Major factors affecting the diversity of aquatic insects in 13 streams with contrasting riparian vegetation in the river Tana, North Norway

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Benthic invertebrate samples, taken in August and October 2000, 2001, 2002 at three sites in each of 13 streams (total 39 sites over a 200 km stretch of river), were used to: (i) classify the species/taxa into groups according to their occurrence; (ii) compare species/taxa richness and biodiversity across all sites; (iii) detect environmental variables responsible for differences between sites. Of 87 recorded taxa, 79 were aquatic insects, 19 were common to 12 streams, 19 were rare (found in ≤2 streams), and the remaining 49 were found in most, but not all, streams in both months. Multivariate analysis separated the latter 49 taxa into benthic assemblies flowing through: (i) willow forest; (ii) non-forested alpine habitat; (iii) birch (October only); (iv) birch and mixed birch-pine (August only); (v) mixed birch-pine habitat (October only). Multiple regression evaluated the relationships between 12 environmental variables and: (i) the residuals from a power function relating benthic density and variation in number of taxa among sites; (ii) Simpson and Shannon-Wiener diversity indices. Overhanging cover and stream width affected positively the larger number of species/taxa and diversity in August, with diversity also affected positively by moss cover. In both months, instream cover had a positive, and water velocity a negative, effect on species/taxa richness, whilst their effects on diversity were the exact opposite. The importance of overhanging and instream cover in this study has shown that enhancing riparian vegetation should always be an important factor in stream restoration and conservation projects.

Key words: aquatic insects, diversity indices, environmental factors, multivariate analysis, subarctic rivers.

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Introduction

Comparative studies (Petersen *et al.* 1995, Sandin 2003) have shown that naturally acid boreal streams have diverse ecosystems (Dangles *et al.* 2004). In recent years, several studies on functional feeding diversity (Frainer *et al.* 2014), metapopulation ecology (Göthe *et al.* 2012, Kärnä *et al.* 2015) and regional faunistic and taxonomic studies (Ekrem *et al.* 2012) are published from stream systems in northern Fennoscandia.

Stream insects are essential food resources for the young stages of anadromous fishes in subarctic river systems (Bergersen 1989, Erkinaro

& Niemelä 1995, Amundsen & Gabler 2008, Johansen *et al*. 2011). Larvae of Ephemeroptera, Plecoptera and Trichoptera are particularly important (Sánchez-Hernández *et al*. 2015) because they are abundant, grow large and provide prey at all seasons because of variations in life cycles and emergence times.

Tana is the largest river system in northern Europe and holds the largest naturally reproducing stock of Atlantic salmon (*Salmo salar*, Linnaeus, 1758) in Europe (Anon. 2015). Because of their high importance as food for salmon, stream invertebrates, predominantly insect larvae, were sampled in the Tana as part of a study on juvenile salmon (parr) ecology in the river system (Johansen *et al*. 2005a, b). Focus was on smaller nursery streams because Johansen *et al*. (2005a) found that parr moved there after spending their first year close to the spawning grounds in the larger tributaries of the system. A sampling programme on macroinvertebrates was undertaken over a three-year period in 13 streams with contrasting riparian vegetation. Data from three sites in each stream were used to: (i) classify the species/taxa into groups according to their occurrence; (ii) compare species/taxa richness and biodiversity across all sites; (iii) detect environmental variables responsible for differences between sites.

Decomposition of riparian leaf litter has a central role in the detritus-based food webs of northern streams (McKie & Malmqvist 2009, Frainer *et al.* 2014). There may, however, be different nutritional values of the litter from different vegetation (Sandin 2009, Hladyz *et al*. 2009, Gessner 2010). Some trees may be particularly beneficial as pointed out in Norway for willows (*Salix* spp.) by Brittain (1974) and Lillehammer (1974) for, respectively, mayflies and stoneflies. The Tana catchment has four major riparian vegetation types (willow, birch (*Betula*), pine (*Pinus*) and barren alpine). Our main hypothesis was that the insect assemblies should be different among streams with different riparian vegetation types. In particular, we expected that the species/taxa richness and the functional feeding groups should be different.

As a positive relation between density and diversity is commonly found (Gotelli & Colwell 2011, Rosenzweig *et al*. 2011), we expected this to be the case also in the present study. But several environmental factors may also have an impact on diversity (Sandin & Johnson 2004, Suurkuukka *et al*. 2014). Therefore, we measured a set of abiotic and biotic factors and compared their influence on diversity across the streams in the study.

Supported by funding from the Norwegian Taxonomy Initiative, a comprehensive faunistic and taxonomic study of insects along humid and freshwater habitats in Finnmark County was undertaken in 2010. The first results were published in eight papers in the Norwegian Journal of Entomology 59 (2). Almost all the material was of adults collected at 116 localities along watercourses across the county (Ekrem *et al*. 2012, Kjærstad *et al*. 2012). Many were along the Alta-Kautokeino, Lakselv and Pasvik river systems (see map in Ekrem *et al*. 2012). Only seven locations were in the Tana catchment. Of these, two were at lakes, four were along the Karasjohka tributary and one from the lower part of the main river. No collections were taken along the small streams included in the present study, or at any other smaller streams in the system. Therefore, the present material should supplement and increase our knowledge of freshwater insects in the largest and northernmost county in Norway, on the border between the European Arctic and boreal climate zones.

