Contrasting effects of anthropogenic and natural acidity in streams: a meta-analysis

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Large-scale human activities including the extensive combustion of fossil fuels have caused acidification of freshwater systems on a continental scale, resulting in reduced species diversity and, in some instances, impaired ecological functioning. In regions where acidity is natural, however, species diversity and functioning seem to be less affected. This contrasting response is likely to have more than one explanation including the possibility of adaptation in organisms exposed to natural acidity over evolutionary time scales and differential toxicity due to dissimilarities in water chemistry other than pH. However, empirical evidence supporting these hypotheses is equivocal. Partly, this is because previous research has mainly been conducted at relatively small geographical scales, and information on ecological functioning in this context is generally scarce. Our goal was to test whether anthropogenic acidity has stronger negative effects on species diversity and ecological functioning than natural acidity. Using a meta-analytic approach based on 60 datasets, we show that macroinvertebrate species richness and the decomposition of leaf litter—an important process in small streams—tend to decrease with increasing acidity across regions and across both the acidity categories. Macroinvertebrate species richness, however, declines three times more rapidly with increasing acidity where it is anthropogenic than where it is natural, in agreement with the adaptation hypothesis and the hypothesis of differences in water chemistry. By contrast, the loss in ecological functioning differs little between the categories, probably because increases in the biomass of taxa remaining at low pH compensate for losses in functionality that would otherwise accompany losses of taxa from acidic systems. This example from freshwater acidification illustrates how natural and anthropogenic stressors can differ markedly in their effects on species diversity and one aspect of ecological functioning.

Keywords: stress; acid rain; aquatic insects; ecosystem function; leaf litter decomposition; meta-analysis

1. INTRODUCTION

The release of acidifying substances through human activities has caused widespread acidification of freshwater systems across continental scales, with consequent reductions in species diversity and ecological functioning in many regions (Schindler 1988; Rosemond *et al.* 1992; Driscoll *et al.* 2001). In addition to anthropogenically acidified systems, many naturally acidic freshwaters are found (Collier *et al.* 1990; Renberg *et al.* 1993; Laudon & Bishop 1999), in which acidic conditions have prevailed over evolutionary time scales. In such regions, freshwater biota has had sufficient time to adapt to low pH, and species diversity—in contrast to the reductions observed in anthropogenically acidified systems—may therefore not be lower than in circumneutral environments (cf. the evolutionary species pool hypothesis, Taylor *et al.* (1990) and Pither & Aarssen (2005)). On the other hand, anthropogenic acidity may be more harmful due to its effects on metal speciation and the increased bioavailability of toxic metals (Campbell & Stokes 1985; Herrmann *et al.* 1993), whereas humic substances in naturally acidic water may ameliorate metal toxicity (Kullberg 1992; Kullberg *et al.* 1993). However, the empirical support for these hypotheses is unclear. The reported relationships suggest that the effect of pH on biotic responses may vary

from weakly negative to positive for both types of acidity (e.g. Rosemond *et al.* 1992; Dangles *et al.* 2004).

Inconsistencies in the associations between acidity and biotic responses may reflect truly different relationships in different regions, for instance, due to dissimilar biogeographical histories or different patterns of covariation between acidity and other factors including productivity. Considering species distributions and ecological functioning in multiple regions would help clarifying these issues. Furthermore, many studies in streams have been limited by a low number of replicates, resulting in low statistical power. As a result, inconsistencies may have been caused by limitations in study design rather than reflecting true ecological effects of pH. Moreover, ecological functioning may not be generally impaired at low pH levels if acid-resistant taxa increase in biomass and thereby compensate for potential losses in functionality caused by reductions in species diversity (Walker 1992; Johnson *et al.* 1996; Niyogi *et al.* 2002). We may therefore expect different responses of measures of diversity and ecological functioning.

