Landscape-controlled chemistry variation affects communities and ecosystem function in headwater streams

Zlatko Petrin, Brendan McKie, Ishi Buffam, Hjalmar Laudon, and Björn Malmqvist

Abstract: We show that benthic freshwater communities of naturally acidic streams in boreal catchments differ depending on properties of the surrounding landscape. Although low pH usually is associated with negative impacts on species diversity and ecosystem function, here decomposition by insects and microbes as well as the abundance of leaf-eating insects were generally high at low pH and at humic sites influenced by mire-dominated compared with forest-dominated surroundings. Moreover, in situ growth experiments showed that the survival of two of the most abundant insect species was higher when they originated from mire-influenced sites, underscoring their tolerance to low pH. However, species diversity generally increased with pH and was greater at forest-influenced than at mire-influenced sites. Although less diverse, acidic and humic streams proved to be functional and supported distinct macroinvertebrate assemblages. Diversity and function in naturally acidic streams are apparently greatly influenced by the prevailing kinds of landscape-driven influences on water chemistry. In conclusion, well-known negative impacts of anthropogenic acidity on diversity and function may not apply to naturally acidic systems that are chemically and biologically heterogeneous.

Résumé : Nous démontrons que les communautés benthiques d'eau douce de cours d'eau naturellement acides dans des bassins versants boréaux diffèrent selon les caractéristiques du paysage environnant. Bien qu'un pH faible soit normalement associé à des impacts négatifs sur la diversité spécifique et le fonctionnement de l'écosystème, néanmoins dans notre étude, la décomposition par les insectes et les microorganismes, ainsi que l'abondance des insectes consommateurs de feuilles, sont généralement élevées aux valeurs basses de pH et dans les sites humiques influencés par un environnement dominé par les tourbières plutôt que par les forêts. De plus, des expériences de croissance in situ montrent que la survie des deux espèces d'insectes les plus abondantes est supérieure lorsque celles-ci proviennent des sites influencés par les tourbières, ce qui souligne leur tolérance aux pH bas. Toutefois, la diversité spécifique croît généralement en fonction du pH et elle est plus élevée aux sites dominés par les forêts qu'à ceux dominés par les tourbières. Bien que moins diversifiés, les cours d'eau acides et humiques s'avèrent fonctionnels et ils contiennent des peuplements distincts de macroinvertébrés. La diversité et le fonctionnement dans les cours d'eau naturellement acides sont apparemment fortement influencés par les effets du type dominant de paysage sur la chimie de l'eau. En conclusion, les impacts négatifs bien documentés de l'acidité causée par l'activité humaine sur la diversité et le fonctionnement peuvent ne pas s'appliquer à des systèmes naturellement acides qui sont hétérogènes des points de vue chimique et biologique.

[Traduit par la Rédaction]

Introduction

Anthropogenic acidity in fresh waters has generally been connected to detrimental impacts on ecosystem structural attributes, such as the diversity and composition of biological assemblages, and functional attributes related to important ecosystem processes (Otto and Svensson 1983; Rosemond et al. 1992; Guérold et al. 2000). Yet recent research indicates assemblages inhabiting naturally acidic systems can often be functional and diverse (Collier et al. 1990; Dangles et al. 2004*a*). However, little is presently known about what factors allow organisms to thrive under naturally acidic conditions or how natural variation in acidic water chemistry affects function and structure. Such naturally acidic freshwater environments are widespread in northern Sweden — and probably widely across the boreal region — in a forest landscape characterized by abundant wetlands rich in dissolved organic carbon (DOC). The acidity stems mainly from the lack of buffering bases in the bedrock (Laudon and Bishop 1999; Bishop et al. 2000) and the comparatively high content of humic acids in streams and lakes (Laudon and Bishop 2002). Paleoecological studies suggest such naturally acidic systems have likely persisted in the region over several thousand years (Renberg et al. 1993; Korsman 1999), and

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given their abundance and persistence over evolutionary time scales, an adapted and specialized fauna may have developed (evolutionary species pool hypothesis, Pither and Aarssen 2005). Thus, streams in northern Sweden comprise a natural laboratory to study how interacting water chemistry variables characterizing acidity status — including pH, DOC content, and inorganic aluminium (Al_i) concentration — alter ecological features such as ecosystem processes and species diversity.

In representative naturally acidic headwater streams in northern Sweden, two types of water chemistry regimes associated with acidic episodes during spring snowmelt have been identified. The regimes bracket a gradient from low to high pH and from high to low DOC levels with varying Al speciation and Al_i concentration (Cory et al. 2006; Buffam et al. 2007). In forested catchments, snowmelt water percolates through the soil pushing DOC-rich, old soil water into the stream channel (Bishop et al. 2004). As runoff in spring greatly exceeds baseflow discharge, most of the stream water consists of such old water, while little freshly melted snow contributes to its composition (Laudon et al. 2004*b*). Thus, at forest regime sites, DOC content increases during snowmelt episodes and — because of the large amount of humic acids and lack of buffering bases in the bedrock — pH decreases (Laudon et al. 2004*a*). In contrast, wetland-dominated catchments are less sheltered from the winter cold, and the water-saturated ground is covered by a continuous ice layer. Accordingly, most of the snowmelt water flows on top of the ice into the stream channel, diluting the DOC-rich old water from the wetland (Laudon et al. 2004*a*). Consequently, DOC content at mire regime sites is reduced during episodes relative to baseflow conditions, as is pH, because buffering bases are absent from snow and wetland water. Hence, forest and mire regimes contrast at baseflow conditions (low versus high DOC content and relatively high versus low pH, respectively), but become chemically similar during the spring flood (Buffam et al. 2007). However, pH levels at mire regime sites are more consistently low compared with forest regime sites (Laudon et al. 2004*a*; Buffam et al. 2007). The buffering capacity increases as the stream water flows into larger channels because larger streams tend to have higher groundwater inputs. They also tend to have lower DOC concentrations, likely because of the dominance in the landscape of forested areas and in-stream photochemical mineralization and microbial decomposition of DOC (Köhler et al. 2002). Thus, larger streams exhibit less extreme water chemistry dynamics, qualitatively resembling those in forest-dominated catchments (Buffam et al. 2007).

