

Millennial-scale relationships of diatom species richness and production in two prairie lakes

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Abstract

Insight into the causes and consequences of changes in aquatic biodiversity requires an improved understanding of the nature of the relationships between species richness and ecosystem function over a much longer temporal perspective than we currently possess. We used high-resolution paleoecological records from two prairie lakes to show that diatom species richness (as fossil frustules) was negatively correlated ($r^2 = 0.09\text{--}0.24$, $p < 0.001$) with diatom production (as fossil pigments) during the past 2,000 yr. By comparing analyses from intervals of fresh and saline waters, we demonstrate that these significant richness–production relationships arose during freshwater periods ($r^2 = 0.13\text{--}0.45$, $p < 0.001$) and could be eliminated ($r^2 < 0.02$, $p > 0.1$) by abiotic disturbances such as droughts. Procrustes analyses of the concordance of species change within freshwater communities and the change in richness–production relationships through time revealed that shifts in diatom community composition could have a large influence in determining the negative relationship between richness and production. Finally, significant correlations ($r^2 = 0.09\text{--}0.24$, $p < 0.0001$) between past diatom species richness and ratios of stable isotopes (primarily $\delta^{15}\text{N}$) suggested that C and N biogeochemical cycles are also linked to changes in algal biodiversity. Taken together, these analyses suggest that the ongoing disruption of climate and biogeochemical systems by humans may obscure the relationship between aquatic biodiversity and ecosystem function in the future.

Concern over the impacts of biodiversity loss on ecosystem function has led to substantial efforts to quantify the nature of species richness–ecosystem production relationships. Whereas large-scale spatial surveys suggest that species richness varies in a unimodal fashion with production (Dodson et al. 2000; Mittelbach et al. 2001; Chase and Leibold 2002), short-term experiments have identified both positive and negative linear relationships (Proulx and Mazumder 1998; Dodson et al. 2000; Downing and Leibold 2002). Although differences between spatial and experimental results may reflect the existence of scale-dependent causal mechanisms (Loreau et al. 2001), neither approach provides much insight over timescales longer than a decade (Dodson et al. 2000). This lack of temporal perspective is of considerable concern both because the mechanisms that generate spatial

patterns may be different from those leading to temporal change, and because such observations from small-scale experiments may be poor predictors of ecosystem dynamics (Symstad et al. 2003). In those few studies that have examined the effects of productivity on species richness in individual lakes (Dodson et al. 2000, Interlandi and Kilham 2001), the relationship has tended to be negative, as have short-term experimental manipulations of productivity in terrestrial systems (Mittelbach et al. 2001). Here, using paleolimnological data, we have the opportunity to test this relationship over a much larger timescale using natural fluctuations in production as our treatment.

Recent work has demonstrated the pitfalls of investigating production–diversity relationships in isolation (e.g., Loreau et al. 2001). Thus, ecologists have focused on how disturbance (Cardinale et al. 2000; Mulder et al. 2001), species identity (Downing and Leibold 2002; Symstad et al. 2003), and other ecosystem processes (Loreau et al. 2001) influence this relationship. To date, the role that disturbance plays remains controversial. Model simulations predict that disturbance can either reduce the slope of positive diversity–production correlations (Cardinale et al. 2000) or can induce either positive or negative correlations, depending on whether disturbance intensity is either high or low (Kondoh 2001). Experimental analyses are also equivocal, with disturbances resulting in both positive and negative changes in richness–production relationships (Proulx and Mazumder 1998; Mulder et al. 2001). Similarly, the role that species identity plays is contentious. Most short-term experiments suggest that although community composition can influence richness–production relationships, the magnitude of this effect may de-

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pend on the particular functional group or trophic level manipulated (Downing and Leibold 2002; Symstad et al. 2003). Finally, we are only now beginning to examine how ecosystem processes other than production might influence or be influenced by species richness. Consequently, Loreau et al. (2001) have suggested that future investigations need to move beyond the simplistic approach of studying two variables in isolation and must address possible feedbacks between richness, production, environmental disturbance, and other ecosystem processes.

In this paper, we used high-resolution paleolimnological records of water chemistry, diatom species richness and production, and ecosystem processes (C and N cycling) in two prairie lakes during the past 2,000 years to investigate the effect of production on richness. This study had four objectives. First, we wished to characterize the shape of the algal richness–production relationship over 2,000 yr for comparison with short-term, within-lake experiments (positive, negative, or no linear correlation; Dodson et al. 2000; Interlandi and Kilham 2001; Downing and Leibold 2002), and large-scale spatial surveys (unimodal relation; Dodson et al. 2000; Chase and Leibold 2002). Second, we sought to test whether observed relationships were altered by disturbance, in this case by the presence of extreme climatic events (droughts). Here models and short-term experiments suggest that production–richness relationships should respond to disturbance, but analyses disagree on the magnitude and direction of response (Cardinale et al. 2000; Kondoh 2001; Mulder et al. 2001). Third, we used matrix concordance analyses to determine whether there was a significant effect of species identity on the richness–production relationships (cf., Dodson et al. 2000; Mittelbach et al. 2001). Finally, we sought to identify whether other major ecosystem processes (C and N cycling) covaried with historical changes in algal species richness and lake production. Because our analyses were based exclusively on paleoecological reconstructions of past lake conditions, our identification of causal mechanisms underlying richness–production relationships was necessarily speculative. However, we have taken advantage of the improved temporal coverage provided by fossil studies to determine whether richness–production models derived from experiments and spatial surveys are equally valid for explaining historical relationships.

