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ARTICLE

Estimation of pollen productivity and dispersal: How pollen assemblages in small lakes represent vegetation

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Abstract

Quantitative understanding of vegetation dynamics over timespans beyond a century remains limited. In this regard, the pollen-based reconstruction of past vegetation enables unique research opportunities by quantifying changes in plant community compositions during hundreds to thousands of years. Critically, the methodological basis for most reconstruction approaches rests upon estimates of pollen productivity and dispersal. Previous studies, however, have reached contrasting conclusions concerning these estimates, which may be perceived to challenge the applicability and reliability of pollen-based reconstruction. Here we show that conflicting estimates of pollen production and dispersal are, at least in part, artifacts of fixed assumptions of pollen dispersal and insufficient spatial resolution of vegetation data surrounding the pollen-collecting lake. We implemented a Bayesian statistical model that related pollen assemblages in surface sediments of 33 small lakes (<2 ha) in the northeastern United States, with surrounding vegetation ranging from 10¹ to >10⁵ m from the lake margin. Our analysis revealed three key insights. First, pollen productivity is largely conserved within taxa and across forest types. Second, when local (within a 1-km radius) vegetation abundances are not considered, pollen-source areas may be overestimated for some common taxa (Cupressaceae, *Pinus*, *Quercus*, and *Tsuga*). Third, pollen dispersal mechanisms may differ between local and regional scales; this is missed by pollen-dispersal models used in previous studies. These findings highlight the complex interactions between vegetation heterogeneity on the landscape and pollen dispersal. We suggest that, when estimating pollen productivity and dispersal, both detailed local and extended regional vegetation must be taken into account. Also, both deductive (mechanistic models) and inductive (statistical models) approaches are needed to better understand the emergent properties of pollen dispersal in heterogeneous landscapes.

KEYWORDS

Bayesian statistical model, pollen dispersal, pollen productivity, pollen-based vegetation reconstruction, pollen–vegetation relationship

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INTRODUCTION

Global environmental changes can affect vegetation composition on regional to global scales, including community turnover (Willis et al., 2010) and ecosystem transformations (Jackson, 2021; Nolan et al., 2018). These vegetation dynamics can take decades, centuries, or millennia to unfold, and have large consequences for global carbon and energy budgets (Bonan, 2008; Bonan & Doney, 2018). A primary approach to studying long-term vegetation dynamics is through geohistoric records, using “proxies” such as fossil pollen deposited in lakes, wetlands, and hollows. The interpretation of changes in pollen records across space and over time provides insights into the history of vegetation, climate, disturbance, and human impacts on ecosystems (e.g., Marsicek et al., 2018; Mottl et al., 2021; Nolan et al., 2018). Whereas analyses of pollen data have been ongoing for more than a century (Edwards et al., 2017), the urgent need to better understand vegetation response to anthropogenic climate change has led to a recent surge in developing and applying a variety of quantitative methods toward reconstructing past vegetation from fossil pollen data (Dawson et al., 2019; Mazier et al., 2012; Theuerkauf & Couwenberg, 2018; Trachsel et al., 2020; Williams et al., 2011; Zanon et al., 2018).

Fundamental to most of these reconstruction approaches is the robust estimation of pollen productivity and dispersal. Pollen productivity is typically defined as the number of pollen grains produced per unit relative abundance of a plant taxon. Pollen dispersal describes how far airborne pollen grains have traveled before being deposited. Although most pollen grains are deposited near their source, a substantial amount of pollen deposited in a lake has derived from distant sources owing to the leptokurtic (i.e., fat-tailed) shape of pollen-dispersal kernels (Jackson & Lyford, 1999; Prentice, 1985). Both pollen productivity and dispersal vary among taxa (pollen taxa are typically defined at the genus or family level due to the limitations of pollen identification) but are often assumed to be invariant within taxa. Therefore, beyond the poorly studied effects of intraspecific variation, pollen taxa may include multiple species that can differ in pollen productivity and dispersal.

