Quaternary Science Reviews 98 (2014) 60–73

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Inferring local to regional changes in forest composition from Holocene macrofossils and pollen of a small lake in central Upper Michigan

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ARTICLE INFO

Article history:
Received 2 November 2013
Received in revised form
28 May 2014
Accepted 31 May 2014
Available online 19 June 2014

Keywords:
Holocene
Plant macrofossils
Pollen
Michigan
North America
Paleoecology
Forest history
Vegetation
Scale

ABSTRACT

Vegetational response to climatic change involves processes of population and community dynamics within local stands, which scale up to landscape-level changes in vegetation composition and broad-scale changes in species distributions. Understanding these dynamics poses a critical challenge to paleoecological explanation, because of the broad range of scales at which these dynamics take place and interact. We present an 8600-year paleoecological record of local and regional changes in forest composition from a small (2.6 ha) lake in central Upper Michigan. Plant macrofossils provide a spatially precise record of local forest composition, while pollen data provide a spatially integrated record of regional vegetational changes. Temporal patterns among different macrofossil types within species show overall coherence, indicating that changes in macrofossil abundance generally record changes in local tree abundance. Temporal patterns in macrofossil sequences correspond to patterns in pollen sequences, indicating that local changes contributed to the large-scale changes in the surrounding region. The pollen and macrofossil records show nearly continuous turnover in vegetation composition throughout the past 8600 years; the longest period without major compositional change was ca 1600 years, and dynamics at multidecadal to multicentennial scales are observed during many periods. Coordinated application of temporally precise sequences of pollen and macrofossil data at multiple sites can support inferences concerning vegetation dynamics at multiple spatial and temporal scales, and test mechanistic hypotheses.

1. Introduction

A central goal of paleoecology is to infer properties and dynamics of past individuals, populations, communities, and ecosystems from multiple lines of fragmentary, incomplete evidence. In terrestrial plant paleoecology, pollen analysis has been employed to these ends for nearly a century (Von Post, 1916), and Quaternary plant macrofossil analysis is long past its sesquicentennial (Steenstrup, 1841; Vaupell, 1851). Quaternary pollen records are legion across much of the terrestrial globe (Williams et al., 2004; Bartlein et al., 2011; Brewer et al., 2012), and plant macrofossil records, though sparser, number in the hundreds in some regions (e.g., Betancourt et al., 1990; Jackson et al., 1997; Binney et al., 2009). Ecological applications of pollen and macrofossil records rest on a foundation of empirical studies of taphonomic processes, comparative studies of modern assemblages and vegetation, and formal and conceptual models for correcting biases and facilitating interpretation.

In spite of the widespread application of pollen and plant macrofossil data and the considerable body of knowledge underlying their interpretation, substantial uncertainties remain. Pollen assemblages represent distance-weighted integrations of vegetation composition extending from the immediate vicinity of the

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http://dx.doi.org/10.1016/j.quascirev.2014.05.030
0277-3791/Published by Elsevier Ltd.

depositional basin out to tens of kilometers away, with distance-weightings varying among taxa according to their pollen-dispersal properties (Prentice, 1985; Sugita, 1994; Jackson and Lyford, 1999). By itself, a pollen assemblage corresponds to no single entity that might otherwise be of interest to ecologists; its primary interest lies in its having recorded features of vegetation that can no longer be observed directly. In aggregating innumerable individuals, populations, and patches over a broad landscape, a pollen assemblage conveys a sense of 'average' composition of regional vegetation. However, the regional signal may be distorted by pollen from vegetation near the depositional site, which may differ substantially from the regional average (Bradshaw and Webb, 1985; Jackson, 1990, 1994).

Differentiating between pollen deriving from local and distant sources has long been a central challenge in pollen analysis; insufficient ability to do so is a major source of uncertainty in ecological and biogeographic applications (Davis et al., 1991; MacDonald, 1993; McLachlan and Clark, 2004). A few tools, based on empirical and theoretical understanding of pollen dispersal, are available to support such differentiation. The proportion of local pollen in sediments is inversely (and non-linearly) related to the size of the depositional basin (Prentice, 1985; Jackson, 1994; Sugita, 1994, 2007a, 2007b). Thus, site selection can dampen or amplify local representation, depending on the purpose of the study (Jacobson and Bradshaw, 1981). Application of pollen-dispersal models to spatial networks of small and large basins can support identification of local and regional sources and detect spatial patchiness of vegetation (Sugita, 1994, 2007a, 2007b). Initial applications are promising (Soepboer et al., 2010; Sugita et al., 2010), but are necessarily restricted to regions rich in depositional basins of suitable size.