Here we used meta-analysis to test the hypothesis that acidity has stronger negative effects on biotic responses in regions where acidity is anthropogenic than where it is natural. The meta-analytic approach also allowed us to distinguish whether variation between studies reflects true variation between regions or low statistical power, and to test whether the functional relationships with pH are linear or nonlinear. We limited our analyses to stream ecosystems studying two types of ecological variables: the

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diversity of macroinvertebrate species and the rates of decomposition of leaf litter, an important ecological function in streams (e.g. Gessner & Chauvet 2002).

2. MATERIAL AND METHODS

We searched the Web of Science (ISI Web of Knowledge, The Thomson Corporation, <http://portal.isiknowledge.com/portal.cgi>) and reference lists in relevant publications for papers presenting data on species richness and/or ecological process rates along pH gradients. In some instances, data for the same effects in the same streams were provided in different papers. Then, we selected a single study to avoid statistical dependence, pseudo-replication and inflated degrees of freedom. We considered only studies in which the pH at the studied sites was circumneutral to acidic and the pH range was greater than one unit. Thus, we excluded studies in which mainly or exclusively alkaline sites or highly acid streams were examined. A minimum of four streams had to be included in each study, to allow coefficients and variances for the second-order polynomial models to be estimated, and a final requirement was that acidity could be classified as being predominantly natural or caused by human activity. For 83% of the datasets, this classification was based on information provided by the authors of the studies, or else on our knowledge about the geographical distribution of anthropogenic acidity. However, it is important to note that the sources of acidity are mixed in some regions and that the classification into natural and anthropogenic sources is therefore not perfect.

We identified a total of 103 studies that met these criteria. Many response variables were not analysed further because they were reported in very few studies, or only for one of the categories: anthropogenic and natural acidity. However, sufficient studies were found to compare the effects of the two kinds of acidity on the species richness of macroinvertebrate communities, and decomposition rates in fine and coarse mesh bags, which provide indications of the rates of decomposition by microbes and by both microbes and invertebrates, respectively. The 60 included datasets are listed in the electronic supplementary material. The mean value of the pH gradients was similar between streams of the two acidity categories across studies for all response variables (table 1). However, the pH gradient tended to be longer in the natural acidity category for macroinvertebrate species richness. Many chemical factors control species distributions and ecological process rates, but here we were interested in the ecological effects of pH across other environmental gradients.

As effect size, we used the slopes obtained by the linear regression of the response variables against pH. In addition, we fitted the second-order polynomials to test for nonlinear relationships, and we checked whether the coefficients of the nonlinear regressions varied systematically with pH, which would indicate a sigmoid response of the dependent variables to pH. We considered streams as independent replicates within studies and for this reason employed a mixed model analysis of covariance rather than a simple linear regression, where multiple sites were sampled in replicate streams or when multiple samples were taken on different dates. Moreover, study locations downstream of confluences were removed from the analyses if further sites in multiple branches upstream of that confluence had been sampled, as such downstream sites constituted dependent sites that could not be rigorously statistically accounted for.

Table 1. Summary of pH gradient lengths and mean gradient $\text{pH} \pm \text{s.d.}$ across studies for the anthropogenic and natural acidity categories. (The number of studies is given in parentheses.)

response variable	$\text{pH}_{\text{anthropogenic}}$	$\text{pH}_{\text{natural}}$
<i>pH gradient length</i>		
macroinvertebrate species richness	2.3 ± 0.7 (27)	2.6 ± 0.9 (12)
decomposition rate in fine mesh bags	2.3 ± 0.5 (6)	2.5 ± 0.3 (4)
decomposition rate in coarse mesh bags	2.5 ± 0.7 (7)	2.5 ± 0.3 (4)
<i>mean gradient pH</i>		
macroinvertebrate species richness	5.9 ± 0.4 (27)	5.8 ± 0.5 (12)
decomposition rate in fine mesh bags	5.9 ± 0.1 (6)	5.5 ± 0.5 (4)
decomposition rate in coarse mesh bags	5.8 ± 0.3 (7)	5.5 ± 0.5 (4)