Inconsistent estimates of pollen productivity and dispersal from different studies can cast doubt on the reliability and applicability of quantitative pollen-based vegetation reconstruction. Pollen productivity estimates for a given taxon can differ by one or more orders of magnitude across regions (Broström et al., 2008; Li et al., 2018; Mazier et al., 2012; Prentice & Webb III, 1986) or time scales (e.g., interannually or decadal; please refer to Kuoppamaa et al., 2009; Minckley et al., 2012), and this has raised concerns about the applicability of pollen productivity estimates across space and time (e.g., Broström

et al., 2008; Li et al., 2018). Therefore, productivity estimates are often validated and applied only within the same region (Hellman et al., 2008a, 2008b; Sugita et al., 2010). For pollen dispersal, the appropriate spatial scale for relating lake-pollen data to the surrounding vegetation remains unclear, with a 100-fold difference among studies in assumed or estimated pollen-source areas. Specifically, some studies have identified the “relevant source areas of pollen (RSAP)” (Sugita, 1994) for pollen deposited in small- or medium-sized lakes as ranging from a few hundred meters to a few kilometers (e.g., Bradshaw & Webb, 1985; Bunting et al., 2004; Han et al., 2017; Hellman, Bunting, et al., 2009), whereas recent data-driven studies have estimated the primary lake-pollen source area to be in the order of hundreds of kilometers for almost all tree taxa (Dawson et al., 2016; Kujawa et al., 2016).

Apparent contradictions in pollen productivity and dispersal may arise due to poorly specified dispersal kernels or inadequate information on landscape heterogeneity (e.g., the spatial distribution of pollen-source taxa) (Li et al., 2018; Liu, 2015). Notably, two prominent types of pollen-vegetation models, namely extended R-value (ERV) models (Bunting et al., 2013; Prentice & Webb III, 1986; Sugita, 1994) and Spatio-Temporal Empirical Prediction from Pollen in Sediments (STEPPS) models (Dawson et al., 2016; Paciorek & McLachlan, 2009), are based on different assumptions. In studies using ERV-type models, the dispersal functions (weights) applied to actual or simulated vegetation data are constructed a priori, using either distance-weighting heuristics or pollen-transport models. These dispersal function assumptions (Jackson & Lyford, 1999; Theuerkauf et al., 2013) underlie the estimation of the RSAP, which are typically hundreds of meters in radius, and determine the areal extent of vegetation surveys (Bunting et al., 2004; Hellman, Bunting, et al., 2009; Hellman, Gaillard, et al., 2009; Li et al., 2018) that are typically in the order of a few kilometers. In contrast, studies based on the STEPPS model (Dawson et al., 2016, 2019; Trachsel et al., 2020) simultaneously estimate pollen productivity and dispersal from a network of vegetation and pollen data, and the estimated dispersal kernels suggested that vegetation from hundreds of kilometers away still strongly influenced pollen assemblages. The spatial resolution of vegetation data used in the STEPPS model, however, is much coarser than in ERV models. For example, in the STEPPS model “local” vegetation surrounding a lake is represented by mean vegetation composition within the corresponding coarse 8 km × 8 km grid cell. This could result in misrepresentation of critical local pollen sources (Liu, 2015; Paciorek & McLachlan, 2009), and observed pollen may be misattributed to more distant vegetation.

In this study, we aimed to rigorously quantify pollen productivity and dispersal by combining the strength

of ERV models (a hierarchy of finely resolved vegetation data near the lake) and the STEPPS model (geographically extensive vegetation data, empirically estimated dispersal, and uncertainty quantification), but overcoming their respective limitations. We implemented a Bayesian statistical model to relate pollen assemblages at 33 small lakes (<2 ha) from three study regions in the northeastern United States to their surrounding vegetation. Our model was informed by detailed forest inventory data that had been resolved at various distances within 1 km from the lakeshore (local), and extended from 1 to 300 km from the lakeshore (regional). Using these data, the approach simultaneously quantified the influences of pollen productivity and dispersal. We addressed the following questions: (Q1) how much do pollen productivity estimates vary within taxa across three study regions of different forest types in the northeastern United States? (Q2) What are the pollen-dispersal characteristics (i.e., how does the probability of pollen deposition decline with distance from the pollen source), and how effectively do mechanistic models of pollen dispersal capture the observed patterns? Finally, (Q3) how important is local and regional vegetation for accurately estimating pollen productivity and dispersal? Respectively, these questions correspond to the three major factors influencing how pollen deposited in lakes represents the surrounding vegetation: pollen productivity, dispersal, and landscape heterogeneity. Therefore, we expect this work to help refine our understanding of pollen productivity and dispersal patterns, and to motivate a new generation of quantitative pollen-based reconstructions to understand vegetation dynamics.

