

Integrating neo- and paleolimnological approaches to refine interpretations of environmental change

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Abstract With the development of quantitative transfer functions to relate community structure to physicochemical variables, reconstructions of past environmental conditions have been possible and have enhanced our understanding of various ecosystem processes. There are cases, however, in which this approach is not applicable, or does not provide enough information for the questions being asked. In these cases, some alternatives are to conduct experiments or to examine the distribution of species at a finer spatial resolution. These two approaches have been used as alternatives to or in conjunction with the development of transfer functions. In this review, I discuss the ways in which these two approaches are now being used in paleolimnological studies to enhance our understanding of the ecology of the species found in sediment records and thus refine interpretations of environmental change. My focus is primarily on studies that deal with establishing clearer relationships between environmental variables and the growth or distribution of organisms. I present examples of how these approaches have been integrated in a variety of studies, including those designed to: (1) refine and enhance reconstructions that are based on transfer functions; (2) develop new paleolimnological tools to reconstruct

environmental change; (3) explore mechanistic links in the relationships between organisms and commonly reconstructed environmental variables; and (4) pose and test hypotheses based on patterns in the sediment record. These cases demonstrate that the use of these approaches was essential to clarify species-environment relationships as well as lake responses to disturbance. As in all disciplines, however, there are many challenges in this area of research. In particular, the quantitative integration of these approaches with the sediment record is a major challenge, due to disparate spatial and temporal scales. This research can also be quite labor-intensive, and provides information on fewer taxa than in the calibration set approach. It also requires interdisciplinary training and/or collaboration in fields that have historically been less integrated, hence they may require greater effort. These issues may hinder the use of these approaches because of the perceived difficulty. I discuss these challenges and address possible solutions.

Keywords Paleolimnology · Experimental methods · Diatoms · Calibration set

Introduction

The development of calibration sets and transfer functions to relate community structure to physicochemical variables has allowed paleolimnologists to reconstruct quantitatively past environmental

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conditions (Birks 1995), which has enhanced our understanding of various ecosystem processes. In this approach, the species assemblages of interest are collected from the surface sediments of numerous lakes (typically at least 30 lakes) in a region, and species distribution patterns are related to environmental variables that are measured from one to several times over the season in which the sediments were collected. Once a small sub-set of variables are identified that are correlated to species distribution patterns within this calibration set, transfer functions can be developed for these variables and used to perform reconstructions. Comparisons between historical data and the developed transfer functions reveal fairly good performance of these models in some cases (e.g. Bennion et al. 1996; Laird et al. 1998a), but not all (e.g. Sayer 2001; Battarbee et al. 2002; Bigler and Hall 2003). This approach has allowed paleolimnologists to document successfully lacustrine changes such as acidification and eutrophication (e.g. Charles and Whitehead 1986; Renberg 1990; Anderson and Renberg 1992; Anderson and Rippey 1994; Hall and Smol 1996), as well as regional changes in climate (Fritz et al. 1991; Laird et al. 1998b; Pienitz et al. 1999).

There are cases, however, in which this approach has limited success. Lakes with very slow sedimentation rates are one example, as surface sediment assemblages may represent several years of community structure while the physical and chemical measurements only capture discrete snapshots of environmental conditions over that period. There is also difficulty in applying this approach to lakes with strong vertical habitat gradients, such as alpine lakes and very large lakes. In these systems, some species can flourish under nutrient-poor conditions in surface waters while others are abundant in the low-light, nutrient-rich deep waters. The calibration set approach does not allow us to distinguish which species inhabit each area. Similarly, in lakes with strong seasonal fluctuations in chemistry, such as saline lakes, surface sediment assemblages will contain a mix of freshwater and saline taxa deposited at different times of the year, which may result in poor ecological inferences if annual mean chemical conditions are used. Depending on the nature of the study, the use of calibration sets also may not provide enough information for the questions being asked, particularly when mechanistic information is

important. There are also many cases (some discussed below) in which environmental variables covary, making it difficult to separate effects. Some alternatives in these situations are to conduct experiments or to examine the distribution of species at a finer spatial resolution. These two approaches have been used as alternatives to or in conjunction with the development of transfer functions.