We then calculated the mean values of the regression coefficients (linear and quadratic terms) using the inverse of the sample variances as weights. To test for differences between regions with anthropogenic and natural acidity, we used a random effects model, allowing for different studies to estimate various effect sizes (Gurevitch & Hedges 1999). Similar to the *F*-statistic in an analysis of variance, the computed test statistic *Q* relates the amount of heterogeneity within each category to the amount between the categories. Non-independence of observations is a ubiquitous problem in meta-analyses (Englund *et al.* 1999). Here we were concerned that the non-independence of multiple observations from the same study could bias effect size estimates. However, reducing the dataset such that only one effect estimate per study was included did not affect any of our conclusions. To study whether potential confounding factors modified the estimated effects of anthropogenic and natural acidity, we compared models with such excluded and included factors. The potential confounders were study region, functional feeding and taxonomic group of study organisms, taxonomic resolution, which means whether the biota was identified to species, genus or family level, causes of anthropogenic acidity and leaf species used in decomposition experiments. To evaluate the robustness of our test results, we removed the data from the most influential studies, those with the highest weights, from both acidity categories and repeated the analyses. A change in the outcome would then indicate the possibility that the outcome depends on particular studies rather than representing an ecological trend that is valid across a wider range of studied sites. We presented only the results of these procedures when they suggested that the findings were not robust or affected by confounding factors. We analysed the data using the MiMA function (Viechtbauer 2006) with the software R v. 2.5.1 (R Development Core Team 2007).

3. RESULTS

The association between acidity and the species richness of macroinvertebrates was stronger for anthropogenic acidity than for natural acidity (figure 1a). In fact, the rate of macroinvertebrate species loss with increasing acidity

Figure 1. Effect size estimates for the species richness of macroinvertebrates and the rates of decomposition of leaf litter in regions with anthropogenically acidified and naturally acidic streams. (a) Mean species richness lost for each unit of pH. (b) Mean change in the rate of species richness loss. (c) Mean loss in the daily rate of leaf litter decomposition in coarse and fine mesh bags per unit of pH decline. (d) Mean change in the rate of decomposition in coarse and fine mesh bags. In (c,d), the symbols represent the following: squares, coarse; triangles, fine. All error bars denote $\pm 95\%$ CI around the respective means. Insets: estimated relationships between taxonomic richness and mean gradient pH for (a) linear and (b) second-order polynomial functions for regions with anthropogenic acidity (solid lines) and natural acidity (dashed lines). Note that the functions are not exact, but only illustrate the general shape of the relationships, as the parameters were estimated as weighted means and the weights of the different parameters were not constant within each dataset.

was three times larger where acidity was anthropogenic than where it was natural ($Q=7.5$, $n=39$, $p=0.006$; figure 1a). The coefficient of the second-order polynomial was also larger where acidity was anthropogenic than where it was natural ($Q=12.8$, $p=0.001$; figure 1b). At the same time, the coefficient tended to increase with increasing acidity ($p=0.014$). For the anthropogenic acidity category, the positive coefficient of the second-order polynomial indicated that the function relating macroinvertebrate species richness to pH was convex (figure 1b). By contrast, no such pattern was observed for the natural acidity category (figure 1b).

Anthropogenic but not natural acidity reduced the rates of decomposition of leaf litter in coarse and fine mesh bags (figure 1c). However, the extent of the loss of function did not differ between the two acidity categories (coarse mesh bags: $Q<0.1$, $n=11$, $p=0.849$; fine mesh bags: $Q=0.9$, $n=10$, $p=0.348$). Nevertheless, for fine mesh bags, the loss in function tended to be larger where acidity was anthropogenic, whereas, for coarse mesh bags, the loss in function was larger where acidity was anthropogenic when

the study region was included in the model ($Q=34.5$, acidity category: $p=0.007$, region: $p<0.001$). The coefficients of the second-order polynomials did not differ between the acidity categories for either type of mesh bags (coarse mesh bags: $Q=1.1$, $n=11$, $p=0.884$; fine mesh bags: $Q=5.0$, $n=10$, $p=0.102$; figure 1d), nor did they change with pH (coarse mesh bags: $p=0.309$; fine mesh bags: $p=0.864$). For fine mesh bags, however, the coefficient was negative in the natural acidity category. The loss in function due to natural acidity may therefore only have increased notably once higher levels of acidity were reached.

