Response of macroinvertebrate assemblages of boreal streams to acid stress

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SUMMARY

1. Use of ecological criteria to exclude streams affected by stressors not of interest here (e.g. nutrient enrichment, liming) resulted in a strong acidity gradient as exemplified by principal component analysis. For example, the first PC axis explained 31.1% of the variance and was clearly related to acidity, e.g. pH buffering capacity and the ratio ANC/H+ were strongly correlated with this axis (loadings > 0.20).

2. Linear and multivariate regression techniques were used to assess the effects of land use and water chemistry (in particular acidity variables) on macroinvertebrate community structure.

3. Correlation revealed a number of significant predictor variables. Stepwise regression of four selected biological metrics (taxon richness, diversity EPT taxa and the Henrikson & Medin acid index) showed that, with the exception of one metric (Shannon diversity), acidity variables were selected as the first explanatory variable. For example, for richness and the acid index minimum ANC was the first variable selected and explained 37.4% and 68.6%, respectively, of the among-stream variance. Similarly, CCA ordination of community composition and environmental variables showed the importance of acidity variables, in particular in the southernmost (Central Plain) ecoregion.

4. Use of lag responses of acidity variables or modeled (flood) minimum pH or ANC did not improve explanatory power.

5. Plots of the Henrikson & Medin acid index showed significant relationships with in-stream measures of acidity. For pH, the first three classes (i.e. class 1 to 3) showed gradual increases in acid index scores. The latter two classes (class 4 and 5), on the other hand, were not as clearly defined (higher variability). Regarding buffering capacity (ANC), the two highest classes (class 4 and 5) showed high among-site variability, in particular when acid scores were regressed against mean ANC. At ANC < 0.02 meq/L very low acid index scores were noted. Very low acid index scores were noted at inorganic Al concentration > 100 µg/L indicating biological impairment.

INTRODUCTION

For several decades emissions of N and S have negatively affected the integrity of surface waters in Sweden and elsewhere. In the early 1990s it was estimated, for example, that some 14,000 or 15% of Swedish lakes with a surface area < 1 km^2 and about one-fifth of all streams could be regarded as being adversely affected by acidification (Bernes 1991). Although natural recovery of water chemistry has been documented in a number of lake ecosystems in Sweden (Wilander 1997) and across Europe (Stoddard et al. 1999), and more recently changes in lake biology have also been reported (e.g. Raddum et al. 2001), acidification is still considered as a major pressure deleteriously affecting the structure and function of lakes and streams in Sweden.

To better understand how to manage and restore the structure, function and biodiversity of aquatic habitats, more knowledge is needed on how organisms respond to human-induced as well as natural environmental changes. In a recent study, Johnson et al. (2004 and submitted) evaluated the response of lake littoral macroinvertebrate communities to natural and human-induced (acidification) stressors. These authors found that lake macroinvertebrate communities were responding to large-scale (regional patterns in landscape type/use) as well as more site-specific patterns in water chemistry. In particular, Johnson et al. (submitted) showed that the littoral communities were best correlated with pH and buffering capacity (alkalinity/acidity). As a continuation of this work, this study was designed to correlatively assess relationships between stream-riffle macroinvertebrate communities and physico-chemical metrics (variables) indicative of acid stress. Moreover, similar to the study on lake benthos by Johnson et al. (2004), focus here is on determining if riffle macroinvertebrate communities are responding in a similar way to acidification stress and, if so, to determine if the ecological classification or threshold levels suggested by Johnson et al. (2004) are applicable for stream (riffle) macroinvertebrate communities. In particular, this study focuses on (i) the importance of different time lags (e.g. extreme values or lag-phase (t_1) responses), (ii) the best chemical predictor of among-stream differences in macroinvertebrate assemblage structure and composition and (iii) determination of threshold or ecological breakpoints along acid-stress gradients (pH, alkalinity/acidity, ANC).

METHODS

Study streams

The streams included in this study are taken from the national lake and stream register (www.ma.slu.se) as well as regional monitoring programs. In the late 1990s, Sweden initiated a long-term monitoring program of multiple habitat types and trophic levels to follow the effects of acidification and recovery of regionally representative stream ecosystems (e.g. Wiederholm & Johnson 1997). Stream categories consist of (i) sites not deemed to be affected anthropogenic stressors and (ii) sites judged to be stressed by acidification and nutrient enrichment. Figure 1 and Table 1 shows the geographic position of the individual sites (coordinates and ecoregion) as well as the total number and interval of years sampled.

Fig. 1. Location of the 49 study streams by ecoregion.

Benthic macroinvertebrates were collected using three different methods. A *standardized kick-sample* consisted of five kick-samples (60 sec x 1 m for streams) taken from each site (one site per stream). *M42 sample* consisted of multiple samples collected either using transect or multihabitat sampling, with the number of replicate samples varying from 1 to 9 (mean 1.4 samples stream^{-1} year^{-1}). The number of replicate *Surber samples* as varied (mean 2 samples stream^{-1} year^{-1}, range = 1 – 4). The size of the area sampled varied between streams. However, a preliminary analyses (CCA ordinations) on macroinvertebrate abundance and presence/absence data revealed no difference, indicating that the effects of different sampling methods might be marginal, hence only abundance data are used here. In addition to community composition, four relatively common metrics were used to compare the response of stream macroinvertebrate communities to acid stress. Two metrics, Shannon diversity (Shannon 1948) and Henrikson & Medin acid index (1986) are recommended for assessing the ecological integrity of inland waters (Anonymous 1999). The two other metrics, taxon richness and the number of Ephemeroptera, Plecoptera and Trichoptera taxa (EPT taxa) are commonly used in studies of ecological assessment.

Samples processed by the Department of Environmental Assessment were sorted and the animals identified according to quality control and assurance protocols (a SWEDAC certified laboratory; see also Wilander *et al.*, 1998; 2003). Identification was done to the lowest taxonomic unit possible, usually to species or species groups, with the exception of oligochaetes and chironomids. QA/QC procedures of the other labs involved in the processing of regional-monitoring samples varied.

In addition to macroinvertebrate samples, water samples were collected and analyzed for a number of water chemistry variables (e.g. nutrients, water color, conductivity, base cations and anions and acidity metrics), following international (ISO) or European (EN) standards when available (Wilander *et al.*, 1998; 2003). The sites where macroinvertebrate samples were taken were also classified according to substratum particle size and vegetation, and the riparian zones (shoreline stretches, 50 m long and 5 m wide, adjacent to the areas sampled) and catchments were classified according land use and vegetation cover.

To more unequivocally analyze the effects of acidity on macroinvertebrate communities, streams judged to be affected by other anthropogenic stressors were removed from the data set. Consequently, streams affected by agriculture (e.g. > 20 % of the catchment classified as agriculture), urbanization (> 0.1 % of the catchment classified as urban), and liming were removed from the data sets. Sites with a mean pH > 7.5 were also excluded in order to place more focus on the acidity gradient. Invoking these exclusion criteria resulted in a dataset consisting of 49 streams distributed across the country (Table 1).