In this review, I discuss the ways in which these two approaches (experiments and higher-resolution spatial analyses of species distribution patterns) are now being used in paleolimnological studies and thus enhance our understanding of the biology and ecology of the species found in sediment records to refine interpretations of environmental change. My focus is primarily on studies that deal with establishing clearer relationships between environmental variables and the growth or distribution of organisms. I present examples of how these approaches have been integrated in a variety of studies, including those designed to: (1) refine and enhance reconstructions that are based on transfer functions; (2) develop new paleolimnological tools to reconstruct environmental change; (3) explore mechanistic links in the relationships between organisms and commonly reconstructed environmental variables; and (4) pose and test hypotheses based on patterns in the sediment record. I also discuss challenges to using these approaches and some possible solutions. Most of my examples come from diatom-based studies because this is my area of research, but I believe that these examples should generally be applicable across paleolimnology. This review is focused on examples from the last ten years, but I remind the reader of several excellent examples of these approaches prior to this time (Kilham et al. 1986, 1996; Smith 1990; ; Gasse et al. 1997).

Examples of integrated studies

Studies designed to refine and enhance reconstructions that are based on transfer functions

An example of this type of study is provided by Bradshaw and Anderson (2003), who investigated diatom-based inferences of eutrophication patterns in Danish lakes. One of the issues in the Danish diatom calibration set is that *Cyclostephanos dubius* (Fricke)

Round has a very high total phosphorus (TP) optimum, and hence has a strong effect on TP reconstructions, such that even modest increases in this taxon result in high inferred TP concentrations. Given the strong effect of this species on TP reconstructions, the authors investigated whether TP was the main factor controlling the abundance of this taxon by examining its distribution patterns both seasonally from the water column as well as from surface-sediment samples. The seasonal samples were collected over ten years from five Danish lakes, and revealed that the abundance of *C. dubius* was positively correlated with nitrate. Analysis of the surface sediment assemblages, however, indicated that TP, lake depth, silica, and chlorophyll *a* had the strongest influence on the abundance of this species. Nitrogen variables were not correlated with *C. dubius* abundance in the surface sediment samples.

The implications of these results depend upon the questions being posed. If the key questions focus on whether changes in trophic status have occurred, the resulting inferences would likely remain the same, as total nitrogen and total phosphorus concentrations tend to co-vary. However, if the object is to identify the driver of ecosystem change in an effort to devise potential remediation strategies, this distinction becomes more important and clearly warrants the use of more detailed studies to improve our inferences.

Through their investigation of chironomid oxygen requirements, Brodersen et al. (2004) provide one of the best examples of how to integrate the calibration set approach with experimental results. Chironomid fossil assemblages are frequently used to reconstruct temperature; part of the influence of temperature on chironomids is via effects on oxygen concentrations. However, in addition to the direct effects of temperature, there are multiple ecosystem processes affecting oxygen concentrations in the hypolimnion, including lake depth, ice cover, stratification, lake productivity, and respiration. As a result, chironomid distribution patterns in calibration sets are often correlated with temperature, oxygen, TP, and/or total nitrogen (Quinlan and Smol 2001; Brodersen and Anderson 2002; Brooks et al. 2001). The calibration set approach does not permit the separation of effects of these variables on chironomid assemblages because of the high degree of co-variation among these variables.

To clarify the oxygen requirements of chironomids, Brodersen et al. (2004) quantified the oxy-regulatory

