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ORIGINAL PAPER

Towards better integration of ecology in palaeoecology: from proxies to indicators, from inference to understanding

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Abstract The special issue titled "Putting the Ecology into Palaeoecology" stems from a session with that name that was held at the 2015 International Paleolimnological Association meeting (International Paleolimnology Symposium) in Lanzhou, China. We briefly describe the motivation for the session, and summarise the contributions to this special issue. Additionally, we discuss our perceptions and concerns about the progress, challenges and future directions of palaeolimnology, stressing the importance of meaningful integration of ecological principles and thinking into palaeoapproaches.

Keywords Palaeoecology · Early warning indicators · Transfer functions · Ecology · Proxy

Introduction

The subject of this special issue is the integration of ecology into palaeoecology. We see a pressing need to bring more ecological thinking into palaeoecology and a parallel need for contemporary lake ecology toembrace a longer-term perspective. This need for a longer-term perspective is increasingly recognised, a fact illustrated by the EU initiative on Long Term Ecosystem Research (LTER). The benefit of studying ecosystems over a number of years stems from the fact that many ecological processes (e.g., dispersal, population dynamics, growth, food-web dynamics, succession, species extinction) that drive biological change tend to operate over timescales that are greater than the typical length of contemporary aquatic ecological studies (1–3 years), and in many cases might involve decades for change to occur. Palaeoecology has enormous potential to provide this long-term perspective on ecosystem change, but the significance of this contribution rests on a better integration of ecological thinking into palaeo studies.

The origins of this special issue stem from the recent history of palaeolimnology, in particular the proliferation of quantitative environmental reconstructions from lake sediments based on transfer-

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function models. The transfer-function approach has many appealing aspects from a lake-management perspective (Anderson 1997; Bennion et al. 1996), but the generality and usefulness of transfer-function models have been increasingly questioned (Sayer 2001; Velle et al. 2010), with caution sounded from the beginning (Fritz et al. 1993). A discussion of the limitations of transfer functions is presented in detail elsewhere (Whitmore et al. 2015), but is briefly revisited here because it highlights broader potential issues and challenges for palaeolimnology as a whole. The kernel of the problem is the attempt to infer change in a single chemical/biological/climatic variable from biological communities (e.g. diatoms, chironomids, cladocerans, pollen) almost always shaped by multiple, interacting forces. Thus, at their core, transfer functions are inherently non-ecological. As a consequence we call for a greater consideration of ecological theory in palaeoeoecology and for the development of much more robust, ecologically meaningful models capable of taking multiple structuring variables into account. This would increase the acceptance of palaeo approaches in general ecological investigations and provide the long-term perspective so desperately needed to inform ecological theory and aquatic ecosystem management.

The transfer-function approach emphasises the use of remains in sediments as proxies, or substitute measures, for variables of interest. The concept of a proxy has become prevalent, but the term has increasingly lost its meaning through incorrect use. Furthermore, the term ‘multi-proxy’ has become common, even when biological assemblages in cores are not used as a proxy for another variable. Here, we stress the need for a shift away from seeing biological remains as “proxies” for something else, and instead call for their use as indicators to track ecological change in ecosystems on realistic timescales (decades to centuries) over which change actually occurs in aquatic environments.

Palaeolimnology has been greatly strengthened by studies that consider several lines of biological evidence. Analysis of the remains of several biological groups provides multiple lines of evidence, potentially from different levels of the food web, and of terrestrial and aquatic origin, to provide a much fuller picture of the nature and causes of environmental change (Bennion et al. 2015; Sayer et al. 2016). However, the use of multiple biological groups does not, in itself, represent the complete integration of ecology into the palaeo discipline. Multi-indicator studies might have the potential to provide a broader picture of ecosystem response, but we should go further and ask questions such as “Can we investigate the ecological processes that shape biological communities using a long-term perspective?” Echoing previous calls for better integration of modern ecology and palaeoecology (Smol 1991; Battarbee et al. 2005; Reid and Ogden 2006; Sayer et al. 2010a), we urge palaeolimnologists to apply their methods to address key ecological questions and theories, and to identify mechanisms of change by combining short- and long-term perspectives. We encourage investigations that address a variety of ecological subjects such as predation, competition, succession, diversity, speciation as well as other topics at the community and landscape levels.