Statistical analyses

<u>Constrained ordination</u>

Direct gradient analysis (also known as constrained ordination, ter Braak and Smilauer 1997-1998) was used to select environmental variables that could explain significant amounts of the variability in structural composition among the stream macroinvertebrate communities. Detrended correspondence analysis (DCA) of square-root transformed species abundance, with downweighting of rare taxa, detrending by segments and non-linear rescaling was used to determine the biological turnover, or gradient length, of the species dataset. From this the appropriate model (ordination procedure) for the constrained ordination was chosen. DCA gradient lengths from 2.279 (Central Plain) to 3.157 (Fennoskandian shield) for axis 1 and from 1.98 (Central Plain) to 3.115 (Fennoskandian shield) for axis 2. Although gradient lengths for the Central Plain ecoregion were borderline (< 2.5 SD) and indicate that a linear response model would better fit the species data, for comparison a unimodal fit (i.e. CCA) was used in all analyses. In CCA the species abundance data were square-root transformed and, where necessary, the environmental variables were transformed ($\log_{10}$ or arcsine of square root) in order to approximate normally distributed random errors. Constrained ordinations were run using the species downweighting option and forward selection of environmental variables. Significance of the environmental variables was tested with 499 Monte Carlo permutations and Bonferroni corrected p-values.

<u>Partial constrained ordination</u>

The total variation in an ecological data set can be partitioned into: (i) unique or pure variation from a specific variable, (ii) common variation contributed by all measured variables and (iii) random error. Constrained ordination, as used above, does not explicitly test for the unique effect of the categories of spatial scale on taxonomic and functional composition. A number of techniques have been developed recently, however, for analyzing and partitioning the variance of multi-scale studies. The approach used here is based on constrained ordination (ter Braak and Smilauer 1997-1998); partial constrained ordination is used to explore the relationships between single environmental variables and biological response variables. Here, partial constrained ordination (pCCA) was run to remove the effect of year or other variables of interest (e.g. importance of acid variables and/or time lags; chemical variables (mean, median and extreme values) for t_0, (same year measures) and t_1 (measures with a one year lag).

A number of ordinations were done to analyze the importance of water chemical metrics on stream macroinvertebrate community structure. First, correspondence analysis of macroinvertebrates and principal components analysis were used to examine the data sets. Canonical correspondence analysis of macroinvertebrates, geographic position, land use/type, stream hydromorphological descriptors and water chemistry was used to assess the importance of mean, extreme (minimum and maximum within-year values) and lag-phase (one and two year lags) responses on littoral communities. Partial correspondence analysis (pCCA) was run on macroinvertebrates and water chemistry (mean, median, extreme values) with year run as a covariable. Three separate ordinations were run using: (i) all data (all regions), (ii) streams in the Fennoskandian shield (ecoregion 2, middle and southern boreal) and streams in the Central Plain (ecoregion 3, boreonemoral and nemoral) regions. Too few sites were available to analyze the Boreal Highland ecoregion. Additionally, two CCAs were run as described above but water chemistry was restricted to lag-variables to determine the influence of time lags on biological response.

Table 1. Selected attributes of the acid and reference study streams. Region 1 = Arctic/alpine and boreal highlands (arctic/alpine and northern boreal), 2 = Fennoskandian shield (middle and southern boreal), 3 = Central Plain (boreonemoral and nemoral).

Name	X-coordinate	Y-coordinate	Region	No. Years	Min Year	Max Year
Dammån	632137	147160	1	1	1997	1997
Ejgstån	654552	123925	1	1	1997	1997
Gnyltån	638065	139975	1	1	1997	1997
Lillån (Oskarsström)	630695	132775	1	1	1997	1997
Lillån-Bosgårdsån	631840	133310	1	1	1997	1997
Lommabäcken Nedre	650920	143244	1	2	1995	1996
Morån	634570	150290	1	1	1997	1997
Norrhultsbäcken	633316	146198	1	1	2001	2001
Pipbäcken Nedre	633070	131710	1	2	1995	1996
Svedån Sved	643455	140114	1	2	2001	2002
Trollbäcken	624725	133411	1	5	1994	2002
Alep Uttjajåkkå	739283	163835	2	4	1997	2002
Bergmyrbäcken	728070	165120	2	14	1997	2003
Bjurbäcken	718265	171875	2	11	1998	2003
Byskebäcken	721688	175512	2	5	1999	2003
Fusbäcken	707965	169175	2	5	1999	2003
Härån (Storån)	684705	153450	2	1	1997	1997
Höjdabäcken	710354	155465	2	3	2001	2003
Kläppsjöbäcken	706580	156068	2	6	1997	2003
Kniptjärnsbäcken	694150	147630	2	6	1997	2003
Kvarnbäcken (Sävarån)	713650	171380	2	5	1999	2003
Kvarnån	703626	153615	2	2	1997	1999
Kärmsjöbäcken	708485	154920	2	6	1997	2003
Lagbäcken	713965	151910	2	5	1999	2003
Laxtjärnsbäcken	730224	165025	2	3	1995	2000
Lill-Fämtan	675032	135400	2	2	1995	1996
Malmån	699100	156210	2	6	1997	2003
Muddusälven	741419	169012	2	3	2000	2002
Myrkanalen	710100	167625	2	6	1999	2003
Mälskarbäcken	718900	154895	2	8	1999	2003
Navarån	694466	154745	2	6	1997	2003
Rokån	726035	174360	2	16	1996	2003
Röjvattsbäcken	709945	164845	2	6	1999	2003
Stormyrbäcken	690530	152405	2	2	1995	1996
Stridbäcken (ovan dos)	704905	167235	2	5	1999	2003
Surmyrdalsbäcken.elfiske	706765	167095	2	8	2000	2003
Sörjabäcken (Lillån)	673815	153365	2	6	1997	1999
Ulvsjöån	690197	154176	2	6	1997	2003
Viksbäcken	699970	163455	2	6	1997	2003
Viskansbäcken	692688	153260	2	2	1997	1999
Västerån. Gravå	711680	171085	2	8	2000	2003
Akkarjåkkå	753460	165285	3	16	1996	2003
Fiskonbäcken. v.vid mynn	720990	147270	3	4	2000	2003
Kvarnbäcken(Luspsjön)	722505	155370	3	5	1999	2003
Rändan	693301	135878	3	1	1997	1997

Storbäcken (Njakafjäll)	720330	149500	3	5	1999	2003
Stråfulan	684875	133226	3	2	1998	1998
Viepsajåkkå	737675	158280	3	16	1996	2003
Yl. Kihlankijoki	752250	182525	3	16	1996	2003

RESULTS

The acid and reference streams studied here were relatively small (median catchment size = 31 km^2) and ranged from lowland (e.g. Ejgstån, 7.4 m a.s.l.) to alpine (e.g. Rändan, 664 m a.s.l.) ecosystems (Table 2). Most streams nutrient poor (mean TP of 12.6 ± 9.03 µg/L), but a nutrient gradient was evident (range = 3.67 µg TP/L to 52.3 µg TP/L). Catchments were predominantly forested (mean = 74%, 10-percentile = 59% forest) and water color reflected a gradient from brown- to clear water systems and the input of allochthonous carbon (mean 0.179 ± 0.112 absF, range = 0.022 to 0.444). Relatively broad gradients in the acidity metrics studied here were clearly evident; pH and alkalinity/acidity averaged 6.22 ± 0.84 and 0.133 ± 0.208, respectively, but ranged from very acid (pH = 4.3, alkalinity/acidity = -0.0906 meq/L) to well buffered (pH = 7.38, alkalinity/acidify = 0.499 meq/L) (Fig. 2).