In all our models, except the one for the decomposition of leaves in coarse mesh bags that included the region, we found significant residual heterogeneity (all $p\leq 0.005$). This suggests that variation among studies in the reported effect sizes reflects truly different effects, rather than low statistical power. Apart from the type of acidity, the study region may have been one of the factors accounting for the different effect estimates, at least for the decomposition of leaf litter in coarse mesh bags.

4. DISCUSSION

Our results suggest that anthropogenic acidification generally has a stronger effect on macroinvertebrate species richness than natural acidity. We identified two possible explanations for this difference: adaptation over evolutionary time scales (cf. the evolutionary species pool hypothesis, Taylor *et al.* 1990) and Pither & Aarssen (2005)) and systematic differences in acidic water chemistry (e.g. Herrmann *et al.* 1993; Kullberg *et al.* 1993; Kowalik *et al.* 2007). Given that anthropogenic acidification stems from the deposition of mineral acids in all but two studies, whereas natural acidity often derives from humic compounds including tannins, systematic differences in the chemistry of acidic waters are likely to occur between regions with anthropogenic and natural acidity. Anthropogenic acidification may change the metal speciation or increase the bioavailability of toxic metals (Campbell & Stokes 1985; Herrmann *et al.* 1993; Kowalik *et al.* 2007). Mineral acids may for instance cause increased concentrations of labile aluminium that is toxic to a wide array of freshwater organisms and may reduce species richness (e.g. Herrmann *et al.* 1993). Humic substances in naturally acidic waters, on the other hand, may complex-bind toxic metals reducing their toxicity (Kullberg 1992; Kullberg *et al.* 1993). This chemical process may have ameliorated negative, indirect effects of acidity, thereby contributing to the relatively high species richness that has been observed in humic streams (Kullberg 1992; Kullberg *et al.* 1993). However, the ecological effects of humic substances depend on their concentration, and higher levels of dissolved organic carbon may well be toxic to aquatic organisms, whereas higher concentrations of some metals, including aluminium, may partly ameliorate the adverse effects of acidification (Kullberg 1992; Herrmann *et al.* 1993; Kullberg *et al.* 1993). More research will be needed to resolve this issue. If, however, the chemical causes of acidity are generally of little importance for the structure of macroinvertebrate communities (cf. Winterbourn & McDuffett 1996), or if pH controls species assemblages across other environmental gradients, for instance in aluminium (Fölster *et al.* 2007), then adaptation to high levels of acidity following extended exposure to low pH is likely to explain the relatively higher species diversity in naturally acidic streams. Such adaptation is particularly probable when naturally acidic freshwaters have been both abundant in the region and persisted over evolutionary time scales (cf. Taylor *et al.* 1990; Pither & Aarssen 2005). Conversely, the low diversity in regions with anthropogenic acidification can be explained by the comparatively short duration of anthropogenic acidification.