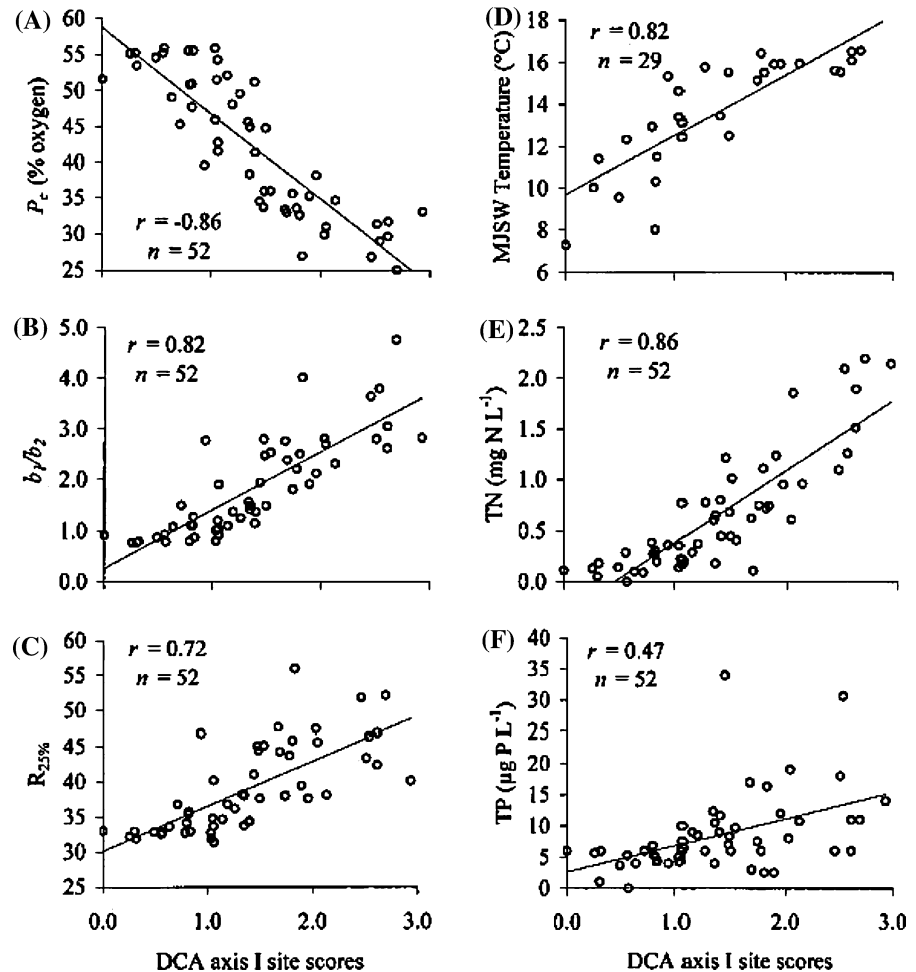
capacity of 16 chironomid taxa from West Greenland lakes in respiration chambers. The experimentally determined values for critical oxygen levels (P_c ; the point down to which certain species can regulate their oxygen uptake) were merged with chironomid assemblage structures from 52 lakes to determine the oxy-regulatory capacities for each assemblage. When the overall assemblage structure was expressed using detrended correspondence analysis (DCA), axis 1 was as strongly correlated to the experimentally measured variables of oxy-regulatory capacity as it was to surface water temperature and nutrient data from the calibration set (Fig. 1). This study demonstrates that the oxy-regulatory capacity can explain, in part, the distribution patterns of chironomids in these lakes as a result of changes in temperature and nutrients, hence it provides important mechanistic information that would otherwise be unclear from the training set approach alone. It also provides a novel example of how experimental data can be merged quantitatively with the calibration set approach.

Studies designed to develop new paleolimnological tools to reconstruct environmental change

Many paleoenvironmental reconstructions rely on the relationship between a chemical component of an organism (e.g. frustule or shell composition, alkenones) and an environmental variable. Field studies can provide a good basis for these relationships, but, as with species-environment relationships, these studies often do not provide clear mechanistic information about these correlations. Experimental manipulations can help to clarify these relationships between environmental variables and organic chemical records, providing critical data that increase confidence in the use of these records. There are numerous examples of integrated studies of this type from the paleoceanography literature on the use of alkenones and organism-specific isotopes (De la Rocha et al. 1997; Herbert 2001; Prahl et al. 2003; Prahl et al. 2006), but far fewer in paleolimnological studies.