Study area

The subarctic river Tana (Teno in Finnish) is situated on the border between Norway and Finland (river mouth at 70°45' N, 28°30' E, Figure 1). The catchment area is 16 386 km^2. The Tana supports the largest fishery of Atlantic salmon in Europe, with mean annual catches of 200 metric tonnes in the river and 200 metric tonnes in the sea outside the river outlet (Moen 1991, Anon. 2015). In addition to the main river, there are over thirty tributaries with genetically distinct spawning stocks of salmon (Anon. 2015).
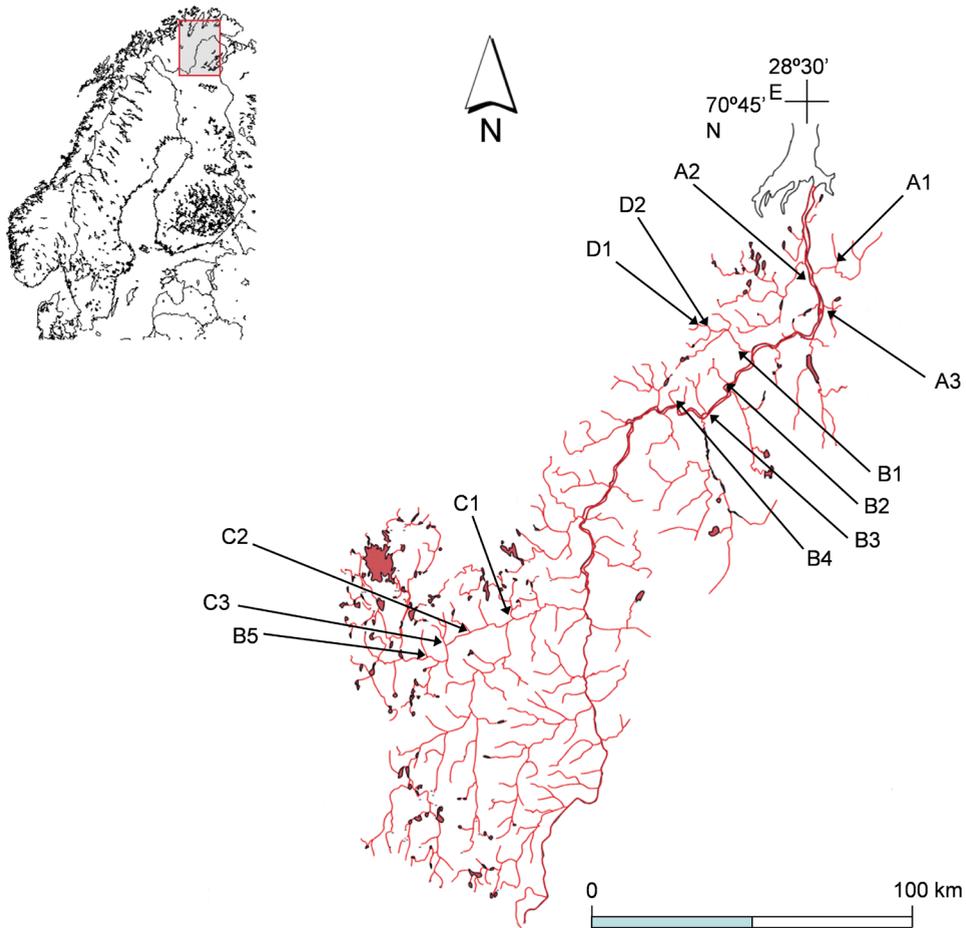
FIGURE 1. Locations of the 13 streams sampled in the subarctic Tana river system; riparian vegetation was willow (streams A1–A3), birch (streams B1–B5), mixed birch and pine (streams C1–C3), and non-forested alpine (D1–D2).

Methods

Sampling of benthos. Invertebrate samples were taken in 13 second, third and fourth order streams flowing either into the main Tana river or into major tributaries of the Tana (Table 1, Figure 1). The distance between stream A1 nearest the river mouth and stream B5 furthest from the river mouth was over 200 km (Figure 1). Four different categories of riparian vegetation are found in the Tana catchment: (A) willow (*Salix* spp.), (B) birch (*Betula pubescens*), (C) a mixture of birch and pine (*Pinus sylvestris*) and (D) non-forested

alpine. Three of the streams were in category A, five in B, three in C and two in D. There were three sampling sites in each stream so that the total number of sampling sites was 39. All sites were in riffle habitats because these occupied most of these fast-flowing streams. The distances between the three sites within the stream increased with the length of the stream and are provided in a previous study (Johansen *et al*. 2005a). The ice-free period is from early June to the end of October. Fieldwork in the early part of the summer is difficult because of frequent and unpredictable floods. Therefore benthic samples were taken in early August and

TABLE 1. General characteristics of the 13 streams sampled. Codes A1 to D2 correspond to those in Figure 1.

Name	Order	Length (km)	Gradient (m/km)	Altitude of mouth (m)
A1 Govdagåljohka	3	9.7	24.7	30
A2 Nuorttit Mohkkeveajjohka	3	6.0	28.7	10
A3 Ruossajohka	3	12.0	15.0	15
B1 Marssajohka	2	5.7	23.7	105
B2 Galbajohka	4	15.0	17.5	60
B3 Levsejohka	3	13.0	17.6	70
B4 Vuolit Vidis	3	9.8	21.7	80
B5 Cærrugæsjohka	3	8.4	12.6	270
C1 Geaimmejohka	4	18.4	10.4	135
C2 Ravdojohka	3	7.0	25.3	195
C3 Jerguljohka	3	13.0	15.5	230
D1 Cagnajohka	3	5.5	10.0	260
D2 Bihtusjohka	3	12.4	6.8	245

early October 2000, 2001 and 2002.

A sample of five sampling units was collected from each site using a Hess-Waters sampler (Waters & Knapp 1961), which samples a bottom area of 0.089 m². Mesh size of the bag in the sampler was 390 μm. This mesh size will not retain the smallest larvae with a length <0.4mm. However, such small larvae can rarely be identified to species. The sampler was pushed into the substratum with the collecting bag lying downstream. The substratum inside the cylinder was then disturbed, while larger stones were handpicked and brushed. The current carried the invertebrates into the collecting bag. The sampling units were chosen randomly at each site. Benthic densities were expressed as numbers m⁻² (with standard error, SE). Benthos samples were preserved in 70 % ethanol and were later handpicked in the laboratory at 6x magnification. We follow the nomenclature of Bauernfeind & Soldan (2012) for Ephemeroptera and Aagaard & Dolmen (1996) for other taxa. Most Ephemeroptera and Plecoptera were identified to species, using the keys of Engblom (1996) and Lillehammer (1988), respectively. Although very small larvae were rarely taken in the samples, as noted above, a few of these larvae were present but could only be identified to genus (*Baetis*, *Nemoura*, *Leuctra*) or family (some small perlodids). Most Trichoptera were identified to species, using several keys (Lepneva

1970, Lepneva 1971, Solem 1983, 1985, Higler & Solem 1986, Bongard 1990, Wallace *et al.* 2003, Edington & Hildrew 2005), but some small larvae could only be identified to genus (*Agraylea*, *Oxyethira*, *Ceraclea*) or family (some small limnephilids). Few Diptera were identified to species, most only to genus or family. Some of the non-insects could only be identified to major taxa. Each taxon was assigned to one of the following functional feeding groups: (i) predators (feeding on animal prey); (ii) shredders (detritivores living off coarse particulate organic matter e.g. leaves); (iii) browsers (collector-gatherers eating fine particulate organic matter and algal grazers); (iv) filter feeders (collecting particles from the water column) (Merritt *et al.* 2008).

