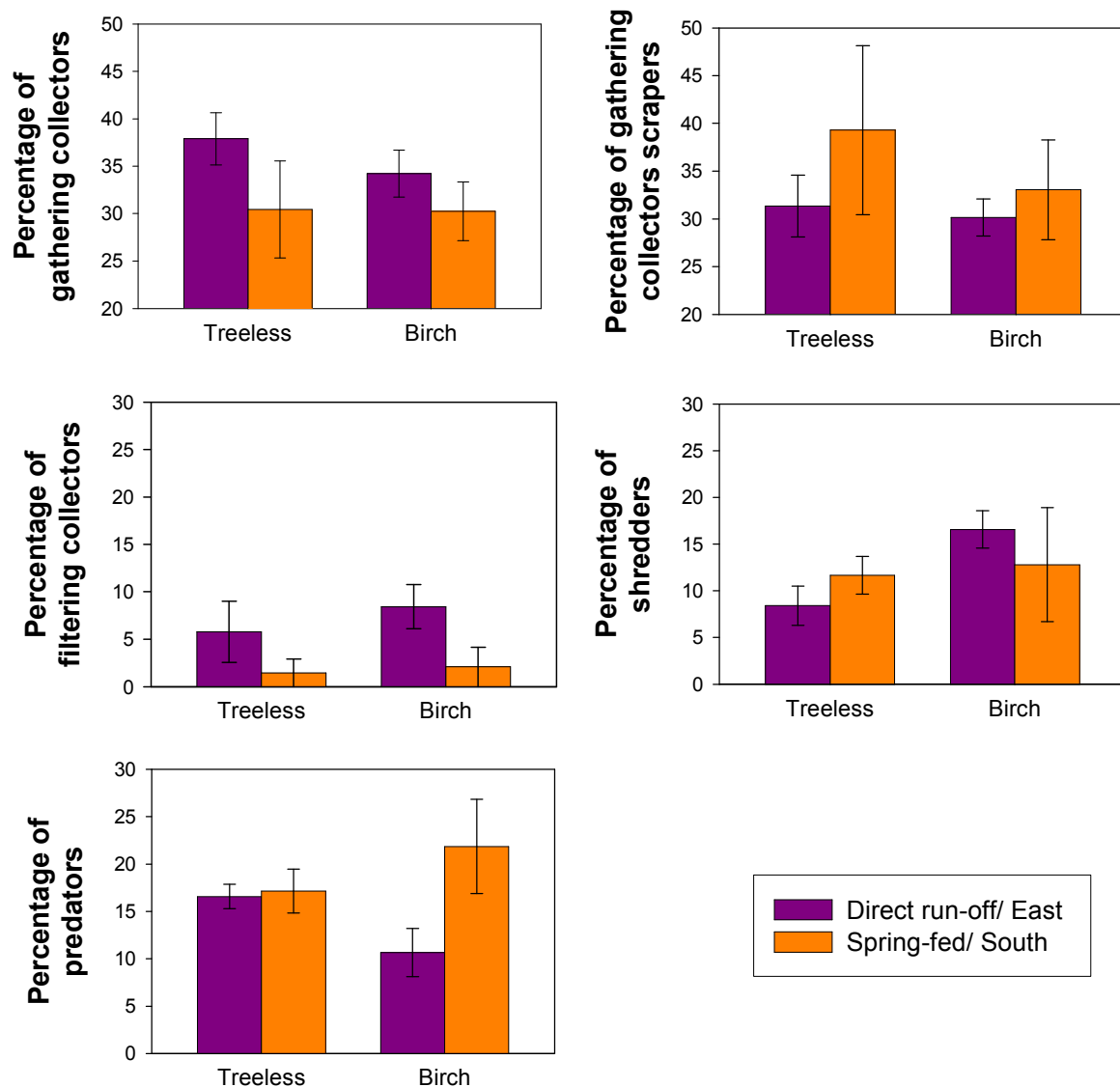


Figure 3.31 Functional feeding groups in July 2008 in spring-fed and direct run-off streams with different catchment types. Analysis, based on invertebrate species presence/absence.

#### 3.3.2.4 Invertebrate assemblages

A principal component analysis, done on species data created four principal components, which all together explained 80.6% of the variance. The first two principal components accounted for 49.6 and 16.1% of the variance. The distribution of samples in PCA and RDA ordination diagrams were very similar, therefore only the RDA diagram is given here. Samples were divided into three groups (Figure 3.32). Samples from direct run-off streams were situated in the lower left of the ordination diagram. Samples taken from colder spring-fed streams (SS1, SS3, SS4 and SB3) were grouped in the upper left of the diagram. The samples from warmer spring-fed streams (SS2, SB1, SB2 and SB4) were located in the right of the ordination diagram farther apart from each other.

Direct run-off streams were distinctive in having much higher numbers of *E. claripennis* than spring-fed streams. The densities of *P. branickii* were low in direct run-off streams, but in spring-fed streams this species was absent. In colder spring-fed streams (SS1, SS3, SS4 and SB3), *Diamesa* species were the most abundant. Warmer spring-fed streams (SS2, SB1, SB2 and SB4) had much higher densities of many taxa than the two other clusters. These taxa were Ostracoda, Oligochaeta, Acarina, Harpacticoidea (Copepoda), *Micropsectra* spp., *D. bohemani/zernyi* and *O. (O.) frigidus* (Figure 3.32). *Thienemanniella* spp. was more abundant in direct run-off streams and in warmer spring-fed streams (SS2, SB1, SB2 and SB4). *E. minor* was found in few times smaller densities in direct run-off streams than in spring-fed streams.

#### 3.3.3 Invertebrate assemblages in relation to stream ecology

Six variables were most important in explaining the variability of invertebrate assemblages, taking into account direct run-off and spring-fed streams (Figure 3.32). These variables were sodium, chlorine, phosphate, pH, percentage of macroalgae cover on stream bottom, and one bottom substrate component, mud. This set of variables explained 64% of the total variance, and the first two axes explained 44.2 and 11.2% of the variance respectively (Figure 3.32).

Sodium, chlorine and phosphate were the most important variables explaining the differences between direct run-off and spring-fed streams (Figure 3.32). The concentrations of these three chemicals were a few times higher in spring-fed than direct run-off streams (Tables 3.1 and 3.13). Macroalgae was an important environmental variable on axis one. It was positively associated with the taxa that were most abundant in warmer spring-fed streams (SS2, SB1, SB2 and SB4): Ostracoda, Oligochaeta, Acarina, Harpacticoidea (Copepoda), *Micropsectra* spp., *Diamesa bohemani/zernyi* and *O. (O.) oblidens*. Mud was the variable that described the bottom of the stream SB4, very high densities of Ostracoda and extremely low densities of *E. minor*. pH was positively associated with *D. aberrata*, *D. bertrami*, *D. latitarsis* group and *Metriocnemus* sp.

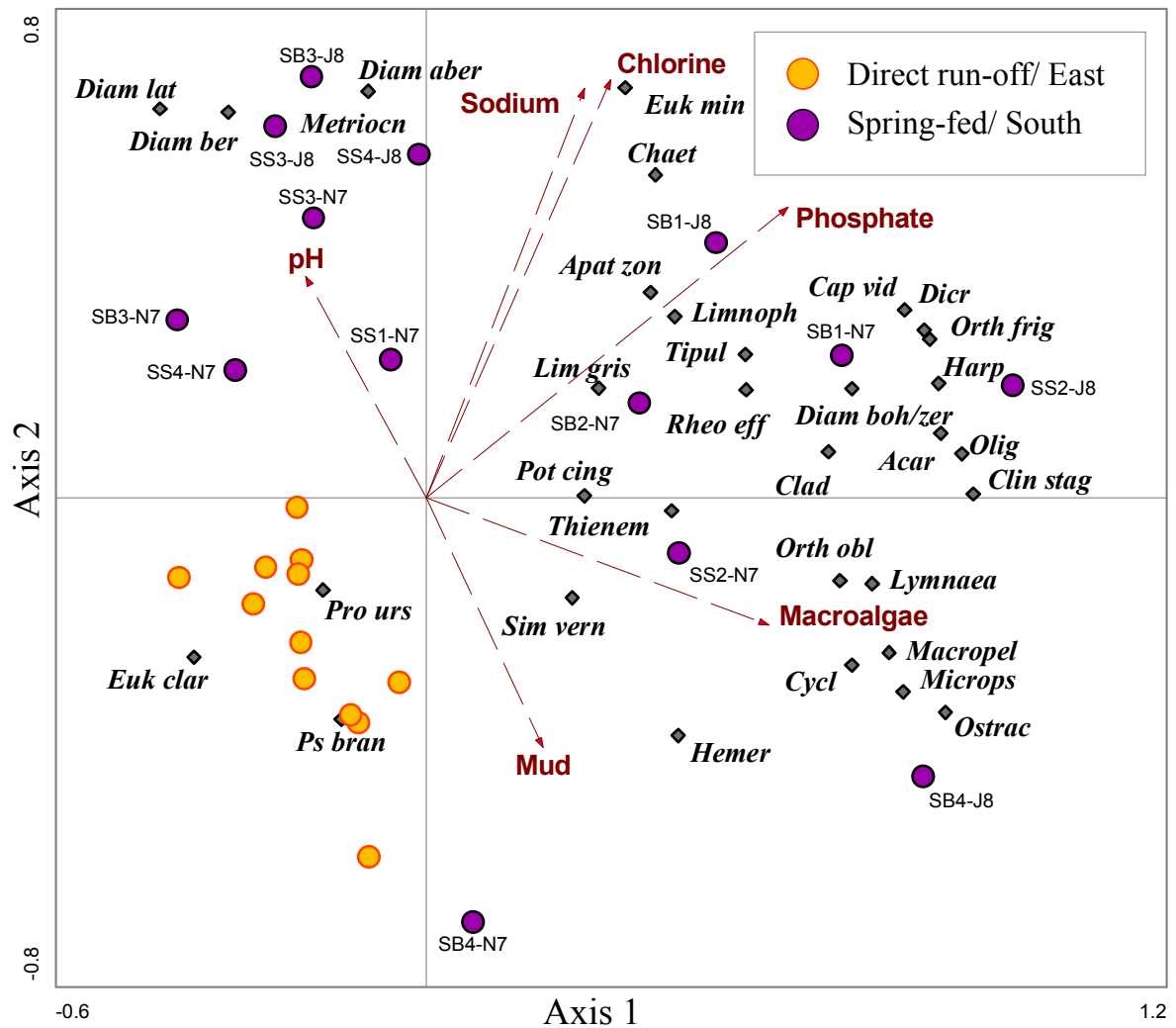


Figure 3.32 RDA ordination diagram based on invertebrate densities and environmental variables in spring-fed and direct run-off streams during two sampling occasions (N7 stands for November 2007, J8 stands for July 2008). Species that were found in less than three samples across the streams and sampling occasions were omitted from the analysis. For explanation on abbreviations for the taxa see a table at page XIX.



