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Biodiversity of Freshwater Diatom Communities during 1000 Years of Metal Mining, Land Use, and Climate Change in Central Sweden

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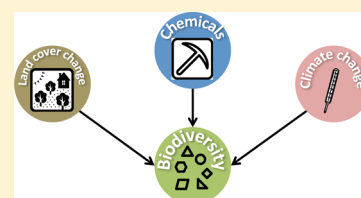
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S Supporting Information

ABSTRACT: We subjected a unique set of high-quality paleoecological data to statistical modeling to examine if the biological richness and evenness of freshwater diatom communities in the Falun area, a historical copper (Cu) mining region in central Sweden, was negatively influenced by 1000 years of metal exposure. Contrary to ecotoxicological predictions, we found no negative relation between biodiversity and the sedimentary concentrations of eight metals. Strikingly, our analysis listed metals (Co, Fe, Cu, Zn, Cd, Pb) or the fractional land cover of cultivated crops, meadow, and herbs indicating land disturbance as potentially promoting biodiversity. However, correlation between metal- and land-cover trends prevented concluding which of these two covariate types positively affected biodiversity. Because historical aqueous metal concentrations—inferred from solid-water partitioning—approached experimental toxicity thresholds for freshwater algae, positive effects of metal mining on biodiversity are unlikely. Instead, the positive relationship between biodiversity and historical land-cover change can be explained by the increasing proportion of opportunistic species when anthropogenic disturbance intensifies. Our analysis illustrates that focusing on the direct toxic effects of metals alone may yield inaccurate environmental assessments on time scales relevant for biodiversity conservation.



INTRODUCTION

From the early 1990s, the species diversity of biological communities (biodiversity) has been recognized to play a key role in processes essential for ecosystem functioning.^{1,2} Extensive meta-analyses of field data on natural and disturbed terrestrial and aquatic ecosystems eventually supported the conclusion that diversity loss reduces ecosystem functions and services.¹ Ecosystem exposure to diverse stressors associated with anthropogenic disturbance at local to global scales was subsequently hypothesized to be one of the driving forces behind the ongoing global decrease in biodiversity.^{3,4} Subsequently, the appreciation by regulatory bodies and society of the potentially deteriorating effects of chemicals on biodiversity has led to a number of environmental policies which aim to prevent pollution and reverse global biodiversity loss.^{5,6}

Approaches to directly observe the effects of chemicals on ecosystems include the use of micro- and mesocosm experiments.⁷ Such experiments are typically designed to unravel how direct effects of a stressor interact with population- and community-level dynamics such as interspecific interaction⁸ or population density.⁹ The duration of these experiments is thus typically chosen to match the length of the species' life cycle, i.e., ranging from days to months.¹⁰ However, it is now well-

recognized that the effects of stressors on freshwater plankton communities also occur on time scales of decades and centuries, i.e., exceeding the typical duration of phenomena studied in plankton community ecology.¹¹ Given the limitations of experimental approaches to understand ecological impacts on such time scales, and in recognition of an important historical component in the community structure of modern-day ecosystems,¹² analysis of high-quality paleoecological records has been proposed as a useful approach to jointly reconstruct the temporal dynamics of community composition and possible influencing factors over time scales ranging from decades to thousands of years.¹³ As a result, paleoecological data are increasingly mined to reconstruct biodiversity fluctuations and to examine the possible causes of such fluctuations.^{14–20}

This study examines if a 1000-year history of metal exposure negatively affected the biodiversity of freshwater communities of diatom algae (Bacillariophyceae), relative to the effects caused by changes in land cover and regional climate. We use the case of lakes in the Falun mining region of central Sweden

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because during the past 2000 years these lakes have experienced dynamic changes in their local aquatic environment caused by both local and regional anthropogenic activity,^{21,22} including 1000 years of copper mine exploitation. To this end, we use statistical modeling to analyze a unique paleoecological data set, which comprises sedimentary records of fossil diatom assemblages and metal concentrations from ten lakes and of terrestrial plant pollen assemblages from three of these lakes. Our analysis includes sedimentary concentrations of eight metals, six pollen-inferred land-cover types, and mean annual and summer temperatures as potential drivers of the richness and evenness of freshwater diatom communities.