In contrast to species richness, the evidence for different effects of anthropogenic and natural acidity on the decomposition of leaf litter was weak. The decomposition of leaves in coarse mesh bags, probably dominated by consumption by macroinvertebrates, was affected more by anthropogenic than natural acidity only when we considered regional differences in the effect sizes. Adaptation and chemical differences in water quality are likely to account for this result. The reduction in microbial decomposition by increased acidity did, however, not significantly differ between the categories. Small differences in the effects of acidity on decomposition are generally consistent with the functional redundancy

hypothesis, i.e. increasing biomass of tolerant organisms compensates for losses in functionality that would otherwise accompany losses of sensitive taxa (Odum 1985; Schindler 1987; Niyogi *et al.* 2002). In systems with high redundancy, ecological functioning is predicted to decrease markedly only at high levels of biodiversity loss, for instance as a consequence of severe environmental stress (Walker 1992; Johnson *et al.* 1996). Thus, the ecological effects of increases in acidity will depend on both the causes of acidity and the ecological variables that are examined.

By summarizing results from a significant proportion of published studies, our analyses constitute a synthesis of the present knowledge about diversity patterns and ecological functioning in regions with anthropogenic and natural acidity. Our analyses included comparisons based on several variants for each of the response variables, thereby integrating information on specific aspects of the variables considered in each of the studies used. By covering multiple regions, we also avoided geographical restrictions and idiosyncrasies related to specific biogeographical processes including differences in the colonization histories among regions. Therefore, we could generalize beyond single systems and taxa (Arnqvist & Wooster 1995). However, the reported studies are biased towards particular regions including North America, western Europe and New Zealand.

Animals and plants are often capable of rapidly adapting to various anthropogenic and natural stressors (e.g. Reznick & Ghalambor 2001), including anthropogenic acidity in freshwater systems (Fischer *et al.* 2001; Derry & Arnott 2007). However, the responses of biota to the same stressor of anthropogenic and natural origin have to our knowledge not been compared before (but see Petrin *et al.* 2007). Such comparisons would indicate the extent to which biota can adapt to novel influences. When anthropogenic stressors are similar to natural stressors, biota may adapt more easily to them (cf. Decker *et al.* 2003). Rapid adaptation to anthropogenic stressors suggests that information on responses to natural stressors could be used to derive the effects of anthropogenic stressors, and vice versa, in assessments of the effects of stressors on species diversity patterns and ecological functioning (Fukami & Wardle 2005). Our results, however, suggest that natural gradients might not be useful for inferring species diversity patterns along anthropogenic gradients owing to probable evolutionary time-lags in regions with anthropogenic stressors (Fukami & Wardle 2005).

In summary, we have shown that anthropogenic and natural acidity may have different consequences for species richness, but also that these differences are not necessarily reflected in ecological functioning. Various explanations have been proposed to account for differences in species diversity between regions with anthropogenic and natural acidity. Some explanations have been specific to particular regions and included differences in biogeographical histories, idiosyncrasies in the composition of the species pools and chemical and biological recovery from acidification (Petrin *et al.* 2007). Other cross-regional explanations have included differences in the quality of acidity and variation in the degree of adaptation depending on time since the onset of acidification (Collier *et al.* 1990; Dangles *et al.* 2004;

Petrin *et al.* 2007). Our approach revealed patterns across different regions and geographical limitations, suggesting that differences in acid quality and/or adaptation may account for the global pattern in macroinvertebrate species richness. However, the data are silent on which of these hypotheses is more likely. In addition, species diversity patterns in particular regions may be controlled by different mechanisms, which are likely to operate on different scales compared with the ones explored in this paper.

