OIKOS 104: 149–155, 2004

Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams

Olivier Dangles, Björn Malmqvist and Hjalmar Laudon

Dangles, O., Malmqvist, B. and Laudon, H. 2004. Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. – Oikos 104: 149–155.

Acidification has strongly affected natural ecosystems due to the deposition of acidifying pollutants in geographical areas with low buffering capacity. Here we show both that taxonomic richness of benthic invertebrates (as a measure of stream health) and breakdown rate of leaf litter (a major process in stream ecosystems) in three naturally acid streams were not significantly different from richness and breakdown rates of three circumneutral control streams in the same area in northern Sweden. In contrast, a comparative data-set representing a gradient from circumneutral to acidified streams in France showed decreasing richness and litter breakdown rates (by 60% and 70% between pH 6.5 and 4.5, respectively) typical of acidified streams. The strong negative effects found in many freshwater systems may be a consequence of low capacity to adjust to rapidly changed conditions. In contrast, organisms in naturally acidic systems, such as streams of the boreal region in catchments with accumulating organic material and a geology poor in buffering substances, seem better adapted as a consequence of protracted exposure to low pH over evolutionary time. These results have implications for the management of streams and rivers in northern Sweden, where considerable efforts are spent on remediation without consideration of the fact that the natural state of many of these systems is acidic.

O. Dangles and B. Malmqvist, Dept of Ecology and Environmental Science, Umeå Univ., SE-90187 Umeå, Sweden. Present address of OD: Institut de Recherche en Biologie de l'Insecte, UMR CNRS 6035, Faculté des Sciences et Techniques, Université François Rabelais, FR-37200 Tours, France (olivier.dangles@univ-tours.fr). – H. Laudon, Dept of Forest Ecology, Swedish Univ. of Agric. Sci., Umeå, SE-901 83, Sweden.

In the past few decades, it has become increasingly clear that acidification negatively affects species diversity and ecosystem function of freshwaters (Schindler 1988, Brakke et al. 1994). Freshwaters may be acid either through impact from strong inorganic acids from atmospheric deposition or by natural processes from organic acidity, or both. In many cases where naturally acidic surface waters occur, anthropogenic acidification can be superimposed on the natural condition exacerbating the acidity of the system. In this context, an important discovery in recent developments of hydrochemical models aiming at disentangling the various sources of acidity (Bishop et al. 2000, Laudon et al. 2001a) was, however, the strong geographic variation in the anthropogenic contribution to low pH values. In areas with low deposition of acidifying substances, natural causes of low pH tend to predominate (Laudon et al. 2001a, Rapp 2001).

Many boreal ecosystems have acidified gradually since the last glaciation (Renberg et al. 1993). Slow weathering rates in combination with the development of peat and wetlands cause low buffering capacity and high levels of natural organic acidity, which are common features of the histosol system throughout a considerable part of the boreal biome (Fitzpatrick 1983). In northern Sweden, such natural processes have lead to a situation where approximately 10% of the country's over 80 000 lakes, most of them in the boreal zone, are

Accepted 17 June 2003

ISSN 0030-1299

naturally acid having a pH below 6.0 (Rapp 2001). Naturally acidifying processes have been shown to be prevalent and important also in freshwaters in other parts of the world, including eastern USA (Driscoll et al. 1989, McGeorge et al. 1991), Nova Scotia (Gorham et al. 1986), northern Great Britain (Jones 1948), parts of the Amazon basin (Williams 1968) and in westland New Zealand (Collier et al. 1990).

The current knowledge of pH-associated changes in aquatic ecosystems mainly derives from studies of recently acidified clearwater habitats. The present view regarding the causes of freshwater acidification does often not consider naturally occurring acids despite the fact that ecological responses can be expected to differ from those in acidified systems. In this study, we argue that while anthropogenic acidification is a recent phenomenon (Battarbee et al. 1989, Jüttner et al. 1997) its effects on biological communities and processes are more severe than are those of natural acidity, which must have been present much longer – for evolutionary time. Thus, we expect to find that systems in regions with a high degree of natural acidity have "adapted" to such conditions (Collier et al. 1990). In this study, we test the two hypotheses that naturally acid streams have comparable species richness to circumneutral stream and that ecosystem processes similarly are not significantly retarded. We have chosen to test the hypotheses using macroinvertebrate taxonomic richness and litter breakdown rates in a set of three acid and three circumneutral streams in central Scandinavia. Leaf litter is the energetic basis of production in low-order streams and its breakdown is a central ecosystem process lending itself as a useful model process (Gessner and Chauvet 2002). To emphasise the difference between acidified and naturally acid streams we also contrast our results with a set of corresponding data on acidified and circumneutral streams from north-eastern France.