## 4 Discussion

A vast amount of researchers in the world have shown that the presence and type of forest in catchments can influence stream invertebrate assemblages (Harding and Winterbourn, 1995; Friberg, 1997; Friberg et al., 1997; Flory and Milner, 1999; Snyder et al., 2002; Thompson and Townsend, 2004; Yoshimura and Maeto, 2006; Yoshimura, 2007; Willacker et al., 2009; Miserendino and Masi, 2010). Barren or scarcely vegetated catchments can, therefore, affect benthic communities in big rivers in Iceland. Rivers originating from well-vegetated catchments have been shown to have a higher invertebrate species richness and densities, and higher fish productivity than rivers draining barren areas (Gíslason et al., 1998; Gíslason et al., 1999; Ólafsson et al., 2002).

Chironomids are the most abundant invertebrate group in direct run-off, glacier-fed and spring-fed streams without lake influence. In this study, the dominant species of chironomids were generally similar to the ones found in the other streams in Iceland (Gíslason et al., 1999; Ólafsson et al., 2000; Gíslason et al., 2001; Stefánsson, 2005; Stefánsson et al., 2006). Since they were the most abundant taxa, chironomids played an important role in this study in determining the differences among the stream characteristics in relation with catchment vegetation, season and environmental variables.

### 4.1 Effect of catchment vegetation on stream ecology

The low concentration of ions and a relatively low conductivity characterized direct run-off streams in the eastern research area. The main reason is thought to be a result of the underlying geology of the island. The old crystalline bedrock in eastern Iceland is relatively stable and weathering rates are slow (Gíslason, 2008). The concentrations of nutrients, such as potassium, sodium, sulphur, phosphate and nitrate are generally low in the water, and ammonium is under detection level, which was demonstrated by the present study. Low values of inorganic ions were one of the factors that determined relatively low conductivities in the streams.

In the present study, no differences in chemical variables were observed in streams with different catchment types. A high sulphur, calcium, sodium, magnesium and phosphate concentration was generally observed in stream AB3. It is very likely, that concentrations of these nutrients in stream AB3 were influenced by higher proportions of birch woodlands within its catchment. Greater territories of birch woodlands supplied higher amounts of litterfall or throughfall, which could determine greater levels of sulphur, calcium, sodium, magnesium and phosphate (Feller, 2005). The presence of large territories of fertile grassland could also supply a considerable proportion of these nutrients.

The stream AS1 also exhibited increased calcium, sodium and magnesium concentration. This is possibly related to the exceptionally large catchment area compared to catchments of the other streams. A high current velocity could also play a role. Concentrations of nutrients derived primarily from chemical weathering (calcium, sodium and magnesium) decrease with increasing discharge due to dilution by less concentrated rainwater (Feller, 2005). High seasonal variations of these elements in stream AS1 could be due to high seasonal variations of current velocity.

In all direct run-off streams, slightly lower concentrations of some elements (calcium, sodium, magnesium and sulphur) were observed during the summer than during the winter. A higher temperature in summer may accelerate weathering and decomposition as well as chemical and microbial reactions, which may then alter chemical movement through soil into the stream (Feller, 2005). However, a higher uptake of nutrients by primary producers in streams and by the riparian vegetation can reduce nutrient concentrations in stream water. A lower temperature during the cooler periods may result in enhanced soil freezing, decreased plant uptake and enhanced stream water ion concentrations (Feller, 2005).

Around three times higher sulphur levels were observed in stream AB3 than in all the other streams. Besides atmospheric deposition, the sulphate level in stream water can be influenced by mineralization of organic matter. Therefore, an increased level of sulphur in AB3 could be determined by greater litterfall. Sulphur oxidizing bacteria is one more way to increase sulphate levels in streams. However, the data were not sufficient enough to check that.

Contrary to the direct run-off streams, the spring-fed streams were distinguishable by having a relatively high ionic concentration. The amount of glassy rocks (hyaloclastites) is generally much higher in younger bedrock than in older. Suck rock formations dissolve much faster in water, which leads to an increase in concentrations of some chemicals (Gíslason et al., 1996; Gíslason, 2008). Old crystalline bedrock in eastern Iceland is relatively resistant and is less prone to weathering than younger rock formations. This determined lower levels of potassium, sodium and sulphur in direct run-off streams. Calcium and magnesium concentrations were similar in both types of streams in the present study. The relative mobility of these elements is less dependent on the age of rocks (Gíslason et al., 1996; Feller, 2005; Gíslason, 2008). The litterfall can also influence greater concentrations of potassium, magnesium, phosphorus, calcium, ammonium, nitrate and sulphate (Feller, 2005).

Temperature, conductivity and concentration of some ions determine the main differences among the spring-fed streams. None of these variables was related to the presence of forest in the catchment. Levels of nutrients did not vary between winter and summer; velocities and temperatures were quite stable between the two seasons as well. This indicates that weathering rates were similar throughout the year. Warmer streams were generally wider than colder ones and more solar energy could reach the water surface. This could be an important factor causing higher production of algae in warmer spring-fed streams than in colder ones.

In general, ecological characteristics of streams in the eastern and southern research areas were very different. Direct run-off streams in the east drained through much larger catchments than spring-fed streams in the south. Only a small part of the catchments in the eastern research area could be considered forested. Whereas in the southern area, only one



catchment (SB4), which was classified as birch forest, was covered by low proportions of birch woodlands. At least half of the areas of the other forested catchments were afforested.

Treeless catchments in the eastern and southern research areas were very different. In the south they were mostly eroded and very poorly vegetated. In the east, heathlands, grasslands and wetlands were covering more than half of the areas of all the treeless catchments. The main vegetation there was grasses, sedges and some dwarf bushes. Bottom substrate composition varied between direct run-off and spring-fed streams. Coarser substrates dominated in direct run-off streams, mainly boulders, cobbles and pebbles. Finer substrates covered the bottoms of spring-fed streams, such as pebbles, gravel and sand.

## **4.2 Relation of stream invertebrate communities with catchment vegetation**

### **4.2.1 Effect of catchment type on invertebrate densities and diversities in the streams**

A number of studies have observed that invertebrate taxonomic richness and density can vary among streams with forested and non-forested catchments. Invertebrate density, biomass and diversity were higher in forest streams than pasture streams in Costa Rica (Lorion and Kennedy, 2009). The number of taxa was highest in deciduous (beech) forest streams and lower in pine forest, scrubland and pastoral streams in New Zealand, but the total densities of individuals were higher in streams with non-forested than forested catchments (Harding and Winterbourn, 1995). Another study from New Zealand showed that streams in tussock and pasture land were richer in species than streams running through pine and broadleaf forests (Thompson and Townsend, 2004).

Streams running through deciduous forests are generally richer in individuals than streams running through conifer forests. In Denmark, the number of taxa and invertebrate density were clearly lower in coniferous forest streams than in streams surrounded by deciduous (beech) forests (Friberg, 1997). In Massachusetts, invertebrate abundance, taxa richness, diversity and unique taxa were greater in a deciduous forest stream than in a stream running through hemlock forest (Willacker et al., 2009). Sometimes conifer forest can support richer invertebrate communities in streams. Streams in hemlock forest had more taxa than streams draining mixed hardwood catchments in Pennsylvania (Snyder et al., 2002).

In eastern Iceland invertebrate density and diversity parameters did not differ significantly between the streams running through the birch woodlands, conifer forest and treeless land. However, some differences could be seen in densities among the streams in relation to catchment composition. The density tended to be higher in the streams running through the birch woodlands than in streams running through the treeless land and conifer forest. However, it was only because of stream AB3, where the densities were about 2–5 times

higher than in all other streams. This stream was also notable for having a better vegetated catchment and higher concentrations of nutrients.

In October 2008, the number of taxa increased greatly in direct run-off streams running through treeless land. During other sampling occasions it was around twice as small as in October 2008. Such a large increase in number of taxa could be attributed to animal drift downstream. Increased current velocity in October 2008 could force the invertebrates to lose contact with the substrate and enter the water column. Drift can increase when population numbers approach food resources needed for their support. Downstream movements can also be associated with life history events such as egg hatching, pupation and emergence. Adults can fly up and down the stream channel or to other drainages (Allan, 1995; Giller and Malmqvist, 1998; Smock, 2006).