Methods

Sediment analyses—Sediment cores were obtained from Humboldt (Saskatchewan; 52°8.62'N, 105°6.61'W) and Chauvin lakes (Alberta; 52°41.41'N, 110°6.02'W) in the northern Great Plains region of central Canada to reconstruct past changes in diatom production, species richness, and ecosystem processes. The surrounding landscape is presently agricultural, converted with the advent of European settlement in the early 1900s, but was once at the northern edge of short-grass prairie. These closed-basin lakes are presently eutrophic and were chosen for their sensitivity to climatic fluctuations that constitute substantial environmental disturbances (e.g., droughts; Laird et al. 2003). Cores were collected during the summers of 1998 and 1999 using standard

gravity (surficial sediments; 0–15 cm) and piston coring equipment. Overlap and correlation between cores was estimated using profiles of sediment geochemistry and diatom species composition. Total core length for Humboldt was 176.5 cm, whereas a 191.0-cm core was collected in Chauvin Lake. Cores were sectioned continuously into 0.25-cm intervals and every other sample was analyzed for fossil remains after sample lyophilization for 24 h (Leavitt and Findlay 1994). Sediment chronologies were based on alpha spectrometric analysis of ²¹⁰Pb activities of recent sediments (1850–present), constant rate of supply calculations, and 4–8 accelerator mass spectrometric analyses of ¹⁴C in seeds, leaves, woody debris, or sediment (Laird et al. 2003; Leavitt et al. unpubl. data). Radiocarbon ages were calibrated to calendar years (A.D.) with CALIB 4.0 (Stuiver et al. 1998). Regression analyses revealed that relationships between ¹⁴C age and burial depth were best described by linear models ($r^2 > 0.89$, $p < 0.0001$), and suggested that sediment mass accumulation rates (dry mass, g cm⁻² yr⁻¹) were relatively constant through time, before European land-use practices.

Fossil diatom frustules were identified to species and were used to reconstruct past diatom species richness as well as changes in lake depth and water salinity. Sediments were digested and diatoms were isolated and enumerated using standardized paleoecological procedures (Wilson et al. 1996; Laird et al. 2003). Species richness was estimated as the total number of unique taxa identified in each sediment interval after standardized counting intensity (~350–500 diatoms sample⁻¹). There was no statistical relationship between counting intensity and species richness. Past lakewater salinity was estimated from changes in the relative abundance of fossil diatoms using inference models that relate diatom species composition to modern lake chemistry (Wilson et al. 1996). The predictive ability of these diatom-inference models is strong and highly significant, as judged from the relationship between inferred and observed salinity in a suite of modern lakes (bootstrapped $r^2 = 0.8–0.9$, $p < 0.001$; Fritz et al. 1999). Our model used a calibration set of 287 lakes, consisting of 79 sites from the prairie region (Fritz et al. 1993; Fritz unpubl. data) and 208 lakes from British Columbia (Wilson et al. 1996) that resulted in predictive model as strong as earlier models (bootstrapped $r^2 = 0.86$, $p < 0.0001$), but with an expanded set of appropriate analogs for reconstructing salinity from the diatom assemblages encountered in these cores. Models for lake depth are summarized by Cumming et al. (2002). In general, the model was less robust than that of salinity (bootstrapped $r^2 = 0.60$), but still capable of quantitative reconstructions of major changes in basin morphology.

Fossil pigments were used to characterize changes in the production of diatoms during the past 2,000 years. Concentrations of sedimentary carotenoids, chlorophylls, and derivatives (nanomoles of pigment per gram of dry mass) were analyzed by high-performance liquid chromatography for each sample (Leavitt and Findlay 1994). Whole-lake experiments (Leavitt et al. 1997), mass-balance budgets (Leavitt and Carpenter 1990), and ecosystem simulation models (Cuddington and Leavitt 1999) show that concentrations of fossil pigments are most strongly correlated to total annual phytoplankton standing crops (wet wt, mg m⁻²) and sum-

marize phytoplankton abundance in taxonomic units equivalent to algal functional groups (Leavitt and Findlay 1994). When expressed as rates of pigment accumulation in sediments ($\text{nmol cm}^{-2} \text{ yr}^{-1}$), these estimates are equivalent to rates of algal production (e.g., Guilizzoni et al. 1983; reviewed in Leavitt 1993). Because mass accumulation rates (dry mass, $\text{g cm}^{-2} \text{ yr}^{-1}$) were constant through time in our lakes (see above), and because pigment accumulation is estimated as the product of mass accumulation rates and pigment concentrations, our fossil pigments also recorded changes in algal production. Consequently, we used diatoxanthin, the signature pigment from diatom taxa, to estimate primary production by diatoms.

Our analyses focus on the relationship between the species richness and production of diatoms, a significant component of overall benthic and planktonic production in shallow prairie lakes (Fritz et al. 1999). Although this relationship is specific to diatoms, strong correlations between total algal production (inferred as fossil β -carotene) and diatom-specific diatoxanthin in both lakes ($r^2 = 0.40\text{--}0.49$, $p < 0.0001$) suggest that our results may also apply to the entire lake ecosystem. Unfortunately, as most algae do not leave physical remains in sediments, we cannot directly test this hypothesis.

Sedimentary isotopic ratios were used to characterize carbon (C) and nitrogen (N) cycling in aquatic ecosystems. Using the same intervals as for diatoms and pigments, inorganic and organic C and organic N samples were prepared using standard methodology (Schelske et al. 1991; Hodell and Schelske 1998) and analyzed on a Thermoquest DeltaPlus^{XL} continuous-flow isotope ratio mass spectrometer. As shown elsewhere, isotope ratios can be excellent integrators of ecosystem processes (Robinson 2001) and, in lake sediments, have been used to track changes in a number of ecosystem attributes including trophic state, food-web structure, and productivity (Hodell and Schelske 1998; Brenner et al. 1999; Gu et al. 1996).