Many studies have addressed the relationships between pH and biotic variables, describing properties of aquatic communities such as ecosystem processes, species richness, and assemblage structure, particularly in regions with substantial anthropogenic acidification of freshwater ecosystems (Otto and Svensson 1983; Rosemond et al. 1992; Guérold et al. 2000). However, little attention has been paid to these relationships in naturally acidic systems (Dangles et al. 2004*a*; McKie et al. 2006), especially with respect to DOC and Al_i dynamics. DOC has potentially both ameliorating and toxic effects (Kullberg et al. 1993; Thomas 1997; Steinberg et al. 2006). The effects of Al_i — appearing widely toxic to freshwater biota — depend on pH and the DOC content of the water (Hall et al. 1985; Burton and Allan 1986; Herrmann 2001).

We carried out three studies investigating (study 1) differences between forest and mire regime sites in ecosystem function and benthic macroinvertebrate species diversity, (study 2) the specific effects of pH, DOC content, and Al_i concentration on ecosystem function and species diversity along a gradient of natural acidity, and (study 3) the effects of forest vs. mire regime on growth and survival of two of the most abundant insect species. If the effects of low pH in naturally acidic were similar to those in anthropogenically acidified systems (Otto and Svensson 1983; Rosemond et al. 1992; Guérold et al. 2000), then we hypothesized low pH would (*a*) depress species richness and (*b*) impair ecosystem function (study 1) and reduce insect growth and survival at mire compared with forest regime sites (study 3) and along a gradient of natural acidity (study 2). Alternatively, if the high levels of humic compounds ameliorated toxic effects of low pH and high Al_i concentration, or if the biota tolerated or were adapted to high acidity levels, then uniformly low pH and high DOC levels would favour species richness and support ecosystem function (study 1) and insect growth and survival at mire compared with forest regime sites (study 3) and along a gradient of natural acidity (study 2).

Materials and methods

Study sites

The studies were carried out at Vindeln Experimental Forests in northern Sweden (64°15′N, 19°48′E, elevation 160–320 m above sea level). The landscape is dominated by mixed coniferous forest and wetlands (Buffam et al. 2007) on moraine soil on top of gneiss bedrock. Mean annual precipitation amounts to ~600 mm, with a third falling as snow, and mean annual air temperature is around 1 °C (Löfvenius et al. 2003). In most years, snow covers the ground from the end of October until the beginning of May. The studies were initiated during the snowmelt episode in 2003 and replicated more extensively in the same season in 2004.

We selected the sites utilized in studies 1 and 3 (Table 1) to independently represent two distinct landscape types, forest and mire, that occurred in close proximity upstream of the study sites. These streams are of low order and have small catchments (Table 1). On average, wetlands comprised a higher proportion of the catchment area at mire (29%) than forest (3%) regimes sites, thus reflecting our choice of landscape use upstream of the study sites (Table 1). However, the percentage of wetlands in the catchment was high at Fulbäcken (12%) compared with other forest regime sites (1%–3%) — although wetlands were in this case located far from the actual study site — and the percentage of wetlands was relatively low at the mire regime site Bergmyrbäcken (6%). In contrast, the sites in study 2 represented the complete gradient of stream size, water chemistry, and landscape use occurring in the study area, with catchment size consequently varying considerably (Table 1). Each site comprised a reach with hard bottom substratum surrounded by forest. Stortjärnen is a lake outlet stream.

Table 1. Location and description of study sites.

Site name	Latitude (N)	Longitude (E)	Study year	Order	Area (km^2)	Wetland (%)	Study	Regime
Risbäcken	64°14′54″	19°48′29″	2003–2005	1	0.60	3	1,2,3	F
Västrabäcken	64°15′10″	19°46′33″	2003–2005	1	0.13	1	1,2,3	F
Lillmyrbäcken	64°15′23″	19°47′04″	2003–2004	1	0.03	76	1,2	M
Kallkälsmyren	64°15′34″	19°46′26″	2003–2005	1	0.19	50	1,2,3	M
Stortjärnen	64°15′39″	19°45′38″	2003–2004	1	0.95	39	2	X
Stortjärnbäcken	64°15′03″	19°46′23″	2004	1	1.40	27	2	X
Kallkälsbäcken	64°15′06″	19°46′36″	2003–2004	2	0.50	17	2	X
Fulbäcken	64°14′51″	19°46′08″	2004–2005	2	2.51	12	2,3	F
Nyängesbäcken	64°14′15″	19°47′29″	2003–2004	2	3.11	15	2	X
Stormyrbäcken	64°15′25″	19°47′12″	2004	2	3.25	27	2	X
Nymyrbäcken	64°14′27″	19°48′55″	2004	3	5.71	18	2	X
Långbäcken	64°13′59″	19°47′14″	2003–2004	3	7.25	11	2	X
Åhedbäcken	64°13′33″	19°46′16″	2004	3	12.61	6	2	X
Övrekrycklan	64°14′49″	19°50′19″	2003–2004	4	19.66	14	2	X
Krycklan	64°11′54″	19°52′08″	2003–2004	4	66.82	9	2	X
Kryckeltjärnbäcken	64°14′31″	19°49′23″	2004	1	0.84	1	1	F
Mullkälenbäcken	64°13′27″	19°46′03″	2004	1	0.19	1	1	F
Mesbäcken	64°12′22″	19°46′52″	2004	1	0.29	2	1	F
Bergtjärnbäcken	64°16′01″	19°47′55″	2004	1	0.99	12	1	M
Bastumyrbäcken	64°12′06″	19°49′40″	2004–2005	1	0.97	15	1,3	M
Lappmyrbäcken	64°12′45″	19°53′40″	2004	2	2.75	23	1	M
Långslåttbäcken	64°15′39″	19°43′16″	2004–2005	1	1.87	19	1,3	M
Bergmyrbäcken	64°14′51″	19°44′02″	2004	1	0.61	6	1	M