Environmental variables. Twelve environmental variables were measured. Three transects were chosen randomly within each site. Stream width was measured in cm at each transect. Water depth (cm) and mean water velocity (at 0.6 times total water depth) were measured vertically every 20 cm across each transect. Velocities were measured with an Ott miniature current-meter. Classification of substratum used the following scale: sand/gravel (<2 cm), pebble (2–7 cm), cobble (7–25 cm) and boulder (>25 cm). A quadratic frame (sides 70 cm) was put down on the stream bottom, and a picture was taken of the streambed within the frame. The substratum

composition in each picture was analysed using the open source computer program ImageJ (National Institutes of Health). Percentage moss cover was also assessed from these streambed pictures. Instream cover was defined as: (i) submerged structures (except substratum) beneath which fish could hide from a view overhead, (ii) undercut banks or overhanging cover <50 cm above the water surface, and (iii) broken water surface. Area of riparian overhanging cover was quantified from a picture taken downstream, using ImageJ to measure the relative percentage of overhanging vegetation and clear sky from a half-circle going from river bank to bank. Conductivity (μS cm^{-1}, standardized to 25°C) was measured with a Hanna Instruments HI 9033 conductivity meter, while pH was measured with a Hanna Instruments HI 9025C pH meter. A detailed description of the habitat in each sampling site was performed in 2000. In following years, we examined each site to make sure that the habitat had not changed markedly.

Statistical analysis. Although most Ephemeroptera, Plecoptera, Trichoptera and Coleoptera were identified to species, other taxa, especially the Diptera, were identified to only genus or family. However, this varying level of identification was consistent between samples and, therefore, there was no particular bias towards a particular taxon in the statistical analyses. Similarity of the benthic assemblages between the 13 streams was examined using Non-metric Multi-Dimensional Scaling (NMDS; Torgerson 1952), a non-parametric robust method for exploring biological community data (Cao *et al.* 1996). A matrix of taxonomic Bray-Curtis similarities based on proportionate abundance data between each pair of streams was calculated and converted into a distance matrix in which distance (or dissimilarity) is 1 - similarity. The NMDS then arranged streams in an ordination into dimensions (axes) by iteratively adjusting between-stream distances to represent the ranks of stream dissimilarities. To reduce noise and enhance the detection of relationships, rare species were removed from the analysis. Therefore, the analyses were applied to the taxa that varied among most streams. The chief advantage of NMDS is that it, unlike other methods, is a distribution-free method.

Differences in number of taxa among the different vegetation categories were tested with one-way analysis of variance (ANOVA). A Tukey-Kramer Honestly Significant Difference (HSD) *post-hoc* pairwise comparison (Kramer 1956, Tukey 1949) was performed on significant ANOVAs to identify the source of the variation.

When sample size and sampling pattern are standardized, as in the present study, indices of diversity provide a useful summary of biodiversity, especially when comparisons are made among different locations (Magurran 2004). Two indices were used in order to strengthen the results:

(i) For a finite community, the index (D) of Simpson (1949) is:

$$D = \sum [n_i (n_i-1)] / [N (N-1)] \qquad (1)$$

where n_i = the number of individuals in the *i*th species, N = total number of individuals. As D increases, diversity decreases. In the present study the index was used as 1-D so that it increased with increasing diversity and the assemblage became more even.

(ii) The Shannon-Wiener index (H') (Shannon & Weaver 1949), is:

$$H' = -\sum p_i \ln p_i \qquad (2)$$

where p_i is the proportion of individuals found in the *i*th species.

Both D and H' were estimated for each site in each of the three years to provide nine estimates for each stream, with SE's for the mean values. As preliminary analyses indicated no significant differences among sites or years within each stream, the nine samples were combined to estimate the overall indices for a sample of 45 sample units from each stream. Separate values were given for the August and October samples.

A ridge regression analysis was performed to relate taxon richness and each index of diversity to environmental variables. Ridge regression, using the statistic Mallow's C_p as the main criterion in selecting the best subset of independent variables, was chosen to remedy potential problems caused by co-linearity (Neter *et al.* 1989).

TABLE 2. List of species/taxa found in the different streams in August and October. Functional feeding groups: p = predator, s = shredder, b = browser and f = filter feeder.

	Functional feeding group	August													October												
		A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2	A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2
EPHEMEROPTERA																											
Ameletus inopinatus Eaton, 1887	b	x																									
Siphlonurus lacustris Eaton, 1870	b																										x
Metretopus borealis (Eaton, 1871)	b					x								x													x
Baetis fuscatus (Linnaeus, 1761)	b						x				x		x	x													x
Baetis lapponicus (Bengtsson, 1912)	b	x	x		x		x	x			x		x	x													x
Baetis macani Kimmins, 1957	b													x													x
Baetis muticus (Linnaeus, 1758)	b	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Baetis rhodani (Pictet, 1843)	b	x	x		x	x	x	x			x	x	x	x			x			x		x		x	x	x	x
Baetis subalpinus Bengtsson, 1917	b	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Baetis indet.	b	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Paracinygmula joernensis (Bengtsson, 1909)	b				x																						
Heptagenia dalecarlica (Bengtsson, 1912)	b		x		x	x			x	x	x	x	x		x		x	x	x		x	x	x	x	x	x	x
Heptagenia sulphurea (Müller, 1776)	b				x	x	x		x	x	x	x	x	x		x		x	x		x	x	x	x	x	x	x
Leptophlebia marginata (Linnaeus, 1767)	b								x	x	x	x	x	x						x	x	x	x	x	x		
Paraleptophlebia werneri Ulmer, 1835	b												x														
Ephemerella aurivillii (Bengtsson, 1908)	b	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Ephemerella ignita (Poda, 1761)	b	x																									
Ephemerella mucronata (Bengtsson, 1909)	b						x							x													
PLECOPTERA																											
Arcynopteryx compacta (McLachlan, 1872)	p	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Diura nanseni (Kempny, 1900)	p	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Isogenus rubecula (Newman 1833)	p	x	x	x	x	x	x	x	x	x		x	x	x				x		x	x		x	x	x		
Isoperla grammatica (Poda, 1761)	p				x		x	x										x	x								x
Perlodidae indet.	p	x	x	x	x	x	x		x	x	x	x	x	x													
Siphonoperla burmeisteri (Pictet, 1841)	p				x	x		x	x	x		x						x	x				x	x	x	x	x
Taeniopteryx nebulosa (Linnaeus, 1758)	s	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x	x	x	x	x
Brachyptera risi (Morton, 1896)	s	x																		x	x	x					
Amphinemura borealis (Morton, 1894)	s	x			x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	x	x	x