All variables except richness were \log_{10} -transformed before analysis to normalize distributions. Because of negative $\delta^{13}\text{C}$ values, a constant was added before transformation ($\log_{10}[x + 30]$) of these two variables.

Statistical analyses—We used both linear and nonlinear regressions to characterize the general form of the relationship between diatom richness and production in Chauvin and Humboldt lakes. For the nonlinear case, we fit the model $R = a + bP + cP^2$, where R was diatom species richness and P was production (as \log_{10} -transformed diatoxanthin concentration). We then compared r^2 values among linear and nonlinear models to check for any substantial increase in goodness of fit.

Rates of diatom community change were estimated from percentage composition data as chord distance per sediment interval (Hall et al. 1999). Chord distance is a dissimilarity coefficient appropriate for estimating rates of change from percentage data. Correlation analyses were then used to evaluate how rates of community change covaried with diatom production, species richness, and diatom-inferred changes in lake depth and water salinity.

Potential climatic disturbances (droughts) were defined as

intervals during which diatom-inferred salinity was above average values recorded during the past 2,000 years. Thus, each salinity time series (Fig. 1A) was detrended by linear regression and used to identify periods of relatively fresh (negative deviations) and saline lake conditions (positive deviations). Linear and nonlinear regressions of diatom species richness and production were compared among fresh and saline subsets to determine if the relationship changed as a result of climatic extremes.

The influence of species identity on richness–production relationships was investigated using a randomized Procrustes analysis to test for a concordant relationship between a matrix that described community structure and one containing species richness and production data (PROTEST analysis with 9,999 randomizations; Jackson 1995). In this procedure, correspondence analysis (CA) was used to ordinate a species-by-sample matrix populated with square root-transformed relative abundances (%) of common diatoms (i.e., present in $>0.5\%$ of all samples from a given lake). Here sample scores from the first two CA axes were used as variables for the community structure matrix. CA is the preferred ordination technique for sparse data input matrices (Jackson 1993). Significant concordance between richness–production and community structure matrices demonstrates that changes in species identity are strongly related to concurrent changes in richness and production.

We also developed a simple visual technique to quantify the interactions between diatom production, species richness, and community composition. In this case, we used CA axis 1 (CA1) scores to summarize diatom community composition. We then used the maximum (positive) and minimum (negative) CA1 scores from each lake's CA to define the ends of a color spectrum that ranged from 400 nm to 700 nm. Using this approach, each diatom assemblage could be assigned a 'color' according to its CA1 score. Sediment intervals were then ordered according to wavelength (CA1 score), and richness or production values for the same sediment intervals were overlain to examine how each varied as a function of community change. This qualitative analysis allows visual representation of the Procrustes analysis and can be used to screen for nonlinear relationships between changes in richness, production, and community composition.

Forward stepwise multiple regression was used to further quantify the relationship between species richness, production, and ecosystem function. Here, richness was considered as the dependent variable, and individual independent variables representing production ([diatoxanthin]), N cycling ($\delta^{15}\text{N}$), and organic ($\delta^{13}\text{C}_{\text{organic}}$) or inorganic C cycling ($\delta^{13}\text{C}_{\text{inorganic}}$) were added to the model ($F_{\text{entry}} = 1.0$, $F_{\text{removal}} = 0.0$). The best model was obtained when all variables included explained a significant, independent amount of variance in species richness.

Results

Radiocarbon dating revealed that both sediment cores spanned approximately 2,000 yr, resulting in an average temporal resolution of ~ 2.5 yr per sediment interval in both