Note: Order: stream order; area: catchment area; wetland: percentage of wetlands in catchment; study: study carried out (1, differences between forest and mire regime sites in ecosystem functioning and benthic macroinvertebrate species diversity; 2, effects of pH, DOC content, and Al_i concentration on ecosystem functioning and species diversity along a gradient of natural acidity; 3, effects of forest and mire regime on growth and survival of the two most abundant insect species.); regime: inferred water chemistry regime (F, forest; M, mire; X, mixed water chemistry regime).

Water chemistry

At 15 sites used in study 2 (Table 1), we collected water samples every 1–3 days during the snowmelt episodes (beginning to end of May in 2003, mid-April to mid-May in 2004 and 2005), weekly at lower flow in the period from March until June, otherwise monthly. At the additional sites used in studies 1 and 3, we took water samples three times before and during the study period to characterize the hydrochemical regime. The study periods consisted of 16 April – 3 June 2003, 26 April – 4 June 2004, and 12 May – 2 June 2005. We measured pH, DOC (by combustion and analysis as CO_2 (Shimadzu TOC-V_{PCH} analyzer) after acidification and sparging of filtered (0.45 µm) water samples), and Al_i concentration (as the difference between total and organic aluminium (inductively coupled plasma optical emission spectroscopy using Varian Vista AX instrument) after fractionation using a cation exchange column) (for details see Cory et al. 2006; Buffam et al. 2007).

Mean pH during the study periods ranged from 4.9 to 6.0 at forest regime sites, 4.0 to 5.8 at mire regime sites, and 4.0 to 6.5 across all studied streams. The lowest pH value (3.8) was measured at a mire regime site. Mean total organic carbon levels ranged from 8.4 to 24.1 $\text{mg}\cdot\text{L}^{-1}$ at forest regime sites, 12.4 to 34.1 $\text{mg}\cdot\text{L}^{-1}$ at mire regime sites, and 8.4 to 34.1 $\text{mg}\cdot\text{L}^{-1}$ across all sites. Mean Al_i concentrations ranged from 67 to 81 $\mu\text{g}\cdot\text{L}^{-1}$ at forest regime sites, 1 to 8 $\mu\text{g}\cdot\text{L}^{-1}$ at mire regime sites, and 0 to 81 $\mu\text{g}\cdot\text{L}^{-1}$ across all sites.

Species diversity (studies 1 and 2)

To estimate species richness, abundance, and composition of benthic macroinvertebrates, we collected five replicate quantitative benthic samples at each site in the beginning of June using a Surber sampler (GB Nets, Cornwall, UK; mesh: 500 µm; area: 0.1 m^2), agitating the bottom substrate to a depth of ~10 cm and standardizing to 1 min sampling time. We preserved all samples in 70% ethanol, sorted them in the laboratory, and identified all macroinvertebrates to the lowest possible taxonomic level, usually species, but genus for a few caddisfly and beetle taxa and most Diptera, and family for Ceratopogonidae, Chironomidae, and Simuliidae. Worms and mites were classified as Oligochaeta and Acari, respectively. Finally, we computed both species density (i.e., the number of taxa recorded per unit area) and sample-based, rarefied taxonomic richness to account for differences in invertebrate abundance among sites, as more species are recorded by chance when more individuals are collected (Gotelli and Colwell 2001).

Ecosystem function (studies 1 and 2)

Leaf litter decomposition is an important ecosystem process in headwater streams (Gessner and Chauvet 2002) that was modelled by measuring leaf mass loss. Therefore, we picked alder leaves from the same plant stand prior to abscission in autumn before the respective field season and enclosed air-dried leaves (1 g *Alnus glutinosa* (L.) Gaertner in 2003, 4 g *Alnus incana* (L.) Moench in 2004) in coarse and fine mesh bags (mesh size 10 and 0.5 mm, respectively).

Macroinvertebrates were able to enter coarse, but not fine, mesh bags. At each site, we exposed five replicates of each bag type in 2003 and six in 2004 by attaching one pair of fine–coarse mesh bags to stakes that were hammered into the stream bed. After an exposure period of 47–48 days in 2003 and 36–37 days in 2004 (mid-April to beginning of June), mesh bags were retrieved and stored at –20 °C until further processing. Macroinvertebrates from coarse mesh bags were preserved in 70% ethanol, and the remaining leaves were separated from other detritus and mineral particles. Leaves were dried at 50 °C to constant weight and combusted at 550 °C for 4.5 h, providing ash-free dry mass estimates (Benfield 1996). We computed the instantaneous decomposition rate (*k*) based on a negative exponential decay function accounting for mass loss due to leaching and handling (Benfield 1996). To estimate decomposition mediated through consumption by leaf-eating insects (shredding) in coarse mesh bags, we subtracted the microbial contribution measured in the corresponding fine mesh bags. As decomposition rates are temperature-dependant and the mean temperature varied among sites, we used the Boltzmann factor to correct the decomposition rates for temperature effects based on metabolic theory (Brown et al. 2004). We also identified all macroinvertebrates from coarse mesh bags to the lowest possible taxonomic level, as was done for the species diversity studies.