METHODS

Study sites and data

The study area is located in the northeastern United States, and included 33 small lakes (area < 2 ha) from three regions of different forests (Figure 1). Dense forests around the 14 Fish Creek (FC) sites in the central Adirondack Mountains in New York State consist of old-growth hardwood and mixed stands (dominant genera are *Fagus*, *Acer*, *Betula*, *Tsuga*, and *Picea*), selectively logged stands (often dominated by *Fagus*), and second-growth stands (dominated by the aforementioned taxa and *Pinus*). Nine sites from the eastern Adirondack Mountains (EAD), also in New York State, are mostly surrounded by second-growth, mixed hardwood/coniferous forests (dominant genera are *Acer*, *Betula*, *Fraxinus*, *Pinus*, *Quercus*, and *Tsuga*), often dominated by *Pinus*. The 10 southern New England (SNE) sites are in *Quercus*-dominated second-growth forests. Vegetation in these regions has been described in detail by

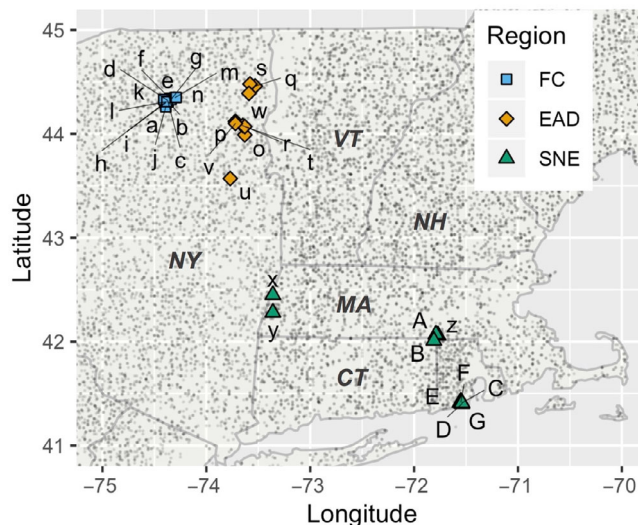


FIGURE 1 The study sites include 33 small lakes (area < 2 ha) located in three regions in the northeastern United States: 14 lakes in Fish Creek, New York State (FC, blue squares), nine (9) in the eastern Adirondack Mountains, New York State (EAD, yellow diamonds), and 10 in the southern New England including Massachusetts, Connecticut, and Rhode Island (SNE, green triangles). Because some sites are closely clustered and their symbols largely overlap on the map, the positions of the symbols are slightly moved for clearer presentation. Correspondence between letters and sites is given in Appendix S1: Table S1. Locations of Forest Inventory and Analysis (FIA) plots measured between 2000 and 2012 are represented by the small, dense, gray points

Jackson (1990, 2019). Using lakes from the three different regions, our model will allow uncertainty estimations across different vegetation compositions as well as within pollen taxa (i.e., the species of *Betula*, *Pinus*, and *Quercus* differ to some extent among regions).

Due to the varying taxonomic resolution of pollen identification, pollen types were grouped by taxa (often genus, sometime species or family) rather than species. Our analysis focused on 13 arboreal taxa (*Abies*, *Acer rubrum*, *A. saccharum*, *Betula*, *Fagus*, *Fraxinus*, *Larix*, *Picea*, *Pinus*, *Populus*, *Quercus*, Cupressaceae, and *Tsuga*), which included all taxa exceeding 5% in pollen assemblages or vegetation proportions at any site.