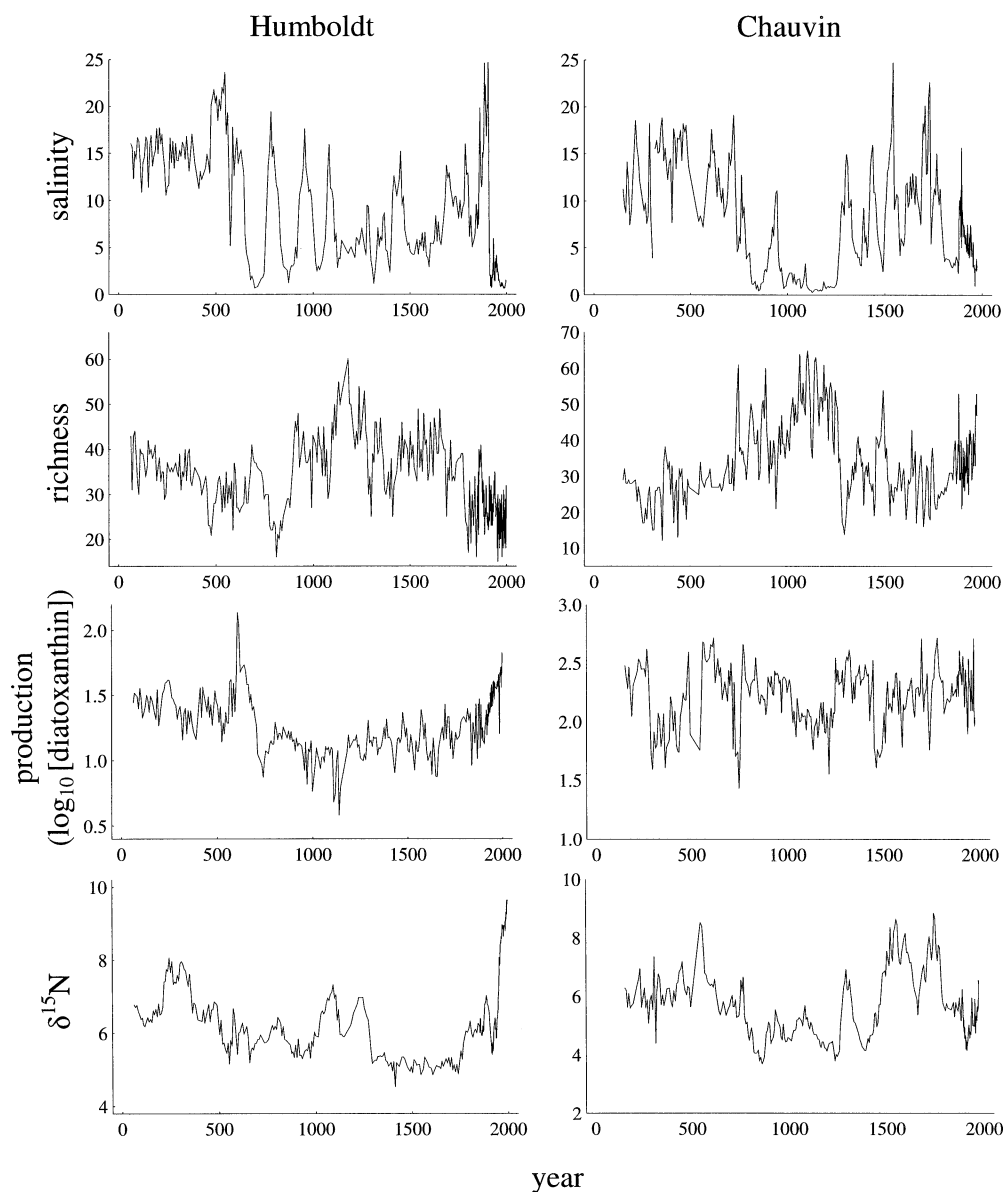


Fig. 1. Historical changes in diatom-inferred lake salinity (‰), fossil diatom species richness, diatom production (\log_{10} [diatoxanthin concentration]; nanomoles of pigment per gram of organic matter), and sedimentary $\delta^{15}\text{N}$ isotope ratios (‰) during the past 2,000 yr in Humboldt Lake, SK, and Chauvin Lake, AB, Canada.

lakes. Diatom-inferred salinity varied 0–20‰ in each lake, whereas pigment-inferred production varied by over 10-fold (Fig. 1). Diatom species richness in each sample ranged 12–65 species in Chauvin Lake and 15–60 species in Humboldt Lake, although the total species pool was substantially greater at each site. Historical values of sedimentary $\delta^{15}\text{N}$ and organic $\delta^{13}\text{C}$ ranged $\sim 5\%$ in both lakes, spanning 3.7‰ to 9.6‰ for $\delta^{15}\text{N}$ and -28.4% to -22.9% for $\delta^{13}\text{C}_{\text{organic}}$. In contrast, inorganic $\delta^{13}\text{C}$ values ranged from -18.5% to 2.1‰ (not shown). Such large changes provide ample variation with which to establish richness–production relationships and test hypotheses related to biodiversity and ecosystem function.

Our first objective was to test for an overall relationship between richness and production. We found a significant negative linear relationship between diatom richness and production in both lakes (Fig. 2). Regressions were strongest in Humboldt Lake ($r^2 = 0.24$, $p < 0.0001$), although the pattern was also highly significant in Chauvin Lake ($r^2 = 0.09$, $p < 0.0001$). Even though our gradients of diatom production encompassed nearly two orders of magnitude, there was no support for a unimodal model at either site, and attempts to fit quadratic equations to these data resulted in no improvement in fit or explained variance.

Comparison of freshwater and saline intervals suggested that disturbance may modify richness–production relation-

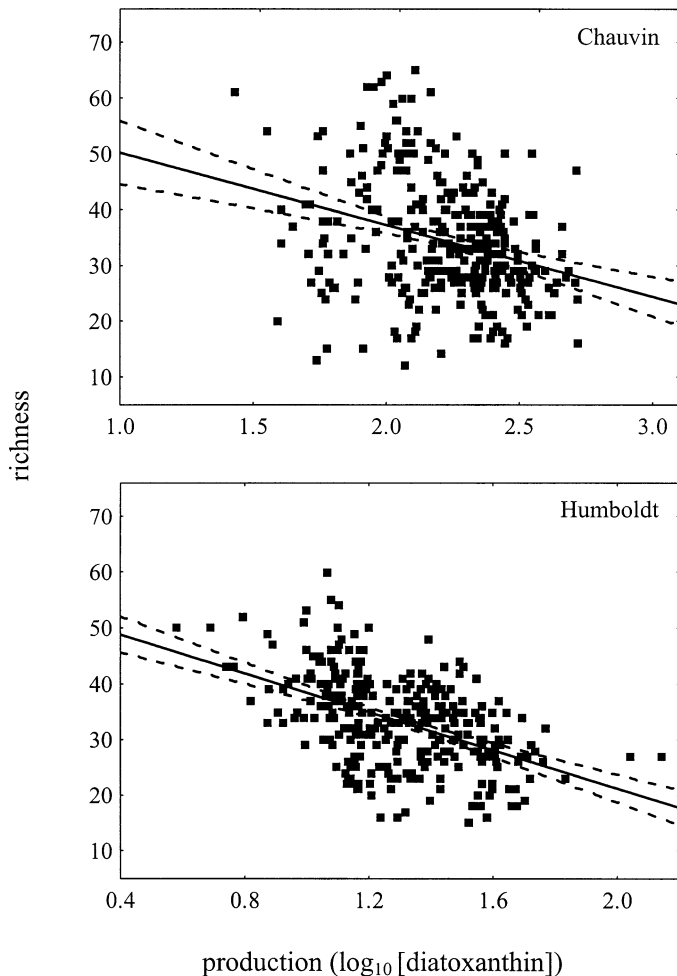


Fig. 2. Relationship between diatom species richness and production in Chauvin Lake, AB and Humboldt Lake, SK for all historical intervals. Linear regressions ($\pm 95\%$ confidence limits) are significant at $p < 0.0001$. Diatom production as in Fig. 1.

ships over long timescales (Fig. 3). In both lakes, the negative relationships between diatom richness and production were enhanced during freshwater periods, whereas no significant statistical relationship could be identified during saline intervals. This pattern was most pronounced in Humboldt Lake ($r^2_{\text{fresh}} = 0.45$, $p < 0.0001$; $r^2_{\text{saline}} < 0.02$, $p = 0.09$), but was also clearly evident in Chauvin ($r^2_{\text{fresh}} = 0.13$, $p < 0.0001$; $r^2_{\text{saline}} < 0.001$, $p = 0.94$). Because of the lack of any significant relationship during saline periods in either lake, the remainder of the analyses were based on data from freshwater periods only.