MATERIAL AND METHODS

Study Site and Data Description. The Falun region in central Sweden is renowned for its long history of copper (Cu) production, as mines had been in continuous use for nearly 1000 years before they were closed in 1993^{23,24} (Figure 1,

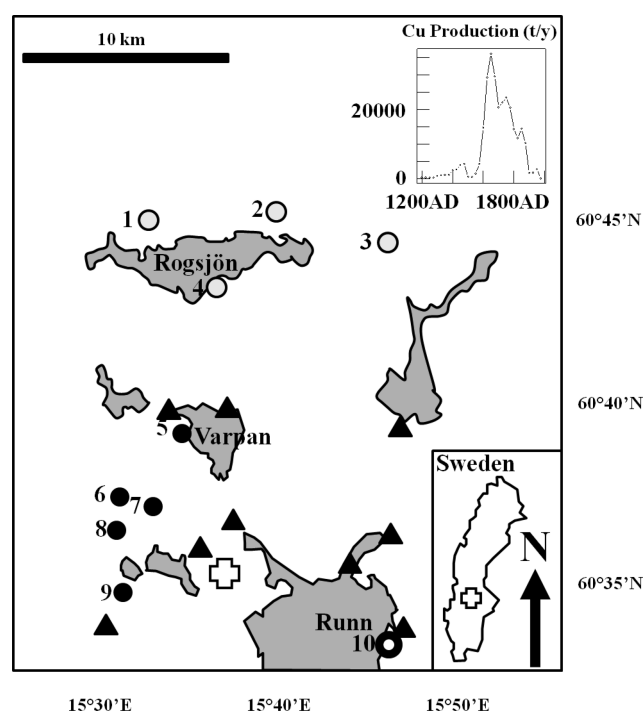


Figure 1. Map of the Falun mining region with the ten lakes considered in the present study indicated by symbols with Arabic numerals: Tjännängstjärnen (1), Rudtjärnen (2), Kvarntjärnen (3), Uvbergstjärnen (4), Varbotjärnen (5), Djuptjärnen (6), Nästjärnen (7), Karlsbotjärnen (8), Stugutjärnen (9), and Hagstjärnen (10). Lakes with the same symbol were assumed to share the same land-cover history. Triangular symbols locate the metal smelters. The location of Falun in Sweden and the copper production history are shown in the insets. The four lakes not considered in this study are not shown on this map. Reproduced with permission from *J. Paleolimnol.*, 2001, 26, 89–107, copyright Springer.²⁵

reproduced with permission from *Journal of Paleolimnology*, 26, 2001, 89–107, copyright Springer). Historically, the Falun Cu mine has been of global importance, producing over 60% of the world's Cu during its peak activity in the 17th century (Figure 1 inset).

Between 1994 and 1996, sediment cores were obtained from fourteen lakes within the Falun region to produce long records of past changes in the local freshwater diatom communities.²⁵

This produced data on the abundance (frustules per gram wet sediment) and species composition of diatom fossils (representing >50 taxa in total), and on the concentrations of eight metal elements (cobalt, nickel, copper, zinc, cadmium, lead, iron, and manganese) between 0 and 2 m sediment depth, representing between 600 and 2000 years of each lake's environmental history.²⁵ For three of the fourteen lakes (Hagtjärnen, Rudtjärnen, and Nästjärnen) also fossil-pollen records of terrestrial vegetation were available,²⁵ allowing reconstruction of changes in land cover around these three lakes. On the basis of ²¹⁰Pb-dating of the upper portion of the records, we constructed simple age-depth models for each of these lakes (Figure S1 of the SI) to convert sediment depths to time BC or AD. Our time series cover the period between 200 BC and 1962 AD, i.e., before the liming of these lakes in the 1980s.²⁵ All details on the coring, subsampling, diatom and pollen identification and counting, and metal analyses are presented in Ek and Renberg.²⁵

The Falun region encompasses only ~400 km² of central Sweden, such that all lakes are subject to the same processes of large-scale atmospheric dynamics, such that temporal patterns of decadal to century-scale climate variability can be assumed to have been uniform among them. We described the main trends of regional temperature history in two ways: using the mean annual temperature in northern Norway inferred from stalagmite $\delta^{18}\text{O}$,²⁶ and the mean summer temperature in northern Finland inferred from an independent set of diatom community composition data.²⁷ Although not from within the Falun region, these data, which have been used previously to reconstruct hemisphere-wide climate trends,²⁸ give a good representation of the Dark Ages Cool Period, the Medieval Climate Optimum and the Little Ice Age, which are the three most prominent climate anomalies of the last 2000 years in western and northern Europe.²⁶ To emphasize these longer-term trends, we smoothed the original high-resolution proxy time series with filters comparable to those applied in the original publications (cubic spline smoothers with 40 and 10 degrees of freedom for annual and summer temperature, respectively).