5. FUTURE RESEARCH

An important focus of future studies should be to distinguish between the two remaining hypotheses to expand the knowledge about the different effects of anthropogenic and natural acidity on species diversity patterns. In some regions, sulphate from marine sediments that are now located above sea level, following isostatic rebound since the last glaciations, is naturally released into streams. Here, the stream water chemistry is likely to be similar to that in regions with anthropogenic sulphur deposition. Conversely, where human activities cause the release of large quantities of humic substances into the stream water, for instance by land-use change including ditching and peat mining, the chemistry of anthropogenically acidified streams may resemble that of naturally humic, acidic streams. Comparing such systems may allow the effects of acid quality to be distinguished from those of adaptation. Common garden experiments, for instance by transplanting macroinvertebrates between regions with different causes of acidity and comparing the performance of the organisms, might also help in revealing whether freshwater biota is adapted to low pH. Finally, the presence of adapted biota in acidic streams may reflect two different processes: adaptation *in situ* after exposure to acidic conditions in abundant naturally acidic freshwater systems over evolutionary time scales (cf. the evolutionary species pool hypothesis, Taylor *et al.* 1990), or immigration of already adapted organisms from neighbouring regions. Distinguishing between these two alternative mechanisms, for instance by studying the degrees of endemism and nestedness in regions with natural acidity, may allow us to assess the adaptability of freshwater biota to low pH in general and the consequences for species diversity and ecological functioning.

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REFERENCES

- Arnqvist, G. & Wooster, D. 1995 Meta-analysis: synthesizing research findings in ecology and evolution. *Trends Ecol. Evol.* **10**, 236–240. (doi:10.1016/S0169-5347(00)89073-4)
- Campbell, P. G. C. & Stokes, P. M. 1985 Acidification and toxicity of metals to aquatic biota. *Can. J. Fish. Aquat. Sci.* **42**, 2034–2049.
- Collier, K. J., Ball, O. J., Graesser, A. K., Main, M. R. & Winterbourn, M. J. 1990 Do organic and anthropogenic acidity have similar effects on aquatic fauna? *Oikos* **59**, 33–38. (doi:10.2307/3545119)
- Dangles, O., Malmqvist, B. & Laudon, H. 2004 Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. *Oikos* **104**, 149–155. (doi:10.1111/j.0030-1299.2004.12360.x)
- Decker, M. B., Breitburg, D. L. & Marcus, N. H. 2003 Geographical differences in behavioral responses to hypoxia: local adaptation to an anthropogenic stressor? *Ecol. Appl.* **13**, 1104–1109. (doi:10.1890/1051-0761(2003)13[1104:GDIBRT]2.0.CO;2)
- Derry, A. M. & Arnott, S. E. 2007 Adaptive reversals in acid tolerance in copepods from lakes recovering from historical stress. *Ecol. Appl.* **17**, 1116–1126. (doi:10.1890/06-1382)
- Driscoll, C. T. *et al.* 2001 Acidic deposition in the north-eastern United States: sources and inputs, ecosystem effects, and management strategies. *Bioscience* **51**, 180–198. (doi:10.1641/0006-3568(2001)051[0180:ADITNU]2.0.CO;2)
- Englund, G., Sarnelle, O. & Cooper, S. D. 1999 The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology* **80**, 1132–1141.
- Fischer, J. M., Klug, J. L., Ives, A. R. & Frost, T. M. 2001 Ecological history affects zooplankton community responses to acidification. *Ecology* **82**, 2984–3000.
- Fölster, J. *et al.* 2007 A novel environmental quality criterion for acidification in Swedish lakes—an application of studies on the relationship between biota and water chemistry. *Water Air Soil Pollut. Focus* **7**, 331–338. (doi:10.1007/s11267-006-9075-9)
- Fukami, T. & Wardle, D. A. 2005 Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proc. R. Soc. B* **272**, 2105–2115. (doi:10.1098/rspb.2005.3277)
- Gessner, M. O. & Chauvet, E. 2002 A case for using litter breakdown to assess functional stream integrity. *Ecol. Appl.* **12**, 498–510. (doi:10.1890/1051-0761(2002)012[0498:ACFULB]2.0.CO;2)
- Gurevitch, J. & Hedges, L. V. 1999 Statistical issues in ecological meta-analyses. *Ecology* **80**, 1142–1149.
- Herrmann, J., Degerman, E., Gerhardt, A., Johansson, C., Lingdell, P. E. & Muniz, I. P. 1993 Acid-stress effects on stream biology. *Ambio* **22**, 298–307.
- Johnson, K. H., Vogt, K. A., Clark, H. J., Schmitz, O. J. & Vogt, D. J. 1996 Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* **11**, 372–377. (doi:10.1016/0169-5347(96)10040-9)
- Kowalik, R. A., Cooper, D. M., Evans, C. D. & Ormerod, S. J. 2007 Acidic episodes retard the biological recovery of upland British streams from chronic acidification. *Global Change Biol.* **13**, 2439–2452. (doi:10.1111/j.1365-2486.2007.01437.x)
- Kullberg, A. 1992 Benthic macroinvertebrate community structure in 20 streams of varying pH and humic content. *Environ. Pollut.* **78**, 103–106. (doi:10.1016/0269-7491(92)90016-4)
- Kullberg, A., Bishop, K. H., Hargeby, A., Jansson, M. & Petersen, R. C. 1993 The ecological significance of dissolved organic carbon in acidified waters. *Ambio* **22**, 331–337.
- Laudon, H. & Bishop, K. H. 1999 Quantifying sources of acid neutralisation capacity depression during spring flood episodes in Northern Sweden. *Environ. Pollut.* **105**, 427–435. (doi:10.1016/S0269-7491(99)00036-6)
- Niyogi, D. K., Lewis Jr, W. M. & McKnight, D. M. 2002 Effects of stress from mine drainage on diversity, biomass, and function of primary producers in mountain streams. *Ecosystems* **5**, 554–567.
- Odum, E. P. 1985 Trends expected in stressed ecosystems. *Bioscience* **35**, 419–422. (doi:10.2307/1310021)