TABLE 2. continued

	Functional feeding group	August													October												
		A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2	A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2
Amphinemura standfussi (Ris, 1902)	s	×	×	×																							
Amphinemura sulcicollis (Stephens, 1836)	s	×	×	×				×	×				×	×												×	×
Nemoura avicularis Morton, 1894	s		×	×												×											
Nemoura cinerea (Retzius, 1783)	s	×	×	×		×										×										×	×
Nemoura viki Lillehammer, 1972	s	×	×	×																							
Nemoura indet.	s	×	×		×	×	×			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Protonemura meyeri (Pictet, 1841)	s	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Capnia atra Morton, 1896	s	×	×	×	×	×		×	×	×		×	×	×	×	×		×	×	×	×	×	×	×	×		
Capnopsis schilleri (Rostock, 1892)	s	×				×				×		×			×					×							
Leuctra digitata Kempny, 1899	s	×	×		×	×	×		×	×	×	×	×	×												×	×
Leuctra fusca (Linnaeus, 1758)	s	×	×	×	×	×		×	×	×	×	×	×	×												×	×
Leuctra hippopus Kempny, 1899	s							×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Leuctra nigra (Olivier, 1811)	s	×	×	×	×	×	×	×	×	×		×	×		×											×	×
Leuctra indet.	s	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
COLEOPTERA																											
Colymbetinae indet.		×				×																					
Elmis aenea (Müller, 1806)	b	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Limnius volckmari (Panzer, 1793)	b						×			×		×	×													×	
Hydraena britteni Joy, 1907	p	×	×	×	×	×		×	×	×	×	×		×	×	×	×			×	×	×					
MEGALOPTERA																											
Sialis fuliginosa Pictet, 1836	p							×			×																
TRICHOPTERA																											
Rhyacophila nubila (Zetterstedt, 1840)	p	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Glossosoma intermedium (Klapálek, 1892)	b	×	×	×			×						×														
Agraylea indet.	b				×			×	×	×	×	×															
Oxyethira indet.	b		×	×	×	×			×	×	×	×															
Philopotamus montanus (Curtis, 1813)	f	×	×	×		×		×	×	×		×					×	×								×	
Plectrocnemia conspersa (Curtis, 1834)	f	×	×	×		×		×	×				×		×	×	×				×	×				×	
Polycentropus flavomaculatus (Pictet, 1834)	f	×			×	×		×	×	×		×	×	×	×		×	×	×				×	×	×	×	×

TABLE 2. *continued*

	Functional feeding group	August													October												
		A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2	A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2
Ceratopsyche nevae (Kolenati, 1858)	f									x																	
Hydropsyche pellucidula (Curtis, 1834)	f				x					x	x	x															
Hydropsyche siltalai Döhler, 1963	f				x	x				x	x	x	x										x	x	x		
Arctopsyche ladogensis (Kolenati, 1859)	f									x													x	x	x		
Micrasema gelidum McLachlan, 1876	f		x	x	x	x				x	x	x	x	x	x	x	x										
Lepidostoma hirtum (Fabricius, 1775)	b									x	x																
Apatania stigmatella (Zetterstedt, 1840)	b	x	x	x				x	x	x					x	x		x	x	x	x	x		x			
Apatania wallengreni McLachlan, 1871	b	x	x					x	x						x	x	x										
Apatania zonella (Zetterstedt, 1840)	b	x	x	x	x		x	x	x		x	x	x		x	x	x	x	x	x			x	x			
Chaetopteryx villosa (Fabricius, 1798)	s	x	x	x					x				x	x	x	x	x	x									
Halesus digitatus (Schrank, 1781)	s	x	x					x	x						x	x	x	x						x			
Potamophylax cingulatus (Stephens, 1837)	s	x	x	x				x		x		x			x	x	x							x			
Limnephilidae indet.	b	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Silo pallipes (Fabricius, 1781)	b	x																									
Ceraclea indet.	b									x																	
DIPTERA																											
Tipula rufina Meigen, 1818	s	x	x					x	x	x	x		x	x		x											
Antocha indet.	b		x							x																	
Dicranota indet.	s	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Elaeophila trimaculata Zetterstedt, 1838	b		x	x			x			x			x								x						
Psychodidae indet.	b	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
Simuliidae indet.	f	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Chironomidae indet.		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Culicoides indet.	b	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Dasyhelea indet.	p				x	x		x	x	x																	
Chelifera indet.	p	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Wiedemannia indet.	p	x	x		x			x	x	x			x	x													
NON-INSECTS																											
Planaria		x				x		x	x	x	x	x	x	x							x	x	x				

TABLE 2. *continued*

	Functional feeding group	August													October												
		A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2	A1	A2	A3	B1	B2	B3	B4	B5	C1	C2	C3	D1	D2
Nematoda		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Lymnaea peregra (Müller, 1774)	b									×															×		
Gyraulus acronicus (Férussac, 1807)	b												×	×												×	×
Pisidium indet.	f												×	×												×	×
Gammarus lacustris Sars, 1863	b												×	×												×	×
Oligochaeta		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Hydracarina		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

Results

Fundamental differences among streams. Of 87 taxa recorded in August and October in the 13 streams, 79 were aquatic insects (Table 2). The 19 taxa listed in Table 3 were common (mean densities $> 20\,m^{-2}$) to all, or nearly all (12), streams. 13 taxa were common in both August and October (Table 3, left column). Of the six taxa common in October (Table 3, right column), five (*D. nanseni*, *A. compacta*, *P. meyeri*, Limnephilidae and *Culicoides*.) were also common in all except one stream in August. *L. hippopus* was probably also present in August but could not be identified because of the small size of the larvae.