Material and methods

Six streams, with high levels of dissolved organic carbon (DOC), were selected in the county of Västerbotten (northern Sweden), a region which has long been regarded as a reference area, not significantly affected by acid deposition (Warfvinge et al. 1995). Three of these were control streams having permanently slightly acidic to circumneutral (pH 6.0–6.6) water, whereas the other three streams showed low pH-values (4.0–4.6) prone to drop in connection with run-off events (Table 1). The hydrochemistry of all streams, excluding Kullabäcken, was monitored in the Episode Project 1996–2001 in northern Sweden (Laudon et al. 2001a, b). Acid neutralising capacity, pH, conductivity and DOC were also analysed for all streams on three occasions over the study period (August 2001–November 2001) using sampling and analytical techniques described in detail by Laudon et al. (2001a).

Breakdown of alder (*Alnus incana* L.) leaves collected just before abscission was measured as mass loss using 4.0 g of air-dried (Gessner et al. 1999) leaves in litterbags of two different mesh sizes (0.3 and 5 mm). Despite potential drawbacks (Bärlocher 1997), the use of fine mesh bags provides relevant data on the contribution of microbes and shredding invertebrates (Dangles and Guérold 2001). Ten replicate bags of each type were secured to the bank with plastic-coated wire. The exposure started in early September 2001 and lasted for 8 weeks, a time sufficient to show considerable leaf mass loss. After retrieval the remaining leaf material was weighed after drying (48 h at 50°C) and ashing (4 h at 550°C) and decomposition rates estimated after adjustment for initial leaching (48 h).

Macroinvertebrates were sampled by taking 10 quantitative, random Surber samples (area 0.05 m^2, mesh size 0.20 mm) within a 50 m study reach of each stream. Animals were identified to species (except for chironomids, oligochaetes and very young larvae) and were dried and weighed as above.

Macroinvertebrate richness was estimated for each of the six streams using a Pareto-style extrapolation (Turner et al. 2001): $S = P^{(1 - N^{-qN^{q}})}$, where S is the number of species and N is the number of individuals in the sub-set of samples; P is the estimated number of species and q is the parameter of curvature of the collector's curve. The procedure used sample and indi-

Table 1. Description of the study streams in Sweden. pH, DOC and ANC_{Gran} are range values. Measured values at the time of sampling in the present study are given in brackets.

Stream	Catchment size (km^2)	Location	Number of samples	pH	DOC (mg l^{-1})	$ANC^{\dagger}_{Gran}$ (μEq l^{-1})
Control streams						
Sörbäcken	62	64 20′ N 18 39′ E	54	5.68–6.98 (6.58)	8–21 (17)	24–410 (154)
Bladtjärnsbäcken	40	63 42′ N 18 59′ E	15	5.90–6.74(6.49)	8–18 (14)	73–181 (84)
Kullabäcken	20	63 52′ N 20 11′ E	9	5.82–6.44 (5.97)	9–13 (12)	72–150 (124)
Naturally acidic streams						
Stridbäcken	10	63 31′ N 19 18′ E	179	3.97–5.29 (4.05)	9–21 (17)	−109–18 (−64)
Pålböleån	112	63 57′ N 20 36′ E	15	4.26–5.97 (4.37)	16–39 (33)	−48–77 (−22)
Åhedån	61	63 41′ N 19 56′E	26	4.21–6.58 (4.62)	11–41 (26)	−30–200 (19)

† Average charge balance ANC (acid neutralization capacity) converted to ANC_{Gran} (Köhler et al. 2000).

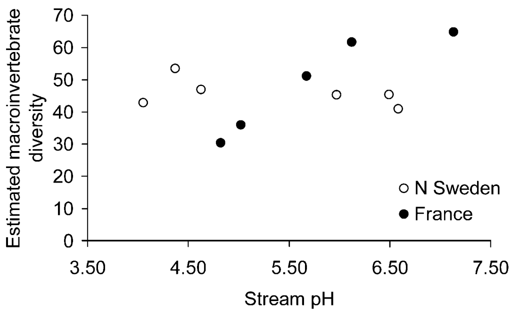

Fig. 1. Estimated benthic macroinvertebrate taxonomic richness vs pH in N Swedish and French streams.

vidual shuffling, sampling without replacement, in 500 runs. Similar results were achieved when using observed species richness and with rarefied species richness (Gotelli and Colwell 2001).