One example of this approach that has applications in both paleolimnology and paleoceanography involves the use of stable oxygen isotopes ($\delta^{18}\text{O}$) in diatom silica to reconstruct temperature. While several investigators demonstrated that fluctuations

Fig. 1 Comparison of correlations between variation in chironomid assemblage structure in West Greenland lakes and (a–c) the weighted averages of the modeled respiratory constants (determined with experiments) and (d–f) environmental variables. (a) Critical limit (P_c , %), (b) ratio between slopes in piecewise regression (b_1/b_2), and (c) $R_{25\%}$ (% of max respiration), (d) Mean July surface-water temperature ($^{\circ}\text{C}$), (e) TN (mg N l^{-1}), and (f) TP ($\mu\text{g P l}^{-1}$). All correlations are significant ($P < 0.001$). Figure from Brodersen et al. (2004; Fig. 5), reprinted with permission from the American Society of Limnology and Oceanography



in $\delta^{18}\text{O}$ values of diatom silica was suggestive of temperature variation (Riotti-Shati et al 1998; Shemesh and Peteet 1998), a clear demonstration of the temperature dependence of oxygen isotope fractionation between biogenic silica and water was needed to use $\delta^{18}\text{O}$ values of diatom silica as a paleothermometer. Field studies can be used to examine the isotopic values of water and diatom frustules in relation to temperature (Schmidt et al. 2001), but this approach still fails to establish a clear relationship between temperature and the $\delta^{18}\text{O}$ values of diatom silica. To address this, Brandriss et al. (1998) conducted a series of culturing experiments with two diatom species grown under different temperatures in water with two different $\delta^{18}\text{O}$ values. These experiments demonstrated that the fractionation of

oxygen isotopes between water and diatom silica were strongly correlated with temperature (Fig. 2). However, additional experiments by Schmidt et al. (2001) with marine phytoplankton showed that the relationship between $\delta^{18}\text{O}$ values of diatom silica and temperature varied and was not consistent with that demonstrated by Brandriss et al. (1998). Although results have varied across some experiments, and many questions remain about the use of $\delta^{18}\text{O}$ of diatom silica as a paleothermometer (as reviewed by Leng and Barker 2006), these experiments advance our understanding in this area and, more importantly, provide stronger evidence than field observations in documenting certain relationships. They also further our ability to develop new paleolimnological tools.

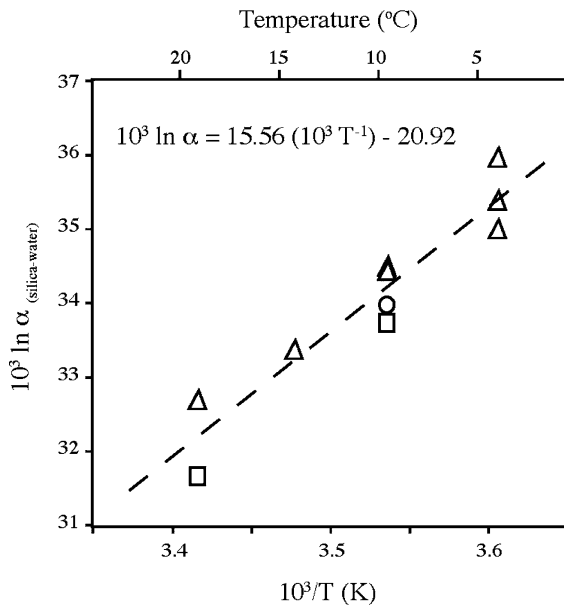


Fig. 2 Results of oxygen isotope fractionation experiments conducted at different temperatures using cultured *Stephanodiscus niagarae* and *Aulacoseira subarctica* presented in Brandriss et al. (1998). Each symbol represents a separate culture experiment: triangles indicate *S. niagarae* (light water); squares indicate *S. niagarae* (heavy water); circle indicates *A. subarctica* (light water). Figure modified from Fig. 1 in Brandriss et al. (1998), reprinted with permission from Elsevier

Studies designed to explore mechanistic links in the relationships between organisms and commonly reconstructed environmental variables