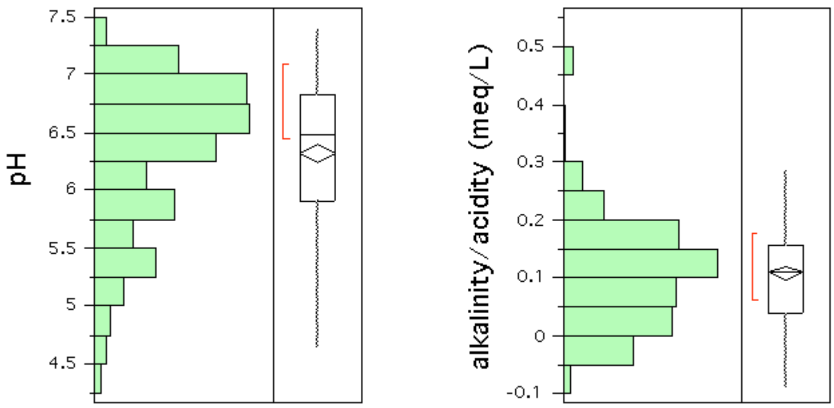

Figure 2. Distribution plots of pH and alkalinity/acidity for acid and reference streams.

Table 2. Selected physico-chemical variables of the 49 study streams.

Variable	Units	Mean ± 1sd
Catchment characteristics		
Altitude	m a.s.l.	268 ± 154
Precipitation	mm	727 ± 132
Runoff	mm	394 ± 101
Annual temperature	°C	2.05 ± 2.30
Catchment area	km^2	414 ± 1878

Forest	%	74 ± 24
Mire	%	10 ± 10.5
Agriculture	%	0.796 ± 2.63
Urban	%	0.0593 ± 0.255
Water	%	2.96 ± 4.42
Water physicochemical		
Temperature	°C	5.31 ± 2.17
Conductivity	mS/m25	3.56 ± 3.17
pH		6.22 ± 0.84
Alkalinity/acidity	meq/L	0.133 ± 0.208
SO_4*	meq/L	0.065 ± 0.066
SO_4_IC	meq/L	0.070± 0.073
BC*	meq/L	0.269 ± 0.271
ANC	meq/L	0.198 ± 0.218
ANCalk	meq/L	0.191 ± 0.202
ANCmod1	meq/L	0.143± 0.207
ANCmod2	meq/L	0.152 ± 0.205
ANCmod3	meq/L	0.161 ± 0.204
ANCmod4	meq/L	0.170 ± 0.204
ANCmod5	meq/L	0.179 ± 0.203
ANC/H^+	unitless	3099 ± 13906
BC*/SSA*	unitless	5.16 ± 2.98
BC*/SO_4*	unitless	5.48 ± 3.22
Al_ICP	unitless	140 ± 104
WHAM Ali	µg/L	15.9 ± 35
Al^{3+}	µg/L	4.28 ± 17
H^+Al^{3+}	µeq/L	0.476 ± 1.89
Ca/Ali	unitless	11973 ± 35267
Ca/Al^{3+}	unitless	39600000 ± 403000000
Ca	meq/L	0.167± 0.241
Mg	meq/L	0.067 ± 0.044
Na	meq/L	0.08 ± 0.077
K	meq/L	0.011 ± 0.007
Cl	meq/L	0.049 ± 0.08
Fl	mg/L	0.120 ± 0.107
Si	mg/L	2.86 ± 0.93
NH_4-N	µg/L	13.6 ± 14.2
NO_2+NO_3-N	µg/L	72 ± 176
TP	µg/L	12.6 ± 9.03
TN	µg/L	387 ± 225
Water Color	Abs_filtered 420/5	0.179 ± 0.112
TOC	mg/L	9.06± 4.75

Indirect gradient analysis of physico-chemical variables

The first three PC-axes explained 64% of the variation in the dataset (n = 43 variables) (Table 3). The first axis explained 31.1% of the variance and was clearly related to acidity. For example, pH buffering capacity and the ratio ANC/H^+ were strongly correlated with this axis (loadings > 0.20). The second PC axis explained another 22.6% of the variance and was related to latitude (X-coordinate), and likely represents a gradient in temperature and hence potential productivity. Catchments classified as agriculture and SO_4* were positively, while latitude was negatively correlated with this axis. The third axis explained another 10% of the residual variance and seemed to represent a longitudinal gradient, with, for example, altitude and mean annual runoff negatively related to this axis. Most streams exhibited relatively low among-year variability in stream chemistry (Fig. 3). However, one stream (Lagbäcken) showed high among-year variability along the first PC axis. This stream had higher pH (6.66) and buffering capacity (alkalinity/acidity = 0.500 meq/L) in 2003 compared to the other four years (range pH 6.44-6.51and alkalinity/acidity 0.157 – 0.217 meq/L for 1999 to 2002).

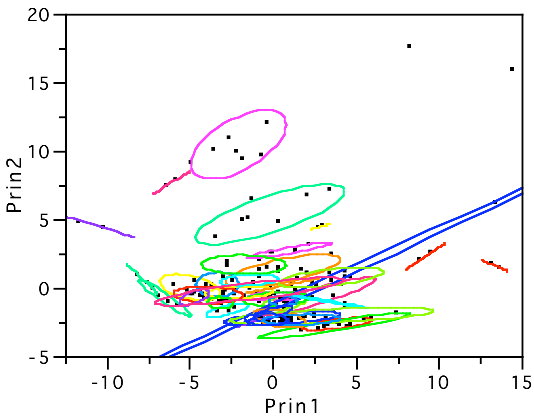

Figure 3. Streams plotted against PC axes 1 and 2. Ellipses show the 95% CL around the individual stream sites (i.e. among-year variance).

Table 3. Principle components analysis of selected physico-chemical variables of 49 streams. Annual mean values were used when available. Loadings ≥ 0.20 are shown in bold text.

	PC1	PC2	PC3
Eigenvalue	13.47	9.73	4.30
Percent	31.3	22.6	10.0
Cum Percent	31.3	54.0	64.0
		Eigenvectors	
X-coordinate	0.054	**-0.246**	0.145
Y- coordinate	-0.041	-0.145	**0.333**
Altitude (m a.s.l.)	0.093	-0.179	**-0.229**
Annual Precipitation (mm)	-0.082	0.199	-0.182

Annual Runnoff (mm)	0.028	-0.017	**-0.293**
Catchment area (km2)	0.018	0.021	**0.222**
% forest	-0.097	0.093	0.030
% mire	-0.024	-0.056	**0.237**
% agri	0.026	**0.252**	-0.016
%urban	-0.043	0.092	-0.061
% water	0.026	-0.008	0.049
% rock	-0.069	0.037	-0.165
pH	**0.233**	-0.095	-0.059
Alkalinity/Acidity (meq/l)	**0.267**	-0.013	-0.027
SO_4*	0.033	**0.279**	-0.027
BC* (meq/l)	**0.216**	0.176	0.061
ANC (meq/l)	**0.255**	0.048	0.096
ANCalk (meq/l)	**0.258**	0.032	0.074
ANCmod1	**0.268**	-0.007	-0.013
ANCmod2	**0.267**	0.000	0.002
ANCmod3	**0.267**	0.007	0.018
ANCmod4	**0.265**	0.014	0.034
ANCmod5	**0.263**	0.022	0.051
ANC/H^+	**0.222**	0.009	-0.056
BC*/SSA*	0.150	-0.160	0.063
BC*/SO_4*	0.148	-0.150	0.069
TOCc (mg/l)	-0.137	0.128	**0.283**
WHAM-modeled Ali (µg/L)	-0.162	0.098	-0.159
Al^{3+} (µg/L)	-0.131	0.057	-0.161
H^+Al^{3+} (µeq/l)	-0.131	0.057	-0.161
Ca/Ali	0.104	-0.058	-0.172
Ca/Al^{3+}	0.097	-0.059	-0.111
Ca (meq/l)	**0.216**	0.164	0.019
Mg (meq/l)	0.145	**0.237**	-0.003
Na (meq/l)	0.013	**0.270**	-0.074
K (meq/l)	0.091	**0.234**	0.137
Cl (meq/l)	-0.004	**0.272**	-0.123
Conductivity_25 (mS/m25)	0.104	**0.284**	-0.073
NH_4-N (µg/L)	-0.015	0.163	0.194
NO_2+NO_3-N (µg/L)	0.022	**0.267**	-0.039
TP (µg/L)	-0.033	0.103	**0.334**
TN_ps (µg/L)	-0.036	**0.261**	0.129
Water color (Abs._F 420/5)	-0.139	0.096	**0.325**

Stepwise linear regression

Stepwise regression of selected biological metrics showed that, with the exception of one metric (Shannon diversity), acidity variables were selected as the first explanatory variable (Table 4). Indeed, more than one acidity variable was often included in each of the four different models. The number of significant variables ranged from seven for Henrikson & Medin acid index to nine (taxon richness and Shannon diversity); coefficients of determination were > 85% for all models.