Non-metric multidimensional scaling (NMDS) was carried out to examine the patterns of biological similarity with respect to benthic assemblages among sites. This ordination method attempts to maximise the fit between measured dissimilarities (we used Bray-Curtis coefficients) and distance between resulting data points within a predefined number of spatial dimensions (Legendre and Legendre 1998). The goodness of fit was estimated with a stress function, which ranges from 0 to 1, with values close to zero indicating a good fit. We further determined which species contributed most to distinguishing the two types of streams (acid and neutral) by performing a SIMPER analysis on density data for all macroinvertebrate taxa. Both analyses were carried out using the ecological community analysis package PRIMER v5 (Clarke and Gorley 2001) after square root transformations.

A parallel study was performed in November 1999 on a set of five streams in the Vosges Mountains (NE France), a region subjected to recent anthropogenic acidification as a result of atmospheric deposition (Dambrine et al. 1998). The selected streams presented a gradient in acidification status (pH 4.8–7.1) due to small-scale differences in mineral composition of the underlying bedrock (Dangles et al. 2001 for details on stream chemistry). The French material was derived in a very similar manner except for using *Alnus glutinosa* (Gaertner) leaves in four replicate litter bags of each type (Dangles 2000).

We used a two-way ANOVA on log-transformed data to test for the effects of location (Sweden vs France) and acidity status (circumneutral vs acid) on macroinvertebrate taxonomic richness. We are aware that using data-sets obtained in different studies is not ideal for ANOVAs. The high similarity of the two experimental protocols and the high repeatability of the French results over time (1996–2000) should, however, make our test acceptably robust. Differences in breakdown rates among Swedish sites (using percent leaf mass loss as response variable) were tested in one-way ANOVA. Regression analysis was used to assess the effect of stream pH on litter breakdown in the French streams. All analyses were performed using Statistica 5.5 for Windows.

Results

We found no significant difference in taxonomic richness among the Swedish streams whereas in the French study a 60% reduction in richness was observed (Fig. 1). In the 2-way ANOVAs there was no difference in taxonomic richness between regions (N Sweden, France): $F_{1,6} = 1.71$; $p > 0.05$, a significant effect of acidity: $F_{1,6} = 10.47$; $p = 0.018$, and a significant interaction term, region × acidity $F_{1,6} = 19.98$; $p = 0.0048$ due to the richness difference in French streams coupled to acidity but lack of such a difference among Swedish streams. An interesting feature of the humic streams was that they supported a very distinctive fauna compared to circumneutral ones: 27% of the taxa in the Swedish streams were found exclusively in the naturally acid streams, as compared to only 4.2% in the French acidified streams.

The NMDS ordination described further the overall differences in community composition among the Swedish streams (Fig. 2). Stress was low (0.01) indicating a high degree of representation. Axis 1 of the NMDS was strongly correlated (Spearman rank correlation, $P < 0.001$) with pH ($r = 0.94$) followed by ANC ($r = 0.89$). Axis 2 was best correlated with the area of the stream catchment ($r = 0.60$). In the NMDS "map"

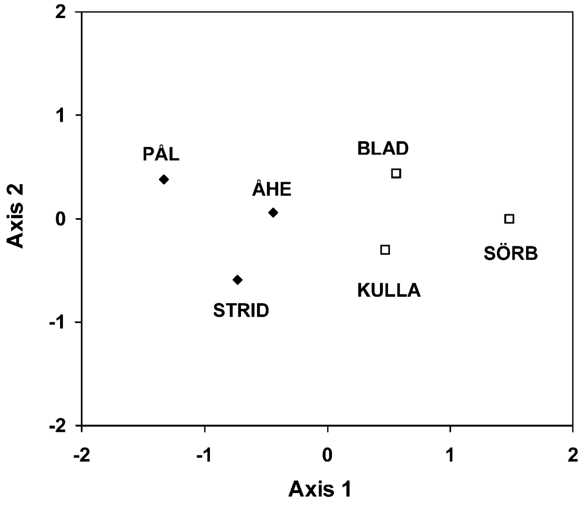

Fig. 2. NMDS plot of sites based on macroinvertebrate data from six Swedish streams. Neutral control streams (Kullabäcken, Bladtjärnsbäcken, Sörbäcken) are shown as open squares and naturally acidic (Stridbäcken, Pålböleån, Åhedån) streams as black diamonds.