Invertebrate densities were higher in spring-fed streams, draining birch forests, than streams draining barren land. These differences were related to water temperature. Higher invertebrate densities and number of taxa were found in warmer spring-fed streams than colder ones. Catchment type had no effect on invertebrate communities in spring-fed streams.

#### **4.2.2 Effect of forest presence in the catchment on stream invertebrate assemblages**

It has been demonstrated that even though invertebrate densities and number of taxa are similar among streams running through different catchment types, differences can be seen in community structure, as in a temperate forest region of Japan (Yoshimura and Maeto, 2006). There, the study focused on comparing the total abundance of individuals and number of families between coniferous and deciduous broad-leaved forest streams. None of these parameters differed significantly between streams running through different forest types. Still, some families of insects were more abundant in deciduous broad-leaved forest streams and some other families were more abundant in coniferous forest streams. In New Zealand, the abundances and number of taxa of stream invertebrates varied only slightly between two types of forested catchments and open sites, but some differences could still be found in community structures according to the catchment type (Friberg et al., 1997).

In the present study, invertebrate density and diversity in direct run-off streams did not differ significantly among treeless land, birch forest and conifer forest. Some differences in invertebrate taxonomic compositions were however observed between the streams running through the treeless land and forested catchments. Splitting the invertebrate data based on two periods (winter and summer) helped to detect those differences. In winter the major differences between streams within treeless and forested catchments were the proportions of some taxa. The composition of the whole catchment explained these differences. The catchments defined as forested were almost fully covered with forests 400 metres upstream from the sampling station of each stream. The composition of each catchment within these 400 metres also explained some of the differences of invertebrate communities in the streams draining treeless and forested catchments.

However, the composition of the catchment within the 400 metres did not help to detect the differences in stream invertebrate communities, according to how well the catchment is vegetated. Stream AB3 was always an outlier in this research. The majority of taxa were

much more abundant in this stream during winter and summer. Its catchment was the best vegetated; proportions of birch woodlands and fertile grassland were the highest. Greater invertebrate densities throughout the whole year in stream AB3 were closely related to the composition of the whole catchment. The composition of the catchment within the 400 metres did not explain the greater invertebrate densities in this stream.

In summer, invertebrate communities in direct run-off streams were related to the presence of forest as well. Higher invertebrate densities in streams AB3, AG2 and AG3 could be explained by higher proportions of birch woodlands in their catchments. Higher invertebrate densities were not related to the catchment characteristics of the 400 metre segment of these streams. However, the highest total riparian biomass values within the 400 metre catchment segment were observed around the streams AB3, AG2 and AG3. This shows that more densely vegetated catchment areas can determine higher invertebrate densities in direct run-off streams.

The presence of forest, its proportions within a catchment and the amounts of riparian biomass had an influence on invertebrate communities in direct run-off streams. Streams with more densely forested catchments are presumably able to support denser invertebrate communities. The effect of catchment vegetation on stream invertebrate densities is better explained by the composition of the whole catchment rather than when catchments were confined to 400 metres upstream from each sampling station. The composition of the catchment within the 400 metres upstream from the sampling stations helps only to detect the fact that streams with forested and non-forested catchments can support slightly different invertebrate communities, but the composition of the whole catchment explained more fine differences among the streams. It helps to understand, that the streams with more densely-vegetated and more forested catchments have more abundant invertebrate communities.

The presence of forest within the catchment did not affect invertebrate community structures in spring-fed streams in southern Iceland. Densities and proportion of taxa were highly associated with the stream water temperature.

#### **4.2.3 Effect of catchment type on invertebrate functional feeding groups in the streams**

It is difficult to place most chironomid species into a functional feeding group, because the majority of them can fall into more than one group. The larvae may exhibit a different feeding behaviour according to food quality, sediment composition and larval instar (Berg, 1995). Many chironomid taxa in this study can be regarded as gathering collectors and scrapers. *P. branickii* has been classified as a gathering collector (Merritt and Cummins, 1996). The results of this study indicated that it can also feed as predator. The whole bodies of other chironomid larvae were observed in the gut contents of *P. branickii*, which indicate their potential predatory behaviour. Some taxa in the study were facultative shredders. They could feed as gathering collectors, scrapers and predators as well.

The composition of functional feeding groups can be highly influenced by catchment vegetation. According to some studies, shredders are more abundant in streams, surrounded by forests because forests provide more allochthonous material (Harding and Winterbourn, 1995). Unshaded streams with non-forested catchments tend to have more

species that feed on algae and FPOM i.e., gathering collectors and scrapers (Dudgeon, 1989; Thompson and Townsend, 2004).

Differences in shredder assemblages can be expected between deciduous and coniferous forest streams. Pine needles decompose slowly and provide a low-quality food for stream invertebrates (Friberg and Jacobsen, 1994; Collen et al., 2004). So, according to some studies, shredder communities should be more abundant in deciduous forest streams than in streams running through a conifer forest (Willacker et al., 2009). The other studies demonstrated that conifer forests and hardwoods support equally abundant shredder communities in streams. Differences were only found in relative proportions of some trichopteran and plecopteran shredder species (Whiles and Wallace, 1997). Sometimes shredders can be more abundant in coniferous forest, than in deciduous forest streams (Murphy and Giller, 2000).

Relative densities of shredders might increase in streams within forested catchments compared to non-forested catchments due to higher allochthonous inputs in former ones. The relative density of scrapers and gathering collectors should have increased in the streams running through the treeless land due to higher primary production. The results of this study did not support these hypotheses, since the proportions of all five functional feeding groups in spring-fed and direct run-off streams did not show any significant difference among catchment type. Gathering collectors and gathering collectors scrapers were the dominant groups in all streams.

Shredders were found in a very small proportion in the streams (average 1.2–4.6% per direct run-off stream and around 0.3–5.1% per spring-fed stream, when the analysis was based on invertebrate densities). Shredder communities in Icelandic streams are generally sparse (Petersen et al., 1995; Gíslason et al., 1999), similar to some other regions of the world. For example, in Brazil, very low abundances of shredding chironomids were found in forested and pasture reaches of two rivers (less than 1% of total midge abundance), even densities of fallen leaves were quite high at forest reaches of both rivers (Sonoda et al., 2009). Lack of shredders was observed in the streams, surrounded by savannah grasslands and rainforests in New Guinea (about 0.4% of total macroinvertebrate populations) (Dudgeon, 1989).

One of the possibilities of low abundances of shredders in Iceland is its geographical location. Iceland is an isolated island in the North Atlantic, and it has low numbers of species and families of potential shredders. The other possibility of low shredder abundances could be the scarce vegetation cover in catchments. Forests in Iceland only cover about 1.5% of the country (Traustason and Snorrason, 2008). The forests surrounding the direct run-off streams were not dense enough, not continuous and the trees were not very tall. Forests covered only a small fraction of each catchment.

Forests in the southern research area covered more than half of each catchment (except SB4), classified as birch forested. However, the catchments were not large and surrounding forests were sparse. Such forests could not provide much debris and support more abundant shredder communities than the streams running through the barren catchments. So, there is a possibility that shredder communities in Iceland have no chance to be more abundant due to a lack of allochthonous matter. In spring-fed streams though, there were more of shredding Trichoptera and Tipulidae species found, compared to direct run-off streams. These species are just facultative shredders and can also feed as gathering

collectors, scrapers and predators. So, their presence could be influenced by higher primary production as well.

One more possible effect influencing scarcity of shredders is low retention of organic matter. However, there is a limited knowledge about retentiveness in streams in Iceland. Substrate, gradient, stream geomorphology and hydraulic regime are all important factors influencing retention in streams (Allan, 1995). Icelandic streams are usually rapid, originating in the mountains and generally have a higher gradient than streams in other Nordic countries (Petersen et al., 1995). The differences of altitude in the origin and sampling station of each direct run-off stream were relatively high, indicating high gradients. Such streams are distinctive for low retention levels of debris and conditions like that are unsuitable for the establishment of some caddis fly taxa (Flory and Milner, 2000).

Small differences related to catchment vegetation could still be seen in shredder communities in direct run-off streams. The highest density of shredding caddis larvae *P. cingulatus* was found in stream AB3. Higher numbers of shredders there, compared to the other streams, could be related to a better-vegetated catchment and high autumn litterfall. The difference of origin and sampling station altitudes of this stream was one of the lowest compared to the other streams, indicating that the gradient in stream AB3 should also be low. The annual fluctuations in velocity were one of the smoothest and the substrate was quite heterogeneous. Such factors could increase detritus retention and therefore can be beneficial for the establishment of *P. cingulatus*.

The other difference, related to catchment composition is the obligate shredder the stonefly species *C. vidua*. It was not present in the streams draining the treeless land, while it was found in small numbers in streams in forested catchments. This species was the most abundant in stream AB3, which was running through the best vegetated catchment. This is in accordance with the results of Harding and Winterbourn (1995) and Thompson and Townsend (2004), who found that the streams in forested catchments can be richer in stonefly taxa than the streams in non-forested catchments.

Most invertebrates in direct run-off and spring-fed streams were gathering collectors and gathering collectors scrapers. This indicates that the main food base in the streams is FPOM and algae. Large pieces of organic matter (CPOM) are not a good food source for those functional feeding groups. Since shredder communities were low, high densities of gathering collectors suggest the effect of other factors of conversion of CPOM into FPOM. One of the possible factors is physical abrasion and fragmentation of debris in the rapid lotic environment. The other source of FPOM could be DOM. Considerable quantities of DOM originating from terrestrial decomposition processes can enter the stream or leach from the debris that falls into a stream. There, DOM can be converted into larger particles in the stream by flocculation and microbial assimilation (Cummins, 1974; Giller and Malmqvist, 1998).