Invertebrate growth and survival (study 3)

To measure growth and survival of the two most common stonefly shredder species in the catchment, *Nemoura cinerea* (Retzius) and *Nemurella pictetii* Klapálek, we collected insects at two sites representing forest and mire regimes (Risbäcken and Kallkälsmyren, Table 1) using electroshocking (Taylor et al. 2001). Prior to the experiment, we kept the animals at 4 °C in aerated containers with alder leaf litter as substrate and food. For the experiment, we picked similar-sized nymphs, carefully avoiding damaged individuals, and enclosed them in cylindrical plastic containers (height 25.0 cm, width 7.5 cm, eight individuals per container) with 1 g (dry weight) of prewetted alder leaves (*Alnus incana*) that served as food and substrate. Both openings were covered with a 0.3 mm mesh. We replicated each treatment and controls without insects four times with both shredder species originating from both streams (reciprocal cross experiment). Allocation of insects to treatments was randomized. We exposed the enclosures at three mire and three forest regime streams. Enclosures were attached to the stream bed with stakes (all four treatments plus control at each stake) for 22 days after peak runoff, removed, and then stored at –20 °C until further processing. To measure growth, we pooled and dried the animals from each enclosure at 50 °C and combusted them at 550 °C (see above). We calculated the instantaneous growth rate for each species, regime at stream of origin, and treatment regime based on the weight difference compared with reference animals set aside at the beginning of the experiment from each stream separately. Finally, we corrected for differences in growth rates due to temperature differences among streams using the Boltzmann factor and for differences related to initial body mass variation using the quarter power of initial body masses as correction factor, in accordance with metabolic theory (Brown et al. 2004). We additionally measured leaf litter decomposition rates as described above.

Data analysis

We used mixed-model analysis of variance (ANOVA) to study the effects of regime on leaf decomposition, with decomposition rate as the response variable, regime and mesh type as fixed factors, and site as a random factor (study 1). We applied mixed-model multiple linear regression (MLR) to study the effects of water chemistry on shredding and microbial decomposition with pH, DOC content, and $\mathrm{Al_i}$ concentration as covariates and site as a random factor running separate analyses for the 2 years (study 2). We used a conditional *F* test to assess the significance of fixed effects (Pinheiro and Bates 2000). As the residuals were heteroscedastic, we employed a variance model representing each site by a different variance (Pinheiro and Bates 2000). Other model assumptions were met. We also studied if shredder abundance differed among streams of varying water chemistry using generalized linear mixed models (GLMM), with shredder abundance as the response variable, regime as the main factor (study 1), or in different analyses, mean pH, DOC content, and $\mathrm{Al_i}$ concentration as covariates (study 2), and site as a random factor. We used a quasi-Poisson error distribution, reflecting the nature of the count data and to model the dispersion factor at the same time (Venables and Ripley 2002).

We used analysis of similarities (ANOSIM), similarity percentages for species' contributions (SIMPER), and nonmetric multidimensional scaling (MDS) on Bray–Curtis similarities of square-root-transformed species abundance data to study differences in the composition of shredder assemblages colonizing coarse mesh bags in forest and mire regime streams (study 1; Clarke 1993). ANOSIM constitutes a method to test statistically whether groups of sampling units (e.g., two habitat types) differ significantly from each other on the basis of differences in species similarity matrices. The ANOSIM statistic *R* reflects the degree of similarities within compared with between groups: values close to 1 would, in our case, indicate that forest and mire regime streams differ, whereas values around 0 would imply that they do not. ANOSIM is conceptually similar to MDS in how similarities among sites are defined and preferable to multivariate ANOVA (MANOVA) for testing divergence in community composition when parametric assumptions are unlikely to be met, for instance when the number of species is substantially greater than the number of samples (Clarke 1993). SIMPER returns the relative contribution of each species to dissimilarities between and within groups of sampling units, thus highlighting which particular species drive the difference between, in this case, forest and mire regime sites. Likewise, we studied the impact of water chemistry regime (study 1) and separate water chemistry variables (study 2) on benthic macroinvertebrate abundance, rarefied richness, species density, and assemblage structure using ANOVA, GLMM, ANOSIM, SIMPER, MDS (study 1), MLR, and GLMM (study 2). We did not fit stream as a random factor when studying the effects on rarefied richness, as only one value was available for each stream comprising replicate measurements.

Table 2. Effects of water chemistry regime and decomposer (shredders versus microbes) on decomposition rate and effects of water chemistry regime on shredder and macroinvertebrate abundance, rarefied richness, and species density.

Effect	df	*F*	*p*
Decomposition rate			
Regime	9	4.6	0.061
Decomposer	102	71.4	<0.001
Regime × decomposer	102	37.5	<0.001
Shredder abundance			
Regime	10	4.5	0.061
Macroinvertebrate abundance			
Regime	10	12.0	0.006
Rarefied richness			
Regime	7	2.5	0.154
Species density			
Regime	10	4.7	0.056

Note: df, denominator degrees of freedom; *F*, conditional *F* test statistic of analysis of variance (ANOVA); *p*, probability level.

Similarly, we studied if growth, survival, and shredding by *Nemoura cinerea* and *Nemurella pictetii* depended on regime at origin and exposure using separate mixed-model ANOVAs and GLMM with growth rate, number surviving, and decomposition rate as response variables; regime at origin, exposure and species identity as main factors; and stream as a random factor (study 3).