In regions with closed-basin, saline lakes, analyses of calibration sets often reveal that salinity (or a closely related variable such as conductivity) is the primary driver of diatom distribution patterns (Cumming and Smol 1993; Fritz et al. 1993; Gasse et al. 1995). This relationship has been used to develop diatom-based transfer functions to reconstruct salinity, and hence, drought frequency, in areas such as the Northern Great Plains (NGP; Fritz et al. 1991). Comparisons have revealed good, but of course, not perfect, agreement between diatom-inferred salinity and historical drought indices (Laird et al. 1998a). Certainly, we recognize that salinity is not the only factor that controls diatom distributions across these saline lakes. Indeed, phytoplankton surveys conducted in the spring of 2004 and 2005 in a set of saline lakes in the NGP revealed that, while the conductivity values

of the four lakes were essentially identical in both years, the phytoplankton communities (largely dominated by diatoms in the spring) differed in two of the lakes between the two years (Saros, unpublished; Fig. 3). In particular, in Stink Lake, while the conductivity was 7.6–7.8 mS cm^{-1} during the two sampling periods, the diatom community switched from two species with salinity optima around 3 g l^{-1} (as defined by the NGP calibration set of 66 lakes; Fritz et al. 1993) in 2004 to an assemblage dominated by *Cyclotella quillensis* Bailey, a species with an optimum of 20.6 g l^{-1} , in 2005.

The relationship between diatoms and salinity is further complicated by the co-variation between salinity and ion composition, the effects of which are difficult to fully partial out from each other in calibration sets. In the NGP calibration set, taxa such as *Anomoeneis costata* (Kütz.) Hust. are associated with bicarbonate-dominated lakes, whereas those such as *Chaetoceros elmorei* Boyer are mainly found in sulfate-dominated waters. Other taxa, such as *Cyclotella quillensis*, show no apparent association with brine type (Fritz et al. 1993). Ion composition can affect nutrient cycling in lakes as well as nutrient uptake by algae (Mohleji and Verhoff 1980; Cole et al. 1986; Caraco et al. 1989), hence there are direct and indirect effects of ion composition on diatoms. This may partially explain why certain taxa such as *Cyclotella quillensis* and *Chaetoceros elmorei* co-dominate infrequently in these lakes despite having similar salinity tolerance ranges (Fig. 4).

To further explore this possibility, Saros and Fritz (2000) examined the growth rates of these two species under varying salinity, ion composition (sulfate or bicarbonate), and nitrogen source (ammonium or nitrate). Two nitrogen sources were tested because sulfate can inhibit the uptake of molybdate (Cole et al. 1986), an essential trace element for nitrate use, but not for ammonium use. For *Cyclotella quillensis*, growth rates on ammonium were equal under all salinity and brine conditions, whereas growth on nitrate was lowest in the sulfate medium. In contrast, while growth rates of *Chaetoceros elmorei* were also equal on ammonium under all conditions, this species was unable to grow under any conditions when nitrate was the provided nitrogen source.

These experiments revealed a physiological difference between these two species that may partially