High densities of filtering collectors such as the blackfly species *S. vernum* in AG2 and AG3, and much higher in AB3 indicate a sufficient FPOM supply. The autumn litterfall in these three streams was higher than the other direct run-off streams, so most likely FPOM levels there were the highest comparing to other streams. By feeding on FPOM the simuliids produce masses of faecal pellets that are larger than the captured organic matter. The faecal pellets might also have a greater significance in FPOM base in streams (Cummins, 1974; Cummins et al., 1989; Giller and Malmqvist, 1998; Wotton et al., 1998;

Wotton and Malmqvist, 2001). A higher density of *S. vernum* could also be related to more shading in AG2, AG3 and AB3 compared to other streams. Timm (1994, in Flory and Milner (2000)) found that *S. vernum* adults only laid eggs in shaded forest reaches and avoided open areas.

The algal biomass was relatively low in the direct run-off streams; still it played an important role as a food source for gathering collectors and scraping invertebrates in AB3, AG2 and AG3 in the summer. In spring-fed streams, algal biomass was quite high, especially in the warmer streams. It could benefit the higher densities of individuals in warmer streams than in colder ones. Algae can either be eaten directly by scrapers or enter the FPOM pool (Cummins, 1974). The importance of algae on stream invertebrates has been shown in several studies. In New Zealand streams, a significant correlation was found between algal biomass and invertebrates that can feed as gathering collectors and scrapers (Friberg et al., 1997). Chironomid scraper communities were positively correlated with algal biomass in streams in Britain (Winterbourn et al., 1992). Reduced growth of algae significantly reduced densities of gathering collector mayfly species, which use algae as an important food source in small stream in New York (Fuller et al., 1986). Algae can even be eaten by shredders (Friberg and Jacobsen, 1994; Franken et al., 2005).

### **4.3 Effect of seasonality on stream invertebrate communities**

The densities of Chironomidae species are known to have distinct seasonal trends in direct run-off rivers in Iceland. Some species are more abundant during summer, others during winter (Stefánsson, 2005). In direct run-off streams in the eastern research area, very clear seasonal variations were found. Total invertebrate densities and number of taxa in most of the streams were highest in October 2008, lower in July 2008 and very small in May 2008 and 2009.

Relative densities of the dominant chironomid species in this study were similar to the findings of Stefánsson (2005), in a direct run-off river in the south-western part of Iceland. In the present, study the relative density of *E. claripennis* was lowest in the beginning of July 2008 and highest in November 2007 and February 2008. In the study by Stefánsson (2005), the proportion of this same species was lowest by the end of June and highest in the middle of March. The relative density of *E. minor* in the present study was highest in November 2007 and October 2008. Stefánsson (2005) also found the relative density of the same species to be highest in October. The relative density of *Thienemanniella* spp. in this study increased in July 2008 and decreased in winter. In the study by Stefánsson (2005), the proportion of this species was highest in the spring and summer, lowest in the winter.

Such cycles of invertebrates in the direct run-off streams were greatly affected by seasonal temperature fluctuations. Temperature is an important variable controlling egg development and larval growth. In summer, maximum stream water temperature was not higher than 14.8 °C. The temperature in October 2008, when most of the species were most abundant, was 0.6–4.2 °C. Such summer and autumn temperatures were suitable for development of chironomids. The optimum growth temperature for some chironomid larvae was observed to be 1.7–18.0 °C (Tokeshi, 1995). Egg development was positively

associated with temperature ranging between 4.5 and 30.0 °C. Many chironomid species do not grow at all under low winter temperatures, but some species keep growing at slower rates (Tokeshi, 1995). Chironomid and simuliid species in high altitude and latitude regions are adapted to live under very harsh conditions. *P. branickii* and some *Diamesa* and *Chaetocladius* species were observed walking and copulating at subzero (-2—1 °C) temperature on snow. Some other chironomid taxa grew slowly during winter beneath the snow and ice packs and emerged successfully through the cracks of melting ice (Lencioni, 2004).

Another factor that could affect seasonal variations in abundances of insect larvae in the streams is photoperiod. This variable is closely related with temperature. In temperate regions photoperiod is a useful cue about seasonal change (Armitage, 1995; Tokeshi, 1995; Giller and Malmqvist, 1998). Longer daylight induces larval development in spring and then decreases in autumn. The chironomid species *E. claripennis* begins larval development in the spring when day length reaches 18:29 hours and ceases in late September, when the day length is 12:06 hours and the average temperature 7.43 °C. *E. minor* and *Thienemanniella* spp. started to develop when the day length was 11:34 (Stefánsson, 2005).

A higher availability of food in the summer could also have a significant effect on stream invertebrate communities. In July 2008, invertebrate densities in direct run-off streams were higher than in February 2008 and 2009, and in May 2008 and 2009, but not as high as in November 2007 and October 2008. A better availability of food, greater supply of debris, higher decomposition rates and increased algal biomass could benefit stream invertebrates in the summer. Opposite direct run-off streams, invertebrate densities in spring-fed streams grew higher in July 2008 compared to November 2007. An especially great increase of densities in the summer was observed in warmer spring-fed streams than in colder ones. Such seasonal shift could be related with high primary production levels.

## **4.4 Association of stream invertebrates with environmental variables**

### **4.4.1 Direct run-off streams**

In winter, the presence of forest influenced invertebrate communities in direct run-off streams. The proportions of some taxa were different in the streams running through treeless land than in birch forest streams. However, altitude also appeared to be important in explaining such differences. Streams with treeless catchments were located at higher altitudes than forested. Altitude was related with the other two variables, water temperature and current velocity.

Aside from streams with treeless catchments, two forested streams were located at higher altitudes than other streams draining forested catchments. These five streams had greater seasonal current velocity fluctuations. Some dominating taxa of chironomids (*E. minor*, *E. claripennis* and *D. latitarsis* group) were strongly negatively associated with the current velocity. The results are in agreement with direct run-off streams in the Westfjords

(Stefánsson et al., 2006), where current velocity was an important indicator of invertebrate community composition in direct run-off streams.

Streams, with sampling stations at higher altitudes exhibited higher seasonal temperature fluctuations. Water temperature played an important role in explaining seasonal abundances of invertebrates as well. One notable stream, with lowest seasonal temperature and velocity fluctuations, was AB3, in which the majority of taxa were the most abundant throughout the year. In all direct run-off streams, the densities of such species as *Micropsectra* spp., *R. (R.) effusus* and *D. bohemani/zernyi* were positively associated with warmer water temperatures. Positive associations of *D. bohemani/zernyi* with temperature contradict other studies. *Diamesa* species are usually considered to be sensitive to a temperature increase (Flory and Milner, 2000; Lencioni, 2004).

Algal biomass and the riparian biomass appeared to be important explanatory variables, i.e., explaining higher invertebrate densities in the streams. High total riparian biomass values led to greater densities of individuals in streams AG2 and AG3 during the summer. Proportions of forests were also high in the catchments of the streams AG2 and AG3. The autumn litterfall into those two streams was much greater compared to the other streams. Therefore, litterfall over the year could cause more debris in the streams and more supply of FPOM, which in turn caused higher densities of stream invertebrates. High total riparian biomass values could explain greater invertebrate densities in AB3 as well. The highest proportion of forest cover and autumn litterfall values were some of the highest of all the streams. Greater levels of some nutrients in this stream could also reflect a higher supply of organic matter from the terrestrial areas.

Chironomids were the most abundant invertebrates in the streams. Litter exclusion experiments showed, that organic matter can serve as food and habitat for some chironomid taxa. Total abundance and biomass of Tanytarsini significantly declined after three years litter exclusion in Appalachian headwater stream, but biomass and abundance of Orthocladiinae did not change after exclusion (Entrekin et al., 2007). The growth of non-tanypodin chironomids, gathering collectors, declined in response to litter exclusion in temperate headwater streams (Johnson et al., 2003).

In summer, greater algal biomass in streams AB3, AG2 and AG3 benefited higher densities of invertebrates. Algae are an important food source for stream invertebrates, mainly scrapers and gathering collectors (Fuller et al., 1986; Winterbourn et al., 1992; Friberg et al., 1997). Silica is considered one of the most critical products for autotrophic production. Cell walls of diatoms are composed of siliceous material, and diatoms are the major periphyton components in cool, shaded streams (Allan, 1995). The supply of silica can influence invertebrate communities indirectly, by affecting the abundance of diatoms, which are the food source for stream invertebrates. This element was an important variable explaining seasonal abundances of invertebrates in direct run-off streams. Lower concentrations of silica in July 2008 could be determined by higher uptake by diatoms, resulting in higher biomass of algae in the streams.

Fish were present in three direct run-off streams (AS2, AS3 and AG1). These three streams were the most accessible to fish because their mouths were low gradient with no obstacles present. The mouths of the other streams were steep. Invertebrate densities in these three streams could be reduced by fish predation. This could explain the very low densities of invertebrates in stream AG1. It is also noteworthy that the sampling station of this stream



was located at the lowest altitude compared to other streams. Fish could therefore enter this stream.