showing the biological similarities the naturally acid streams were well separated from the circumneutral ones. The SIMPER analysis indicated that 16 (including Simuliidae, and early instar larvae of *Nemoura* and *Leuctra*) of the 30 most discriminatory taxa between neutral and acid streams were more abundant in the latter (Table 2). Ephemeropterans (*Baetis*, *Nigrobaetis muticus/niger* and *Ephemerella aurivillii* but not *Leptophlebia marginata*) along with the beetle *Elmis aenea* were among the discriminatory taxa being more abundant in the neutral streams. With regard to shredders small nemourid and leuctrid stonefly larvae as well as those of *Amphinemura borealis* were more abundant in the acid streams, whereas *Leuctra fusca/digitata* and *Protonemura meyeri* were more common in the neutral ones.

Leaf litter breakdown experiments did not reveal any significant differences in breakdown rates among the Swedish streams (coarse mesh bags: ANOVA, $F_{1,4} = 0.18$, $p = 0.696$; fine mesh bags: $F_{1,4} = 1.80$, $p = 0.251$, Fig. 3). This was in contrast to the observations in France, where breakdown was exponentially reduced with decreasing pH (coarse mesh bags: $y = 2.21\ e^{0.52x}$, $r^2 = 0.989$, $p < 0.0001$; fine mesh bags: $y = 6.56\ e^{0.27x}$, $r^2 = 0.925$, $p < 0.0001$).

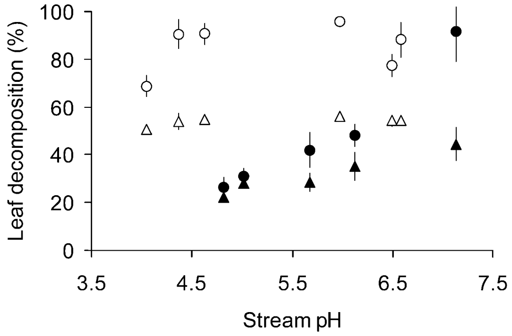

Fig. 3. Leaf mass loss in coarse (circles) and fine (triangles) mesh bags vs pH in N Swedish (open symbols) and French (closed symbols) streams. Means ± 1 SD are shown (N = 10 Sweden; N = 4 France).

Discussion

Our results show that recent anthropogenic acidification has more severe effects on biological communities and processes than has natural acidity. The reductions in taxonomic richness seen in the French streams, and in other acidified streams in the USA and Europe, have all been of similar magnitude (Hildrew et al. 1984,

Table 2. Results of SIMPER analysis for benthic fauna in Swedish streams showing average abundances (ind m^{-2}); percent contribution of each taxon to average dissimilarity (51.1) between the two groups: 'acidic' and 'neutral' streams. Only taxa that contributed up to a total of 75% to the separation of the groups are listed.

Taxa	Average abundances		
	Acid streams	Neutral streams	% contribution
Nemoura	2260	172	8.3
Baetis	0	1185	6.7
Undetermined Simuliidae	2366	990	6.0
Leuctra	596	75	3.7
Elmis aenea Müller	24	509	3.4
Undetermined Chironomidae	3913	5805	3.3
Leptophlebia marginata L.	255	2	3.0
Nigrobaetis muticus/niger	17	269	3.0
Ephemerella aurivillii Bengtsson	0	145	2.4
Simulium (gr. *ornatum*)	22	245	2.3
Simulium (gr. *vernum*)	435	133	2.3
Baetis rhodani Pictet	0	249	2.2
Isoperla grammatica Poda	205	25	2.0
Orthocladiinae	215	38	1.9
Oligochaeta	212	277	1.9
Amphinemura borealis Morton	151	23	1.9
Polycentropus flavomaculatus Pictet	162	0	1.9
Leuctra fusca/digitata	110	245	1.8
Protonemura meyeri Pictet	27	167	1.8
Simulium argyreatum Meigen	1	103	1.8
Ithytrichia sp.	152	0	1.6
Asellus aquaticus L.	44	0	1.5
Hydraena	0	61	1.5
Limnephilinae (instars < III)	151	96	1.4
Capnopsis schilleri Rostock	69	49	1.4
Taeniopteryx nebulosa L.	103	31	1.3
Sericostoma personatum Kirby & Spence	1	31	1.3
Diura nanseni Kempny	0	30	1.2
Baetis digitatus Bengtsson	31	49	1.2
Plectrocnemia conspersa Curtis	55	9	1.1
Brachyptera risi Morton	47	11	1.1