The integration of ecology into palaeoecology to infer mechanisms of change can be accomplished in many ways and can involve using relationships established in contemporary environments to interpret past biological change in a semi-qualitative way (e.g. regression tree models: Davidson et al. 2010). Alternatively, sediment-core data can be interpreted qualitatively using existing knowledge frameworks in limnology and aquatic ecology to develop better understanding of, for example, trophic cascades (Leavitt et al. 1989) and changed seasonality of primary producers (Sayer et al. 2010b). Such approaches aim to get at the nature and causes of ecological change, which contrasts with feeding data into a transfer-function model or using ordinations that simply identify points of change or trends. We urge researchers to explore and test mechanisms that will provide knowledge and that have direct application to aquatic ecological science and aquatic conservation. It follows that interpretation of sediment-core sequences would benefit immensely from improved understanding of the ecology of species that demonstrate changes in abundance through time, and from greater knowledge about the limnological functioning of the aquatic systems that are being studied.

To infer changing ecological processes and mechanisms in the long term and to increase the acceptance and use of palaeo studies in aquatic ecology and conservation, there is a pressing need to get back to basics, and for palaeoecologists to become involved in community and autoecological studies to better understand species preferences, dynamics (over a range of time scales) and interactions. This need is especially true of groups such as diatoms, ostracods, and chironomids for which there are many palaeo studies, but comparatively few in contemporary ecological research. Furthermore, so that ecological information can be inferred confidently from assemblages of species in sediments, it is crucial that we continue to study taphonomy to understand how assemblages are formed and how well fossil assemblages reflect the biocoenoses from which they were derived. This is a fundamental underlying need of palaeoecology that should never be ignored.

Special issue papers

This special issue includes 13 papers that address the issues raised above and demonstrate the value of better integration of ecology in palaeoecology. The papers are summarised according to a number of themes.

Taphonomy

The way in which the living biological community is represented in the sedimentary record is a fundamental issue in palaeolimnology. While this issue is widely recognised and frequently acknowledged, it is less often subject to detailed analysis in field studies. The studies in this special issue that address taphonomic processes in lake systems thus provide a valuable addition to understanding.

Dalton et al. examine sediment distribution patterns in an Irish humic-stained lake using a combination of sediment traps and surface sediment samples, and they explore the transfer of environmental signals from the water column to lake-sediment records. They identify marked spatial and temporal variation in the deposition of aquatic versus terrestrially derived organic matter, and a strong influence of lake-basin position and water depth on a range of parameters including diatom and pigment assemblages. These findings have implications for the interpretation of ecological signals in the sediment record. This study provides an example of how palaeolimnological and contemporary limnological approaches can be integrated through the application of sediment traps, enabling comparisons between sedimentation factors such as sinking rates and particle flux, and phytoplankton dynamics.

On a similar theme, Maier et al. employ sediment traps to compare whole-year diatom assemblages for a 12-year period with the corresponding diatom record of the annually laminated sediment in a varved boreal lake in Sweden. They observe large inter-annual variability of diatom succession and abundance patterns in the traps that are driven by seasonal environmental events, such as winter air temperature and/or autumn runoff, as well as by the thermal structure of the lake. This variability is well reflected in the varved sediments. The study highlights the need to consider short-term environmental events when interpreting annual sediment signals in relation to climate.

Bishop et al. compare modern survey data with sedimentary remains for a single macrophyte species *Najas flexilis*. Detailed modern surveys are compared with very highly spatially resolved sampling of surface sediments across three lakes that represent a gradient of modern *N. flexilis* abundance from occasional to absent. The study shows that *N. flexilis* remains are found even where the plant is currently absent, and that the abundance of seeds at an individual point does not reflect the abundance of the plants at the same location. However, many more seeds are found at sites where plants were abundant, whereas fewer are found at sites where plants are less abundant, and fewer still where plants are currently absent.

Species ecology, habitat preferences

The transfer-function boom drove extensive sampling programmes that yielded abundant distributional information among biological groups with respect to specific water-quality variables. However, less research has been conducted with respect to the broader ecology of individual taxa, including habitat preferences, which would better inform ecological interpretations.