Stream bottom substrate heterogeneity influences invertebrate abundance and diversity (Giller and Malmqvist, 1998). Different substrates harbour different assemblages of animals. The highest diversity of individuals was established for pebble and gravel in river in Lithuania, and the highest number of taxa was found on stone substratum (Ruginis, 2007). In French streams, invertebrate abundances increased with substrate size up to cobble and decreased when the substrate became boulder or bedrock (Beisel et al., 1998). The substrate in stream AB3 was quite diverse and was one of the variables, explaining higher invertebrate densities. Oligochaetes, ostracods, blackflies and caddisflies were found in higher densities in this stream. The interruptions of sand and some mud in the margins of the stream could provide good habitat for oligochaetes and ostracods. Coarse substrate (cobbles and boulders) could serve as a habitat for caddis larvae and simuliids.

#### 4.4.2 Spring-fed streams

Substrate was important but not the main factor explaining invertebrate abundances in spring-fed streams. The substrate of stream SB4 consisted only of sand and mud contrary to the substrate of other streams, which had gravel and stones. Sand and mud could improve living conditions for ostracods, which were found in very high densities and were the dominating taxa in this stream in November 2007.

Temperature was the main factor that explained the differences in invertebrate communities in spring-fed streams. Such cold-adapted species as *D. aberrata*, *D. bertrami* and *D. latitarsis* group were much more abundant in colder streams, compared to the warmer ones. In winter and summer, the temperatures in colder streams were between 2.57 and 3.47 °C.

*Diamesa* species usually live in cold streams, located in high altitudes and latitudes (Lencioni, 2004). They are widespread in glacial-fed rivers in Iceland with common temperatures between 2 and 10 °C (Ólafsson et al., 2000; Gíslason et al., 2001). A strong negative correlation was found between the density of *Diamesa* species and water temperature in a glacial-fed stream in Alaska (Flory and Milner, 2000). Increased water temperature reduced the abundance of these animals. *Diamesa* species could thrive in stream water temperatures around 2 °C. Abundance declined in summer when water temperature increased above 4 °C (Flory and Milner, 2000).

My findings agree with the results of Flory and Milner (2000). The temperatures in warmer spring-fed streams were higher than in colder ones, 3.34 and 7.31 °C. *D. aberrata*, *D. bertrami* and *D. latitarsis* group were non-existent in these streams, or only a few individuals were found. Contrary to these species, *D. bohemani/zernyi* was more abundant in warmer streams and found in very small densities in colder ones. In winter, this species was also positively associated with temperature in direct run-off streams in eastern Iceland.

Higher water temperatures facilitated the establishment of other chironomid species. *R. (R.) effusus* and *Micropsectra* spp. were found only in warmer spring-fed streams. In direct run-off streams in winter, they were positively associated with temperature as well. *Thienemanniella* species only lived in warmer spring-fed streams. *Clinocera*, Muscidae

species, Plecoptera and Oligochaeta were more abundant in warmer spring-fed streams than in colder ones. The study of Flory and Milner (2000) also confirmed a positive effect of temperature on the establishment of some taxa. They concluded that a temperature increase above 2 °C facilitated the establishment of many chironomid taxa, amongst which were some *Eukiefferiella* and *Chaetocladius* species and *P. branickii*. Some non-chironomid taxa, such as Ephemeroptera, Plecoptera, *Clinocera*, Muscidae and Oligochaeta were also not found until temperatures increased above 2 °C.

In July 2008, total densities of individuals increased greatly in warmer spring-fed streams compared to colder ones. Higher temperatures facilitated higher levels of primary production and higher densities of invertebrates. Higher temperatures could influence higher decomposition rates of some allochthonous matter and increase FPOM as well. The differences of altitudes at the origin and sampling station were smaller in warmer streams than in colder ones. That indicates the lower gradient, which could cause increased retention of organic matter. High abundances of algae could also provide a significant amount of FPOM. In July 2008, warmer streams had high levels of primary production and water was full of floating algae.

The proportion of moss cover of the substrates of spring-fed streams led to the presence and increased densities of some invertebrate taxa. Such rare species, as *S. vernum*, *P. cingulatus* and *Limnophyes* sp. were closely related with the cover of moss. The presence of bryophytes has been shown to benefit stream invertebrates in a vast amount of studies. Invertebrate density and richness increased with increasing moss weight in conifer forest streams in Ireland (Clenaghan et al., 1998). Greater invertebrate biomass was found in a spring-fed stream than a mountain stream in arctic Alaska, because spring-fed stream had 1000 times greater bryophyte biomass (Parker and Huryn, 2006).

The present results disagree with the findings of Lee and Hershey (2000) in a fourth order arctic river in Alaska. In their study, moss increased densities of Chironomidae but had no effect on Simuliidae densities. Shredding stoneflies have been shown to be the dominant moss dwellers in a small boreal headwater stream in Finland (Vuori and Joensuu, 1996). Large predatory chironomids, mayflies, and some caddisflies were also found to be more abundant in bryophytes, but blackfly larvae abundances seem not be enhanced by the presence of bryophytes (Vuori and Joensuu, 1996; Stream Bryophyte Group, 1999).

The presence of bryophytes benefits stream invertebrates in a few ways. Bryophytes can have important impacts on nutrient uptake and retention by providing a larger surface area for the development of epiphytic food resources and by trapping organic matter. Mosses are not a preferable food source when they are alive. They replenish the supplies of food after they die by entering the CPOM and FPOM pools. Bryophytes are a good refuge from high current velocity and predators (Cummins, 1974; Stream Bryophyte Group, 1999). Mosses tend to stabilize substrate; therefore, moss-dominated microhabitats are more stable than moss-free habitats. Habitat stability is important to the success of many insect taxa (Vuori and Joensuu, 1996; Lee and Hershey, 2000).

Densities of invertebrates in spring-fed streams could also be affected by fish predation. Fish were present in three of the warmer streams (SS2, SB1 and SB2). The densities of invertebrates (mostly chironomids) in these streams in the summer were still 5–37 times higher than in colder ones. Warmer temperatures and high amounts of potential prey could be a cause of the presence of fish in these streams. Invertebrate communities in one of the

warmer streams, SB4, were not influenced by fish predation. The bottom of this stream was very boggy, made of mud and sand, no stones were present; therefore there was not suitable habitat for fish juveniles there. In November 2007, just a few individuals of chironomids were found there. The dominant taxon was Ostracoda, which lives in the sand and are not visible to fish. The lack of food helps explain the absence of fish in this stream. It is notable that the sampling stations of streams SS2, SB1 and SB2 were located at lower altitudes (88–92 metres) than the sampling stations of all other streams (114–139 metres). This could also help the fish reach the streams as well as if they were close to the main river.

## **4.5 Comparisons of invertebrate communities between different geological areas**

### **4.5.1 Differences in invertebrate communities between direct run-off and spring-fed streams**

Total densities and proportional abundances of invertebrates in the streams differed more between geographical locations than between catchment types. My results agree with the results of Friberg and others (1997) from streams in New Zealand. They found that differences in stream invertebrate communities were smaller between two forest types, than the differences between two geographical locations with different bedrock characteristics. In my study, temperature was the main variable that caused differences in invertebrate communities between spring-fed streams. Presence of forest did not play any significant role in determining stream invertebrate assemblages, but the differences between colder and warmer streams were great.

In the eastern research area, the presence of forest had an effect on stream invertebrate communities. In the summer, direct run-off streams with better-forested catchments seemed to support higher invertebrate densities. In the winter, streams running through forested and treeless catchments supported equally abundant invertebrate communities, but some differences between proportions of taxa could be seen. Some species were slightly more abundant in the streams within forested catchments compared to streams within treeless catchments. An exception was always stream AB3, which had highest proportions of birch forest and fertile grassland in the catchment. The densities of invertebrates there were always higher compared to other streams.

A difference between invertebrate communities in direct run-off and spring-fed streams was total invertebrate density. In November 2007, the densities in spring-fed streams were around 2–3 times higher than in direct run-off streams. In July 2008 these differences grew up even more. Spring-fed streams had more than 30 times higher density than direct run-off streams. My results are consistent with the findings of Gíslason et al. (1999) who detected that densities of individuals were higher in spring-fed rivers and much lower in run-off systems. In July 2008, the number of taxa in direct run-off and spring-fed streams was almost the same. However, Shannon diversity and evenness were higher in direct run-off streams, indicating that invertebrate communities there were more homogeneous and could be considered more diverse.

#### **4.5.2 Factors, affecting the differences between direct run-off and spring-fed streams**

Nutrient levels were the main environmental factors that explained the differences in invertebrate communities between the eastern and southern research areas. Redundancy analysis highlighted sodium, chlorine and phosphate as the main variables. Some other chemical variables (nitrate, total nitrogen, total phosphorus, sulphur and potassium) did not come up in redundancy analysis as the main factors, but their levels were also much higher in the spring-fed streams.

Higher levels of nutrients could influence higher primary production rates in spring-fed streams. Algal biomass there was almost six times greater than in direct run-off streams. Such high differences of primary production may be the main factor determining the differences in invertebrate densities between spring-fed and direct run-off streams. Associations between levels of nutrients, algal growth and invertebrate colonization have been observed with nutrient enriched experimental substrates in streams. In a New Zealand mountain stream, increased levels of nitrate and phosphorus of experimental substrate benefited diatom growth and higher colonization by chironomid larvae (Winterbourn, 1990). In British streams, algal production response to nitrogen and phosphorus enrichment was site specific, but the abundances of chironomid larvae and some stoneflies were positively associated with algal biomass (Winterbourn et al., 1992).

The data regarding allochthonous inputs in spring-fed streams are still in process within the ForStreams project. Different inputs of terrestrial organic matter could also cause the differences between spring-fed and direct run-off streams. One more difference between direct run-off and spring-fed streams was the size of the dominant substrate, but it was not an essential factor determining the differences in invertebrate communities.