Rosemond et al. 1992, Braukmann 2001) as have those observed in anthropogenically acidified streams in south Sweden (Otto and Svensson 1983, Kullberg 1992). Similarly, the reduced leaf breakdown rates observed in the French sites are in accordance with studies in other acidified regions (Chamier 1987, Griffith and Perry 1993). In naturally acidic streams of northern Sweden neither the taxonomic richness of benthic invertebrates nor the breakdown rate of leaf litter was significantly different from richness and breakdown rates of circumneutral control streams in the same area. These results suggest that organisms in naturally acidic freshwater have become adapted through the protracted exposure to low pH over evolutionary time, but also that species composition was different between neutral and acid streams suggesting that species-specific preferences or tolerances may have been involved (Table 2). Further studies including more streams would be needed to verify whether the patterns observed regarding specific differences remain consistent with respect to acidity.

To our knowledge, only the study by Collier et al. (1990) in New Zealand has made comparisons between naturally acidic brown water and anthropogenically acidified clearwater streams. They proposed the existence of adapted stream communities in naturally acid streams, although the evidence they presented in support of the hypothesis was rather weak. In different regions of Europe there is considerable variation in the abilities of macroinvertebrate populations to cope with acidic conditions (Raddum and Skjelkvale 2001). Although dispersal will act as a strong evolutionary force promoting genetic homogeneity, isolation of benthic macroinvertebrate sub-populations, particularly in environments of steep environmental gradients, such as boreal streams, can lead to genetic differentiation of populations through local adaptation or genetic drift. In this sense, an extreme environment, such as a very acid stream, may offer unique conditions favouring the selection for unusual functional adaptations. An alternative hypothesis would be that natural acidity provides a profoundly different environmental filter (sensu Poff 1997), selecting species from a regional pool that possesses traits suitable for coping with extreme environments.

In addition to evolutionary explanations, at least two circumstances may contribute to the seemingly low perturbation of naturally acidic streams in the boreal biome. First, high levels of dissolved humic substances may ameliorate the toxicity of metals, primarily of aluminium, which has documented toxic effects on biota in acidified freshwaters (Driscoll et al. 1980). Where low pH is brought about naturally by high concentration of organic acids, most dissolved aluminium is rendered non-toxic through complexation with dissolved organic matter. Second, fish are sensitive to low pH and tend to be present in reduced numbers, or even disappear from such streams. In the present study, fish have clearly been eradicated from French acidified streams but their exact status in the Swedish acid streams remains uncertain. The information available from repeated electrofishing surveys in these streams by the regional government comes primarily from other parts of the catchments, which, however, all have fish, including brown trout. Absence of fish may favour such invertebrate taxa that are sensitive to fish predation (Stenson 1985), although separating the indirect effects of fish presence from those of acidity would require further investigation.

We think that the current focus on recently acidified streams may have created a misleading picture of the functioning of lotic environments with low pH. Similar conclusions were reached by Perakis and Hedin (2002), who showed that features of dissolved nitrogen transport in rivers differed between intensively disturbed temperate ecosystems where nitrogen is largely present in inorganic form, and unpolluted South American ecosystems, where transported nitrogen is mainly organic. In an analogous way, acidifying compounds in acidified streams mainly consist of inorganic sulphates and nitrates whereas they are mostly present as organic humic acids in naturally acid streams. Although significant progress has been made to reduce acidifying emissions and to mitigate negative effects in freshwater environments by liming affected waters and their catchments (Stoddard et al. 1999, Driscoll et al. 2001), the discussion over the last decades regarding the causes of freshwater acidification has rarely included the influence of naturally occurring acids.