Reconstruction of Diatom Diversity and Land Cover.

The biodiversity of past diatom communities in the Falun-area lakes was quantified using the taxonomic richness (S) and evenness (J) of the recovered fossil diatom assemblages. Richness was calculated as the total number of taxa, i.e., the number of diatom species and subspecies with a reported abundance >0. Evenness was calculated as $J = -(\sum p_i \ln(p_i)) / \ln(S)$ with p_i the relative abundance of diatom taxon i , i.e., the ratio of the counts of this taxon over the total number of counts in the diatom assemblage, and “ln” the natural logarithm.²⁹

Past changes in the land cover surrounding three of the fourteen study lakes were inferred from fossil pollen assemblages by grouping terrestrial plant taxa according to the major types of natural or anthropogenic land cover they represent, based on review papers^{30–42} (listed in Table S1, SI), and on the database “POPweb” (<http://www.geog.qmul.ac.uk/popweb/default.htm>). Pollen taxa, represented as proportional abundances relative to a terrestrial pollen sum of 1, were summed within the groups to obtain quantitative proxies for six land-cover classes: cultivated crops (e.g., cereals), ferns, meadow (grasses and grassland herbs), disturbed land (herbs indicating anthropogenic land disturbance, i.e. “ruderal species”), deciduous forest, and conifers.

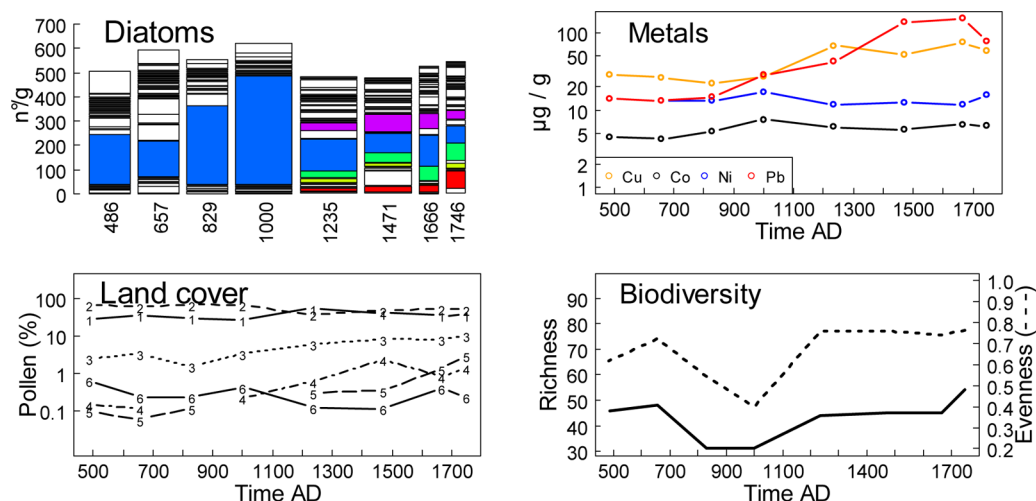


Figure 2. Diatom fossil counts, metal concentrations, land cover, and biodiversity (richness and evenness, left and right axis, respectively) in a representative lake of the Falun region (Hagtjärnen) between 486 and 1764 AD. Color codes for key diatom taxa (upper left panel) are as follows: (red box) *Fragilaria construens* var. *venter*, (yellow box) *Cyclotella comta*, (green box) *Asterionella formosa*, (blue box) *F. construens*, and (pink box) *F. pinnata*. Arabic numbers denote land-cover classes: 1: deciduous forest trees; 2: conifer trees; 3: meadow; 4: herbs indicating land disturbance; 5: cultivated crops; and 6: ferns. Data for the other nine lakes are available in the SI (Figures S2–S10).

The final data set thus comprised a biological and environmental time series for three lakes, including the biodiversity (species richness and evenness) of the diatom community, concentrations of eight metals, pollen-derived proxies for six land cover classes and two temperature variables. However, the sampled sediment depths (and thus ages) differed between diatoms, pollen, and metals. To obtain joint observations at the same points in time, the pollen and metal time series were resampled using the linear interpolation function of the “Rioja” package in R.⁴³ Extrapolation outside the period for which pollen and metal concentrations were available was not allowed. The final data set is unique in its uniformity, because both the diatom and pollen counts of all study lakes were performed by the same analysts, using standardized techniques and uniform taxonomic resolution across sites.