In both Humboldt and Chauvin lakes, rates of diatom community change (as chord distance) in freshwater intervals were negatively correlated with diatom production (\log_{10} [diatoxanthin]; $r = -0.17$ and -0.22 ; $p < 0.05$), but not lake salinity ($p > 0.25$) or diatom species richness ($p > 0.12$). Additional correlations, also using only freshwater intervals, suggested that there were few consistent relationships among salinity, richness, and production; salinity was inversely related to richness and directly related to production in Chauvin Lake, and directly related to richness and

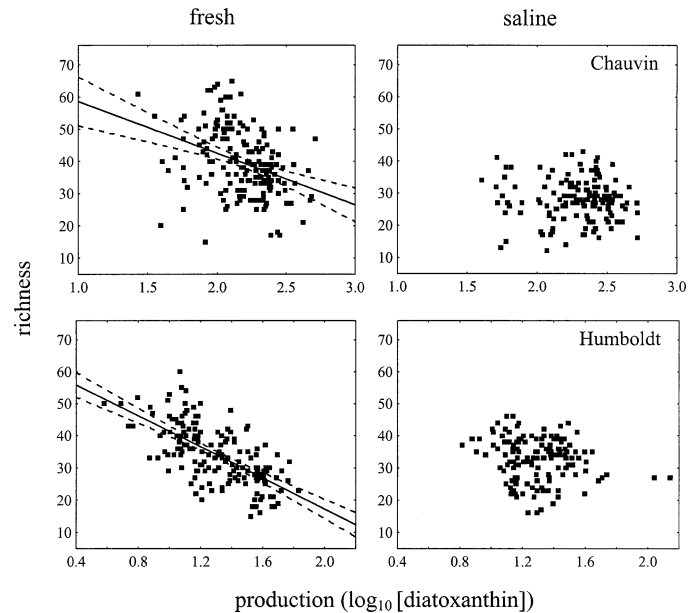


Fig. 3. Relationship between diatom species richness and production in Chauvin Lake, AB and Humboldt Lake, SK for freshwater and saline historical intervals. Freshwater and brackish conditions were defined as negative and positive detrended diatom-inferred salinity values, respectively. Confidence limits as in Fig. 2.

inversely related to production in Humboldt Lake. Instead, species richness was significantly correlated with historical changes in lake depth, particularly in Humboldt Lake ($r = -0.48$, $p < 0.0001$), where richness declined during periods of greater water depth.

Procrustes analysis of freshwater intervals revealed a significant influence of species identity on the relationship between richness and production. Specifically, highly significant concordance values were obtained for comparisons of matrices describing community structure and richness–production relationships in both Humboldt ($m^2 = 0.71$, $p < 0.0001$) and Chauvin lakes ($m^2 = 0.79$, $p < 0.0001$). Such significant matrix concordance suggests that species identity was strongly related to patterns of richness and production in each lake.

Visual comparison of the relationships between production, richness, and community composition (as CA1) also suggested that algal production covaried with changes in species identity (Fig. 4). In both lakes, production (white line) varied substantially as a function of community composition. Species richness (black line) also varied with community composition as documented by our initial analysis (Fig. 2). In general, the rate of change in algal production (slope of production vs. CA1 score) was greatest when species composition changed most, although this effect was less evident for Chauvin Lake than for Humboldt Lake. Given this latter observation and the consistency in community composition observed over a good portion of the fossil record (the red end of the spectrum dominates in both lakes), it is not too surprising that the proportion of variance explained (at least in Chauvin Lake) by our freshwater regressions between richness and production (Fig. 3) is not larger.