Comparing invertebrate communities in the eastern and southern research areas revealed that geological characteristics of the catchment played a great role in determining the differences between the two areas. Bedrock type may influence various habitat factors in the streams, such as availability of nutrients, water quality, temperature and primary productivity. Therefore in this study, all these factors are suggested to have a greater effect on invertebrate communities in Icelandic streams than surrounding forest.

# Conclusions

Treeless and forested catchments in Iceland can support equally abundant and diverse invertebrate communities in direct run-off streams, but the taxa composition may be slightly different. Direct run-off streams running through the forested catchments where the proportions of birch woodland and riparian biomass were greater seemed to support higher invertebrate densities than the streams running through the scarcely forested catchments. The effect of catchment vegetation on stream invertebrate densities is better explained by the composition of the whole catchment rather than when catchments were confined to 400 metres from each sampling station.

Differences in direct run-off stream invertebrate communities were affected by altitude, which was associated with the two variables: temperature and velocity. The streams located at higher altitudes exhibited higher annual temperature and velocity fluctuations, which were also important in explaining invertebrate abundances in streams. Algal biomass determined higher densities of stream invertebrates as well.

The presence of forest in the catchment had no effect on invertebrate communities in spring-fed streams. There, temperature was the main variable in determining the differences in species composition and densities. Different species were found in warmer spring-fed streams than in the colder ones. Invertebrate communities were denser in warmer streams.

Greater differences in invertebrate communities were observed between the two different geological areas that were compared than between catchment types within each area. The younger bedrock supplies a greater availability of nutrients, which supports higher primary production and determines different water quality. Temperature regimes are different in spring-fed streams, compared to direct run-off streams. These factors had a greater effect on invertebrate communities in Icelandic streams than the surrounding forest.



# References

- Abelho, M., Graca, M.A.S., 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in central Portugal. *Hydrobiologia* 324, 195-204.
- Ægisdóttir, H.H., Þórhallsdóttir, E., 2004. Theories on migration and history of the North-Atlantic flora: a review. *Jökull* 54, 1-16.
- Allan, J.D., 1995, *Stream Ecology: structure and function of running waters*. Chapman and Hall, London.
- Anderson, L.E., 1954. Hoyer's Solution as a rapid permanent mounting medium for bryophytes. *The Bryologist* 57, 242-244.
- Anderson, N.H., Sedell, J.R., Roberts, L.M., Triska, F.J., 1978. Role of Aquatic Invertebrates in Processing of Wood Debris in Coniferous Forest Streams. *American Midland Naturalist* 100, 64-82.
- Armitage, P.D., 1995, Behaviour and ecology of adults. In: Armitage, P.D., Cranston, P.S., Pinder, L.C.V. (Eds.), *The Chironomidae. Biology and ecology of non-biting midges*. Chapman & Hall, London, pp. 194-224.
- Arnalds, A., 1987. Ecosystem disturbance in Iceland. *Arctic and Alpine Research* 19, 508-513.
- Artmann, U., Waringer, J.A., Schagerl, M., 2003. Seasonal dynamics of algal biomass and allochthonous input of coarse particulate organic matter in a low-order sandstone stream (Weidlingbach, Lower Austria). *Limnologia* 33, 77-91.
- Beisel, J.N., Usseglio-Polatera, P., Thomas, S., Moreteau, J.C., 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 389, 73-88.
- Berg, M.B., 1995, Larval food and feeding behaviour. In: Armitage, P., Cranston, P.S., Pinder, L.C.V. (Eds.), *The Chironomidae. Biology and ecology of non-biting midges*. Chapman & Hall, London, pp. 136-168.
- Broadmeadow, S., Nisbet, T.R., 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences* 8, 286-305.
- Brönmark, C., Hansson, L., 2005, *The biology of lakes and ponds*. Oxford University Press, New York.

- Clenaghan, C., Giller, P.S., O'Halloran, J., Hernan, R., 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: relationships to physico-chemical and biotic factors. *Freshwater Biology* 40, 175-193.
- Collen, P., Keay, E.J., Morrison, B.R.S., 2004. Processing of pine (*Pinus sylvestris*) and birch (*Betula pubescens*) leaf material in a small river system in the northern Cairngorms, Scotland. *Hydrology and Earth System Sciences* 8, 567-577.
- Coope, G.R., 1986. The invasion and colonization of the North Atlantic islands: a paleoecological solution to a biogeographic problem. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 314, 619-635.
- Cox, T.J., Rutherford, J.C., 2000. Thermal tolerances of two stream invertebrates exposed to diurnally varying temperature. *New Zealand Journal of Marine and Freshwater Research* 34, 203-208.
- Cranston, P.S., 1982, A key to the larvae of British Orthocladiinae (Chironomidae). *Freshwater Biological Association Scientific Publication No. 45*.
- Cummins, K.W., 1974. Structure and function of stream ecosystems. *BioScience*, 631-641.
- Cummins, K.W., Klug, M.J., 1979. Feeding Ecology of Stream Invertebrates. *Annual Review of Ecology and Systematics* 10, 147-172.
- Cummins, K.W., Merritt, R.W., Andrade, P.C.N., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment* 40, 69-89.
- Cummins, K.W., Wilzback, M.A., Gates, D.M., Perry, J.B., Taliaferro, W.B., 1989. Shredders and riparian vegetation. *BioScience*, 24-30.
- Dangles, O., 2002. Aggregation of shredder invertebrates associated with benthic detrital pools in seven headwater forested streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 28, 1-4.
- Dudgeon, D., 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. *Hydrobiologia* 179, 183-194.
- Eaton, A.D., Clesceri, L.S., Greenberg, A.E., 1995, *Standard Methods for the Examination of Water and Wastewater*. American Public Health Association, Washington.
- Einarsson, T., 1994, *Geology of Iceland: rocks and landscape*. Mál og menning, Reykjavik.
- Entrekin, S.A., Wallace, J.B., Eggert, S.L., 2007. The response of Chironomidae (Diptera) to a long-term exclusion of terrestrial organic matter. *Hydrobiologia* 575, 401-413.
- Feller, M.C., 2005. Forest harvesting and streamwater inorganic chemistry in western North America: a review. *Journal of the American Water Resources Association* 41, 785-811.



- Flory, A., Milner, A.M., 1999. Influence of Riparian Vegetation on Invertebrate Assemblages in a Recently Formed Stream in Glacier Bay National Park, Alaska. *Journal of the North American Benthological Society* 18, 261-273.
- Flory, E.A., Milner, A.M., 2000. Macroinvertebrate community succession in Wolf Point Creek, Glacier Bay National Park, Alaska. *Freshwater Biology* 44, 465-480.
- Franken, R.J.M., Waluto, B., Peeters, E., Gardeniers, J.J.P., Beijer, J.A.J., Scheffer, M., 2005. Growth of shredders on leaf litter biofilms: the effect of light intensity. *Freshwater Biology* 50, 459-466.
- Friberg, N., 1997. Benthic invertebrate communities in six Danish forest streams: Impact of forest type on structure and function. *Ecography* 20, 19-28.
- Friberg, N., Jacobsen, D., 1994. Feeding plasticity of two detritivore-shredders. *Freshwater Biology* 32, 133-142.
- Friberg, N., Winterbourn, M.J., Shearer, K.A., Larsen, S.E., 1997. Benthic communities of forest streams in the South Island, New Zealand: Effects of forest type and location. *Archiv Für Hydrobiologie* 138, 289-306.
- Fuller, R.L., Roelofs, J.L., Fry, T.J., 1986. The importance of algae to stream invertebrates. *Journal of the North American Benthological Society* 5, 290-296.
- Giller, P.S., Malmqvist, B., 1998, *The Biology of Streams and Rivers*. Oxford University Press, New York.
- Gíslason, G.M., 1979. Identification of Icelandic caddis larvae, with descriptions of *Limnephilus fenestratus* (Zett.) and *L. picturatus* McL. (Trichoptera: Limnephilidae, Phryganeidae). *Entomologica Scandinavica* 10, 161-176.
- Gíslason, G.M., 2005. Origin of freshwater fauna of the North-Atlantic islands: present distribution in relation to climate and possible migration routes. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 29, 198-203.
- Gíslason, G.M., Adalsteinsson, H., Hansen, I., Ólafsson, J.S., Svavarsdóttir, K., 2001. Longitudinal changes in macroinvertebrate assemblages along a glacial river system in central Iceland. *Freshwater Biology* 46, 1737-1751.
- Gíslason, G.M., Adalsteinsson, H., Ólafsson, J.S., 1998. Animal communities in Icelandic rivers in relation to catchment characteristics and water chemistry. Preliminary results. *Nordic Hydrology*, 129-148.
- Gíslason, G.M., Ólafsson, J.S., Adalsteinsson, H., 1999, Macroinvertebrate communities in rivers in Iceland. In: Friberg, N., Carl, J.D. (Eds.), *Biodiversity in Benthic Ecology*. Proceedings from Nordic Benthological Meeting in Silkeborg, Denmark, 13-14 November 1997. NERI Technical Report, No. 266., pp. 53-61.

Gíslason, G.M., Ólafsson, J.S., Adalsteinsson, H., 2000. Life in glacial and alpine rivers in central Iceland in relation to physical and chemical parameters. *Nordic Hydrology* 31, 411-422.

Gíslason, G.M., Sigfússon, A.T., 1987, Life cycle and food of *Apatania zonella* (Zett.) in a spring-fed stream in SW Iceland (Trichoptera: Limnephilidae). In: Bournaud, M., Tachet, H. (Eds.), *Proceedings of the 5th International Symposium on Trichoptera*. Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 237-242.

Gíslason, S.R., 2008. Weathering in Iceland. *Jökull* 58, 387-408.