We operationally defined the “local scale” as within 1 km from the lakeshore and the extended “regional scale” as spanning 1–300 km from the lakeshore. This distinction was introduced to distinguish major vegetation-survey data sets and accommodate possible major differences in pollen dispersal between the two scales in our model. Unlike the notion of “background pollen” in ERV models, sites within the same region in our model may have different pollen inputs from regional sources owing to vegetation heterogeneity at scales of 10¹ to 10² km. The pollen sampling procedure and the local vegetation-survey protocol followed

Jackson (1990, 2019). At each of the 33 small lakes, modern pollen samples were collected from the top 1 cm of sediments at the center of the lake between 1986 and 1990. During the same period, trees growing within 1 km around the lakeshore were surveyed with varying intensity, including exhaustive or inventory-plot measurements within 20 m, and transects of plotless angle-count (Bitterlich) samples. Total basal area (m^2) was calculated for each tree taxon growing within a 1-km radius, for each of five distance intervals from the shore of each small lake: 0–20, 20–50, 50–100, 100–500, or 500–1000 m. Site information is listed in Appendix S1: Table S1. Pollen counts, local basal areas of taxa at each lake, and detailed descriptions of the sampling methods and data are reported in Jackson (2019).

To estimate contemporary vegetation abundances outside the 1-km radius, we obtained data from the Forest Inventory and Analysis (FIA) program for 349,309 individual trees in 7354 plots between the years 2000 and 2012 (Figure 1). Because some plots were remeasured during this time, in total 10,753 plot-level records were used. The total basal area (m^2) for each tree taxon was calculated for each plot-level record. If a plot location was measured multiple times between 2000 and 2012, the mean basal area of each taxon was calculated. For each lake site, we calculated the mean vegetation abundances of taxa in ring-shaped bands located at different distances from the lake, and a total of 100 “rings” were considered at each lake site. Each ring had a width of 3 km. That is, the smallest/nearest ring had an inner radius of 1 km and an outer radius of 4 km from the lakeshore, whereas the largest/furthest ring had an inner radius of 298 km and an outer radius of 301 km from the lakeshore. We chose the ring width to be 3 km because the coordinates for FIA plots were “fuzzed” within 0.5–1 mile (i.e., 0.8–1.6 km; O’Connell et al., 2017) and some were “swapped” (plot coordinates exchanged between similar private forest plots within the same county); therefore, finer rings in this case would not have resulted in a better resolution. Although vegetation within the 1 km radius was sampled in the late 1980s, more than a decade before the FIA plots were sampled, the change in vegetation composition during that decade (and/or difference due to sampling methods) appeared to be small (Appendix S1: Figure S1).

Furthermore, we assessed spatial patterns of vegetation heterogeneity around each lake using vegetation abundance data from both vegetation surveys at the local scale and forest inventories at the regional scale. To do this, we used squared-chord distance (SCD; Overpeck et al., 1985) to quantify the dissimilarities between vegetation composition (i.e., relative abundances) at different distances from the lakeshore and several “focal” vegetation compositions at 0.02, 0.1, 0.5, 1, 9, 27, and 45 km from the lakeshore.

Bayesian model specification

We developed a Bayesian statistical model that related deposited pollen assemblages with surrounding vegetation at the 33 small lakes. Recall the “pollen-source topography” analogy: Essentially, our model is informed by pollen counts from the lakes as well as the vegetation distribution maps surrounding the lakes, and estimates taxon-specific pollen productivities (estimated for each study region) and parameters describing dispersal patterns (estimated for local and regional scales respectively).

Our model structure was overall similar to that of the STEPPS approach (e.g., Dawson et al., 2016) in terms of the Bayesian implementation and the delineation of a focal area around the site and those areas beyond. However, important data choices and model implementations differed. Our analysis has two distinct features that accommodate complex landscape heterogeneity: (i) the finely resolved and extended spatial information of vegetation abundances (the vegetation distribution map), and (ii) the separate, explicit treatment of local versus regional dispersal. Specifically, we decomposed pollen contributions into local sources (originating within 1 km from the lakeshore) and regional sources (originating beyond 1 km from the lakeshore). We estimated taxon-specific local contributions, which were the proportions of pollen contributed by local vegetation relative to all pollen of the same taxa from all distances. Relative vegetation abundances (i.e., vegetation composition) were distance weighted within their respective scales (local vs. regional). At the local scale, the taxon-specific influences of vegetation on pollen were estimated for the five concentric rings (0–20, 20–50, 50–100, 100–500, and 500–1000 m intervals from the lakeshore) at which local vegetation was finely surveyed. At the regional scale, the taxon-specific influences of vegetation on pollen are estimated for increasing radial rings (1–4, 4–7, 7–10, ..., and 298–301 km from the lakeshore).