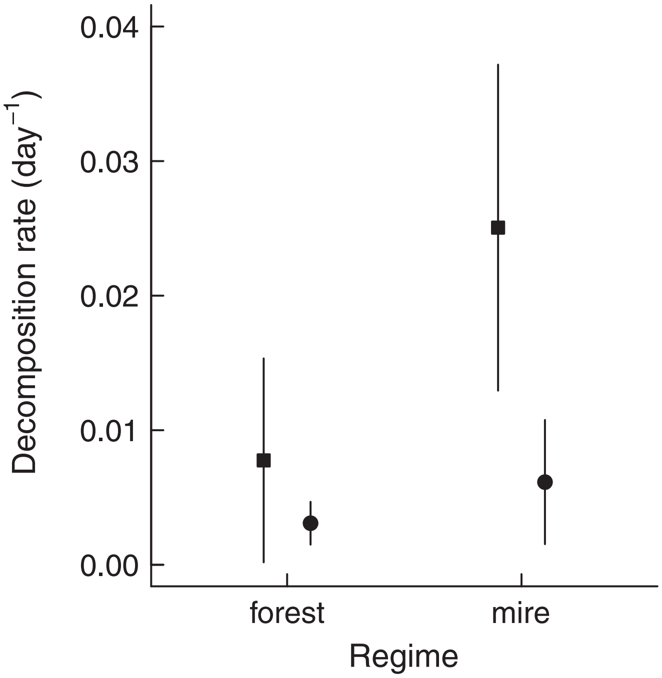
We performed all tests at the level of $\alpha = 0.05$ except otherwise stated and computed the GLMMs and carried out the ANOVAs, MLRs, and model-checking procedures using the statistical software R 2.3.0 with the packages nlme and perturb (Venables and Ripley 2002; R Development Core Team 2005). We used PRIMER 5 for Windows version 5.2.9 (PRIMER-E Ltd, Plymouth, UK) for ANOSIM, SIMPER, and MDS (Clarke 1993). All plots were drawn based on model parameters.

Results

Effects of regime on structure and function (study 1)

Leaf litter decomposition was overall higher because of shredding than because of microbial activity (Table 2, Fig. 1). Moreover, it tended to be higher at mire than at forest regime sites, reflecting elevated shredding and, to a lesser extent, microbial activity (i.e., the effect of regime differed between shredder and microbial activity) (Table 2, Fig. 1). The abundance of shredding macroinvertebrates was on average higher at mire than at forest regime sites, but the variation was large and the difference significant at the 10% level, but not at 5% (mire: mean 62 individuals per sample, 95% confidence interval (CI) 13–301; forest: mean 13 individuals per sample, 95% CI 4–43; Table 2). The compositional differences of shredder assemblages in coarse mesh bags from mire and forest regime streams were not significant because of high variability among streams of the same regime (Table 3). Stream identity, and thus variation among streams, explained a larger proportion of the compositional differences than regime type. Accordingly, ordination using Bray–Curtis similarities indicated overlapping shredder composition in streams of the two regimes (Fig. 2*a*). However, a trend to spatial separation between streams of the two regimes was apparent, suggesting smaller compositional differences between mire and forest regime streams. These differences reflected mainly variation in abundance of the stoneflies *Nemoura cinerea* and *Nemurella pictetii* and the cased caddisfly *Potamophylax cingulatus* (Stephens) (i.e., the species contributing most to dissimilarities between mire and forest regime streams) (Table 4). Only the forest regime site Kryckeltjärnbäcken tended to be associated with the mire regime sites rather than with the other forest regime sites. The stonefly *Protonemura meyeri* (Pictet) and *Potamophylax cingulatus* were found in the Kryckeltjärnbäcken site and some of the mire regime streams, but not in the other forest regime streams.

Fig. 1. Mean decomposition rate (–*k*) due to shredding (■) and microbial (●) activity at four forest and seven mire regime sites in boreal Swedish streams. Vertical bars indicate 95% confidence intervals.



Because macroinvertebrate abundances varied considerably among streams, the rarefaction curves overlapped only partly, so that never more than two-thirds of them could be formally compared, resulting in notoriously low power. Thus, the test results were likely overly conservative, and while there was a tendency towards higher, rarefied richness at forest than at mire regime sites, the difference was not significant (Table 2). Species density was also higher at forest regime sites at the 10% level, albeit not at 5% (Table 2), while abundance was higher at mire regime sites (Table 2). In spite of large differences among streams of the same regime accounting for a large proportion of the variation, benthic macroinvertebrate assemblages exhibited clear compositional differences between mire and forest regime streams (Table 3, Fig. 2*b*) mainly due to differential distributions of the stoneflies *Leuctra nigra* (Olivier), *Nemoura cinerea*, and *Nemurella*

Table 3. Effects of stream identity and water chemistry regime on shredder and macroinvertebrate assemblages.

Effect	*R*	*p*
Shredder assemblages		
Stream	0.499	0.001
Regime	0.019	0.439
Macroinvertebrate assemblages		
Stream	0.564	0.001
Regime	0.545	0.003

Note: *R*, analysis of similarities (ANOSIM) *R* test statistic; *p*, probability level.

pictetii and the families Chironomidae and Simuliidae (Table 4). The mayfly *Leptophlebia marginata* (L.) was found only at mire regime sites, and the predatory caddisfly *Plectrocnemia conspersa* (Curtis) was found mostly at these sites, but was also found elsewhere.