Gíslason, S.R., Arnorsson, S., Armannsson, H., 1996. Chemical weathering of basalt in Southwest Iceland; effects of runoff, age of rocks and vegetative/glacial cover. *American Journal of Science* 296, 837-907.

Graça, M.A.S., Canhoto, C., 2006. Leaf litter processing in low order streams. *Limnetica* 25, 1-10.

Gregory, S.V., Swanson, F.J., McKee, W.A., Cummins, K.W., 1991. An Ecosystem Perspective of Riparian Zones: Focus on links between land and water. *Bioscience* 41, 540-549.

Guðjónsson, G., Gíslason, E., 1998, *Vegetation Map of Iceland*. 1:500,000. General overview. Icelandic Institute of Natural History, Reykjavík.

Harding, J.S., Winterbourn, M.J., 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. *New Zealand Journal of Marine and Freshwater Research* 29, 479-492.

Harriman, R., Morrison, B., 1982. Ecology of streams draining forested and non-forested catchments in an area of central Scotland subject to acid precipitation. *Hydrobiologia* 88, 251-263.

Hrafnisdóttir, T., 2005. *Diptera 2 (Chironomidae)*. *The Zoology of Iceland III*, 169.

Hynes, H.B.N., 1975. The stream and its valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 1-15.

Jóhannesson, H., Sæmundsson, K., 1998, *Geological map of Iceland*, 1:500,000. Tectonics. In: *Hist. I.I.N.* (Ed.), Reykjavík.

Johnson, B.R., Cross, W.F., Wallace, J.B., 2003. Long-term resource limitation reduces insect detritivore growth in a headwater stream. *Journal of the North American Benthological Society* 22, 565-574.

Kristinsson, H., 1995. Post-settlement history of Icelandic forests. *Icelandic Agricultural Sciences* 31-35.

- Kristjánsson, B.K., Svavarsson, J., 2004. Crymostygidae, a new family of subterranean freshwater gammaridean amphipods (Crustacea) recorded from subarctic Europe. *Journal of Natural History* 38, 1881-1894.
- Kristjánsson, B.K., Svavarsson, J., 2007. Natural History Miscellany. Subglacial Refugia in Iceland Enabled Groundwater Amphipods to Survive Glaciations. *The American Naturalist* 170, 292-296.
- Ladakis, M., Belias, C., Dassenakis, M., Scoullou, M., Salta, F., 2003, An effective oxidation method for the simultaneous determination of nitrogen and phosphorus in marine sediments. 3rd International Conference IMA, Thessaloniki, Greece, pp. 381-384.
- Lee, J.O., Hershey, A.E., 2000. Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. *Journal of the North American Benthological Society* 19, 697-708.
- Lencioni, V., 2004. Survival strategies of freshwater insects in cold environments. *Journal of Limnology* 63, 45-55.
- Lepš, J., Šmilauer, P., 2003, Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.
- Lorenzen, C.J., 1967. Determination of chlorophyll in pheopigments: spectrophotometric equations. *Limnol. Oceanogr.* 12, 343-346.
- Lorion, C.M., Kennedy, B.P., 2009. Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. *Freshwater Biology* 54, 165-180.
- Magurran, A.E., 2004, Measuring biological diversity. Blackwell Publishing, Oxford.
- Malmqvist, B., Wotton, R.S., Zhang, Y.X., 2001. Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos* 92, 35-43.
- Meleason, M.A., Quinn, J.M., 2004. Influence of riparian buffer width on air temperature at Whangapoua Forest, Coromandel Peninsula, New Zealand. *Forest Ecology and Management* 191, 365-371.
- Merritt, R.W., Cummins, K.W., 1996, An Introduction to the Aquatic Insects of North America. Kendal/Hunt Publishing Company, Dubuque Iowa.
- Merritt, R.W., Cummins, K.W., 2006, Trophic relationships of macroinvertebrates. In: Hauer, F.R., Lamberti, G.A. (Eds.), *Methods in Stream Ecology*. Academic press, Oxford, pp. 585-609.
- Miserendino, M.L., Masi, C.I., 2010. The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. *Ecological Indicators* 10, 311-319.
- Moore, R.D., Spittlehouse, D.L., Story, A., 2005. Riparian microclimate and stream temperature response to forest harvesting: A review. *Journal of the American Water Resources Association* 41, 813-834.

Murphy, J.F., Giller, P.S., 2000. Seasonal dynamics of macroinvertebrate assemblages in the benthos and associated with detritus packs in two low-order streams with different riparian vegetation. *Freshwater Biology* 43, 617-631.

O'Driscoll, J.F., Harrison, S.S.C., Giller, P.S., 2006. Do trees make a difference? An evaluation of the impact of riparian vegetation on the ecology of nutrient poor headwater streams. *Polish Journal of Ecology* 4, 695–700.

Ólafsson, J.S., Adalsteinsson, H., Gíslason, G.M., Hansen, I., Hrafnisdóttir, 2002. Spatial heterogeneity in lotic chironomids and simuliids in relation to catchment characteristics in Iceland. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 28, 157-163.

Ólafsson, J.S., Gíslason, G.M., Adalsteinsson, H., 2000. Chironomids of glacial and non-glacial rivers in Iceland: a comparative study. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 27, 720-726.

Parker, S.M., Huryn, A.D., 2006. Food web structure and function in two arctic streams with contrasting disturbance regimes. *Freshwater Biology* 51, 1249-1263.

Petersen, R.C., Gíslason, G.M., Vought, L.B.M., 1995, Rivers of the Nordic countries. In: Cushing, C.E., Cummins, K.W., Minshall, G.W. (Eds.), *River and Stream Ecosystems. Ecosystems of the World*. Elsevier, Amsterdam, pp. 295-341.

Peterson, B.V., 1977. The blackflies of Iceland. *Canadian Entomologist* 109, 449-472.

Pétursson, J.G., 1999. Skógræktaröldin. Samanteknar tölur úr Ársriti Skógræktarfélags Íslands. [The first 100 years of tree planting in Iceland]. *Skógræktarritið*, 49–53.

Quinn, G.P., Keough, M.J., 2002, *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.

Richardson, J.S., 1994, Stream-forest interactions: potential effects on productivity and biodiversity of benthic communities in interior British Columbia. In: Macdonald, J.S. (Ed.), *Proceedings of the Takla Fishery/Forestry Workshop: a two year review*. Canadian Technical Report of Fisheries and Aquatic Sciences No.2007, pp. 9-14.

Richardson, J.S., 2008. Aquatic arthropods and forestry: effects of large-scale land use on aquatic systems in Nearctic temperate regions. *The Canadian Entomologist* 140, 495-509.

Richardson, J.S., Bilby, R.E., Bondar, C.A., 2005. Organic matter dynamics in small streams of the Pacific Northwest. *Journal of the American Water Resources Association* 41, 921-934.

Ruginis, T., 2007. Environmental impacts on macroinvertebrate community in the Babrungas River, Lithuania. *Ekologija* 53, 51-57.

Sadler, J.P., 1999. Biodiversity on oceanic islands: a palaeoecological assessment. *Journal of Biogeography* 26, 75-87.

Sæmundsson, K., 1979. Outline of geology of Iceland. *Jökull* 29.

Schmid, P.E., 1993, A key to the larval Chironomidae and their instars from the Austrian Danube region streams and rivers. Part 1: Diamesinae, Prodiamesinae and Orthocladiinae. Editorial Board, Vienna.

Sigurðsson, S., 1977, Birki á Íslandi (útbreiðsla og ástund). [Propagation and condition of birch woodlands in Iceland]. In: Ragnarsson, H., Guðmundsson, H., Þorsteinsson, I., Jónsson, J., Blöndal, S., Sigurðsson, S. (Eds.), Skógarmál. Printed by Edda hf., Reykjavík, pp. 146-172

Sjörs, H., 1963, Amphi-Atlantic zonation, nemoral to Arctic. In: Löve, A., Löve, D. (Eds.), North Atlantic Biota and Their History. Pergamon Press, Oxford pp. 109–125.

Sjörs, H., 1967, Nordisk Växtgeograf [In Swedish: Plant geography in the Nordic countries]. Scandinavian University Books. Svenska Bokförlaget, Stockholm.

Smock, L.A., 2006, Macroinvertebrate dispersal. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology. Academic press, Oxford, pp. 465-487.

Snorrason, A., Einarsson, S.F., 2006. Single-tree biomass and stem volume functions for eleven tree species used in Icelandic forestry. Icelandic Agricultural Sciences 19, 15-24.

Snyder, C.D., Young, J.A., Lemarié, D.P., Smith, D.R., 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences 59, 262-275.

Sonoda, K.C., Matthaei, C.D., Trivinho-Strixino, S., 2009. Contrasting land uses affect Chironomidae communities in two Brazilian rivers. Fundamental and Applied Limnology 174, 173-184.

Stefánsdóttir, H.M., 2010, Transport and decomposition of allochthonous litter in Icelandic headwater streams: Effects of forest cover. Faculty of Environmental Sciences. Agricultural University of Iceland, Reykjavík, p. 110.

Stefánsson, S.M., 2005, Mýsamfélög og lífsferlar rykmýs í dragám á Íslandi. (Community structure of midges and chironomid life cycles in Icelandic direct run-off rivers). Faculty of Life- and Environmental Sciences. University of Iceland, Reykjavík, p. 70.

Stefánsson, S.M., Ólafsson, J.S., Adalsteinsson, H., Gíslason, G.M., 2006. The structure of chironomid and simuliid communities in direct run-off rivers in Tertiary basalt bedrock in Iceland. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 29, 2015-2020.