For taxon richness and Henrikson & Medin acid index min ANC was the first variable selected and explained 37.4% and 68.6%, respectively, of the among-stream variability of these metrics. The finding that ANC was a good predictor of the acid index tested here was not surprising since this metric weights acid sensitive/tolerant taxa differently. For EPT taxa, mean inorganic Al (WHAM-modeled) was the first variable selected and explained 38% of the variance in mayfly, stonefly and caddisfly taxa. Macroinvertebrate diversity was more correlated with mean annual runoff (24.5%); acidity variables were first included at step 5, Al explained 5.6% of the variance in diversity.

Table 4. Results of stepwise regression of selected biological metrics and physico-chemical metrics. Independent variables were geographic coordinates, catchment land use/cover and mean and extreme (min, max of acidity variables) water chemistry. SS = sum of squares, R^2 = proportion of the variation in the response variable that can be attributed to terms in the model rather than random error.

Step	*Parameter*	*Seq SS*	*RSquare*
	Taxon richness		
1	min ANC (meq/L)	705.4	0.374
2	min ANCalk (meq/L)	213.3	0.487
3	mean NH4-N (µg/L)	167.5	0.575
4	max H^+Al^{3+} (µeq/L)	129.6	0.644
5	Runnoff (mm)	142.6	0.719
6	mean Ca (meq/L)	70.1	0.757
7	mean TN (µg/L)	68.9	0.793
8	mean Ca/Ali	49.7	0.819
9	min Ca/Ali	63.8	0.853
	Shannon diversity		
1	Runnoff (mm)	3.37	0.245
2	mean TN (µg/L)	1.84	0.379
3	max TOCc (mg/L)	1.76	0.506
4	mean NO_2+NO_3-N (µg/L)	2.15	0.662
5	max Al_ICP (µg/L)	0.78	0.718
6	min Alk./Acid (meq/L)	1.22	0.807
7	mean NH_4-N (µg/L)	0.47	0.841
8	mean ANC/H^+	0.26	0.860
9	mean BC* (meq/L)	0.23	0.877
	EPT taxa		
1	mean WHAM-modeled Ali (µg/L)	485.3	0.380
2	% water	172.2	0.514
3	% agriculture	153.8	0.635
4	mean TN (µg/L)	141.2	0.745
5	X-coor	67.0	0.797
6	max SO_4* (meq/L)	36.0	0.826
7	mean NH_4-N (µg/L)	32.3	0.851
8	mean Ca/Al^{3+}	15.0	0.863
	Henrikson & Medin acid index		
1	min ANC (meq/L)	145.3	0.686
2	mean TOCc (mg/L)	12.4	0.745

3	mean K (meq/L))	9.1	0.788
4	max TOCc (mg/L)	5.0	0.811
5	min ANCalk (meq/L)	4.5	0.833
6	mean Ca/Al^{3+}	2.8	0.846
7	Runnoff (mm)	2.7	0.859

Direct gradient analysis (CCA)

Constrained ordination of stream macroinvertebrate assemblages and physico-chemical variables showed that the first CCA axis explained from 8.5% (Fennoskandian shield, ecoregion 2) to 13% (Central Plain, ecoregion 3) of the among-stream variance in community composition (Table 5). Year, run as a co-variable, explained less than 3% of the variance in each of the three models. Forward selection of significant (Bonferroni corrected p-values) variables was stopped at 10 variables. The resultant models explained from 28% (all regions) to 44% (Central Plain) of the variance in community composition after accounting for the effect of year.

Table 5. Summary results from CCA analysis of stream macroinvertebrate assemblages and physico-chemical variables. Year was run as a covariable.

		CCA axis	Eigenvalue	% Species variance
			All regions	
total inertia	*2.817*	1	0.251	9
sum of all eigenvalues	*2.795*	2	0.164	14.8
sum of all canonical eigenvalues	*0.784*	3	0.094	18.2
		4	0.077	20.9
			Fennoskandian shield	
total inertia	*2.825*	1	0.239	8.5
sum of all eigenvalues	*2.8*	2	0.171	14.6
sum of all canonical eigenvalues	*0.826*	3	0.127	19.2
		4	0.074	21.8
			Central Plain	
total inertia	*1.775*	1	0.224	13
sum of all eigenvalues	*1.726*	2	0.121	19.9
sum of all canonical eigenvalues	*0.758*	3	0.115	26.6
		4	0.081	31.3

The 10 “best” predictor variables varied among the regions studied here (Table 6, see also Appendix 1). When all regions were included in the analyses, ecoregion was the first variable selected accounting for 17% of the total variance (or inertia). Mean WHAM-modeled Al concentration explained another 15% of the residual variance, followed by longitude (Y coordinate, 8%), catchment area (5%) and % water in the catchment (5%). These latter three variables presumably are proxies for east to west and north to south gradients in climate (e.g. degree days) and precipitation. The remaining five variables represented gradients in altitude (step 7, 5%), runoff (step 10, 5%) and % water in the catchment (step 6, 5%), marine influence (median Cl, step 8, 5%) and the effects of urbanization (step 9, 5%)

In the Fennoskandian shield region, min pH was the first variable selected (accounting for 21% of the among-stream variability in stream benthos), followed by three variables indicative of catchment size (area, 10%) and land use (% agriculture, 12%; % urban 8%) and longitude (7%). Similar to when all regions were analyzed together, a latitudinal gradient was evident in the Fennoskandian shield dataset. For example, the three variables X-coordinate (latitude), % forest and runoff explained 4%, 6%, and 5%, respectively of the variability in macroinvertebrate assemblages. Two variables indicative of acid stress were selected in the first 10 steps; namely max Al^{3+} concentration (6%) and mean ratio between base cations and strong acids (BC*/SSA, 4%). λ_1 indicated that Al^{3+} concentration alone was strong predictor of macroinvertebrate communities (i.e. 19% of the variance was explained by this variable when no covariables were included).

In the southernmost region, three variables, namely runoff (step 1, 19%), altitude (step 2, 11%) and precipitation (step 3, 11%) explained 41% of the explained among-stream variance in community composition. Another three variables, % mire (step 5, 8%), max TOCc (step 7, 4%) and water color (absf, step 8, 4%), indicated the importance of terrestrial leaf litter on stream communities in the Central Plain region. However, similar to the Fennoskandian shield region, variables indicative of acid stress were also significant; median BC*/SS (step 6, 5%) and median ANC/H+ (step 10, 3%).