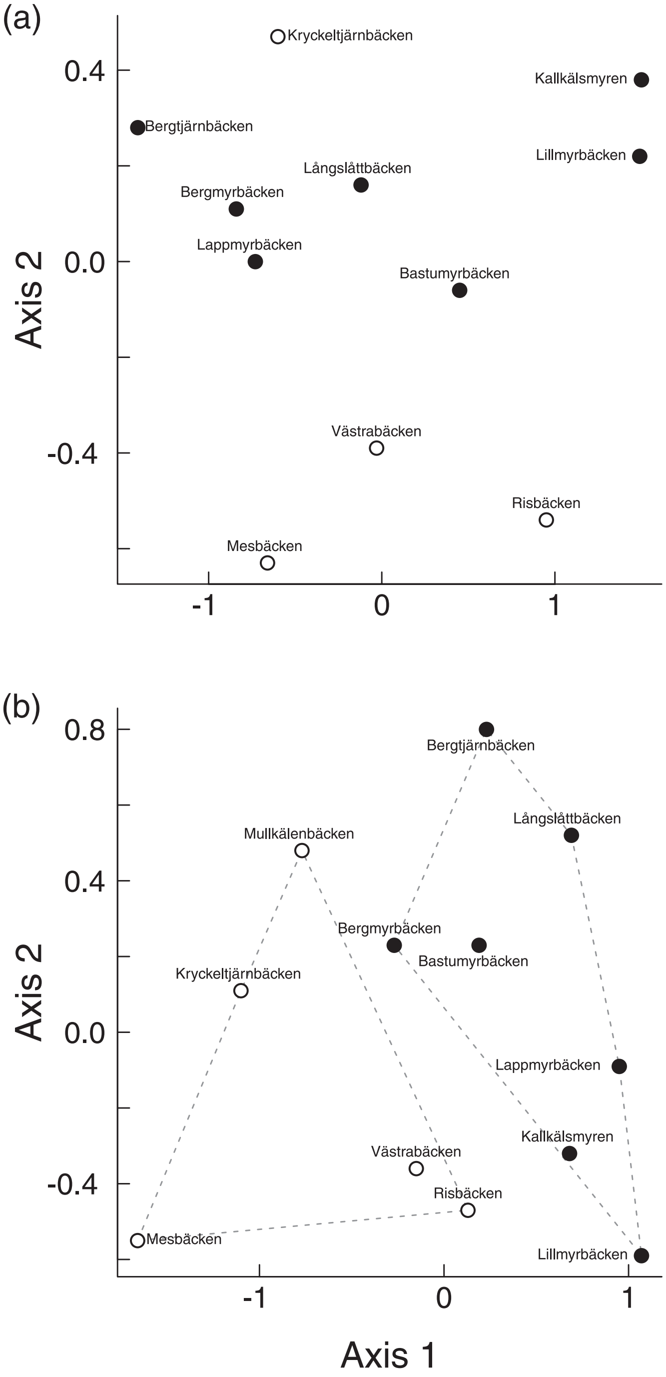
Chemistry, structure, and function across a catchment gradient (study 2)

Decomposition due to both shredding and microbial activity across the entire Krycklan catchment was unrelated to pH, DOC content, and Al_i concentration in 2003 and 2004 (all $p > 0.1$). In 2003, shredder abundance was not related to any of the water chemistry variables (all $p > 0.1$). However, in 2004, shredder abundance was higher at low pH, but not related to any other water chemistry variable (DOC content, Al_i concentration, and interactions: $p > 0.1$; pH: slope = –1.1, $F_{[1,7]} = 109.3$, $p < 0.001$). Rarefied richness did not appear to vary with pH, DOC content, or Al_i concentration in either year (all $p > 0.1$). However, species density increased with increasing pH in both years although only significantly at the 10% level, but not at 5% (DOC content, Al_i concentration, and interactions: $p > 0.1$; pH_{2003}: slope = 0.8, $F_{[1,1]} = 44.8$, $p = 0.094$; pH_{2004}: slope = 0.5, $F_{[1,7]} = 5.4$, $p = 0.053$). In 2003, macroinvertebrate abundance was unrelated to the water chemistry variables (all $p > 0.1$). But in 2004, it was higher at high pH and not related to any of the other water chemistry variables (DOC content, Al_i concentration, and interactions: $p > 0.1$; pH: slope = 0.8, $F_{[1,7]} = 25.5$, $p = 0.002$).

Shredder growth and survival (study 3)

Nemoura cinerea grew faster when originating from forest regime conditions, irrespective of the regime at the site of exposure, while the growth rates of *Nemurella pictetii* did not differ (Table 5, Fig. 3*a*). However, *Nemurella pictetii* showed a tendency towards higher growth rates when exposed to the same conditions as at their origin. The survival of *Nemurella pictetii* of forest regime origin was lower than that of mire regime origin and lower compared with *Nemoura cinerea*, which showed a similar tendency (Table 5, Fig. 3*b*). Furthermore, *Nemurella pictetii* appeared to survive better when exposed to forest regime conditions, irrespective of the regime at origin, but this pattern was not significant (Table 5). Shredding by *Nemoura cinerea* and *Nemurella pictetii* was not related to the regime at the origin of the shredders or at the site of exposure or to species identity (all $p > 0.1$).

Fig. 2. Nonmetric multidimensional scaling plot of the sites on the basis of (*a*) shredder assemblages from coarse mesh bags at four forest (○) and seven mire (●) regime sites (stress: 0.05, two-dimensional solution) and (*b*) benthic macroinvertebrate assemblages at five forest (○) and seven mire (●) regime sites in boreal Swedish streams (stress: 0.07, three-dimensional solution, only the first two dimensions are plotted).



Discussion

Major limiting factors for stream organisms generally include pH and related water chemistry variables, such as DOC content, alkalinity, and Al_i concentration (Herrmann et

Table 4. Species contributions (SIMPER) to dissimilarities of shredder and benthic macroinvertebrate assemblages (from coarse mesh bags and Surber samples, respectively) between forest and mire regime sites.