Statistical Model: General Description. The goal of the statistical modeling was to examine if the biodiversity of the fossil diatom assemblage is negatively related to the sedimentary concentrations of eight metals, taking into account eight additional covariates (six land-cover classes and mean annual and summer temperatures) as potential confounding factors. To this end, we first attempted to fit generalized linear models (*glms*) to the diversity data:

$$g^{-1}(E[y_i|x_{ij}, \text{lake}_i]) = \text{lake}_i + \sum(\beta_j \times x_{ij}) \quad (1)$$

where g is a link function, i.e. a function that relates the predictors to the mean response $E[y_i|x_{ij}, \text{lake}_i]$, lake_i is a factorial predictor allowing time-averaged biodiversity to vary among lakes, and β_j are the coefficients expressing the effect of the observation x_{ij} (the i -th observation of the j -th predictor) on observation y_i . We initially excluded temporal autocorrelation of the response variable from the model structure, i.e., *glms* were fitted under the assumption that all observations are mutually independent. Subsequently we tested—using likelihood-ratio tests—if extension with an autocorrelation structure in a generalized linear mixed model (*glmm*) was supported by the data. Fitting of the *glms* was performed separately for species richness (counts, thus Poisson distributed and g = natural

logarithm) and evenness (Normally distributed and g = identity).

After fitting the *glms*, we tested the assumption that relations between predictors and biodiversity were linear by inspecting the residuals from the *glms*. The *glms* for which the residuals changed in a nonlinear way with changing predictor values were rejected and these analyses were repeated using generalized additive models (*gams*), a recently suggested tool for detecting nonlinear effects in paleoecological time series.⁴⁴ Unlike *glms*, *gams* do not a priori assume linear relationships between the predictors and the response variable. Instead, these relationships—and their complexity—are estimated directly from the data by fitting smoothers f_j :

$$g^{-1}(E[y_i|x_{ij}, \text{lake}_i]) = \text{lake}_i + \sum f_j(x_{ij}) \quad (2)$$

where g is a link function, i.e., a function that relates the predictors to the mean response $E[y_i|x_{ij}, \text{lake}_i]$, lake_i is a factorial predictor allowing time-averaged biodiversity to vary among lakes, and f_j are thin-plate regression splines, expressing the effect of the observation x_{ij} , which is the i -th observation of the j -th predictor.⁴⁵ Note that eq 2 only differs from the *glm* formulation (eq 1) in that it uses a smoother f instead of a linear relation between the means of y and x . The same link functions and distributions were used as for the *glms*. During *gam* fitting, a trade-off between the complexity and the predictive capacity of the smoothers prevents overfitting. Technical background on *gams* can be found in Wood.⁴⁵ As with *glms*, we initially excluded temporal autocorrelation of the response variable from the model structure. We tested for autocorrelation in the same way as for *glms*, i.e., by combining with a mixed model and subsequent likelihood-ratio testing. To ensure that potential autocorrelation was not obscured by overly parametrized smoothers, we restricted the degrees of freedom of the fitted smoothers to 4.

Model Selection and Validation for Lakes Hagtjärnen, Rudtjärnen, and Nastjärnen. We followed two different approaches to model selection, both implemented using the R packages *mgcv* (additive modeling),⁴⁶ *nlme* (linear modeling)⁴⁷ and the R *base* package⁴⁸ (details listed in the SI). A first

approach included any significant predictor into the model. A second approach adopted a forward model-selection procedure based on Akaike's Information Criterion (AIC). The AIC is a goodness-of-fit measure that penalizes model complexity so that lower AICs imply a better trade-off between the goodness-of-fit and model parsimony. The AIC is known to be an estimator of the prediction error; by minimizing AIC overfitting is avoided.

Model Selection and Validation for Seven More Falun Lakes. For eleven of the fourteen Falun lakes studied by Ek and Renberg,²⁵ no pollen data were available. To increase the data availability for statistical analyses, we assumed that reconstructed land-cover dynamics for the three principal lakes also applied to seven other lakes (Tjämnängstjärnen, Kvarntjärnen, Uvbergstjärnen, Varbotjärnen, Djuptjärnen, Karlsbotjärnen, and Stugutjärnen) located within 5 km of one of these three lakes (Table S2, SI). The four other lakes were excluded from this analysis, either because they were located >5 km from the lakes providing land-cover reconstruction (Laktjärnen and Mörttjärnen), or because of general data scarcity (Stångtjärnen and Önsbackadammen). This assumption increased the number of available data points from $n = 34$ to $n = 86$. The model selection and validation procedures outlined above were then repeated for this extended data set.