Comparison of the three models showed the importance of geographic variability (climate proxies and land use/cover) and acidity as robust predictors of community composition. For example, ecoregion delineation in the "all ecoregion" model and latitude and/or longitude were significant predictors in all three models. Climate variables were better correlated with stream assemblages in the southernmost region (Central Plain), whilst catchment land use/cover variables were better predictors of stream assemblages in the Fennoskandian shield. Regarding acid stress, more acid-variables were selected in the top 10 in the Central Plains regions (three variables explained 16% of the variance in stream communities). However, min pH alone explained 21% of the among-stream variance in the Fennoskandian shield.

Table 6. The first 10 significant variables selected in direct gradient analysis (CCA) of stream macroinvertebrate assemblages and physico-chemical variables. Lamda 1 (λ_1) shows the variability explained without covariables. Model shows the first ten significant variables (forward selection with Monte Carlo permutation tests and Bonferroni corrected p-values) and in parenthesis the variation explained with covariables. Year was run as a covariable.

Variable	λ_1 All ecoregions	model	λ_1 Fennoskandian shield	model	λ_1 Central Plain	model
Ecoregion	0.17	1 (17%)	na		na	
X-coordinate	0.16		0.11	9 (4%)	0.15	
Y-coordinate	0.09	4 (8%)	0.16	5 (7%)	0.17	9 (3%)
Altitude	0.12	7 (5%)	0.08		0.15	2 (11%)
Precipitation	0.09		0.06		0.17	3 (11%)
Runnoff	0.07	10 (5%)	0.05	8 (5%)	0.19	1 (19%)
Catchment area km^2	0.08	5 (5%)	0.1	3 (10%)	0.12	
% forest	0.09		0.07	6 (6%)	0.1	
% mire	0.04		0.08		0.1	5 (8%)
% agriculture	0.1	3 (8%)	0.12	2 (12%)	0.14	
% urban	0.05	9 (5%)	0.05	4 (8%)		
% water	0.15	6 (5%)	0.11		0.13	
mean BC*/SSA	0.1		0.11	10 (4%)	0.13	

mean WHAM Al	0.15	2 (15%)	0.2		0.07	
median ANC/H^+	0.15		0.2		0.1	10 (3%)
median BC*/SS	0.11		0.12		0.14	6 (5%)
median WHAM Al	0.14		0.19		0.07	4 (8%)
median Cl	0.05	8 (5%)	0.06		0.11	
median Abs._F	0.12		0.1		0.09	8 (4%)
min pH	0.14		0.21	1 (21%)	0.12	
max TOCc	0.08		0.11		0.07	7 (4%)
max Al^{3+}	0.15		0.19	7 (6%)	0.06	

<u>CCA with lag water chemistry variables</u>

CCA of stream macroinvertebrate assemblages and geographic, catchment characteristics and lag physico-chemical variables showed that the first CCA axis explained from 5.4% (Fennoskandian shield, ecoregion 2) to 14.4% (Central Plain, ecoregion 3) of the among-stream variance in community composition (Table 7). Year, run as a co-variable, explained from 1.2% (Fennoskandian shield) to 3.4% (Central Plain) of the variance in macroinvertebrate composition. Ten-variable models explained slight less variability compared to the non-time lag models above; from 21% (Fennoskandian shield) to 34% (Central Plain) of the variance in community composition was explained by lag physico-chemical variables.

Table 7. Summary results from CCA analysis of stream macroinvertebrate assemblages and geographic position, catchment characteristics and lag (t_l) physico-chemical variables. Year was run as a covariable.

		CCA axis	**Eigenvalue**	**% Species variance**
		Fennoskandian shield		
total inertia	*2.474*	1	0.131	5.4
sum of all eigenvalues	*2.445*	2	0.113	10
sum of all canonical eigenvalues	*0.503*	3	0.071	12.9
		4	0.053	15.1
		Central Plain		
total inertia	*1.658*	1	0.231	14.4
sum of all eigenvalues	*1.601*	2	0.133	22.8
sum of all canonical eigenvalues	*0.548*	3	0.117	31.1
		4	0.066	34.2

Table 8 shows the variance explained by the individual lag water chemistry variables. In both regions, geographic position (X and/or Y-coordinates) and cacthment characteristics explained more variance in macroinvertebrate composition compared to water chemistry. For example, catchment area explained 10% of the variance in the Fennoskandian shield and geographic position and runoff each explained 21% of the variance in the Central Plain ecoregion. Regarding acidity variables, mean Al^{3+} and mean WHAM-modeled Al each explained 5% of the variance for streams in the Fennoskandian shield, whereas mean SO4* and mean BC*/SSA each explained 15% of the variance in the Central Plain. Comparison of extant with lag water chemistry showed that whereas min pH was best predictor of stream composition in the Fennoskandian shield region, this variable in lag form explained only 3% of the variance (for extant values of λ_1 see Appendix 1). Similarly, for the Central Plain ecoregion lag values did not improve the explanatory power of the acidity variable. Lag median BC*/SS explained 14% (λ1) of the variance in stream composition in this region compared to ca 15% (mean).

Table 8. Lambda 1 (λ_1) values (variance explained with only year run as a covariable) CCA of stream macroinvertebrate assemblages and geographic position, catchment characteristics and lag (t_1) physico-chemical variables. Year was run as a covariable. Acidification metrics are shown in bold.

Fennoskandian shield (eco 2)		**Central Plain (eco 3)**	
Variable	*Variance explained*	*Variable*	*Variance explained*
mean BC*	**0.02**	**mean WHAM Al**	**0.05**
mean ANCmod4	**0.02**	**mean Ca/Ali**	**0.09**
mean ANCmod3	**0.02**	**mean ANC**	**0.10**
mean ANCmod2	**0.02**	mean TOCc	0.10
mean ANCmod1	**0.02**	**mean BC***	**0.10**
mean ANCmod5	**0.02**	**mean H^+Al^{3+}**	**0.10**
mean ANCalk	**0.02**	**mean Al^{3+}**	**0.10**
mean alkalinity/acidity	**0.02**	**mean ANCalk**	**0.10**
mean SO_4*	**0.03**	**mean Ca/Al^{3+}**	**0.11**
mean ANC	**0.03**	**mean ANCmod5**	**0.1**
mean pH	**0.03**	**mean ANCmod4**	**0.11**
mean ANC/H^+	**0.03**	**mean pH**	**0.11**
% urban	0.03	**mean ANCmod3**	**0.11**
Runnoff	0.03	**mean ANCmod2**	**0.11**
Precipitation	0.03	**mean ANC/H^+**	**0.11**
Altitude	0.04	**mean ANCmod1**	**0.11**
% agriculture	0.04	**mean alkalinity/acidity**	**0.11**
mean TOCc	0.04	% mire	0.12
Y-coordinate	0.04	% forest	0.12
mean Ca/Ali	**0.04**	**mean BC*/SO4**	**0.14**
mean H^+Al^{3+}	**0.04**	**mean BC*/SSA**	**0.15**
mean Ca/Al^{3+}	**0.04**	**mean SO_4***	**0.15**
mean WHAM Al	**0.05**	% water	0.15
mean Al^{3+}	**0.05**	Altitude	0.16
% water	0.06	Catchment area km^2	0.17
% mire	0.06	% agriculture	0.17
mean BC*/SO_4	**0.07**	Precipitation	0.19
mean BC*/SSA	**0.07**	X-coordinate	0.21
% forest	0.07	Y-coordinate	0.21
X-coordinate	0.09	Runnoff	0.21
Catchment area km^2	0.10		

pCCA with acidity variables as covariables

Partial constrained ordination (pCCA) was run to determine the combined influence of acidity variables on macroinvertebrate composition. The unique effect of acidity variables was similar between the Fennoskandian shield and Central Plain ecoregions (29.1% and 27.8%, respectively). By contrast, slightly more variance in community composition was accounted for by "other" environmental variables in the Central Plain ecoregion (39.0%) compared to the Fennoskandian shield (24.4%). Consequently, more variance remained "unexplained" in the Fennoskandian shield (46.5%) compared to the Central Plain (33.1%).