Taxon[a]	Species contribution (%)	Regime
Shredders		
Nemoura cinerea (Retzius) (P)	38.7	Mire
Nemurella pictetii (Klapálek) (P)	21.6	Mire
Potamophylax cingulatus (Stephens) (T)	11.7	Mire
Small *Nemoura* sp. (P)	9.1	Forest
Micropterna sequax (McLachlan) (T)	6.5	Forest
Leuctra nigra (Olivier) (P)	4.2	Mire
All listed shredder taxa	91.8	
Benthic macroinvertebrates		
Chironomidae (D)	18.5	Mire
Leuctra nigra (Olivier) (P)	12.9	Mire
Nemoura cinerea (Retzius) (P)	11.8	Mire
Nemurella pictetii (Klapálek) (P)	11.6	Mire
Simuliidae (D)	11.3	Mire
Oligochaeta	4.8	Forest
Plectrocnemia conspersa (Curtis) (T)	4.6	Mire
Potamophylax cingulatus (Stephens) (T)	3.8	Mire
Ceratopogonidae (D)	3.4	Forest
Leptophlebia marginata (L.) (E)	1.9	Mire
Dicranota sp. (D)	1.8	Mire
Brachyptera risi (Morton) (P)	1.7	Mire
Agabus sp. (C)	1.4	Forest
Molophilus sp. (D)	1.3	Forest
All listed benthic taxa	90.8	

Note: Regime refers to the water chemistry regime at which the respective taxon is more abundant.
[a] E, Ephemeroptera; P, Plecoptera; T, Trichoptera; C, Coleoptera; D, Diptera.

al. 1993; Courtney and Clements 1998; Vinson and Hawkins 1998). Critical levels of these factors restrict biodiversity, affect food resource quality, and impose physiological constraints, which together negatively affect ecosystem processes (e.g., primary production, grazing, and leaf litter decomposition) (Hall et al. 1980; Herrmann et al. 1993; Ledger and Hildrew 2005). Although differences in diversity between the catchment types were not clear in all instances in our study, trends were apparent and differences in community structure, function, and shredder survival were strong and consistent.

In agreement with our expectations, species diversity was often higher at forest than at mire regime sites and at higher pH. However, in contrast with previous studies (e.g., Otto and Svensson 1983; Rosemond et al. 1992; Guérold et al. 2000), leaf litter decomposition, as our measure of ecosystem function, and shredder abundance were higher at mire regime sites and at low pH. Thus, any effect of reduced species diversity at mire regime sites and sites with low pH on decomposition (Jonsson and Malmqvist 2000; Jonsson et al. 2001) was compensated by higher shredder abundances, particularly of the stoneflies *Nemoura cinerea* and *Nemurella pictetii* and of the efficient caddisfly shredder *Potamophylax cingulatus* (Dangles and Guérold 2001). Although impaired ecosystem process rates have been reported for streams with low pH (Otto and Svensson 1983; Dangles et al. 2004*b*), leaf litter decomposition rates in naturally acidic, larger streams in northern Sweden do not appear to vary with acidity (Dangles et al. 2004*a*). Such a lack of response contrasts with the results from our present study, which was performed in headwater streams contrasting strongly in hydrochemistry.

The variation in macroinvertebrate assemblages across sites of differing water chemistry regime also pertained to shredders. In contrast with circumneutral streams, anthropogenically acidified (Otto and Svensson 1983; Rosemond et al. 1992) and naturally acidic streams (Dangles et al. 2004*a*), as in our study, have assemblages characterized by a dominance of stoneflies and scarcity or lack of mayflies. The dominant stoneflies *Nemoura cinerea* and *Nemurella pictetii* showed higher survival when originating from mire regime sites. These species are known to be acid resistant with a generally broad tolerance to environmental variables (Braukmann 2001), suggesting that they thrive under conditions less suitable for most other freshwater macroinvertebrates.

Although Al_i has been found to negatively affect freshwater biota (Hall et al. 1985; Burton and Allan 1986; Herrmann 2001), we did not detect any effects of Al_i concentration. In our study, the generally low and temporally dynamic Al_i concentration (Cory et al. 2006) possibly clouded any ecological responses.

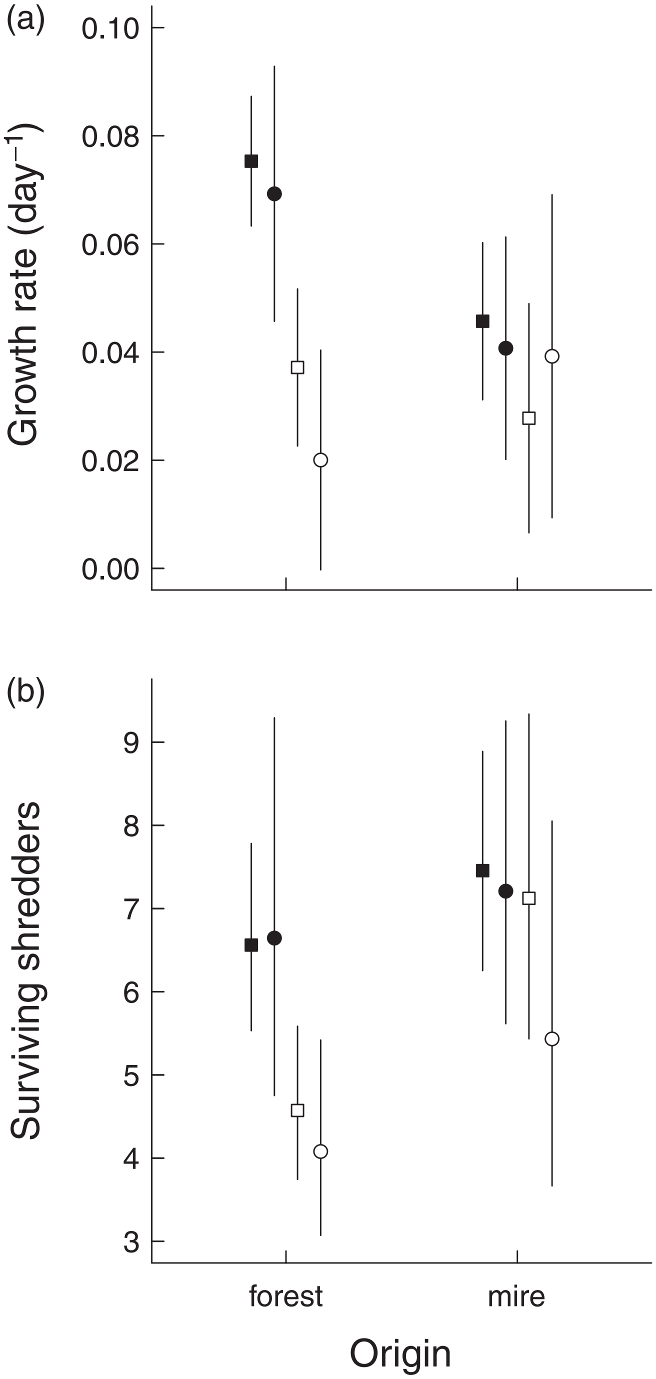
Our results support hypothesis (*a*) of depressed diversity at low pH and mire regime sites, but reject hypothesis (*b*) of impaired ecosystem function under the same conditions. The