■ RESULTS AND DISCUSSION

Reconstructed Biodiversity, Metal Concentrations, and Land Cover. The reconstructed time series of diatom community composition suggested increases in diatom richness and evenness during the last 1000 years in eight of the ten lakes we considered. For example, in Hagtjärnen the diatom community around 1000 AD (i.e., before metal mining and land-cover changes) was dominated by *Fragilaria construens*, after which other taxa, such as *Fragilaria construens* var. *venter*, *Cyclotella comta*, *Asterionella formosa*, and *Fragilaria pinnata* became equally abundant (Figure 2; data from the other lakes are shown in Figure S2–S10, SI). As a result, diatom richness and evenness in Hagtjärnen were 20 and 0.3 higher during these more recent periods than around 1000 AD. In the two remaining lakes, this trend was either less pronounced (Kvarntjärnen) or absent (Stugutjärnen). In the period before copper mining, i.e., between 0 and 1000AD, consistent biodiversity changes across the ten lakes were lacking.

Sedimentary concentrations of Cu ($\mu\text{g/g}$), which originate almost exclusively from effluents of local mining activity, increased during the last 1000 years, most notably in the two lakes situated <2 km from the metal smelters (Figure 1: Stugutjärnen and Varbotjärnen). Also Hagtjärnen is nearby a smelter, but upstream from its effluents hence explaining its relatively low Cu concentrations.²⁵ Sedimentary concentrations of Pb, which are mostly due to the smelters' regional atmospheric pollution but probably reflect input from long-distance sources as well,⁴⁹ showed clear 10- to 100-fold increases in all lakes except Varbotjärnen and Djuptjärnen. In contrast, concentrations of Cd and Ni stayed relatively constant through time. Concentrations of Zn and Mn exhibit similar temporal patterns as Cu, and are therefore not shown. Cd exhibits temporal patterns similar to Co.

The reconstructed land-cover history for the larger Falun mining region based on pollen records from three small lakes suggested increasing anthropogenic presence from AD 1000 onward (Figure 2 and Figures S2–S10, SI; note the logarithmic scale). The intensification of agricultural activity in the Falun

region is reflected by the steady increase of pollen from cereal crops between 1000 and 1800 AD, followed by exponential increase during the last 200 years. Pollen from herbs indicating land disturbance and pollen from cultivated crops increased about 10-fold over time (Table S1, SI), peaking in the 15th century. The change over time in the total number of tree pollen (deciduous forest trees and conifers) over the last 2000 years was relatively modest, indicating that anthropogenic activity seemingly did not include massive deforestation beyond the level reached 2000 years ago, confirming earlier forest-cover reconstructions for central Sweden.⁵⁰

Exploratory data analysis revealed considerable correlations among the covariates (Figures S11 and S12, SI). Correlations among metals were lowest between Mn and Fe; correlations among pollen indicators for meadow, land disturbance, land cultivation, and ferns were always >0.5 (except between ferns and cultivation, for which it was 0.28). Summer temperature was only correlated with two metals. All metals except Mn and Fe had correlation coefficients >0.5 with at least one of the land-cover types meadow, disturbed land, and cropland.

Modeling of Biodiversity in Hagtjärnen, Rudtjärnen and Nastjärnen. Here, we give the final model selection results; a detailed overview of all results and of the validation of model assumptions is available as SI.

Linear models were good approximations of the relations between richness and the covariates included, as no nonlinear relations between residuals and predictors were apparent (B and C panels of Figure S13, SI). Richness could be significantly described by 13 models (12 with one significant predictor in left panel of Table S3 of the SI; one with two significant predictors in Table S4, left panel, SI of the SI). Each of these models explained about 50% of the observed variability through time and between lakes. None of these models suggested negative effects of metal concentrations on the biodiversity of the diatom community. Only deciduous trees and summer temperature had a significant negative coefficient in the linear models, suggesting a negative effect on diatom richness (Table S3, SI). The estimated effects of metals and the other land cover classes on diatom richness were positive (Table S3, SI). The effects on richness as estimated by the single predictor models were robust to the inclusion of additional predictors (Table S3, SI). For example, the coefficient estimated for cultivated crops was about 10, regardless of the model considered (Tables S3–S4SI). When based on the AIC, a model using the proportion of grassland pollen (indicating meadow), an intercept and a lake effect had the lowest AIC (237) among all of the tested models and this AIC could not be lowered by adding predictors.