A complementary approach is paired analysis of pollen and plant macrofossils. In contrast to pollen, macrofossils from lake sediments are indisputably local in origin; airborne dispersal is, except in rare cases, limited to 10^0–10^2 m, and waterborne macrofossils can derive from no further than the catchment boundary. Thus, a macrofossil assemblage derives from a relatively small area surrounding the lake, more analogous to the scale of conventional ecological observation and sampling than that of a pollen assemblage. Macrofossil assemblages, however, are subject to their own biases of representation, and vegetation adjacent to a lakeshore may not be representative of surrounding uplands. Furthermore, sample sizes for macrofossil assemblages tend to be small, owing to low concentrations in sediments (typically at least five orders of magnitude lower than pollen concentrations) and to the low sediment volume obtained in typical lake-sediment cores.

Macrofossil data tend to be treated conservatively in paleoecological inference. In the canonical text of pollen analysis, Knut Fægri asserted that although occurrence of a macrofossil might indicate local presence at a site, "nothing can be concluded from its absence" (Fægri and Iversen, 1975, p. 123). Accordingly, many studies use macrofossil data exclusively as singular indicators of local occurrence. This is reasonable when sample sizes are low, taphonomic biases are high, or sampling is haphazard or opportunistic. However, local presence and absence can be reliably inferred from macrofossil data, provided sample sizes are large enough and taphonomic biases are such that they maximize likelihood of representation in sediments given occurrence in surrounding vegetation (Jackson, 2012). Presence/absence at individual sites can be scaled up to infer past geographic distributions of species (Jackson et al., 1997, 2000; Binney et al., 2009).

Macrofossils are often tabulated and expressed as concentrations (number per unit sediment volume), accumulation rates (numbers per cm^2 per year), or percentages of a designated macrofossil sum. Quantitative macrofossil sequences are often based on small sample sizes and have high inter-sample variability, making it difficult to differentiate between vegetational signal and extraneous noise. Nonetheless, macrofossil and pollen data often show parallel patterns (e.g., Jackson and Booth, 2007), suggesting that macrofossil data can support inferences concerning local-scale vegetation composition and dynamics. Macrofossil data may be underutilized as a source of information concerning vegetational change at local and regional scales, and as a tool for linking the regional changes represented in pollen sequences to the local changes that might be observed at the stand scale.

Effective study design and robust interpretation of macrofossil data can be informed by principles and observations based on empirical studies and theoretical considerations. Because macrofossil sources are largely limited to trees growing within 10^0–10^2 m of shore, airborne macrofossil flux-density to a lake surface will increase as an approximate linear function of shoreline perimeter, but total lake area will increase as an approximate square function of the perimeter. Therefore, all else held constant, macrofossil flux density per unit lake area will decrease rapidly as lake size increases. Macrofossil density in benthic sediments decreases with distance from shore (Wainman and Mathewes, 1990; Jackson and Booth, 2007), owing to attenuating airborne dispersal to the lake surface and to diffusion as airborne, floating, or suspended macrofossils move further from onshore sources. As a general rule, macrofossil preservation in sediments increases with water depth (Jackson, 1989; Jackson and Booth, 2007); lower temperatures and oxygen deficits retard decomposition. Emergent or-floating-leaved vegetation in shallow waters pose physical barriers to dispersal of macrofossils to deeper waters, and will thus decrease macrofossil concentrations in offshore sediments. Steep slopes along a lakeshore will increase adjacency of upland trees to open water, and overhanging trees will contribute macrofossils directly to the water surface while inhibiting emergent vegetation by shading the narrow littoral margin of the lake. Accordingly, small lakes with deep water within 50 m of shore bordered by steep, forested slopes and overhanging trees are ideally suited to yield high concentrations of well-preserved macrofossils.

In this paper, we compare Holocene pollen and macrofossil data, obtained at relatively high (decades to centuries) temporal resolution, from sediments of Tower Lake, a small lake in northern Michigan, specifically selected to maximize representation of plant macrofossils from forest species characteristic of the surrounding upland landscape. We compare the pollen and macrofossil data for 11 tree species, assessing the extent to which patterns in the macrofossil record correspond to those in the pollen record. This comparison supports assessment of the local forest dynamics represented in the macrofossil record in terms of the regional dynamics recorded by pollen. We also compare temporal patterns among different macrofossil types within tree taxa, to determine whether those patterns are attributable to changes in local tree populations or to taphonomic or other factors. We discuss the various factors, taphonomic and other, that can influence macrofossil abundance in lake sediments, and suggest how paleoecological studies can be effectively designed to maximize and differentiate information on both local and regional changes in forest composition. Finally, we discuss the Tower Lake record in terms of the challenges faced by paleoecologists in explaining ecological dynamics that involve multiple temporal and spatial scales, and how these challenges might be addressed by careful consideration of scale and employment of multiple lines of evidence.

2. Site description

Tower Lake (informal name) is an endorheic kettle lake in central Upper Michigan (46°32′31″N, 86°02′13″W, 261 m elevation)