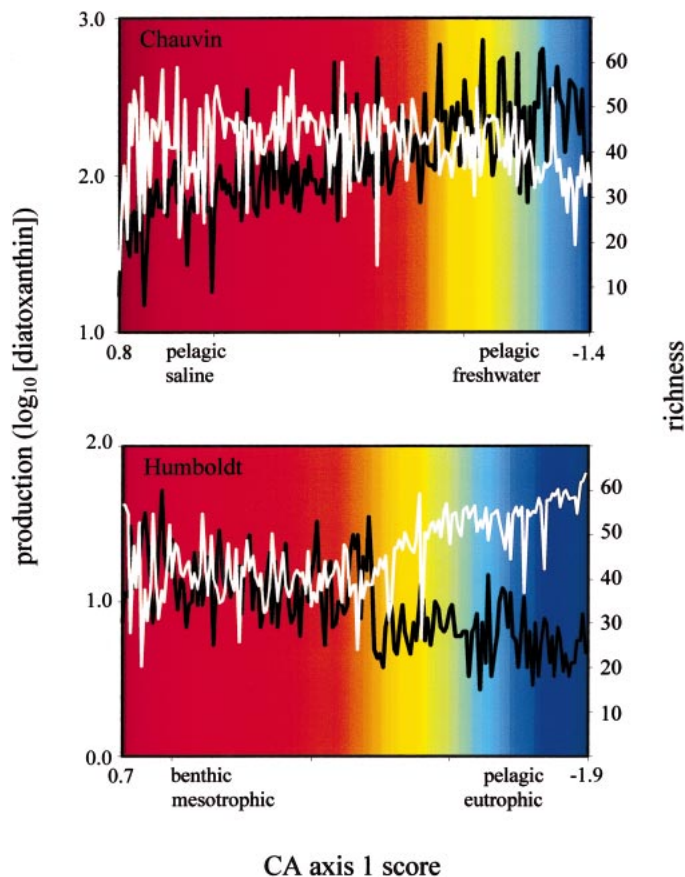


Fig. 4. Fluctuations in diatom production (white) and species richness (black) as a function of diatom community composition in Chauvin and Humboldt lakes during historical freshwater intervals. Correspondence analysis was used to order diatom communities along CA axis 1. Diatom communities were assigned a wavelength range assuming that the extremes of CA axis 1 represented 400 nm and 700 nm. Corresponding estimates of diatom production (as Fig. 1) were plotted according to this gradient of community change to identify how production and richness varied as a function of community change.

Together, these patterns suggest that, at millennial time-scales, community composition appears to play a large role in determining the inverse relationship between richness and production.

Correspondence analysis of fossil assemblages also suggested that the mechanisms underlying community change, and therefore richness–production relationships, may have differed among lakes. For example, the first two CA axes captured 44% (first axis = 28%) of the variation in diatom community structure in Chauvin Lake and 50% of the variation in Humboldt Lake (first axis = 31%). In Chauvin Lake, the pelagic freshwater indicator taxa *Cyclotella michiganiana* and *Fragilaria tenera* (Fritz et al. 1993, Wilson et al. 1996) were strongly associated with the negative end of CA1, whereas *Cy. choctawhatcheeana* and *Chaetoceros muelleri*, both pelagic saline species, had the highest loadings on the positive end. Thus, CA1 represented a pelagic gradient of salinity, despite our inclusion of only freshwater intervals in the analysis. In contrast, the negative end of CA1

of Humboldt Lake was defined by pelagic eutrophic species (*Stephanodiscus hantzschii*, *S. niagarae*, *S. parvus*), whereas benthic mesotrophic saline species plotted at the positive end of the axis (e.g., *Navicula sp. 6 PISCES*, *N. crucicula*, *N. salinarum*). Here, the principle gradient of community change in Humboldt Lake was defined by production and secondarily depth or salinity, consistent with the strong richness–production relationship at this site ($r^2_{\text{fresh}} = 0.45$), and the linear correlation between richness and depth (see above).

In both lakes, negative relationships were recorded between species richness and corresponding sedimentary $\delta^{15}\text{N}$ values during freshwater intervals (Fig. 5). Overall, this trend was more pronounced in Humboldt Lake ($r^2 = 0.23$, $p < 0.0001$) than in Chauvin Lake ($r^2 = 0.09$, $p < 0.0001$), although in both cases, significant regressions were retained even if saline intervals were included in the analyses. Further, correlations between richness and isotopic signatures were significant and negative at both sites even when production was included in multiple regressions (Table 1), despite the observation that relationships between production and $\delta^{15}\text{N}$ were positive in Humboldt Lake ($r = 0.63$, $p < 0.001$) and negative in Chauvin Lake ($r = -0.21$, $p < 0.01$). In contrast, inorganic and organic $\delta^{13}\text{C}$ values were retained only in the final regression model from Humboldt Lake, despite elemental ratios that suggested that the organic sediments of both lakes were composed mainly of algal remains (C:N < 10; Meyers 1997).

Discussion

This study used fossil records spanning two millennia to identify consistent negative relationships between the species richness and production of diatoms in two prairie lakes (Fig. 2). However, comparison of analyses from freshwater and saline intervals (Fig. 3) suggested that richness–production relationships could be eliminated by abiotic disturbances, such as droughts, that greatly increase lakewater salinity and osmotic stress. Similarly, richness–production relationships were strongest in Humboldt Lake, where gradients of community change were defined primarily by shifts in trophic state of the system. Furthermore, both Procrustes and visual analyses (Fig. 4) revealed that species identity had an important influence on richness–production relationships in these aquatic ecosystems. Finally, significant regressions between past diatom richness and isotopic metrics of N (and to a lesser extent C) cycling suggested that other ecosystem functions, such as biogeochemical cycling, may covary with aquatic biodiversity.

The significant negative relationships between diatom richness and production observed here contrast with models developed from spatial (unimodal; Mittelbach et al. 2001) and experimental approaches (positive linear; Proulx et al. 1996; Proulx and Mazumder 1998; Downing and Leibold 2002), but are consistent with short time series from individual lakes (Interlandi and Kilham 2001) and some whole-lake ecosystem enrichment experiments (Dodson et al. 2000). When viewed as part of a unimodal richness–production curve, negative relationships have been hypothe-