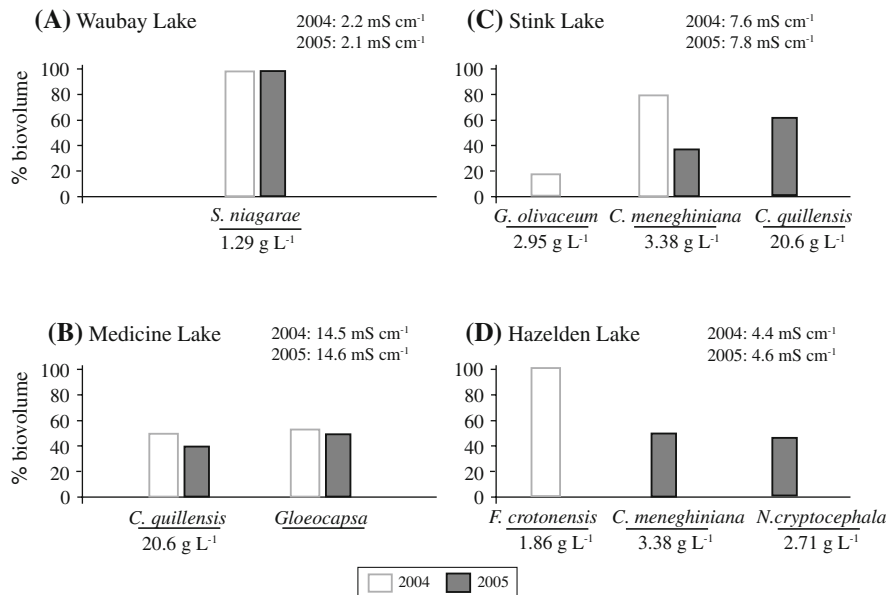


Fig. 3 Spring phytoplankton assemblages from the water columns of four saline lakes in the northern Great Plains (NGP), collected in 2004 and 2005. Conductivity values at the time of sampling are indicated for each lake and date in the upper right corner of each panel. Across the lakes, phytoplankton assemblages consisted almost entirely of diatoms (except

Gloeocapsa, a cyanobacterium in Medicine Lake), and included *Stephanodiscus niagarae*, *Gomphonema olivaceum*, *Cyclotella meneghiniana*, *Cyclotella quillensis*, *Fragilaria crotonensis*, and *Navicula cryptocephala*. The salinity optimum of each diatom, based on the NGP calibration set (Fritz et al. 1993), is indicated under each taxon. Data are from Saros (unpublished)

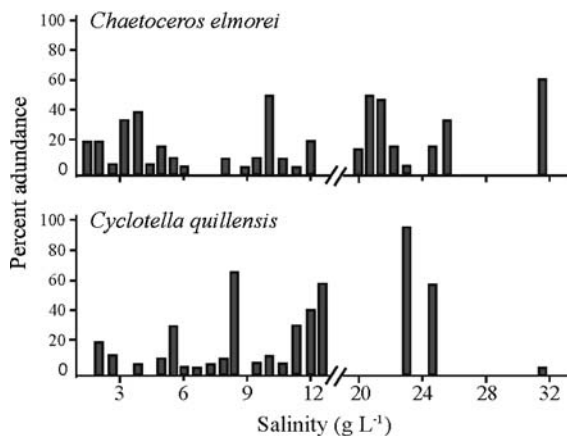


Fig. 4 Distributions of *Chaetoceros elmorei* and *Cyclotella quillensis* in the surface sediments of a sub-set of lakes ($n = 28$) across the northern Great Plains (NGP) over a salinity range. Abundances at each salinity value are based on a sample from one lake, indicating that these two species are generally not abundant in the same systems. The data used to assemble this figure are from Fritz et al. (1993)

explain their infrequent co-dominance despite similar salinity tolerances. Mechanistic studies such as this may allow us to better understand and potentially

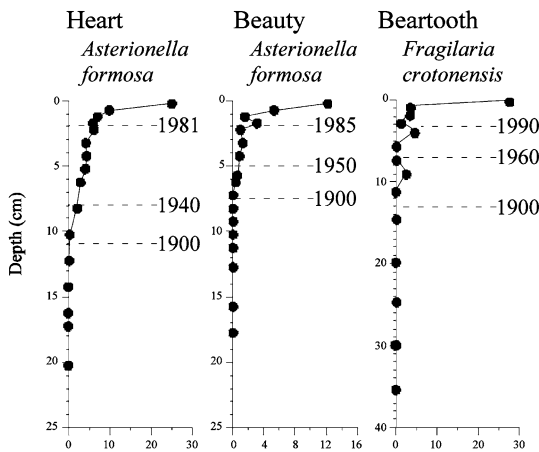
extract more information from patterns in the sediment record. I suggest that combining this type of approach with multi-proxy reconstructions may be a particularly powerful tool to understand the mechanisms behind ecosystem change.