Relations between the predictors and evenness were not well described by the linear models. Most notably for Cd, meadow herbs, herbs indicating land disturbance, and summer temperature, model residuals changed in a nonlinear fashion with changing values of these predictors, showing an optimum in model deviations from the data at intermediate covariate values (Figure S15, SI). Therefore, model selection was performed on additive models as these allow for nonlinear relations. When based on significance, this selection yielded 21 possible models for evenness (10 with one predictor listed in the left panel of Table S5 of the SI; 11 with two predictors in the left panel of Table S6, SI), each explaining about 75% of the observed variation in evenness over the past 2000 years. None of these models suggested a negative effect of metals on evenness. Instead, five models using one metal and three models using

one land cover type suggested positive effects of these covariates on evenness (Figure S16, SI). The effects estimated by single-predictor models were the same as those estimated by the models with two significant predictors. For example, higher sedimentary Zn concentrations correspond to higher evenness values, regardless of the model considered (Figure S16, SI). When performing model selection using Akaike's Information Criterion (AIC), a model using the proportion of conifers and mean summer temperature—besides an intercept and a lake effect—had the lowest AIC value (−85.9).

Modeling Biodiversity in Ten Falun Lakes. Assuming that the history of land-cover change, as reconstructed from pollen found in the sediment of lakes Hagtjärnen, Rudtjärnen, and Nastjärnen, can be used to represent the land-cover history for seven regional lakes nearby, we repeated our analysis based on the significance of model terms and AIC, using the assorted paleoecological data from ten lakes. For both richness and evenness, results were similar to those based on data from the three principal study lakes (right panels of Tables S3–S6, SI). Linear models were only suitable to describe richness, while evenness was described best by nonlinear *gams*. Models with one significant predictor could be extended with a second predictor in rare cases only. Model selection for richness again suggested positive effects of metals and land cover (Table S3, SI). The model for richness with the lowest AIC (612; Table S3, SI) had Cd as the sole predictor. Model selection for evenness confirmed our analysis with data from three lakes only in that none of the selected models suggested a negative effect of metals on evenness (Figure S17, SI). Among all models tested for evenness, a model including the sedimentary Zn concentration and the fraction of conifers—apart from an intercept and a lake effect—had the lowest AIC (−213; Table S6, SI). Validation of model assumptions using residual diagnostics is discussed and depicted (Figures S14 and S17) in the SI.

Fitted Effects of Metals. All evaluated models suggested effects on diatom species richness and evenness of either sedimentary metal concentrations or land cover. Although correlations between these two potential types of environmental stressors impeded determining which of the two significantly contributed to biodiversity variation, mining activity—quantified by sedimentary metal concentrations—clearly did not reduce biodiversity during 1000 years of copper mining. These results comply with findings on shorter (decadal) time scales. For example, Cattaneo et al.⁵¹ found no relationship between diatom community composition and modern-day metal exposure of lakes across the Abitibi mining region in Quebec (Canada). An impoverished diatom community—dominated by *Achnanthes minutissima* and *Brachysira vitrea*—was reported only in sediment samples with extremely high Cu concentrations (up to 8000 $\mu\text{g/g}$; three times higher than the maximum Cu concentration found in the present study). In another study, the same authors calculated the effects on diatom diversity of metal-induced structural community changes in surface-sediment samples from the Rouyn-Noranda mining region in Quebec.⁵² Only in lakes with Cu concentrations exceeding 1000 $\mu\text{g/g}$ (up to 3000 $\mu\text{g/g}$) did they find that diatom richness and evenness were 40 and 0.25 units lower than in lakes with sedimentary metal concentrations between 0 and 500 $\mu\text{g/g}$. Couillard et al.⁵³ reached similar conclusions for the same mining region using deeper (0.5 m) sediment cores, representing the recent past. In the present study, there was only one lake where Cu exceeded 1000 $\mu\text{g/g}$

on three subsequent occasions (Stugutjärnen). Although suggested by the data (Figure S7, SI), our model analyses did not find negative metal effects on diversity in this lake. To test if a negative metal effect was hidden in the fitted coefficients for the “lake” predictor (essentially the lake-specific time-averaged diversity) we plotted the fitted coefficients against the corresponding time-averaged Cu concentration. The two lakes with the highest sedimentary Cu concentrations had coefficients that were in the lower range of those estimated for the less polluted lakes, but no consistent trend was found between the fitted lake effect and Cu (Figure S18, SI).