Rare taxa were defined as those found in only one or two streams and at mean densities less than $20\,m^{-2}$ (Table 4). Of the 22 rare taxa from August, 18 were not collected in October, probably because they were in the egg stage or very small early instars. Three species classified as rare in August were found in several streams in October; this discrepancy was probably also due to their life cycles, all emerging as adults in the spring/early summer. *Nemoura avicularis* was the only taxon that was rare in both months. The five remaining rare taxa in October were all common in August.

The final group of 49 species/taxa were those found in most, but not all streams, in August and October. This group was used in the NMDS analysis to compare the benthic assemblies in streams with different riparian vegetation types (Figure 2). In both August and October, the three streams flowing through predominantly willow forest were grouped together to the left (A1–A3 in Figure 2a, b), while the five streams flowing through predominantly birch woodlands were located in the middle (B1–B5 in Figure 2a, b). The three streams flowing through a mixed birch-pine forest were located together on the right in August (C1–C3, Figure 2a) and in the upper part in October (Figure 2b). The fauna in mixed birch/pine streams was not distinct from that of predominantly birch streams in August when species/taxa richness was high, but formed a distinct group in October. The two streams flowing through a non-forested alpine habitat

TABLE 3. Common species/taxa found in all streams in the samples from August and October.

Taxa (August and October)	Taxa (October only)
Baetis muticus (Linnaeus, 1758)	*Arcynopteryx compacta* (McLachlan, 1872)
Baetis spp.	*Diura nanseni* (Kempny, 1900)
Ephemerella aurivillii (Bengtsson, 1908)	*Protonemura meyeri* (Pictet, 1841)
Taeniopteryx nebulosa (Linnaeus, 1758)	*Leuctra hippopus* Kempny, 1899
Leuctra spp.	Limnephilidae
Elmis aenea (Müller, 1806)	*Culicoides* indet.
Rhyacophila nubila (Zetterstedt, 1840)	
Dicranota indet.	
Simuliidae	
Chironomidae	
Chelifera indet.	
NON-INSECTS	
Hydracarina	
Oligochaeta	

TABLE 4. Rare species/taxa found in only one or two streams in the samples from August and October (a = absent in samples from the other month; * = common in samples from the other month).

Taxa (August)		Taxa (October)	
Ameletus inopinatus Eaton, 1887	a	*Nemoura avicularis* Morton, 1894	
Siphlonurus lacustris Eaton, 1870	a	*Nemoura cinerea* (Retzius, 1783)	*
Baetis macani Kimmins, 1957	a	*Capnopsis schilleri* (Rostock, 1892)	*
Paracinygmula joernensis (Bengtsson, 1909)	a	*Philopotamus montanus* (Curtis, 1813)	*
Paraleptophlebia werneri Ulmer, 1835	a	*Tipula* indet.	*
Ephemerella mucronata (Bengtsson, 1909)	a	*Eloeophila trimaculata* Zetterstedt, 1838	*
Ephemerella ignita (Poda, 1761)	a		
Isoperla grammatica (Poda, 1761)	*		
Brachyptera risi (Morton, 1896)	*		
Nemoura avicularis Morton, 1894			
Limnius volckmari (Panzer, 1793)	a		
Colymbetinae	a		
Sialis fuliginosa Pictet, 1836	a		
Ceratopsyche nevae (Kolenati, 1858)	a		
Arctopsyche ladogensis (Kolenati, 1859)	*		
Ceraclea indet.	a		
Lepidostoma hirtum (Fabricius, 1775)	a		
Silo pallipes (Fabricius, 1781)	a		
Antocha indet.	a		
NON-INSECTS			
Gyraulus acronicus (Férussac, 1807)	a		
Pisidium indet.	a		
Gammarus lacustris Sars, 1863	a		
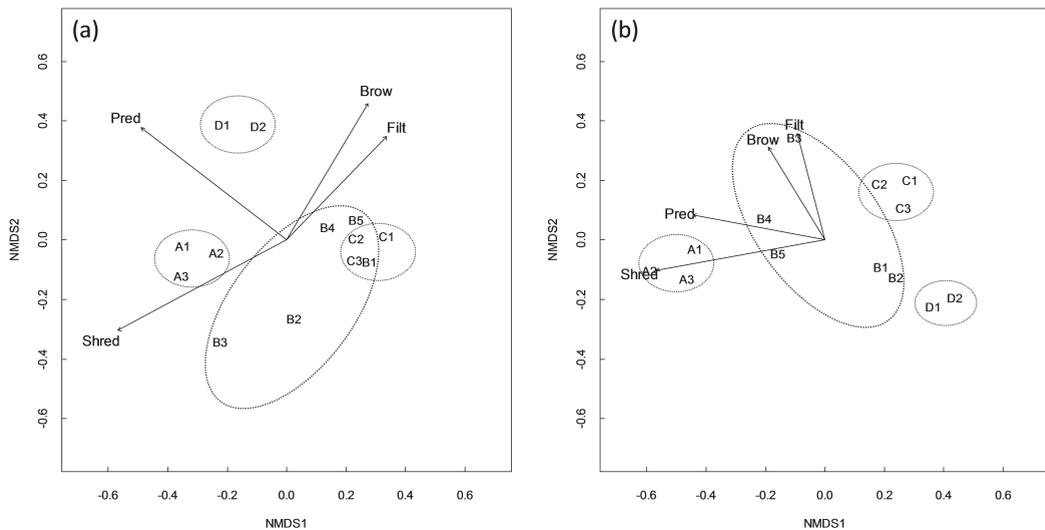
FIGURE 2. The relationship between the first two axes of the Non-metric Multi-Dimensional Scaling (NMDS) plot of the 13 stream samples in the subarctic Tana river system in (a) August and (b) October. The streams are shown by codes (A1-D2, see Table I). Vectors showing functional feeding groups are superimposed over the NMDS plot (Pred = predators; Shred = shredders; Brow = browsers; Filt = filter feeders).

formed a distinct group at the top in August (D1–D2, Figure 2a) and to the right in October (Figure 2b).