Considering acidity's current importance in environmental management plans and for understanding surface water recovery, there is both practical and theoretical interest in determining to what extent water acidity has an effect on both the structure and function of stream systems. Moreover, studies of naturally acid systems are rare despite the potentially great value of understanding the extent to which their biota are able to adapt and how well such systems perform in comparison with circumneutral systems. In this context, important as our results are for understanding the functioning of naturally acid ecosystems in boreal forested regions, this study also has specific implications. For example, in Sweden the costs for liming freshwater ecosystems with the specific objective of restoring the natural biodiversity of 8000 lakes and 12000 km of streams (Appelberg and Svenson 2001) amount to approximately US$25 million annually since 1991 (Bishop et al. 2001). We believe that the management of boreal streams and rivers would be considerably improved by taking into consideration the fact that the natural state of many of these systems is acidic.

Acknowledgements – The authors are grateful to Kevin Bishop, Jérôme Casas, Mark Gessner and Simon Rundle for helpful comments on the manuscript. This research was supported by the European Science Foundation (LINKECOL Programme) to O.D. at the University of Umeå.

References

Appelberg, M. and Svenson, T. 2001. Long-term ecological effects of liming – The Iselaw Programme. – Water Air Soil Pollut. 130: 1745–1750.

Bärlocher, F. 1997. Pitfalls of traditional techniques when studying decomposition of vascular plant remains in aquatic habitats. – Limnetica 13: 1–11.

Battarbee, R. W., Stevenson, A. C., Rippey, B. et al. 1989. Causes of lake acidification Galloway, south-west Scotland: a paleoecological evaluation of the relative rates of atmospheric contamination and catchment change for two acidified lakes with non-afforested catchment. – J. Ecol. 77: 651–672.

Bishop, K., Laudon, K., Hruska, J. et al. 2001. Does acidification policy follow research in northern Sweden? The case of natural acidity during the 1990's. – Water Air Soil Pollut. 130: 1415–1420.

Bishop, K. H., Laudon, H. and Köhler, S. 2000. Separating the natural and anthropogenic components of spring flood pH decline: a method for areas that are not chronically acidified. – Water Resour. Res. 36: 1873–1884.

Brakke, D. F., Baker, J. P., Bohmer, J. et al. 1994. Physiological and ecological effects of acidification on aquatic biota. – In: Steinberg, C. E. W. and Wright, R. F. (eds), Acidification of freshwater ecosystems: implication for the future. John Wiley & Sons Ltd, pp. 275–312.

Braukmann, U. 2001. Stream acidification in south Germany: chemical and biological assessment methods and trends. – Aquat. Ecol. 35: 207–232.

Chamier, A.-C. 1987. Effect of pH on microbial degradation of leaf litter in seven streams of the English Lake District. – Oecologia 71: 491–500.

Collier, K. J., Ball, O. J., Graesser, A. K. et al. 1990. Do organic and anthropogenic acidity have similar effects on aquatic fauna? – Oikos 59: 33–38.

Clarke, K. R. and Gorley, R. N. 2001. PRIMER v5: User manual/tutorial. Plymouth Marine Laboratories, Plymouth, UK.

Dambrine, E., Pollier, B., Poswa, A. et al. 1998. Evidence of current acidification in spruce stands in the Vosges Mountains, north-eastern France. – Water Air Soil Pollut. 105: 43–52.

Dangles, O. 2000. Approche du fonctionnement de ruisseaux forestiers soumis à des processus d'acidification: décomposition des litières, rôle des macroinvertébrés benthiques et application vers une gestion conservatoire. – PhD thesis. Univ. of Metz, France.

Dangles, O. and Guerold, F. 2001. Influence of shredders in mediating breakdown rates of beech leaves in circumneutral and acidic forest streams. – Arch. Hydrobiol. 151: 649–666.

Dangles, O., Guerold, F. and Usseglio-Polatera, P. 2001. Role of drifted particulate organic matter in the macroinvertebrate colonization patterns of leaf bags in headwater streams. – Freshwat. Biol. 46: 575–586.

Driscoll, C. T., Baker, J. P., Bisogni, J. J. et al. 1980. Effect of aluminium speciation on fish in dilute acidified waters. – Nature 284: 161–164.

Driscoll, C. T., Fuller, R. D. and Schecher, W. D. 1989. The role of organic acids in the acidification of surface waters in the eastern US. – Water Air Soil Pollut. 43: 21–40.

Driscoll, C. T., Lawrence, G. B., Bulger, A. J. et al. 2001. Acidic deposition in the north-eastern United States: sources and inputs, ecosystem effects, and management strategies. – BioScience 51: 180–198.