Setting class boundaries

Regression of selected biological and acidity metrics

Results of regression analysis of biological metrics and direct ordination of community composition revealed a number of acidity variables that explained significant amounts of the variance in macroinvertebrate assemblage composition. Linear regression was used to compare the response of three biological metrics to selected acidity gradients. Not surprisingly, the Henrikson & Medin acid index gave the best fit against several of the acidity variables (Table 9). Coefficients of determination ranged from 0.097 (mean BC*/SSA) to 0.451 (min pH). Taxon richness was also related to the acidity variables; with the exception of mean BC*/SSA all relationships were highly significant ($p < 0.0001$), however coefficients of determination were generally much lower than those noted for the Henrikson & Medin acid index. R^2 values ranged from 0.069 (mean WHAM-modeled Al) to 0.292 (min ANC). By contrast, results of Shannon diversity were equivocal; six of the eight relationships showed a significant response with the acidity variables, whist two (mean BC*/SSA and mean WHAM-modeled AL) did not and coefficients of determination were low (< 11%).

Table 9. Linear regression of selected acidity and biological variables. Coefficient of determination (R^2) and root mean square error (RMSEP) ; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. n = 255 observations.

	Taxon richness		Shannon diversity		Henrikson & Medin acid index	
	R^2	RMSEP	R^2	RMSEP	R^2	RMSEP
mean pH	0.10***	9.095	0.013*	0.8433	0.394***	2.253
min pH	0.131***	8.932	0.028**	0.8368	0.451***	4.749
mean alkalinity/acidity	0.067***	9.256	0.018*	0.8429	0.28***	2.455
min alkalinity/acidity	0.154***	8.816	0.056***	0.8247	0.383***	2.274
mean ANC	0.131***	8.932	0.038**	0.8326	0.276***	2.463
min ANC	0.292***	8.066	0.109***	0.8011	0.382***	4.749
mean BC*/SSA	0.015*	9.513	-0.004 (ns)	0.8503	0.097***	4.749
mean WHAM-modeled Al	0.069***	9.246	0.003 (ns)	0.8474	0.163***	2.648

Ecological breakpoints of threshold values

The Henrikson & Medin acid index was regressed against mean and minimum pH, ANC and inorganic Al (WHAM-modeled) to determine if biological threshold or breakpoints were evident (Figs. 4 – 6). According to Johnson et al. (2004), five class boundaries used for pH and four were used for ANC. For pH the five classes used are pH < 5 (class 5 = extremely acid) and 5 < pH ≤ 5.6 (class 4 = very acid), 5.6 < pH ≤ 6.2 (class 3 = acid), 6.2 < pH ≤ 6.8 (class 2 = weakly acid) and pH > 6.8 (class 1 = neutral-alkaline). For buffering capacity (ANC) the five classes are < 0 meq/L (class 1), 0 – 0.02 meq/L (class 2), 0.02 – 0.05 meq/L (class 3), 0.05 – 0.20 me/L (class 4) and > 0.20 meq/L (class 5). For WHAM-modeled inorganic Al, three classes were designated; namely, < 20 µg/L (class 1), 20 – 100 µg/L (class 2) and > 100 µg/L (class 3). A score of 6.0 is considered as the cutoff below which sites are deemed to be showing the effects of acid stress (Anonymous 1999).

Clear responses to mean and minimum pH were evident (Fig. 4). At pH < 5 the Henrikson & Medin acid index showed low scores < 3, indicating biological impairment. Moreover, the relatively low among-stream variance in acid scores (between 0 and 3) reinforces the conjecture that streams are very stressed. By contrast, class 4 (pH 6.2 – 6.8) and class 5 (pH > 6.8) showed considerable variation, with the majority of the sites having a Henrikson & Medin acid index score > 6. Slight differences were noted between the response of the acid index against mean versus minimum pH, with a threshold value (ca pH 6.5) being more evident when acid score values were plotted against minimum pH. These findings indicate that classes 1, 2 and 3 are affected by acid stress, but the somewhat higher variance associated with sites > pH 6 makes class delineation more difficult.

Streams with minimum ANC > 0.20 meq/L generally had acid scores > 6 (i.e. no or little impairment). This pattern was, however, not as evident when acid scores were plotted against mean ANC. Considerable variability was noted at ANC > 0.05 meq/L ANC (i.e. class 4 and 5), in particular when acid scores were plotted against mean ANC. No clear differences were noted between the two ANC classes 2 and 3 (i.e. scores with the ANC interval 0.02 to 0.05 meq/L varied 1 to 4). However, close to 0.020 meq/L the variance in acid index scores seemed to decrease and below this cut-level scores (three streams) were < 2.

The effects of inorganic Al on stream macroinvertebrate assemblages was assessed using two classes. At 20 µg/L Al effects on acid index scores were evident, with the exception of one stream having score > 6. The pattern was reinforced at Al concentrations > 100 µg/L. All stream sites had index scores < 5 and the majority (n = 6) had scores ≤ 2 when plotted against maximum Al.

In summary, plots of the Henrikson & Medin acid index showed significant relationships with in-stream measures of acidity. Comparison of the stream biological-acidity gradients with those studied by Johnson et al. (2004) suggest that streams display more variability across the acidity gradients studied here. For pH, the first three classes (i.e. class 1 to 3) showed gradual increases in acid index scores. The latter two classes (class 4 and 5), on the other hand, were not as clearly defined (higher variability) as those using lake assemblages (Johnson et al. 2004). Regarding buffering capacity (ANC), the two highest classes (class 4 and 5) showed high among-site variability, in particular when acid scores were regressed against mean ANC. Very low acid index scores were noted at inorganic Al concentration > 100 µg/L indicating biological impairment.