The ANOVA comparing the number of species in streams flowing through the different vegetation types was statistically significant in August ($F_{3,581}$=37.36, $p<0.001$) and October ($F_{3,551}$=122.14, $p<0.001$). In August, the *post-hoc* HSD comparison identified a significantly higher ($p<0.001$) number of species/taxa in the willow (A1–A3) and mixed birch/pine streams (C1–C3) than in birch (B1–B5) and non-forested alpine streams (D1–D2) (Figure 3a). All *post-hoc* HSD comparisons were significant in October (all $p<0.001$; Figure 3b).

When the functional feeding groups (Table 2) were superimposed as vectors on the results of the NMDS analyses, they showed distinct patterns (Figure 2a, b). In both months, shredders (17 taxa in August, 7 in October) were found chiefly in the streams flowing through willow forest (A1–A3) and two of the birch forest streams (B2, B3). This shows that overhanging vegetation was clearly important for shredders. Predators were relatively more common in the non-forested alpine streams

(D1–D2) in August (8 taxa) but not in October (4 taxa). In both months, filter feeders (6 taxa in August, 5 in October) and browsers (20 taxa in August, 11 in October) were predominant in the remaining streams flowing through birch (B1, B4, B5) and mixed birch-pine forest (C1–C3).

Taxon richness and diversity. Taxon richness, the number of species/taxa present in a stream, is the simplest measure of biodiversity. As noted earlier, most taxa were identified to species and most of the remainder to genus. The relationship between the number of taxa recorded at each site (S) and the mean number of invertebrates at the site ($N\,\mathrm{m}^{-2}$) was described by a power function:

$$S = a\,N^b \qquad (3)$$

where values of the intercept a and power b are given in the legend to Figure 4. As the number of taxa was very different in August and October, the two months were treated separately (Figure 4). Equation 3 was a good fit ($p<0.01$) in both months and the R^2 value indicated that benthic density explained a large amount of the variation in the number of taxa in the different sites, 55 % in August and 59 % in October.
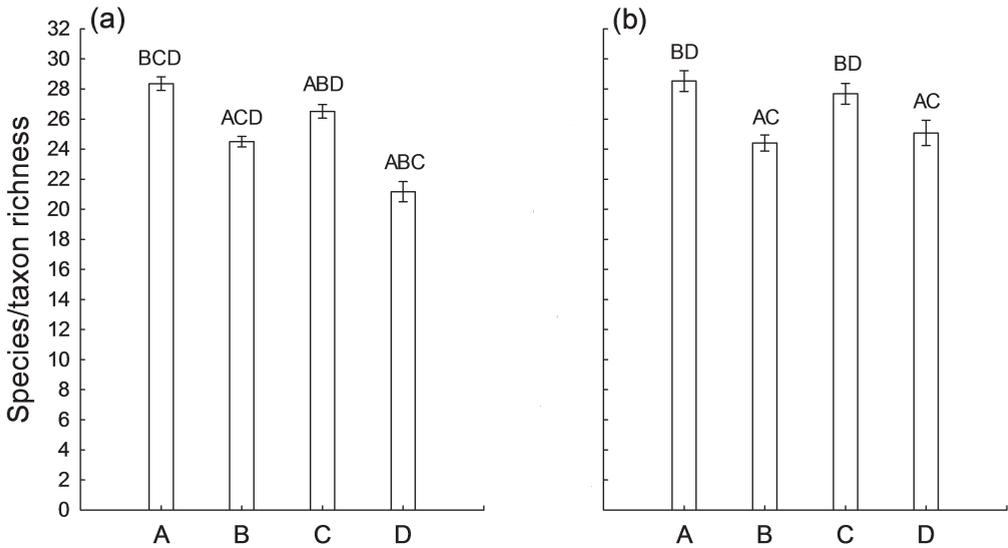
FIGURE 3. The average number of species/taxa (± SE) in benthic samples from streams flowing through different vegetation categories in (a) August and (b) October. Vegetation categories are A = willow, B = birch, C = mixed birch/pine, D = non-forested alpine. Significant *post-hoc* HSD comparisons are indicated by letters above the bars.
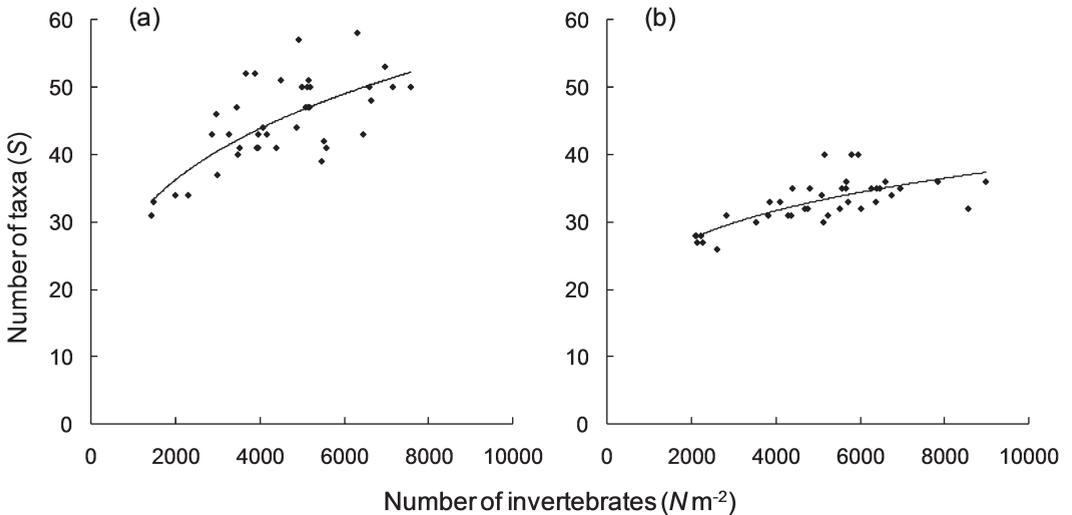
FIGURE 4. Relationship between the number of species/taxa recorded at each site (S) and the mean number of invertebrates at the site (N m-2) in: (a) August, (b) October. Curves given by Eqn. 4 with $a = 4.50$, $b = 0.27$ in August, $a = 5.81$, $b = 0.20$ in October ($n = 39$ in both months).
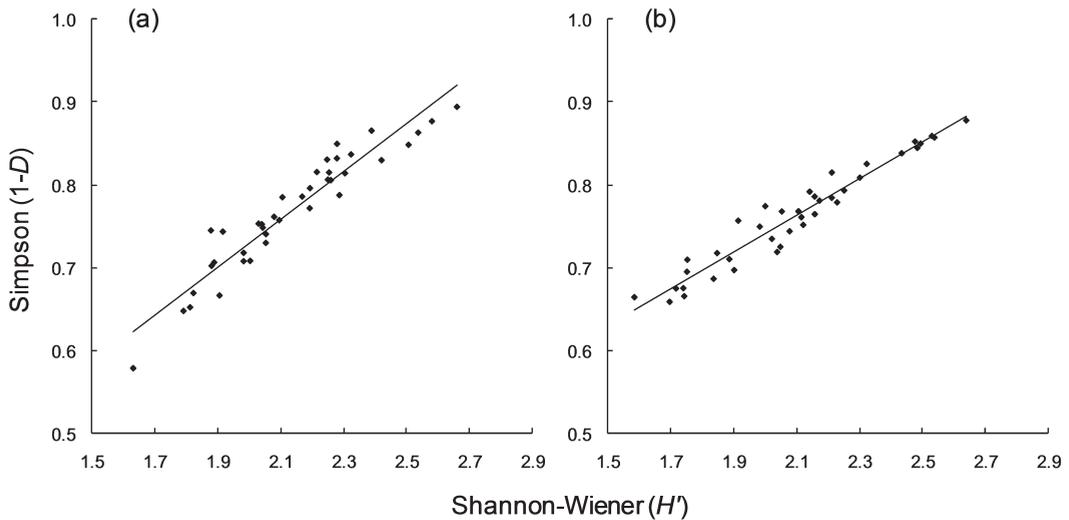
FIGURE 5. Relationships between Simpson's index (1-*D*) and the Shannon-Wiener index (*H′*) for the 13 streams in: (a) August, (b) October. Regression line given by: 1-*D* = *a* + *b H′*, where *a* = 0.15, *b* = 0.29 in August, *a* = 0.30, *b* = 0.22 in October (*p*<0.001 for both months).