Fitzpatrick, E. A. 1983. Soils: their formation, classification and distribution. – Longman.

Gessner, M. O. and Chauvet, E. 2002. A case for using litter breakdown to assess functional stream integrity. – Ecol. Appl. 12: 498–510.

Gessner, M. O, Chauvet, E. and Dobson, M. 1999. A perspective on leaf litter breakdown in streams. – Oikos 85: 377–384.

Gorham, E., Underwood, J. K., Martin, F. B. et al. 1986. Natural and anthropogenic causes of lake acidification in Nova Scotia. – Nature 324: 451–453.

Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – Ecol. Lett. 4: 379–391.

Griffith, M. B. and Perry, S. A. 1993. Colonization and processing of leaf litter by shredders in streams of contrasting pH. – Freshwat. Biol. 30: 93–103.

Hildrew, A. G., Townsend, C. R., Francis, J. et al. 1984. Cellulolytic decomposition in streams of contrasting pH and its relationship with invertebrate community structure. – Freshwat. Biol. 14: 323–328.

Jones, J. R. E. 1948. The fauna of four streams in the 'Black Mountain' district of south Wales. – J. Anim. Ecol. 17: 51–65.

Jüttner, I., Lintelmann, J., Michalke, B. et al. 1997. The acidification of the Herrenwieser See, Black Forest, Germany, before and during industrialisation. – Wat. Res. 31: 1194–1206.

Köhler, S., Laudon, H., Wilander, A. et al. 2000. Estimating organic acids dissociation in natural surface water using total alkalinity and TOC. – Water Res. 34: 1425–1434.

Kullberg, A. 1992. Benthic macroinvertebrate community structure in 20 streams of varying pH and humic content. – Environ. Poll. 78: 103–106.

Laudon, H., Westling, O., Löfgren, S. et al. 2001a. Modelling preindustrial ANC and pH during spring flood in northern Sweden. – Biogeochemistry 54: 171–195.

Laudon, H., Westling, O., Vøllestad, L. A. et al. 2001b. Naturligt sura och försurade vatten i Norrland (in Swedish with English summary) – Swedish Environ. Protection Agency. Report 5144, Stockholm, Sweden.

Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier Science.

McGeorge, J. E., Jagoe, C. H., Risley, L. S. et al. 1991. Litter decomposition in low pH streams in New Jersey pinelands. – Verh. Internat. Verein. Limnol. 24: 1711–1714.

Otto, C. and Svensson, B. S. 1983. Properties of acid brown water streams in south Sweden. – Arch. Hydrobiol. 99: 15–36.

Perakis, S. S. and Hedin, L. O. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. – Nature 415: 416–419.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – J. N. Am. Benthol. Soc. 16: 391–409.

Raddum, G. G. and Skjelkvale, B. L. 2001. Critical limit of acidifying compounds to invertebrates in different region of Europe. – Wat. Air Soil Pollut. 130: 825–830.

Rapp, L. 2001. Critical loads of acid deposition for surface water, exploring existing models and a potential alternative for Sweden. PhD thesis. Swedish Univ. of Agric. Sci., Uppsala, Sweden.

Renberg, I., Korsman, T. and Anderson, N. J. 1993. A temporal perspective of lake acidification in Sweden. – Ambio 22: 264–271.

Rosemond, A. D., Reice, S. R., Elwood, J. W. et al. 1992. The effects of stream acidity on benthic invertebrate communities in the south-eastern United States. – Freshwat. Biol. 27: 193–209.

Schindler, D. W. 1988. Effects of acid-rain on freshwater ecosystems. – Science 239: 149–157.

Stenson, J. A. E. 1985. Biotic structure and relation in the acidified Lake Gårdsjön system: a synthesis. – Ecol. Bull. 37: 319–326.

Stoddart, J. L., Jeffries, D. S., Lükeviler, A. et al. 1999. Regional trends in aquatic recovery from acidification in North America and Europe. – Nature 401: 575–578.

Turner, W., Leitner, W. and Rosenzweig, M. 2001. WS2M-Software for the measurement and analysis of species diversity. Published at http://eebweb.arizona.edu/diversity/

Warfvinge, P., Löfgren, S. and Lundström, U. 1995. Implication of natural acidification for mitigation strategies in northern Sweden. – Water Air Soil Pollut. 85: 499–504.

Williams, P. M. 1968. Organic and inorganic constituents of the Amazon River. – Nature 216: 937–938.