Pla et al. synthesise a very large quantity of diatom data from a single Pyrenean lake. They identify species preferences for different habitats and different species assemblages among habitats. Deep-lake sediment samples are found to represent whole-lake gamma diversity. The study also shows how pH reconstructions based on species from different habitats can yield different results. This can be explained by inter-habitat differences in productivity, and thus dissolved inorganic carbon concentration, and hence pH.

Prentice et al. integrate macrofossil data from a previous study with new data on testate amoeba from Loch Leven, Scotland, which has a long history of eutrophication. The history of eutrophication-driven change in submerged plants is compared with changes in testate amoeba. The study shows that the testate amoeba community changed at the same time as plant macrofossil assemblages. Indicator-species analysis shows that certain rhizopod taxa are associated with specific aquatic vegetation, and reflect eutrophication-induced change.

Emson et al. report a surprisingly strong relationship between the comparatively rare diatom taxa *Lemnicola hungarica* and *Sellaphora saugerresii* and the minute floating-leaved species of *Lemna* (Araceae), which leave scant evidence in lake sediments of their past presence. The investigators examine diatoms in surface sediments of small ponds in Norfolk, England that show periods of *Lemna* dominance. Sediment cores from Bodham Rail Pit are examined at high resolution, and these diatom indicators closely track known annual abundances of *Lemna* over a 20-year period. This study discloses species-specific host preferences of epiphytic diatoms and the potential to use those relationships to assess macrophytes that leave little evidence in sediments. The study would not have been possible without a combination of modern data and high-resolution historic analyses, as well as careful attention to the importance of examining the ecological significance of rare taxa. This epiphyte/host relationship appears to hold promise for ecological interpretation in a wide range of lake sizes and geographic regions.

Drivers and mechanisms

Whilst it is not strictly speaking possible to isolate causality with certainty using the palaeo record, it may be possible to isolate the most probable mechanisms of change, or to reduce the plausible hypotheses to one. Pennington (1981) noted that only hypotheses that explain all sets of paleolimnological data should be regarded as true. Thus we need to be cautious when inferring causes of change in the long term, but it is clear that when contemporary ecological and palaeoecological studies are combined, important insights often emerge (Sayer et al. 2010a).

Whitmore et al. present a palaeolimnological study of sediment cores from seven shallow, subtropical Florida lakes to explore the reasons for diatom successions from *Aulacoseira*- to fragilarioid-dominated assemblages, which they report are typically associated with eutrophication. They conclude that cyanobacteria are responsible for reducing planktonic *Aulacoseira* in favour of fragilarioid taxa, with the most likely mechanisms being reduced light availability, cyanobacterial allelopathy or other aspects of competitive exclusion, while climate warming is not seen as a likely cause of the observed species shifts. This is an important finding because increases in fragilarioid taxa have often been interpreted as statistical noise in paleolimnological reconstructions, whereas in subtropical Florida lakes, they indicate a progression to hypereutrophic conditions and dominance by cyanobacteria.

Reid et al. explore the relative influence of local land-use changes and flow regulation as drivers of change in floodplain lakes (billabongs) on a dryland river floodplain in Australia. They present evidence that the impact of drivers varies with hydrological connectivity. The effect of land-use change is greater for more isolated billabongs and the effect of hydrological change is greater for more connected billabongs. Reid et al. attribute this pattern to stronger coupling of isolated billabongs to the local catchment, as compared to more connected billabongs, which are more strongly coupled to the hydrology of the parent stream. This study demonstrates the ability of palaeo approaches to disentangle the effects of multiple stressors, and it highlights how hydrology and geomorphology can interact to influence the sensitivity of shallow-lake ecosystems to specific stressors.

McGowan et al. examine seasonal patterns in epilithic diatom assemblages in the littoral zone of 19 Arctic lakes along a climate gradient in Western Greenland to better understand diatom ecology, and hence to better inform palaeoecological reconstructions. Complex relationships with water-chemistry gradients are observed with various nutrients (e.g. nitrate-nitrogen and silicate) and alkalinity being the most influential factors, depending on the season and distance from the coast. A novel aspect of this study is its determination of functional attributes of diatoms, through which it is possible to gain a greater understanding of how community structure differs in spring versus summer. Finally, the knowledge gleaned about species ecology is applied to previously published diatom records to determine whether additional ecological information can be extracted from the sediment record. The use of *Epithemia* spp. as indicators of nitrogen limitation to infer long-term changes in lake nitrogen cycling provides a salient example of the insights gained from the contemporary ecological studies.

