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The effects of anthropogenic land cover change on pollen-vegetation relationships in the American Midwest

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ABSTRACT

Fossil pollen assemblages provide information about vegetation dynamics at time scales ranging from centuries to millennia. Pollen-vegetation models and process-based models of dispersal typically assume stable relationships between source vegetation and corresponding pollen in surface sediments, as well as stable parameterizations of dispersal and productivity. These assumptions, however, are largely unevaluated. This paper reports a test of the stability of pollen-vegetation relationships using vegetation and pollen data from the Midwestern region of the United States, during a period of large changes in land use and vegetation driven by Euro-American settlement. We compared a dataset of pollen records for the early settlement-era with three other datasets of pollen and forest composition for two time periods: before Euro-American settlement, and the late 20th century. Results from generalized linear models for thirteen genera indicate that pollen-vegetation relationships significantly differ ($p < 0.05$) between pre-settlement and the modern era for several genera: *Fagus, Betula, Tsuga, Quercus, Pinus*, and *Picea*. The estimated pollen source radius for the 8 km gridded vegetation data and associated pollen data is 25–85 km, consistent with prior studies using similar methods and spatial resolutions.

Hence, the rapid changes in land cover associated with the Anthropocene affect the accuracy of ecological predictions for both the future and the past. In the Anthropocene, paleoecology should move beyond the assumption that pollen-vegetation relationships are stable over time. Multi-temporal calibration datasets are increasingly possible and enable paleoecologists to better understand the complex processes governing pollen-vegetation relationships through space and time.

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1. Introduction

Fossil pollen records and other paleoecological proxies provide evidence of ecological dynamics over centuries to millennia. These records therefore expand knowledge of community composition, environmental change, and ecological dynamics at timescales that are not possible to observe directly. Knowledge of long-term community dynamics elucidate many aspects of ecological patterns and processes, including study of historical ecosystems (Birks et al., 2000), climate-driven species range expansions and contractions (Davis and Shaw, 2001), causes of abrupt change in ecological systems (Booth et al., 2012), and processes that give rise

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to the emergence of no-analogue communities (communities that are ecologically dissimilar to any found today; Jackson and Overpeck, 2000; Williams and Jackson, 2007). This knowledge also provides historical baselines for understanding and managing disturbance and restoration. (Birks, 1996; Foster and Motzkin, 2003; Hotchkiss et al., 2007; Lynch et al., 2014).

Accurate reconstruction of past vegetation requires an understanding of the relationship between the composition of pollen and the composition and structure of its source. This relationship is complicated by differences among taxa in dispersal vector, pollen productivity (number of pollen grains per individual organism), and the morphology of pollen grains, all of which affect dispersal (Cain, 1939; Erdtman, 1943). Pollen data are typically represented as relative abundances, which are further complicated by the interdependence of each taxon on all others, known as the Fagerlind effect, (Fagerlind, 1952; Davis, 1963; Prentice and Webb, 1986; Davis et al., 1991a; Davis and Shaw 2001). Studies consistently show a positive relationship between pollen and plant abundances. These studies demonstrate that smaller basins capture pollen from smaller source areas than larger basins (e.g. Tauber, 1965; Jacobson and Bradshaw, 1981; Bradshaw and Webb, 1985; Prentice, 1985; Jackson, 1990; Sugita, 1994). The relevant pollen source area for small basins, such as forest hollows, is on the scale of tens of meters (Calcote, 1995; Jackson and Kearsley, 1998). Studies that include medium and large lakes show larger source areas. When using both larger lakes and gridded vegetation datasets with a spatial grain >1 km^2, studies produce correspondingly larger estimates of pollen source area, on the order of 10–50 km radii or larger (Bradshaw and Webb 1985; Williams and Jackson 2003; Dawson et al., 2016).

Palynologists have spent decades studying these relationships and building models to estimate the composition of vegetation from pollen data. Empirical investigations into pollen-vegetation relationships typically rely upon spatial networks of pollen assemblages paired with observations about the surrounding vegetation (Bradshaw and Webb, 1985; Jackson, 1990; Davis et al., 1991b; Calcote, 1995; Parshall and Calcote, 2001; Williams, 2002; Williams and Jackson, 2003; Bhattaharrya et al., 2011). Early methods ranged from relatively simple linear regression models (Webb et al., 1981; Bradshaw and Webb, 1985) to R-values based on ratios of pollen productivity (Davis, 1963). These methods also included extended R-value (ERV) models that address the Fagerlind effect (Parsons and Prentice, 1981; Prentice and Webb, 1986; Prentice et al., 1987). Process-based pollen dispersal models, such as the Landscape Reconstruction Algorithm (LRA), use diffusion-based dispersal kernels (Sutton, 1953) and information about pollen fall speeds and productivity to estimate the pollen loadings produced by plant communities around a basin (Prentice, 1985, 1988; Sugita, 1994). STEPPS, a Bayesian hierarchical model, also models pollen dispersal from and to gridded points, while also estimating key parameters such as pollen productivity and dispersal, including the uncertainty of these estimates (Paciorek and McLachlan, 2009; Dawson et al., 2016).