Steindórsson, S., 1964, Gróður á Íslandi (Vegetation in Iceland). Almenna bókafélagið, Reykjavík. (In Icelandic).

Steinman, A.D., Lamberti, G.A., Leavitt, P.R., 2006, Biomass and pigments of benthic algae. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology. Academic press, Oxford, pp. 357-379.

Stream Bryophyte Group, 1999. Roles of bryophytes in stream ecosystems. *Journal of the North American Benthological Society* 18, 151-184.

Svavarsson, J., Kristjánsson, B.K., 2006. *Crangonyx islandicus* sp. nov., a subterranean freshwater amphipod (Crustacea, Amphipoda, Crangonyctidae) from springs in lava fields in Iceland. *Zootaxa* 1365, 1-17.

Swan, C.M., Palmer, M.A., 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. *Oecologia* 147, 469-478.

Sweeney, B.W., 1992. Streamside forests and the physical, chemical, and trophic characteristics of piedmont streams in Eastern North America. *Water Science and Technology* 26, 2653-2673.

Szekely, G.J., Rizzo, M.L., 2005. Hierarchical clustering via joint between-within distances: Extending Ward's minimum variance method. *Journal of Classification* 22, 151-183.

Tecator, 1983a. Determination of orthophosphate in water by flow injection analysis. Application Note 60/83.

Tecator, 1983b. Determination of the sum of nitrate and nitrite in water by flow-injection analysis. Application Note 62/83.

Tecator, 1983c. Determination of chloride in water by flow injection analyses. Application Note 63/83.

Tecator, 1983d. Determination of chloride in water by flow injection analyses. Application Note 63-01/83.

Thompson, R.M., Townsend, C.R., 2004. Land-use influences on New Zealand stream communities: effects on species composition, functional organisation, and food-web structure. *New Zealand Journal of Marine and Freshwater Research* 38, 595-608.

Thordarson, T., Hoskuldsson, A., 2002, Iceland: classic geology in Europe 3.

Timm, T., 1994. Reasons for the shift in dominance between *Simulium* (N.) *vernum* and *Simulium* (S.) *ornatum* (Diptera: Simuliidae) along the continuum of an unpolluted lowland stream. *Archiv für Hydrobiologie*, 199-210.

Tokeshi, M., 1995, Life cycles and population dynamics. In: Armitage, P.D., Cranston, P.S., Pinder, L.C.V. (Eds.), *The Chironomidae. Biology and ecology of non-biting midges*. Chapman & Hall, London, pp. 225-268.

Traustason, B., Snorrason, A., 2008. Spatial distribution of forests and woodlands in Iceland in accordance with the CORINE land cover classification. *Icelandic Agricultural Sciences* 39-47.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 130-137.

- Von Schiller, D., Marti, E., Riera, J.L., Sabater, F., 2007. Effects of nutrients and light on periphyton biomass and nitrogen uptake in Mediterranean streams with contrasting land uses. *Freshwater Biology* 52, 891-906.
- Vuori, K.M., Joensuu, I., 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: Do buffer zones protect lotic biodiversity? *Biological Conservation* 77, 87-95.
- Wallace, J.B., Eggert, S.L., 2009. Benthic Invertebrate Fauna, Small Streams. *Encyclopedia of Inland Waters* 2, 173-190.
- Whiles, M.R., Wallace, J.B., 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. *Hydrobiologia* 353, 107-119.
- Wiederholm, T. (Ed.), 1983, Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica*, Motala.
- Willacker, J.J., Sobczak, W.V., Colburn, E.A., 2009. Stream Macroinvertebrate Communities in Paired Hemlock and Deciduous Watersheds. *Northeastern Naturalist* 16, 101-112.
- Winterbourn, M.J., 1990. Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology* 23, 463-474.
- Winterbourn, M.J., Hildrew, A.G., Orton, S., 1992. Nutrients, algae and grazers in some British streams of contrasting pH. *Freshwater Biology* 28, 173-182.
- Wintermans, J.F.G.M., De Mots, A., 1965. Spectrophotometric characteristics of chlorophylls *a* and *b* and their pheophytins in ethanol. *Biochimica et Biophysica Acta* 109, 448-453.
- Wotton, R.S., Malmqvist, B., 2001. Feces in aquatic ecosystems. *Bioscience* 51, 537-544.
- Wotton, R.S., Malmqvist, B., Muotka, T., Larsson, K., 1998. Fecal pellets from a dense aggregation of suspension-feeders in a stream: An example of ecosystem engineering. *Limnology and Oceanography* 43, 719-725.
- Yoshimura, M., 2007. Comparison of stream benthic invertebrate assemblages among forest types in the temperate region of Japan. *Biodiversity and Conservation* 16, 2137-2148.
- Yoshimura, M., Maeto, K., 2006. Comparison of an aquatic invertebrate assemblage between an old-growth natural forest and planted coniferous forest basins in a Japanese temperate region: the Kuroson stream in the Shimanto River basin. *Landscape Ecol. Eng.*, 81-89.





# Appendixes

Appendix 1 The samples taken from direct run-off streams in eastern research area.

Sampling date	Stream	Measured environmental variables											
		Number of Surber samples	Number of algae samples	Velocity	Depth	Width	Substrate type	Vegetation type of stream bottom	Temperature	Conductivity	pH	Water samples	Litter traps
27-29 Nov 2007 <sup>1</sup>	AS1	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AS2	5 <sup>2</sup>	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AS3	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AB1	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AB2	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AB3	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AG1	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AG2	10	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
	AG3	5 <sup>2</sup>	-	✓	✓	-	✓	✓	✓	✓	✓	✓	-
15-16 Feb 2008 <sup>1</sup>	AS1 <sup>3</sup>	-	-	-	-	-	-	-	✓	✓	✓	✓	-
	AS2 <sup>3</sup>	-	-	-	-	-	-	-	✓	✓	✓	✓	-
	AS3 <sup>3</sup>	-	-	-	-	-	-	-	✓	✓	✓	✓	-
	AB1	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
	AB2	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
	AB3	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
	AG1	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
	AG2	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
	AG3	5	-	-	-	✓	✓	-	✓	✓	✓	✓	-
19-21 May 2008	AS1 <sup>4</sup>	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
7-9 July 2008	AS1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

Continues

Sampling date	Stream	Measured environmental variables											
		Number of Surber samples	Number of algae samples	Velocity	Depth	Width	Substrate type	Vegetation type of stream bottom	Temperature	Conductivity	pH	Water samples	Litter traps
6-8 Oct 2008	AS1 <sup>4</sup>	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	AG3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
23-24 Feb 2009 <sup>1</sup>	AS1 <sup>3</sup>	—	—	—	—	—	—	—	✓	✓	✓	—	—
	AS2 <sup>3</sup>	—	—	—	—	—	—	—	✓	✓	✓	—	—
	AS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AB2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AG1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AG2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
	AG3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	—
26-28 May 2009	AS1 <sup>4</sup>	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AS2	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AS3	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AB1	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AB2	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AB3	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AG1	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AG2	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	AG3	5	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓

<sup>1</sup>All streams were partly frozen and Surber samples were taken randomly from unfrozen gaps

<sup>2</sup>The streams were heavily frozen and only five Surber samples were available.

<sup>3</sup>The streams were heavily frozen and the sampling was not available

<sup>4</sup>Due to snowmelt or high precipitation the current velocity was very strong and the depth was too high. Invertebrate sampling was impossible in the middle of the stream, so samples were taken randomly not further than two metres from each margin of the stream where the depth and current velocity were not so high.

Appendix 2 The samples taken from spring-fed streams in southern research area.

Sampling date	Stream	Measured environmental variables											
		Number of Surber samples	Number of algae samples	Velocity	Depth	Width	Substrate type	Vegetation type of stream bottom	Temperature	Conductivity	pH	Water samples	Litter traps <sup>5</sup>
21-23 Nov 2007 <sup>1</sup>	SS1	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SS2	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SS3	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SS4	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SB1	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SB2	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SB3	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
	SB4	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	—
19-21 Feb 2008	SS1	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SS2	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SS3	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SS4	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SB1 <sup>2</sup>	—	—	—	—	—	—	—	—	—	—	—	—
	SB2	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SB3	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
	SB4	5	—	✓	—	✓	✓	—	✓	✓	✓	✓	—
29-30 May 2008	SS1	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS2	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS3	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS4	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB1	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB2	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB3	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB4	10	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
14-15 July 2008 <sup>1</sup>	SS1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS4	10	6 <sup>3</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB2	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB4	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
29 Sept-1 Oct 2008	SS1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SS4	10	5 <sup>3</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB2	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	SB4	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

*Continues*

Sampling date	Stream	Measured environmental variables										Water samples	Litter traps <sup>5</sup>
		Number of Surber samples	Number of algae samples	Velocity	Depth	Width	Substrate type	Vegetation type of stream bottom	Temperature	Conductivity	pH		
30 Apr -1 May 2009	SS1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SS2	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SS3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SS4	10	5 <sup>3</sup>	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SB1	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SB2	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SB3	10	10	✓	✓	✓	✓	✓	✓	✓	✓	—	✓
	SB4	10	— <sup>4</sup>	✓	✓	✓	✓	✓	✓	✓	✓	—	✓

<sup>1</sup>Sampling occasions analysed in this research.

<sup>2</sup>Stream was not reachable due to winter frost.

<sup>3</sup>The stream bottom did not have enough of stones large enough for chlorophyll *a* analysis.

<sup>4</sup>The bottom of the stream was lacked the stones large enough for chlorophyll *a* analysis.