The fact that no significant negative relationship was found—here or by other authors, as discussed in the previous paragraph—between diatom biodiversity and Cu concentrations up to 1000 $\mu\text{g/g}$ is counterintuitive, because phytoplankton is generally considered sensitive to metals and responds to elevated metal exposure with growth cessation.⁵⁴ In addition, metals in mining areas are typically present as mixtures, exerting joint toxicity to aquatic life. Indeed, most metals followed the same temporal trend, as demonstrated by correlation coefficients >0.5 (Figures S11 and S12, SI), suggesting a common source and a combined exposure to aquatic life. Also, concurrent with metal exposure the lakes were exposed to suboptimal pH resulting from acid mining drainage, potentially causing additional stress. The single metals (e.g., Cu) we used for model construction should therefore be understood as proxies of metal mining activity *sensu lato*, and when considered in isolation, concentrations of one single metal are conservative estimates of the suboptimal conditions to which aquatic life was exposed. When adopting a “single metal” approach, ancient aqueous concentrations of Cu, Zn, and Co in some of the lakes during metal mining, as reconstructed from sedimentary metal concentrations and water-suspended matter partitioning coefficients (L kg^{-1} ; Table S7, SI), overlap with toxicity thresholds for freshwater algae as summarized in EU risk assessment reports (Table S7, SI). Although no data were available to account for historical metal bioavailability, this exercise at least suggests that individual metals must have affected the algal communities inhabiting these lakes (Figure S19, SI). When accounting for the mixture of all metals exerting their toxic effects jointly and simultaneously, between $<0.001\%$ and 100% of the diatom species must have experienced a sum of toxic units (i.e., the sum across all metals of concentration divided by toxicity threshold) exceeding one, suggesting toxicity of the metal mixture⁵⁵ (Figure S20, SI), varying by lake and period (pre-vs postmining). If one assumes that a species is lost when its sum of toxic units exceeds one for several decades, then the ecotoxicological prediction would be that richness reductions between 0.001% and 100% occurred. The possibility of no mining-related stress to freshwater algae seems unlikely, let alone that mining stress would have promoted diversity. Instead, it seems likely that diversity in toxic environments was sustained by sensitive taxa being replaced by tolerant taxa. Indeed, several common diatom taxa have been identified as tolerant to metal pollution and/or to the acidic effluent that characterized early day metal mining, e.g., *Fragilaria construens* var. *venter*,⁵² *Asterionella formosa*,⁵¹ *Aulacoseira perglabra* var. *floriniae*,⁵⁶ *Achnanthes* [*minutissima* agg.] and *Frustulia* [*rhomboides*agg.].⁵⁷ In the present study, the proportions of *F. construens* var. *venter*, *A. [minutissima* agg.] and *A. formosa* indeed appear to have increased or remained constant with increasing metal concentrations, respectively (Figure S21, SI). The fact that these changes in community structure occurred

following metal exposure while biodiversity was not reduced demonstrates that using biodiversity as an end point in nature conservation allows species identities to change as long as biodiversity is unaltered. Thus, if the goal of environmental protection is to maintain the taxonomic composition of a given ecosystem, biodiversity is a too coarse a measure to serve this goal, and alternative techniques may be more suitable.⁵⁸

Fitted Models: Effects of Land Cover. Models including land-cover covariates indicated that meadow, disturbed land, and cropland promoted biodiversity. Again, it should be noted that the importance of these covariates cannot be distinguished from the potential, although questionable, positive effects of metals, because of correlations among them. All tested models that included land cover indicated that some degree of disturbance by changes in land cover is beneficial for the biodiversity of freshwater diatom communities in the studied Swedish lakes. This result complies with the “Intermediate Disturbance Hypothesis” (IDH;⁵⁹), which proposes that peak biodiversity is realized at an intermediate level of disturbance, at which competing taxa tend to coexist because no single species is capable to dominate the community. However, our models never suggested a unimodal relationship as predicted by the IDH, nor did the data (Figure 3). Possibly, this is because our