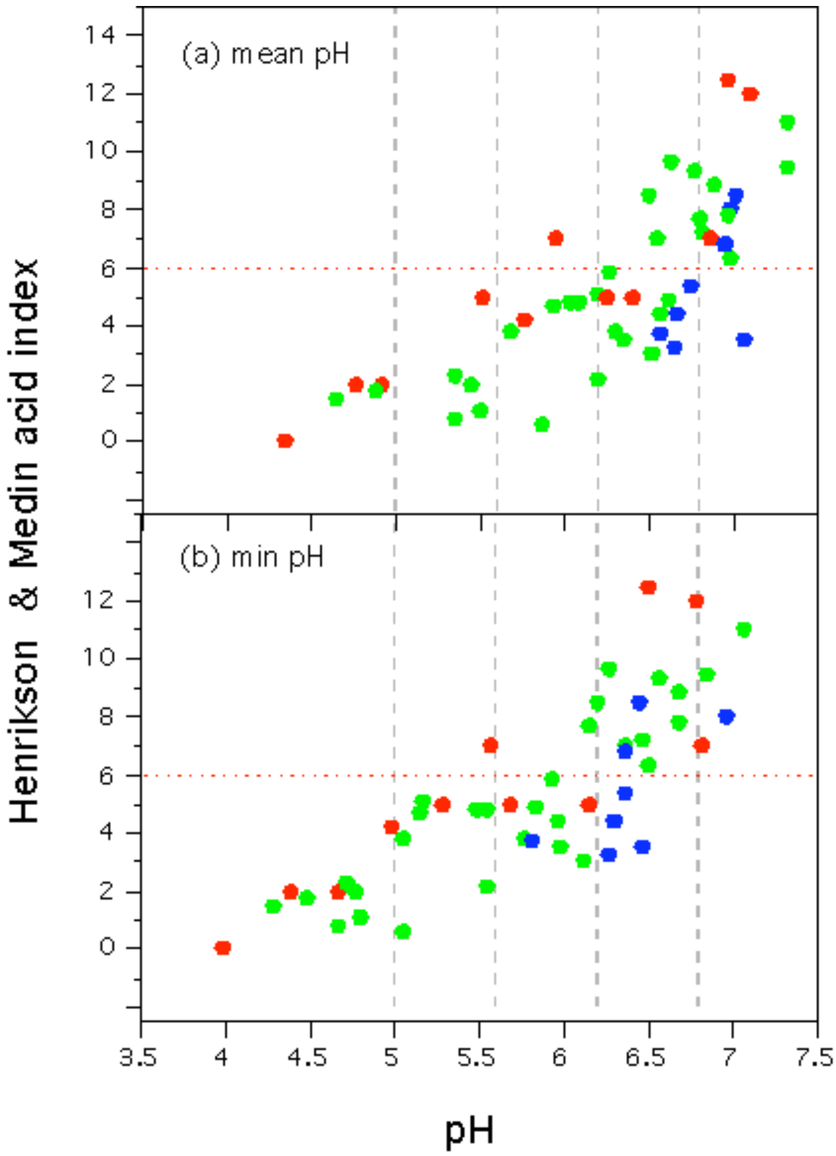

Figure 4. Scatter plots of Henrikson & Medin acid against mean (a) and minimum (b) pH (n = 49 streams). Vertical lines show the class boundaries defined by Johnson et al. 2004. The horizontal line shows the Henrikson & Medin acid index value of 6.0; according to Ecological Criteria this designates the borderline where acid-stress effects may occur (Anonymous 1999). Blue = Boreal Highland, green = Fennoskandian shield, red = Central Plain.

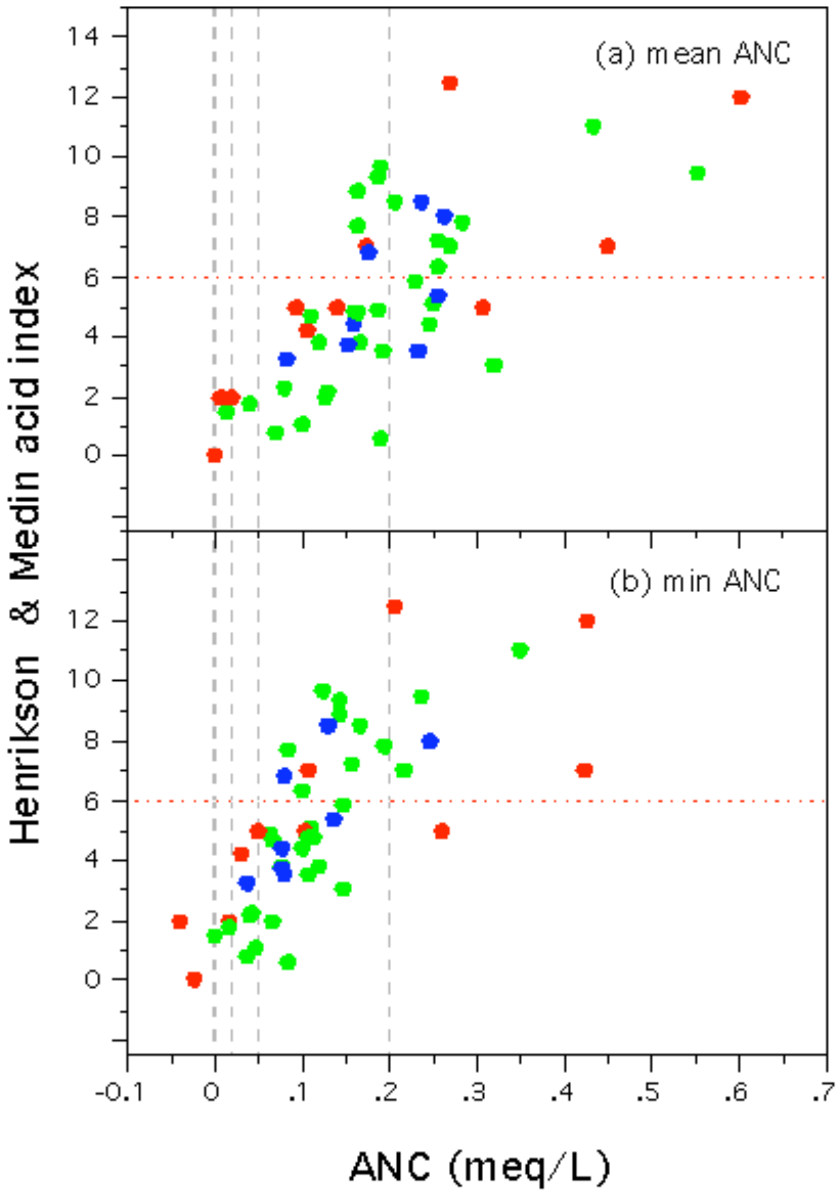

Figure 5. Scatter plots of Henrikson & Medin acid against mean (a) and minimum (b) ANC (n = 49 streams). Vertical lines show the class boundaries defined by Johnson et al. 2004. The horizontal line shows the Henrikson & Medin acid index value of 6.0; according to Ecological Criteria this designates the borderline where acid-stress effects may occur (Anonymous 1999). Blue = Boreal Highland, green = Fennoskandian shield, red = Central Plain.