Our modeling approach was as follows. At site $s = 1, \dots, S$ ($S = 33$; $s = 1, \dots, 14$ belong to the FC region, $s = 15, \dots, 23$ belong to the EAD region, and $s = 24, \dots, 33$ belong to the SNE region), observations of lake sediment-surface pollen samples, vegetation within 1 km, and FIA plots within 300 km were available as described in section “Method - Study sites and data”. To account for observation error, we modeled pollen counts, $Y_{s,t}$, of taxon $t = 1, \dots, T$ ($T = 13$) in the sample from site s (where \mathbf{Y}_s is the vector of site-specific pollen counts, of length T) as coming from a multinomial distribution with probability parameters determined by the relative pollen load, \mathbf{P}_s , for each taxon at that site (\mathbf{P}_s is also a vector of length T and $\sum_{t=1}^T P_{s,t} = 1$):

$$\mathbf{Y}_s \sim \text{Multinomial}(\mathbf{P}_s, N_s) \quad (1)$$

where $N_s = \sum_{t=1}^T Y_{s,t}$ is the total number of pollen grains counted in the sample from site s , summing across all taxa.

$P_{s,t}$ at site s is determined by both local and regional sources of pollen and by the taxon-specific pollen productivities, $\Phi_{r,t}$ (scaling factor, per relative vegetation abundances, therefore unitless) for region $r = 1, \dots, R$ ($R = 3$):

$$P_{s,t} = \Phi_{r(s),t} (\gamma_t \cdot \text{VL}_{s,t} + (1 - \gamma_t) \cdot \text{VR}_{s,t}) \quad (2)$$

where $r(s)$ denotes the region in which site s is location; γ_t is the taxon-specific local weights, representing the proportion of pollen contributed by local trees of taxon t relative to all (local and regional) pollen of that taxon. $\text{VL}_{s,t}$ is the distance-weighted relative abundance of each taxa t within 1 km (local vegetation composition) of site s ; $\text{VR}_{s,t}$ is defined similarly to $\text{VL}_{s,t}$, but for trees occurring beyond 1 km and up to ~300 km from the lakeshore (regional vegetation composition).

We modeled the taxon-specific and region-specific pollen productivities (Φ) hierarchically. We expected $\Phi_{r,t}$ to vary among taxa; in addition, because environmental conditions, phenotypes of trees, and growth forms of trees may vary across regions, $\Phi_{r,t}$ may also vary within taxa across regions. Therefore, for each taxon in region $r = 1, \dots, R$ ($R = 3$, corresponding to FC, EAD, and SNE), we defined the region-level vector of taxon productivities, Φ_r , as varying around the overall taxon-level productivity, Φ^* (both are vectors of length T). Because the productivity of a taxon is only meaningful relative to other taxa (pollen percentages do not measure pollen flux, therefore no absolute pollen productivity can be inferred from pollen data), we imposed a sum-to-one constraint for the relative productivity parameters using a Dirichlet distribution:

$$\Phi_r \sim \text{Dirichlet}(\alpha \cdot \Phi^*) \quad (3)$$

where the scalar parameter, α , was given a relatively non-informative, yet realistic uniform prior:

$$\alpha \sim \text{Uniform}(20, 1000) \quad (4)$$

Sum-to-one constraints were also used for the overall taxon-level productivities, to which we assigned a relatively non-informative Dirichlet prior:

$$\Phi^* \sim \text{Dirichlet}(1, \dots, 1) \quad (5)$$

For the local pollen contributions or weights, γ_t , that represents the contribution of local pollen (values between 0 and 1) relative to regional pollen, we specified relatively non-informative uniform priors:

$$\gamma_t \sim \text{Uniform}(0, 1) \quad (6)$$

for taxon $t = 1, \dots, T$ ($T = 13$).