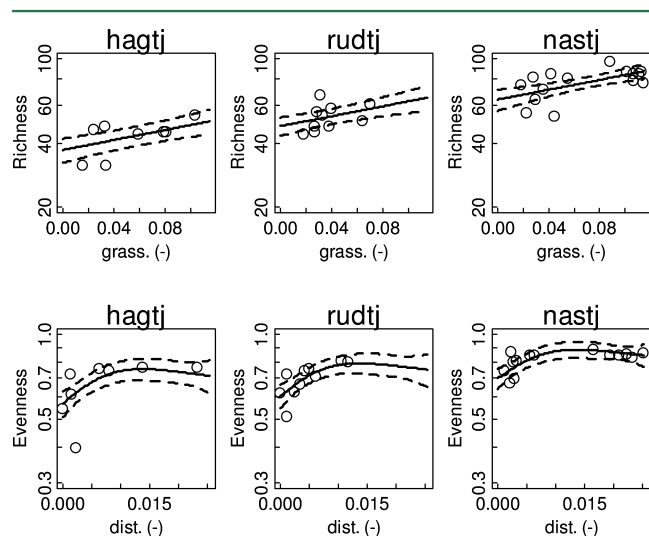


Figure 3. Observed (symbols) and predicted (solid lines) richness (top panels) and evenness (lower panels) in lakes Hagtjärnen (hagtj), Rudtjärnen (rudtj), and Nastjärnen (nastj) as a function of the proportion of herbs indicating land disturbance in the total count of terrestrial pollen. Dashed lines are pointwise 95% confidence intervals.

data—diatom responses to multiple stressors over a 2000-year period—are representative for low- to medium-disturbance levels only. As a result, the “high” disturbance levels that are needed to confirm or reject the unimodal relationship between disturbance and biodiversity in this particular case were not represented. Recent reports have demonstrated that land use intensification can have detrimental effects on the diversity of remains of microbial life in lake sediments.⁶⁰

The beneficial effect of moderate disturbance levels on phytoplankton diversity has been shown valid on short time scales (weeks to months) using experimental setups⁶¹ and theoretical exercises aided by ecological modeling.^{62–65} In these efforts, disturbance has been defined as environmental variability caused by wind-driven water-column mixing,⁶⁶ temperature fluctuation,⁶⁷ lake level,⁶⁶ turbidity⁶⁸ or nutrient

loading.⁶⁹ On long (historical) time scales and specifically for diatom communities, the promotion of aquatic community richness by the relatively abrupt land-cover changes following North American settlement has also been demonstrated.⁷⁰ The underlying mechanisms proposed by these authors, namely the alterations in lake turbidity and nutrient levels following land clearance (deforestation), are the same as those observed in experiments with time scales from weeks to months. In the case of the Falun mining region, massive deforestation did not occur during the period covered by this study (e.g., Figure 2). Still, the modest changes in tree cover were weakly correlated to changes in pollen from cultivated crops, herbs associated with land disturbance and meadow herbs (Figure S22, SI). Land-cover change thus possibly stimulated biodiversity by increasing fluxes of nutrients and suspended materials, as in Watchorn et al.⁷⁰ In addition, the conversion of forested land to meadows and fields may have made the Falun lakes more accessible for immigrant species, thus sustaining the diversity of the local communities. Some support for these hypotheses can be found in the data set in the form of increasing proportions of r-strategist diatom taxa (*Fragilaria construens*,⁷¹ *Fragilaria pinnata*,⁷² *Asterionella formosa*,^{73–76} and *Achnanthes [minutissima agg.]*^{77–79}) as historical levels of disturbance in the Falun region increased. Indeed, the proportions of these opportunistic taxa are positively correlated with pollen percentages of herbs reflecting land disturbance (Figure S22, SI). However, the contribution of land clearing versus nutrient enrichment to this increase in opportunistic taxa remains to be tested.

Implications for Chemical Risk Assessment and Biodiversity Conservation. No ecotoxicological data are available on the effects of chemicals on natural ecosystems over time scales lasting decades to centuries. Toxicity thresholds derived using classic ecotoxicological short-term tests on individual species are therefore not necessarily adequate to assess the sensitivity of ecosystem structure and functioning on these long time scales. In this study, all tested models that included metals as stressors surprisingly suggested increases rather than decreases of biodiversity following exposure to metal pollution, a counterintuitive result for which we have found no previous reports in the literature and which could not be predicted by ecotoxicological paradigms of single chemical toxicity or mixture toxicity. This indicates that available toxicological data cannot predict long-term trends of biodiversity in field ecosystems exposed to a multitude of potential stress factors, including changes in land cover and temperature. Instead, our extensive set of statistical analyses suggests enhancement of biodiversity by modest land disturbance during the last millennium in the Falun mining area. These results urge us to revisit the role of chemicals and chemical risk assessment in the conservation of biodiversity, even in ecosystems adjacent to point sources of chemical pollution.

■ ASSOCIATED CONTENT

● Supporting Information

Details on the additive and linear modeling, Tables S1–S7 and Figures S1–S22. This material is available free of charge via the Internet at <http://pubs.acs.org>.

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Notes

The authors declare no competing financial interest.

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