Studies designed to pose and test hypotheses based on patterns in the sediment record

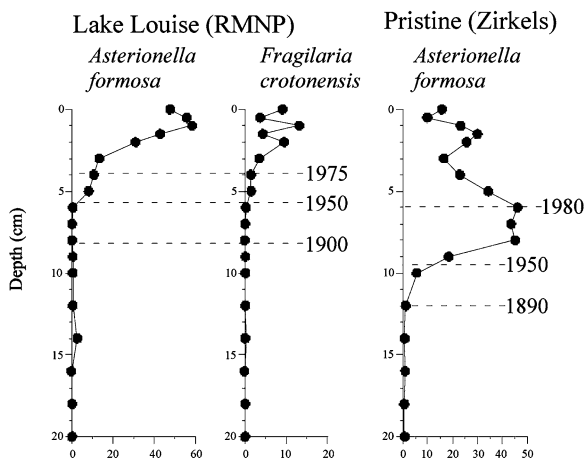
In many regions, we see recurring patterns in species changes in lacustrine sediment records. This is the case, for example, with widespread, consistent increases in *Cyclotella* species since the late 1800s across numerous Arctic lakes (Smol et al. 2005). We have also observed a consistent pattern of change in diatom community structure in lakes of the central and southern Rocky Mountains (Wolfe et al. 2001; Saros et al. 2003), with *Asterionella formosa* Hassall and *Fragilaria crotonensis* Kitton increasing in abundance across numerous lakes in these areas during the last sixty years (Fig. 5a). The timing of change varies between these two regions, with increases in these two species around 1950 in the southern Rockies and sometime generally after 1980

(A)

Beartooth Wilderness lakes



Colorado Rocky Mountains



Relative frequencies (%) based on sums >400 total diatom valves

(B)

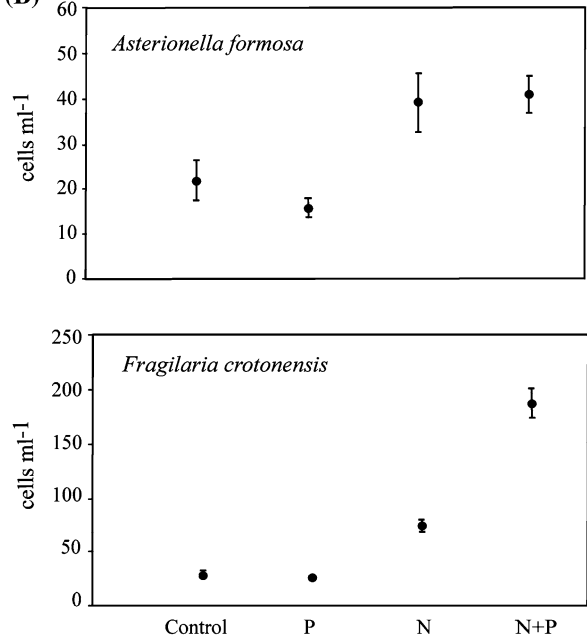


Fig. 5 Example of study designed to test hypotheses posed from widespread patterns in the sediment records. (a) Dated (by excess ^{210}Pb activities) sediment profiles of *Asterionella formosa* and *Fragilaria crotonensis* from a set of representative lakes in the central (Beartooth–Absaroka Wilderness) and southern (Colorado) Rocky Mountains of the United States. Increases in either taxon generally begin after 1950. (b) Results

in the central Rockies. Based on observed increases in atmospheric deposition of nitrogen, lighter $\delta^{15}\text{N}$ values of sedimentary organic material in more recent sediments, and the labeling of *A. formosa* and *F. crotonensis* as “mesotrophic” diatoms, the recent changes in diatom community structure were attributed to enhanced atmospheric N deposition (Wolfe et al. 2001). However, the mesotrophic label was derived from work in lakes that were historically limited by phosphorus (P), and in which P enrichment

of the nutrient enrichment experiments in Beartooth Lake for *Asterionella formosa* and *Fragilaria crotonensis*, with nutrient treatment indicated for each treatment ($n = 3$). Error bars reflect standard error estimates. Figure from Saros et al. (2005; compilation of Figs. 2 and 3), reprinted with permission from the National Research Council Canada

stimulated the growth of these two species, hence there were few data available on their response to N enrichment in N-limited lakes. Furthermore, enhanced N deposition was not the only change occurring in the Rockies over the last century. Widespread fish stocking and changes in climate were also occurring.