Wengrat et al. look at how increases in productivity alter the diversity of diatom assemblages in sediment cores from seven tropical, eutrophic reservoirs in Brazil. The authors provide evidence for a marked decrease in spatial beta-diversity between waterbodies as well as a decrease of alpha-diversity within a site over time, suggesting that eutrophication leads to homogenization of the diatom assemblage. This study serves to illustrate the valuable role of palaeoecology in understanding changes in freshwater biodiversity in response to eutrophication.

Salgado et al. examine modern macrophyte and associated invertebrate communities of Castle Lough, Northern Ireland, and explore how diversity is influenced by spatial heterogeneity of environmental factors. The investigators also document how plant and invertebrate macrofossil assemblages changed over more than a century in sediment cores from three sub-basins in the lake. The results show that modern spatial heterogeneity, particularly with respect to water depth, promotes greater diversity because of habitat complexity, but that eutrophication decreases diversity over time and exerts a homogenising effect on communities. This paper demonstrates the importance of combining modern ecological studies with historical approaches to provide greater understanding of the factors that influence community structure, and how this structure is progressively changed by drivers that arise from human influence.

Long-term changes in biodiversity and biological communities

As noted above, palaeolimnology covers timescales which are otherwise out of reach. Other papers in the special issue use this long-term perspective to better understand community dynamics, species interactions, changes in biodiversity and to enhance our understanding of species ecology:

Bennion et al. show how sedimentary macrofossil records can define ecological reference conditions and assess the condition of lakes, and thereby assist in the setting of conservation objectives and management goals. Based on a sound understanding of present-day plant ecology, they interpret the observed general shift towards macrophyte species more typically associated with eutrophic conditions over the last century. This is further evidence that nutrient-load reduction measures are urgently required. This study demonstrates the value of using modern macrophyte ecology to interpret historical change.

Boxem et al. analyse the plant macrofossils and pollen from sediment cores of a wetland in Ontario, Canada to identify long-term changes in the aquatic plant community. The study shows that plant community composition has been impacted by human activities (deforestation, water regulation), with a notable shift from a sedge-dominated wet-meadow wetland to a cattail-dominated system, the latter of which is known to cause loss of ecosystem diversity. The value of such studies for informing restoration strategies is clearly demonstrated. The recommendation is to reintroduce native sedge species that were present prior to catchment disturbance.

Progress, future challenges and research needs

Despite promising advances in our understanding of many taxonomic groups frequently used in palaeoecology (e.g. diatoms, ostracods, chironomids, and testate amoebae), we still lack sufficient contemporary ecological knowledge. In turn this current lack of knowledge hampers what we can do meaningfully in terms of inferring underlying processes from species compositional patterns.

There remains a large disparity between palaeo and contemporary investigation. While there has been significant growth in the number of diatom-based palaeo studies, with ever more elaborate approaches for environmental inference, there has not been a corresponding growth in diatom ecology studies. There is a fundamental need for greater knowledge of diatom seasonality, species responses to water-column mixing, habitat preferences in terms of light availability, substrate, water depth and influences from competition, grazing and other food-web effects. For example, some diatom studies have looked at seasonality with a view towards more-informed palaeo reconstruction of limnological dynamics, climate and species interactions (Bennion et al. 2012; Kirilova et al. 2008; Köster and Pienitz 2006; McQuoid and Hobson 1997; Sayer et al. 2010a), but many more studies are needed. Such information would be invaluable to the development of more sophisticated palaeolimnological interpretations, and to understanding of the long-term response of diatoms.

Studies on macrophytes have demonstrated great potential for increasing our understanding about ecosystem change (Bennion et al. this issue; Bishop et al. this issue; Boxem et al. this issue; Salgado et al. this issue). For example, studies of plant macroremains, combined with modern studies of seasonality, have allowed us to more confidently infer long-term changes in lake seasonality (Sayer et al. 2010c), changes in plant community structure (Madgwick et al. 2011) and taphonomy (Bishop et al. this issue). In particular, when macrofossils are combined with other groups, such as cladocerans, pigments or diatoms, it is possible to identify the most likely processes and mechanisms driving change in macrophyte abundance, such as shifts from benthic to pelagic production (Davidson et al. 2011) or fish kills (Leavitt et al. 1989; Sayer et al. 2016). This in turn can help to develop our understanding of the mechanisms that control macrophyte distribution on different spatial and temporal scales. A better understanding of the ecology of individual taxa and their associations with other biological groups will help us move away from using sedimentary assemblages as a proxy for a single-chemical variable such as pH or total phosphorus, and towards their use as indicators of ecosystem conditions. This shift from proxies to indicators might seem like semantics, but it represents a different intention towards the study of the sediment record.