However, part of the remaining variation could be explained by environmental factors. The multiple regression analysis used to examine the relationship between the residuals from the power function and the twelve environmental variables was significant both for August and October (*p*<0.01). About half of the remaining variation (50 % in August, 43 % in October) was related positively to instream cover and overhanging cover in both months and also to stream width in August and to conductivity in October, and negatively to water velocity in both months and to conductivity and moss cover in August (Table 5).

The two diversity indices, 1-*D* and *H′*, were very closely correlated for the 13 streams in each month with R^2 of 0.90 in August and 0.94 in October (Figure 5). This increased confidence in the use of both indices as a measure of biodiversity. The multiple regression analysis showed that both indices were related to instream cover and overhanging cover in October, both having positive effects, and to stream width, water velocity, conductivity, moss cover, overhanging cover (all positive), and instream cover (negative) in August (Table 5).

Discussion

The NMDS grouped the 13 streams according to similarities in the composition of their invertebrate communities, and the different groupings corresponded to the four different categories of riparian vegetation in the Tana catchment. The fauna in mixed birch/pine streams was not distinct from that of predominantly birch streams in August when species/taxa richness was high, but formed a distinct group in October. This suggests that the fauna in these streams was related to birch vegetation in August, but not in October at the end of leaf fall from the deciduous birch. This relationship agrees with the River Continuum Concept (Vannote *et al.* 1980) in which the trophic structure of benthic communities is linked to variation in energy input (Hildrew & Townsend 1987). There was also a general reduction in the number of taxa from August to October (Table 2). Most of the missing species in October were in the egg stage or early instars and would not be collected by the sampling method.

The species/taxa found in the August and October samples from the different streams in the Tana river are broadly comparable to samples from boreal streams, e.g. from Norway

TABLE 5. Estimates (± SE) for the August and October samples of the parameter estimates a, b_1, b_2, b_3, b_4, b_5 and b_6 together with partial correlation coefficients (r_p) for b_1-b_6 in multiple regression equations of the form $Y=a+b_1X_1+b_2X_2+\ldots+b_6X_6$ where Y was the dependent variable and $X_1 \ldots X_6$ were the environmental variables (X_1=stream width, X_2=water velocity, X_3=conductivity, X_4=moss cover, X_5=instream cover, X_6=overhanging cover).

Dependent variable	R^2	a	b_1	r_p	b_2	r_p	b_3	r_p	b_4	r_p	b_5	r_p	b_6	r_p
Res. Eqn. 4	0.50	-3.83	1.17	0.51	-15.6	-0.43	-0.052	-0.22	-0.060	-0.44	0.12	0.24	0.073	0.46
(August)		(3.19)	(0.35)		(5.75)		(0.041)		(0.021)		(0.088)		(0.46)	
Res. Eqn. 4	0.43	-3.88			-4.30	-0.23	0.033	0.25			0.067	0.24	0.023	0.34
(October)		(1.44)			(0.033)		(0.022)				(0.046)		(0.011)	
Shannon-Wiener	0.60	1.10	0.085	0.55	1.04	0.45	0.0081	0.48	0.0034	0.40	-0.011	-0.34	0.0044	0.43
(August)		(0.20)	(0.023)		(0.37)		(0.0026)		(0.0014)		(0.0056)		(0.0016)	
Shannon-Wiener	0.47	1.63									0.0069	0.18	0.0059	0.60
(October)		(0.16)									(0.0061)		(0.0013)	
Simpsons	0.57	0.48	0.030	0.59	0.33	0.45	0.0022	0.43	0.00064	0.26	-0.0044	-0.40	0.0014	0.43
(August)		(0.064)	(0.0070)		(0.12)		(0.0008)		(0.0004)		(0.0018)		(0.0005)	
Simpsons	0.46	0.64									0.0021	0.24	0.0012	0.56
(October)		(0.038)									(0.0014)		(0.0003)	

(Bergersen 1987, 1989, 1992, Huru 1980a, 1980b, 1981, 1982, Johansen 1998, Johansen *et al*. 2000, Klemetsen *et al*. 2015), Sweden (Müller 1954, Ulfstrand 1968, Malmqvist & Hoffsten 2000) and Finland (Paavola *et al*. 2000, Heino 2005). Although the streams in the present study are situated in the northernmost part of Norway, their faunal characteristics did not fit those of alpine and Arctic rivers in the classification proposed by Petersen *et al*. (1995), and were closer to the boreal-forest group of streams, but even the latter group was not an exact description. The benthos community recorded in the present study suggests the presence of a separate group, which could be termed the northern deciduous-forest streams.