After observing these consistent, widespread changes in alpine diatoms in the Rockies, we tested the hypothesis that enhanced N deposition was primarily driving these changes. We integrated

results from two types of experiments (resource-physiology and nutrient-enrichment assays) with those from field studies of the vertical distributions of diatoms in the water columns of several alpine lakes. The resource physiology experiments indicated that *A. formosa* and *F. crotonensis* both have higher N requirements than *Staurosirella pinnata* (Ehr.) Williams and Round, a typical alpine diatom that has decreased in relative abundance in the last few decades (Michel et al. 2006). In the nutrient-enrichment experiments, *A. formosa* and *F. crotonensis* both increased under N enrichment (Fig. 5b), but not under P or silica enrichment alone (Saros et al. 2005). Vertical distribution patterns within the water columns of several lakes revealed that these two species were positively correlated with N variables while negatively correlated with P variables (Saros et al. 2005). Considering the results of these three approaches in conjunction with the lighter $\delta^{15}\text{N}$ values of sedimentary organic material in the sediment cores, we concluded that N enrichment from atmospheric deposition was the likely driver of changes in diatom community structure in lakes across the Rockies. This combination of approaches allowed us to test more clearly and demonstrate the drivers of diatom community change than a calibration set alone would have.

Challenges to integrating these approaches

As with any area of science, challenges arise with respect to the successful, widespread use of the types of approaches described here. Experimental work is often viewed as too labor-intensive, particularly for the relatively small number of species for which data can be collected in most experiments. While developing a calibration set also requires a great deal of work, it has the advantage of yielding ecological information on hundreds of taxa. The benefits of experimental work, however, are that it allows us to test hypotheses more explicitly based on our observations from the sediment record, and to identify some of the mechanisms by which environmental change drives community shifts. I suggest that one way to get the most out of the experimental approach is to focus experiments on a sub-set of key species that consistently change across a region. Coupling experiments with observations from a calibration set

can also help to fill in potential gaps in terms of the environmental preferences of diatom taxa.

Another barrier to integrating experimental work into paleolimnological studies is that many paleolimnologists have little to no training in keeping organisms alive. In fact, part of our training consists of how to use harsh chemicals to strip unnecessary components off and out of organisms. We should collaborate with biologists and ecologists, who I suggest would welcome involvement in this type of research as a matter of general interest as well as an innovative application of their work. Looking across the literature and funded proposals in ecology in the United States, my sense is that there has been a general decline in basic autecological studies of aquatic organisms over the last few decades. This may be a consequence of increased competition for funding, which sharply raises the need to produce increasingly innovative proposals. This decline in autecological studies is problematic for paleolimnologists, as we need this type of information to help support our conclusions about patterns in the sediment records. Hence, collaborations with biologists and ecologists have many benefits, including student training in an interdisciplinary setting that can foster the development of the next generation of paleolimnologists with an expanded set of skills.

One of the biggest hurdles to integrating experimental research into paleolimnological studies is the lack of quantitative models to apply experimental results explicitly to sediment records. As discussed above, the study by Brodersen et al. (2004) provides an excellent example of a case in which experimental results could be merged quantitatively with the surface-sediment-chironomid assemblages, but experimental results are not always so well-suited to this merger. If this field is to continue to grow, the development of innovative statistical analyses or models to make explicit links back to the sediment record will be essential. Bayesian methods are providing appropriate frameworks in some cases to integrate various types of data (Muzikar and Granger 2006). A possible area to explore further is the transformation of models that forecast aquatic community structure based on environmental variables into hindcasting models that reconstruct environmental variables based on fossil assemblages. This possibility requires further development, but the recent examples of integration of process-based

models such as MAGIC, PROFILE, and SAFE with paleoecological data (as reviewed by Anderson et al. 2006) provide a good starting point.

Conclusions

The examples presented here highlight research at the interface of neo- and paleolimnology that is helping to clarify relationships between environmental variables and the growth or distribution of species from the fossil record. These studies have provided data to refine environmental reconstructions in a number of ways, by clarifying mechanistic links, as well as by demonstrating species-environment relationships by testing them explicitly through biological or ecological experiments and observations. These examples provide alternative and complementary methods to the widely-used calibration set approach, and, I hope, will foster ideas about new ways to refine our reconstructions and generate new hypotheses regarding lake processes.

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