Table 5. Effects of water chemistry regime at origin (origin), species identity (species), and regime at site of exposure (exposure) on growth and survival of the shredder stoneflies *Nemoura cinerea* and *Nemurella pictetii*.

Effect	*F*	*p*
Growth		
Origin	8.3	0.005
Species	55.9	<0.001
Exposure	1.2	0.334
Origin × species	20.8	<0.001
Origin × exposure	3.4	0.068
Species × exposure	0.1	0.820
Origin × species × exposure	3.4	0.069
Survival		
Origin	18.4	<0.001
Species	29.0	<0.001
Exposure	0.8	0.416
Origin × species	7.0	0.010
Origin × exposure	0.8	0.386
Species × exposure	3.1	0.081
Origin × species × exposure	0.3	0.598

Note: *F*, conditional *F* test statistic of analysis of variance (ANOVA); *p*, probability level. The denominator degrees of freedom (df) were 4 for the effects of regime at site of exposure; otherwise df = 65.

Fig. 3. Mean (*a*) growth rate and (*b*) number of surviving shredder stoneflies, *Nemoura cinerea* (solid symbols) and *Nemurella pictetii* (open symbols), originating from a forest and mire regime site and exposed under forest (squares) and mire (circles) regime conditions at three forest and three mire regime sites in boreal Swedish streams. Vertical bars indicate 95% confidence intervals.



likely mechanisms accounting for the former result include limitation of diversity by low pH (Otto and Svensson 1983; Rosemond et al. 1992) and water chemistry dynamics (Laudon et al. 2005). Mechanisms accounting for the latter result likely include acclimation (Wood et al. 1988; McCahon and Pascoe 1989), tolerance of and adaptation to the corresponding water chemistry regime (Fischer et al. 2001; Dangles et al. 2004*a*), and interactions among various factors (McCahon and Pascoe 1989; Horne and Dunson 1995).

Environmental dynamics may affect the capacity of freshwater biota to acclimate (Thomas et al. 1986; Meeuwig et al. 2004), which we did not study directly. Unpredictably dynamic conditions may stress tolerant or adapted organisms (Thomas et al. 1986), while the relatively stable or predictably dynamic conditions, as usually encountered at mire regime sites, might favour acclimation and the succession of a functional community despite otherwise suboptimal chemical conditions, such as low pH. *Nemurella pictetii* in enclosures grew faster when exposed to conditions similar to those at their origin, suggesting acclimation effects. This result likely did not emerge because of differences in food quality, as variation in food composition in acidic compared with circumneutral streams did not affect the growth of *Nemurella pictetii* (Ledger and Hildrew 2001). However, the overall distinct effects of regime and pH on species diversity and decomposition rates imply other mechanisms for the patterns observed.

Interactions among water chemistry variables, especially ameliorating effects of high DOC levels at low pH, likely contributed to our results on leaf litter decomposition (Kullberg et al. 1993; Thomas 1997). Even if direct effects of DOC may not exist (Qualls and Haines 1990), our results probably would be attributable to indirect effects such as the facilitation of nutrient uptake or complexing of Al (McCahon and Pascoe 1989; Thomas 1997; Dobranskyte et al. 2006).

Additionally, as shredder survival and growth largely depended on the origin of the experimental animals, irrespective of the subsequent regime at the site of exposure, tolerance of or adaptation to low pH also seems to have been instrumental (Dangles et al. 2004*a*). Although both shredder species may be found in dystrophic water, *Nemoura cinerea* — a hardy, ubiquitous stonefly also found in bogs (Brinck 1949; Lillehammer 1988) — showed overall higher survival and growth rates than *Nemurella pictetii*, which is mostly encountered in springs, trickles, and small streams (Brinck 1949; Lillehammer 1988). The results were complex, and further experimentation with more species is necessary to resolve these issues and assess the relative importance of ameliorating effects, acclimation, and tolerance and adaptation for insect growth and survival, community structure, and ecosystem function.

The type of assemblage inhabiting a given system depends on specific interactions between pH and DOC, which may cause species diversity and functional characteristics to reverberate downstream (Gore 1982; Wallace et al. 1982; Cuffney et al. 1990), suggesting a mechanism underlying landscape-level species distributions. This ecological echo may be mediated through dispersal (Gore 1982) and the influence of hydrochemical and ecological properties of headwater streams on downstream reaches (Wallace et al. 1982; Cuffney et al. 1990).

We found large hydrochemical variation particularly in headwater streams (Cory et al. 2006; Buffam et al. 2007). In response to this variation primarily regulated by land use, stream biota formed distinct assemblages with differing species diversities and associated decomposition rates. Consequently, naturally acidic streams are not all the same ecologically, but support a pool of macroinvertebrates that vary in their degrees of tolerance if not adaptation to acidity. Given the large variation in hydrochemical (Cory et al. 2006; Buffam et al. 2007) and ecological attributes of streams (this study), blanket strategies for dealing with environmental impacts are unlikely to be appropriate (e.g., McKie et al. 2006).

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