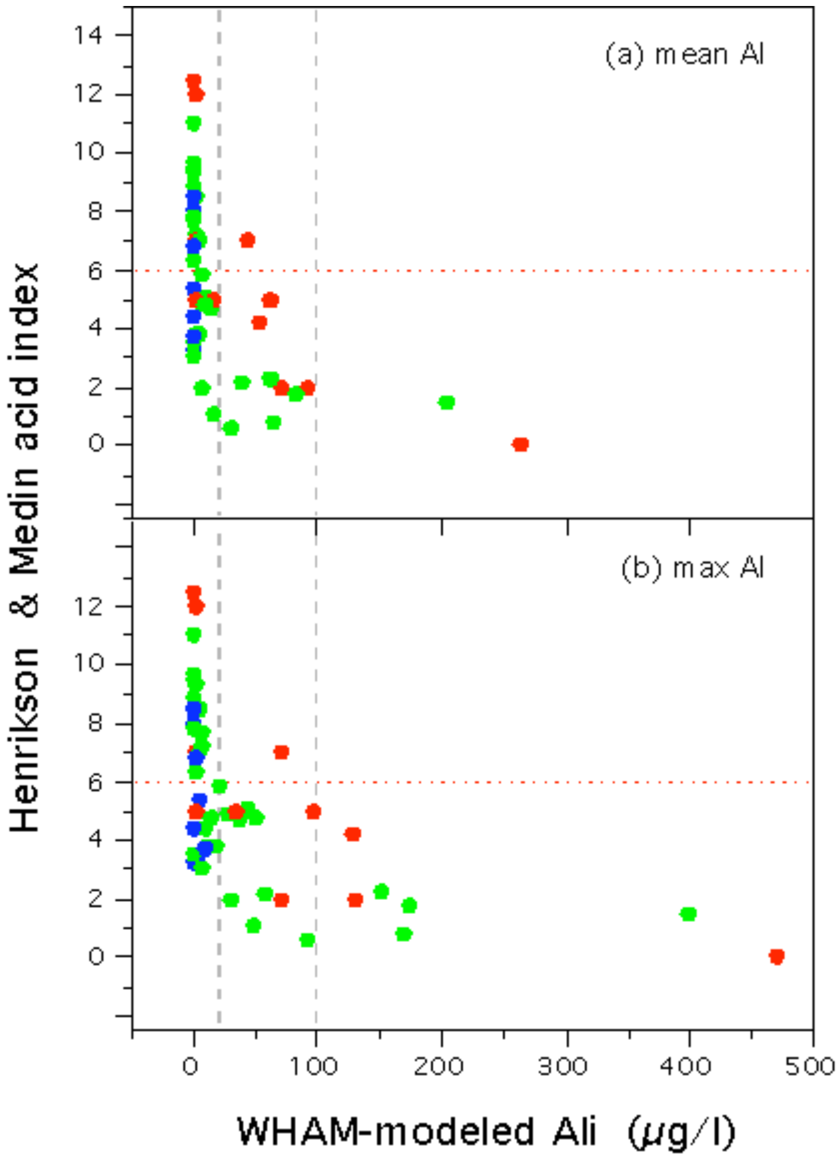

Figure 6. Scatter plots of Henrikson & Medin acid against mean (a) and maximum (b) WHAM-modeled Al (n = 49 streams). Vertical lines show the class boundaries defined by Johnson et al. 2004. The horizontal line shows the Henrikson & Medin acid index value of 6.0; according to Ecological Criteria this designates the borderline where acid-stress effects may occur (Anonymous 1999). Blue = Boreal Highland, green = Fennoskandian shield, red = Central Plain.

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Appendix 1. Summary of results from direct gradient analysis (CCA) of stream macroinvertebrate assemblages and physico-chemical variables. Lamda 1 (λ_1)shows the variability explained without covariables. Model shows the first ten significant (Bonferroni corrected p-values) variables and in parenthesis the variation explained with covariables.

Variable	All ecoregions λ_1	model	Fennoskandian shield (eco 2) λ_1	model	Central Plain (eco 3) λ_1	model
Ecoregion	0.17	1 (17%)	na		na	
X-coordinate	0.16		0.11	9 (4%)	0.15	
Y-coordinate	0.09	4 (8%)	0.16	5 (7%)	0.17	9 (3%)
Altitude	0.12	7 (5%)	0.08		0.15	2 (11%)
Precipitation	0.09		0.06		0.17	3 (11%)
Runnoff	0.07	10 (5%)	0.05	8 (5%)	0.19	1 (19%)
Catchment area km^2	0.08	5 (5%)	0.10	3 (10%)	0.12	
% forest	0.09		0.07	6 (6%)	0.10	
% mire	0.04		0.08		0.10	5 (8%)
% agriculture	0.10	3 (8%)	0.12	2 (12%)	0.14	
% urban	0.05	9 (5%)	0.05	4 (8%)		
% water	0.15	6 (5%)	0.11		0.13	
mean pH	0.15		0.20		0.11	
mean alkalinity/acidity	0.09		0.11		0.09	
mean SO_4*	0.05		0.04		0.11	
mean BC*	0.05		0.09		0.07	
mean ANC	0.08		0.12		0.08	
mean ANCalk	0.07		0.10		0.09	
mean ANCmod1	0.08		0.11		0.09	
mean ANCmod2	0.08		0.11		0.09	
mean ANCmod3	0.08		0.11		0.09	
mean ANCmod4	0.08		0.11		0.09	
mean ANCmod5	0.07		0.10		0.09	
mean ANC/H+	0.13		0.16		0.10	
mean BC*/SSA	0.10		0.11	10 (4%)	0.13	
mean BC*/SO_4	0.09		0.11		0.12	
mean TOCc	0.13		0.10		0.07	
mean WHAM Al	0.15	2 (15%)	0.20		0.07	
mean Al^{3+}	0.14		0.16		0.07	
mean H^+Al^{3+}	0.11		0.12		0.07	
mean Ca/Ali	0.10		0.14		0.11	
mean Ca/Al^{3+}	0.12		0.12		0.10	
mean Ca	0.05		0.08		0.10	
mean Mg	0.07		0.11		0.09	
mean K	0.06		0.07		0.08	
mean Cl	0.05		0.06		0.10	
mean conductivity	0.04		0.07		0.09	
mean NH_4-N	0.12		0.05		0.04	
mean NO_2+NO_3-N	0.12		0.12		0.16	
mean TP	0.07		0.09		0.15	
mean Abs._F	0.12		0.11		0.10	

median pH	0.16		0.20		0.10	
median Alkalinity/Acidity	0.10		0.12		0.10	
median SO_4*	0.05		0.05		0.10	
median BC*	0.06		0.10		0.08	
median ANC	0.08		0.11		0.09	
median ANCalk	0.07		0.10		0.10	
median ANCmod1	0.10		0.12		0.10	
median ANCmod2	0.09		0.12		0.10	
median ANCmod3	0.09		0.11		0.10	
median ANCmod4	0.08		0.11		0.10	
median ANCmod5	0.08		0.11		0.10	
median ANC/H^+	0.15		0.20		0.10	10 (3%)
median BC*/SS	0.11		0.12		0.14	6 (5%)
median BC*/SO_4	0.10		0.12		0.13	
median TOCc	0.14		0.10		0.07	
median WHAM Al	0.14		0.19		0.07	4 (8%)
median Al^{3+}	0.06		0.07		0.09	
median H^+Al^{3+}	0.04		0.05		0.09	
median Ca/Ali	0.11		0.16		0.10	
median Ca/Al^{3+}	0.15		0.18		0.11	
median Ca	0.05		0.08		0.10	
median Mg	0.06		0.13		0.09	
median K	0.06		0.07		0.08	
median Cl	0.05	8 (5%)	0.06		0.11	
median conductivity	0.04		0.08		0.09	
median NH_4-N	0.12		0.06		0.07	
median NO_2+NO_3	0.14		0.12		0.13	
median Tot-P	0.08		0.08		0.15	
median Abs._F	0.12		0.10		0.09	8 (4%)
min pH	0.14		0.21	1 (21%)	0.12	
min Alkalinity/Acidity	0.09		0.13		0.07	
max $_{SO4}$*	0.03		0.02		0.12	
min BC*	0.11		0.14		0.04	
min ANC	0.13		0.17		0.04	
min ANCalk	0.09		0.12		0.05	
min ANCmod1	0.09		0.13		0.06	
min ANCmod2	0.09		0.13		0.06	
min ANCmod3	0.09		0.12		0.05	
min ANCmod4	0.09		0.12		0.05	
min ANCmod5	0.09		0.12		0.05	
min ANC/H+	0.13		0.20		0.09	
min BC*/SO_4	0.11		0.16		0.08	
min BC*/SO4	0.10		0.15		0.08	
max TOCc	0.08		0.11		0.07	7 (4%)
max WHAM Al	0.14		0.20		0.08	
max Al^{3+}	0.15		0.19	7 (6%)	0.06	
max H^+Al^{3+}	0.14		0.17		0.06	
min Ca/Al	0.11		0.17		0.11	
min Ca/Al	0.14		0.19		0.12	
min Ca	0.10		0.13		0.08	

min Mg	0.10	0.15	0.06
min K	0.09	0.09	0.08
max Cl	0.05	0.05	0.07
max NO_2+NO_3-N	0.09	0.10	0.13
TOC_flood		0.07	0.06
ANC_flood		0.14	0.11
pH_flood		0.14	0.09