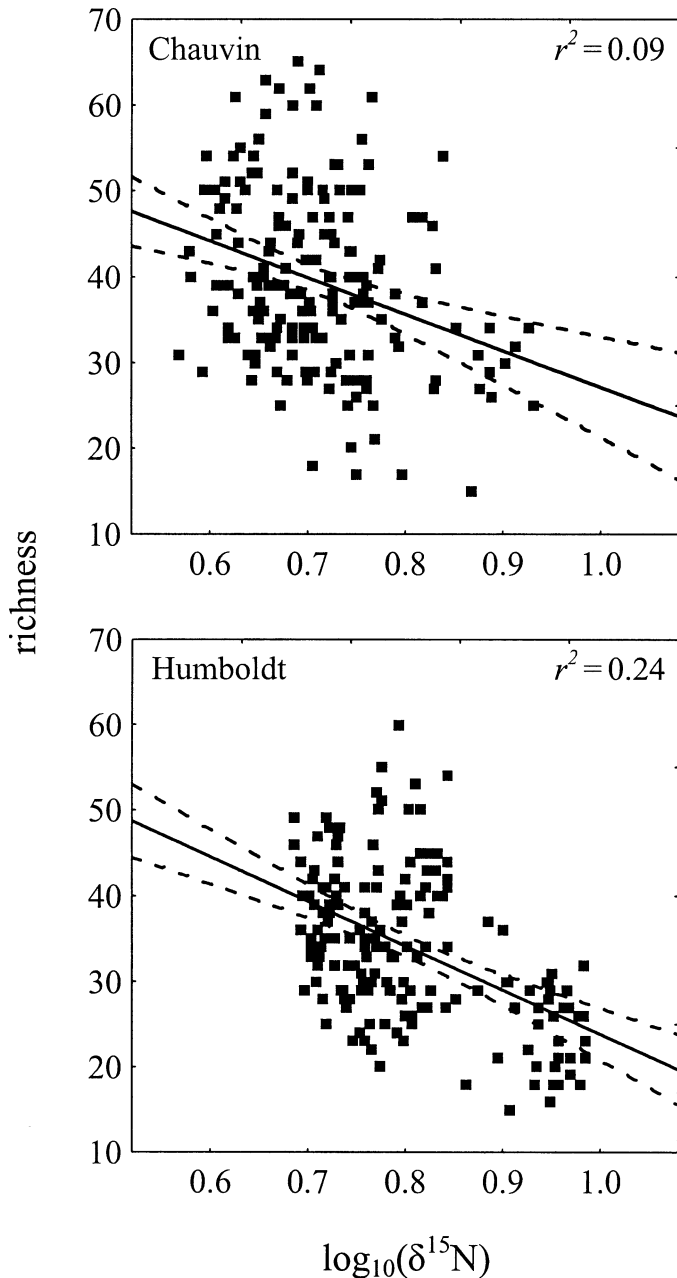


Fig. 5. Relationship between diatom species richness and stable isotope ratios of nitrogen ($\delta^{15}\text{N}$, ‰) in organic sediments deposited in Chauvin Lake, AB and Humboldt Lake, SK during historical freshwater intervals of the past 2,000 yr.

sized to arise because of extreme destabilization of predator–prey cycles (‘paradox of enrichment’), reduction in resource heterogeneity (‘resource heterogeneity hypothesis’ see also Interlandi and Kilham 2001), changes in the number or nature of limiting resources (‘resource-ratio hypothesis’), or changes in prey susceptibility to predators under eutrophic conditions (‘keystone-predation hypothesis’; all reviewed in Leibold 1999). Further, the precise form of the relationship (linear, unimodal) may depend also on the scale of observation (Loreau et al. 2001; Mittelbach et al. 2001; Chase and

Leibold 2002) and degree of disturbance (Cardinale et al. 2000; Kondoh 2001; see below).

Although we cannot distinguish easily among hypotheses, we note that rates of diatom community change declined significantly with increased production, suggesting that the basic mechanism underlying the ‘paradox of enrichment’ (i.e., population destabilization) did not operate in our lakes. Instead, our results are consistent with some expectations of the ‘resource heterogeneity hypothesis’ (Tilman et al. 1982). For example, we note that diatom richness was inversely related to lake depth in both Humboldt and Chauvin lakes as was overall community composition (Fig. 4), suggesting that changes in habitat availability and environmental heterogeneity may play an important role in dictating richness–production relationships (cf. Kerr and Packer 1997; van Rensburg et al. 2002). For example, the depth of Humboldt Lake (now 6.6 m) has varied from 1.4 to 11.3 m in the past 2,000 yr (Leavitt unpubl. data), a range sufficient to regulate growth of rooted macrophytes that are habitat for some diatoms and important regulators of alternative stable states in shallow lakes (Scheffer et al. 1993). However, although our results are consistent with expectations of the resource heterogeneity hypothesis, the lack of information concerning concomitant changes in predation (Proulx and Mazumder 1998) and resource regimes (Interlandi and Kilham 2001) precludes us from more definitive statements concerning the alternate controls (i.e., paradox of enrichment, keystone-predation, and resource-ratio hypotheses) of the observed richness–production relationships in these lakes.

Because human activities are both reducing biodiversity and introducing severe perturbations of the abiotic environment, there is intense interest in documenting the potential interaction between ecosystem disturbance and richness–production relationships. In lakes of the northern Great Plains, droughts increase ionic strength and osmotic stresses that are strong controls of algal community composition (Fritz et al. 1999), although not production (Vinebrooke et al. 1998). To date, modeling exercises suggest either that such disturbance may diminish (Cardinale et al. 2000) or intensify (Mulder et al. 2001) positive linear relationships between richness and production, and that differential effects may be evident depending on the severity of perturbation (Kondoh 2001) and the level of the food web impacted (Proulx and Mazumder 1998). Proposed mechanisms that degrade richness–production relationships include overall loss of species and consequent increases in food-web invasibility, selective elimination of competitively dominant species unique to eutrophic lakes, and switches in the direction of grazer effects on algal diversity (Cardinale et al. 2000; Proulx and Mazumder 1998). Because diatom species richness was correlated with production but not salinity (Fig. 3), yet salinity influenced community composition (Fig. 4), we speculate that disturbance impacts were only partially manifest through overall loss of species richness, but additionally reflect changes in physiological, competitive, and trophic processes as well as functional shifts in community composition. Regardless of the precise mechanism underlying disturbance effects, we note that our analyses suggest that future global warming has the potential to eliminate the relationship between richness and production in lakes of central North America, fur-

Table 1. Forward stepwise multiple regression results obtained by regressing diatom species richness against diatom production (diatoxanthin), inorganic and organic $\delta^{13}\text{C}$, and organic $\delta^{15}\text{N}$ in freshwater sediment intervals.