- Petrin, Z., Laudon, H. & Malmqvist, B. 2007 Does freshwater macroinvertebrate diversity along a pH-gradient reflect adaptation to low pH? *Freshw. Biol.* **52**, 2172–2183. (doi:10.1111/j.1365-2427.2007.01845.x)
- Pither, J. & Aarssen, L. W. 2005 The evolutionary species pool hypothesis and patterns of freshwater diatom diversity along a pH gradient. *J. Biogeogr.* **32**, 503–513. (doi:10.1111/j.1365-2699.2005.01194.x)
- R Development Core Team 2007 *R: a language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna, Austria. See <http://www.R-project.org/>.
- Renberg, I., Korsman, T. & Anderson, N. J. 1993 A temporal perspective of lake acidification in Sweden. *Ambio* **22**, 264–271.
- Reznick, D. N. & Ghelambor, C. K. 2001 The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112**, 183–198. (doi:10.1023/A:1013352109042)
- Rosemond, A. D., Reice, S. R., Elwood, J. W. & Mulholland, P. J. 1992 The effects of stream acidity on benthic invertebrate communities in the south-eastern United States. *Freshw. Biol.* **27**, 193–209. (doi:10.1111/j.1365-2427.1992.tb00533.x)
- Schindler, D. W. 1987 Detecting ecosystem responses to anthropogenic stress. *Can. J. Fish. Aquat. Sci.* **44**, 6–25.
- Schindler, D. W. 1988 Effects of acid rain on freshwater ecosystems. *Science* **239**, 149–157. (doi:10.1126/science.239.4836.149)
- Taylor, D. R., Aarssen, L. W. & Loehle, C. 1990 On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* **58**, 239–250. (doi:10.2307/3545432)
- Viechtbauer, W. 2006 MiMA: an S-Plus/R function to fit meta-analytic mixed-, random-, and fixed effects models [Computer software and manual]. See <http://www.wvbauer.com/>.
- Walker, B. H. 1992 Biodiversity and ecological redundancy. *Conserv. Biol.* **6**, 18–23. (doi:10.1046/j.1523-1739.1992.610018.x)
- Winterbourn, M. J. & McDuffett, W. F. 1996 Benthic faunas of streams of low pH but contrasting water chemistry in New Zealand. *Hydrobiologia* **341**, 101–111. (doi:10.1007/BF00018114)