The use of a greater range of ecological indicators, numerical methods, replication or multiple cores and multiple-site studies (Reid et al. this issue; Salgado et al. this issue; Wengrat et al. this issue) has encouraged researchers to focus on more ecologically based aspects (such as biodiversity) or to pose more ecological questions (as opposed to environmental history questions), and to test hypotheses generated from contemporary ecology and palaeo studies. These include testing ideas about the nature of alternative stable states and catastrophic change (Hobbs et al. 2012; Ogden 2000; Randsalu-Wendrup et al. 2014; Sayer et al. 2010b), trophic cascades (Jeppesen et al. 2001; Leavitt et al. 1989; Sayer et al. 2016) and patterns of biodiversity change (Davidson et al. 2010, 2013; Gregory-Eaves and Beisner 2011).

The above examples demonstrate how useful palaeo approaches are to investigating ecological change, and their potential for addressing and testing ecological theories. It is our view that the future of palaeoecology and palaeolimnology depends on the palaeo community embracing the ‘ecology’ in palaeoecology. It is crucial that we gain an actual understanding of what the presence and relative abundance of species that belong to different biological groups means for a lake. Likewise it is critical to know how they change over seasons, years, decades and centuries. This is entirely different from looking at patterns of variance in axis 1 scores of a particular species group and simply inferring “change” over time. This latter approach has been used to identify early warning indicators (EWIs) that portend a ‘critical transition’ (Wang et al. 2012) or regime shift, which purportedly occurs when an ecosystem shifts between two alternative equilibria (Scheffer and Carpenter 2003), as suggested in shallow lakes as a response to nutrient enrichment (Scheffer et al. 1993). Certain patterns of variance are reportedly diagnostic of ‘flickering’ or ‘critical slowing down,’ which are early warnings of an impending catastrophic shift (Scheffer et al. 2009). This approach of using the palaeo record to identify EWIs through diagnostic patterns in variance, though addressing a potentially interesting and important ecological question, does not integrate ecological or limnological understanding into the study. The identity of the species, their habitat preferences and their ecological significances are not considered, but rather patterns in the variance in the assemblage (autocorrelation) are used. From the perspective of trying to increase our understanding of the ecological processes that lead to, for example, plant loss and reduction in biodiversity and ecosystem services (e.g. carbon storage) in shallow lakes, such studies shed little light. Furthermore, even if such EWIs reliably presage a regime shift, or in the case of shallow lakes the loss of macrophytes, it is questionable whether these early warnings could be adequately detected in real time by an environmental manager (Spears et al. 2017).

We propose the use of more meaningful EWIs that address the loss of resilience or ecological value, and of change in key ecosystem functions (e.g. carbon and nitrogen cycling). Such EWIs should be grounded in well-established mechanisms that can be understood and interpreted by limnologists and lake managers alike. In the case of shallow lakes that are affected by eutrophication and are vulnerable to plant loss, these might include a reduction in the length of the growing season linked to macrophyte species loss (Hilt et al. 2013; Sayer et al. 2010c), more substantial inter-annual variation in plant abundance (Bayley et al. 2007) and shifts from benthic to pelagic production (Davidson et al. 2011; Vadeboncoeur et al. 2003). The identification and understanding of improved EWIs can be obtained from the long-term perspective that paleoecological methods offer, and they are best explored by a combination of ecological and paleoecological methods.

To conclude, we call for greater collaboration between ecologists and palaeoecologists, and for a more concerted effort to employ the long-term perspective provided by palaeolimnology to detect mechanisms that lead to ecological degradation and biodiversity loss in aquatic systems. We emphasise the need to shift away from seeing biological remains simply as proxies of some variable of interest. In addition, we call for better-integrated studies that holistically address ecosystem function and change, and that use palaeolimnology to test fundamental theoretical questions in ecology.

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