The species/taxa classified as common in this study are the same as those commonly found elsewhere in the region (see references listed above). Ephemeroptera and Plecoptera, the two most prominent insect orders in northern rivers, had richnesses of 17 and 20, respectively, in the present material. Their combined richness of 37 is slightly higher or similar to that recorded in Spanselva, Troms (27, Huru 1980b), Barduelva, Troms (29, Huru 1981), Sæterelva, Troms (34, Johansen 1998), Reisaelva, Troms (41, Huru 1980a), Altaelva, Finnmark (38, Huru 1984, Bergersen 1987, 1989, 1992) and Lakselva, Finnmark (39, Huru 1982); see also Table 1 in Klemetsen *et al*. (2015). Several of the Trichoptera species collected in the Tana catchment by Andersen & Hagelund (2012) were found as larvae in our streams (Table 2), including the rare Finnmark species *Ceratopsyche nevae*. *Hydropsyche siltalai* was only recorded in southern Norway by Solem & Andersen (1996). It was found in several of our streams (Table 2) and according to Artskart (2016) there are now sporadic records from all over northern Norway including Finnmark. It was not collected by Andersen & Hagelund (2012) but was listed as one of six additional species for Finnmark by Tobias & Tobias (2010). However, Andersen & Hagelund (2012) remark that proper locality information should be presented before the species in this list can be added. This is now the case for *H. siltalai*, and the regular occurrence in the Tana streams indicates that it is more common and abundant in Finnmark than previously known.

The richness for the Tana streams is lower than in the list of all registered freshwater species in the area (Aagaard & Dolmen 1996; see also Andersen & Hagelund (2012), Boumans & Brittain (2012) and Kjærstad *et al*. (2012)) but that list includes all freshwater habitats and covers a much longer time. Like in most reports referred to above, however, some rare species may nevertheless have been missed. This may be due to several factors. Firstly, samples were taken in only riffle habitats

and a few species restricted to slow-flowing areas may not have been collected. Secondly, although five sampling units from each sampling site twice a year over three years should be adequate (Elliott 1977), some very rare species may have been missed. Finally, the sampling in August and October may have excluded species that emerge during spring. However, this was unlikely because some species emerging in spring were frequently taken in the samples, e.g. *Taeniopteryx nebulosa* and *Capnia atra* (Table 2).

A considerable part of the benthos variation in Tana was explained by environmental variables. Lotic systems appear to be variable and harsh environments, and it is suggested that abiotic factors may have a great influence in these systems (Allan & Castillo 2007). The local diversity at any site is dependent on the regional species pool, but often less than half of the latter is found at any site (Allan & Castillo 2007). This indicates that local environmental factors affect the probability that each species in the regional species pool is able to live and persist locally (Poff 1997). Local-scale factors such as water quality, water velocity, substratum, and riparian and instream vegetation often account for a larger part of species variance than regional-scale factors such as ecoregions and catchment characteristics (Sandin & Johnson 2004). Of the 12 environmental variables that had an effect on richness and biodiversity indices, instream cover and overhanging cover dominated in both months. Overhanging riparian vegetation had a positive effect on juvenile salmon density in the streams (Johansen *et al*. 2005b). The present study has shown that it also has a positive effect on the biodiversity of the benthos. This is probably why there was also a positive relationship between salmon density and the density of the benthos in the 13 streams (Johansen *et al*. 2005b).

A power law was found to be the best description of the relationship between the number of taxa and the number of individuals in the present study. Similar power-law equations have been used to describe species-area relationships, and the positive relationship between the number of species found in an area and the size of that area is well documented (Rosenzweig *et al*. 2011). The wide range of values reported for the slope

of the power law in freshwater systems varies between 0.17 and 0.53 (Sepkoski & Rex 1974, Browne 1981, Elliott & Drake 1981, Brönmark *et al*. 1984). The slopes in the present study, 0.27 in August and 0.20 in October, fall well into that range.

Instream cover had a positive, and water velocity a negative, effect on richness in the present study. However, these same factors had the opposite effect on diversity indices. A possible reason for this lies in the fact that diversity indices such as Simpson's and Shannon-Wiener include a measure of density as well as taxon richness. The relationships suggest that increasing instream cover enhanced the number of species/taxa, but changed the densities of each taxon, leading to a lower diversity. Similarly, increasing water velocity reduced species/taxa richness but a change in the numbers of each taxon led to higher diversity indices.

There are important applied aspects of this study. Stream invertebrates, especially insects, are an important food for fish (Erkinaro & Niemelä 1995, Amundsen & Gabler 2008, Johansen *et al*. 2011) and provide indicators of habitat quality (Allan & Castillo 2007). They also have intrinsic values as major constituents of riverine biodiversity (Allan & Castillo 2007). For these reasons it is desirable to understand their biology, including relationships with environmental factors that influence biodiversity. The Tana River is important because of its large fishery for Atlantic salmon, and Johansen *et al*. (2005b) showed that the migration of salmon parr into nursery streams is related to density of macroinvertebrates. The present study has shown that the benthic communities in a wide range of Tana streams were related to differences in the riparian vegetation. The chief environmental factors affecting invertebrate diversity were overhanging cover and woody instream cover that had fallen in from the banks. Therefore, riparian vegetation, particularly willow and birch, emerged as an important positive factor. Riparian leaf litter is a key component in the food webs of streams (Frainer *et al*. 2014). The riparian vegetation is also a source of drifting terrestrial invertebrates in the streams (Johansen *et al*. 2005a). Therefore,

enhancing riparian vegetation should always be an important factor in stream restoration projects, as shown by Suurkuukka *et al.* (2014) from northern Finland. Most of the riparian vegetation along the Tana streams is still relatively pristine. Because of the high importance for the insect communities and the salmon, conservation of the riparian vegetation should be a goal for the streams in the Tana catchment.

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