Lake	Variable	Model		Variables remaining in model			
		r^2	p -value	partial r	slope	slope SE	p -value
Chauvin		0.28	<0.00001				
	Diatoxanthin			0.455	-19.74	2.95	<0.00001
Humboldt	$\delta^{15}\text{N}$	0.47	<0.00001	0.419	-55.24	9.16	<0.00001
	Diatoxanthin			0.083	-18.25	3.01	<0.00001
	$\delta^{15}\text{N}$			0.075	-11.66	8.08	0.151
	Inorganic $\delta^{13}\text{C}$			0.069	15.21	8.35	0.070
	Organic $\delta^{13}\text{C}$			0.061	31.34	20.40	0.126

ther obscuring the critical role of biodiversity in these aquatic ecosystems.

Our paleoecological analyses suggested that species identity and community composition have a significant influence on the richness–production relationship in these prairie lakes (Fig. 4). Species identity is thought to influence richness–production relationships via three main mechanisms: a sampling effect (Huston 1997), niche complementarity (Loreau 1998), or facilitation (Mulder et al. 2001; Cardinale et al. 2002). However, in each case, ecosystem production is assumed to increase with species richness. In contrast, we find that the opposite relationship may operate on very long time-scales, suggesting the existence of other regulatory mechanisms. In this regard, while our Procrustes analyses demonstrated that changes in community composition were concordant with variation in richness–production relationships, our CA-based visual analysis suggested that species identity influenced both lake production (Fig. 4) and species richness independently. Because rate of change in species composition (as chord distance) was correlated with production alone, whereas richness was correlated with both production and depth, we suggest that habitat heterogeneity (basin depth and morphology) may also play a key role in mediating the interaction between community composition and richness–production relationships.

Changes in diatom species richness were closely related to variations in stable isotope ratios of N, but not consistently with C, suggesting that some basic biogeochemical cycles may also influence aquatic biodiversity, or vice versa (Fig. 5). These patterns remained in multiple regression analyses even when production was included as an independent explanatory variable (Table 1), suggesting that a fundamental relationship may exist between species richness and N cycling, in addition to changes in lake production. Overall, the magnitude of variation in past $\delta^{15}\text{N}$ values in both lakes (Fig. 1) was similar to those observed to arise in other ecosystems as a result of changes in N_2 -fixation, nitrification, and denitrification activities (reviewed in Robinson 2001). Unfortunately, because stable isotope ratios of C and N in sedimentary organic matter integrate biogeochemical processes in both sedimentary and water-column environments (Brenner et al. 1999; Herczeg et al. 2001), there remain significant challenges in the interpretation of sedimentary isotope ratios in terms of underlying mechanisms (Meyers

1997). However, even in the absence of a defined mechanism, we feel that the significant patterns observed between richness and other indices of ecosystem biogeochemistry are instructive and should form the basis for future research. In particular, we note that because climate change and N biogeochemistry are both strongly correlated with species richness in the past, and because both factors are changing, often independently, because of human activities (e.g., Vitousek et al. 1997), it may no longer be possible to identify the unique relationships between biodiversity and ecosystem function. Consistent with this view, we find that richness–production relationships were weaker in Humboldt Lake during the 20th century when urban effluent was discharged into the lake (J. A. Rusak unpubl. data).

To our knowledge, this paper represents a first attempt to use high-resolution paleoecological data to evaluate the role of aquatic biodiversity in ecosystem function. The validity of our analysis, therefore, depends on several assumptions concerning the reliability of diatoms and pigments as indicators of aquatic biodiversity and production. First, we assume that patterns developed from analysis of a subcomponent of primary producer trophic level (diatoms) scales appropriately to the entire lake. While unlikely to be completely true, we note that correlations between diatom-specific diatoxanthin and biomarkers of total production (β -carotene, pheophytin *a*) are uniformly strong in these ($r^2 > 0.4$, $p < 0.0001$) and other lakes (e.g., Vinebrooke et al. 1998), and that diatom pigments composed 25–50% of the algal carotenoid sum in sediments, despite differential preservation issues (see Leavitt 1993). Second, we assume that variations in fossil pigment accumulation rate (see Methods) accurately recorded changes in algal production, as shown in whole-lake experiments, mesocosm experiments, mass-balances, and computer simulation (reviewed in Cuddington and Leavitt 1999). In this regard, prior research demonstrates that variations in sedimentary pigments explain at best 75–90% of change in algal biomass and production (reviewed in Leavitt 1993; Cuddington and Leavitt 1999; Leavitt and Hodgson 2001). Thus, while modest correlations between diatom richness and production in Chauvin Lake may partly arise from biases arising from fossil preservation or degradation independent of production, explanatory power in Humboldt Lake was similar to that recorded in many other studies (e.g., Mittlebach et al. 2001).

Finally, our analysis assumes that each lake represents a sufficient gradient of production (10- to 100-fold) to encompass the full range of variance required to differentiate unimodal and linear models. In this regard, we feel that further research may be needed, as our sites have likely been productive throughout the past 2,000 yr and it is possible that we are missing the oligotrophic end of the production spectrum. Thus, although our data are sufficient to show that a positive linear model does not underlie the observed richness–production relationships, we feel that the addition of further sites and paleoecological indices (e.g., indicators of irradiance, predation, and herbivory) may be required for definitive identification of patterns and causal mechanisms. Instead, we suggest that temporal controls of diversity–function relationships over millennia or centuries may be fundamentally different from those operating on smaller spatial and temporal scales, and that the theory underlying unimodal or positive models may need to be modified to incorporate insights from long time frames.

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