Regardless of form, pollen-vegetation models are always calibrated using pollen and vegetation data for one time period, then applied to infer vegetation from pollen for another time. Different kinds of models make different assumptions. ERV models that are calibrated against spatial datasets of forest composition and pollen assemblages assume a stable relationship through time between pollen and plant abundances. This assumption of temporal stability is largely untested, however, even though previous studies have suggested that the assumption is likely false. Pollen-vegetation relationships vary according to forest type and the relative abundance of high and low pollen producers (Schwartz, 1989; Seppä, 1998; Parshall and Calcote, 2001; Meltsov et al., 2011; Baker et al., 2015), as well as differences in the structure and heterogeneity of vegetation landscapes (Bunting et al., 2004). The source area of pollen also likely changes over time (Nielsen and Sugita, 2005). Process-based models such as LRA avoid assumptions about the stability of the relationship between the compositions of assemblages and plant communities. Instead, they assume that atmospheric properties such as turbulence remain constant over time, as well as the aerodynamics of pollen grains and the relative pollen productivity of taxa. Bayesian hierarchical models such as STEPPS (Dawson et al., 2016; Paciorek and McLachlan, 2009) also effectively assume constant turbulence over time and are calibrated using spatial datasets of pollen and vegetation, although they seek to estimate latent parameters of pollen productivity and dispersal. Both LRA and STEPPS effectively assume that pollen productivity and dispersal are temporally stable – an assumption that may not hold under changing temperatures and concentrations of atmospheric carbon dioxide, past or future (Huusko and Hicks, 2009). The assumption of temporal stability in parameters is pervasive in pollen-vegetation modeling, and ecological modeling more generally, yet is potentially violated by the rapid ecological and environmental changes associated with the Anthropocene.

The transformation of forest composition in the North American upper Midwest by Euro-American settlement and land use, combined with accurate vegetation surveys just before widespread settlement, enables study of the stability of pollen-vegetation relationships across a period of major vegetation change. Before Euro-American settlement (hereafter "pre-settlement"), upper Midwestern forests were principally of comprised temperate hardwood and boreal forest communities north and east of the prairie-forest border, and prairies and oak savannas were found to the south and west (Curtis, 1959). Vegetation ecotones were steeper than those found at present. Frequent fires largely maintained the southern oak savanna and prairie communities (Curtis, 1959; Shea et al., 2014). European land use nearly eliminated these ecosystems and replaced them with agricultural land and late-successional, shade-tolerant deciduous forests. Logging in northern forests resulted in declines in abundances of *Pinus* species, while widespread slash burning and continued logging decreased fire-intolerant boreal species such as *Tsuga canadensis*, and increased early successional genera such as *Betula* and *Populus* (Rhemtulla et al., 2007). In other regions, fire suppression led to an increase in shade-tolerant, fire-sensitive, mostly deciduous species, replacing fire-tolerant conifers (Drobyshev et al., 2008). Recent estimates suggest that 29% of modern upper Midwestern forests have no close compositional analogue in pre-settlement forests in the region.

While paleoecologists have long investigated the profound effects of historic land use on vegetation (e.g. Grimm, 1984; Jacobson and Grimm, 1986; Davis et al., 1991a,b; Hotchkiss et al., 2007), relatively few studies have explored the effects on pollen-vegetation relationships. For the state of Minnesota in the United States, St. Jacques et al. (2008a) demonstrated that the relationships between pollen and climate have shifted significantly from the pre-settlement era to the present, thereby affecting pollen-based climate reconstructions. St. Jacques et al. (2008b, 2015) recommended that pollen-based paleoclimatic inferences should be based on data from pre-settlement era pollen, rather than modern pollen-climate calibration sets, to minimize the distortion and bias produced by 19th- and 20th-century land use. Using historical records in Denmark to estimate the relative source area of pollen, Nielsen and Sugita (2005) showed that the effects of human activity on vegetation patch size alters the pollen source area for fossil pollen sites.

This paper reports an assessment of the constancy of pollen-vegetation relationships by comparing four contemporary and pre-settlement pollen and vegetation datasets. These datasets

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