To calculate $\text{VL}_{s,t}$ and $\text{VR}_{s,t}$, the relative abundances (i.e., the compositions) of local and regional vegetation around site s were weighted based on their distances to the lake (i.e., forests closer to the lake get a higher weight than those further away from the lake):

$$\text{VL}_{s,t} = \sum_{i=1}^I \text{VJCK}_{s,i,t} \cdot \text{wl}_{s,i,t} \quad (7)$$

$$\text{VR}_{s,t} = \sum_{j=1}^J \text{VFIA}_{s,j,t} \cdot \text{wr}_{s,j,t} \quad (8)$$

where $\text{VJCK}_{s,i,t}$ (data, from Jackson, 2019) denotes the taxa compositions (proportional contribution to the total basal area) within the i^{th} consecutive local ring ($i = 1, \dots, I$; $I = 5$) of site s , weighted by the local weights $\text{wl}_{s,i,t}$. Similarly, $\text{VFIA}_{s,j,t}$ denotes the taxa contributions within the j^{th} consecutive regional ring ($j = 1, \dots, J$; $J = 100$) of site s , weighted by the regional weights $\text{wr}_{s,j,t}$.

The outer boundary of the i^{th} consecutive local ring was at DL_i ($\text{DL}_i = 20, 50, 100, \text{ and } 1000$ m for $i = 1, \dots, I$, respectively) from the lakeshore. The inner-most boundary of the most proximate regional ring was at 1 km from the lake shore, and the outer boundary of the j^{th} consecutive regional ring was at DR_j ($\text{DR}_j = 4 \times 10^3, 7 \times 10^3, 10 \times 10^3, \dots, \text{ and } 301 \times 10^3$ meters for $j = 1, \dots, J$, respectively) from the lakeshore. Inspired by equation (8) in Prentice (1985), the local and regional distance weights were similarly defined (b_t parameters are proportional to pollen fall speeds over wind speed and θ is related to the turbulence parameter) as follows:

$$\text{wl}_{s,i,t} = \frac{1}{cl_{s,t}} \left(e^{b_t(R_s^\theta - (\text{DL}_i + R_s)^\theta)} - e^{b_t(R_s^\theta - (\text{DL}_{i+1} + R_s)^\theta)} \right) \quad (9)$$

$$\text{wr}_{s,j,t} = \frac{1}{cr_{s,t}} \left(e^{b_t(R_s^\theta - (\text{DR}_j + R_s)^\theta)} - e^{b_t(R_s^\theta - (\text{DR}_{j+1} + R_s)^\theta)} \right) \quad (10)$$

where R_s is the radius of the lake at site s , and $cl_{s,t}$ and $cr_{s,t}$ are standardizing constants that ensure that $\text{wl}_{s,i,t}$ and $\text{wr}_{s,j,t}$ sum to 1 across all i and j , respectively:

$$cl_{s,t} = 1 - e^{b_t(R_s^\theta - (\text{DL}_I + R_s)^\theta)} \quad (11)$$

$$cr_{s,t} = 1 - e^{b_t(R_s^\theta - (\text{DR}_J + R_s)^\theta)} \quad (12)$$

To facilitate the interpretation of model parameters, we also calculated the cumulative influence of vegetation at different distances for a typical, 30-m radius lake:

$$Fl_{i,t} = \left(1 - e^{b_i \cdot (30^\theta - (DL_{i+1} + 30)^\theta)}\right) / \left(1 - e^{b_i \cdot (30^\theta - (DL_i + 30)^\theta)}\right) \quad (13)$$

$$Fr_{j,t} = \left(1 - e^{b_i \cdot (30^\theta - (DR_{j+1} + 30)^\theta)}\right) / \left(1 - e^{b_i \cdot (30^\theta - (DR_j + 30)^\theta)}\right) \quad (14)$$

$$Flr_{j,t} = \gamma_t + (1 - \gamma_t) \cdot Fr_{j,t} \quad (15)$$

where Fl is the cumulative contribution of pollen from vegetation within different local distances ($Fl = 100\%$ at 1 km from the lakeshore), Fr is the estimated cumulative contributions of vegetation at different regional distances ($Fr = 100\%$ at 301 km) when the model is only informed by regional vegetation, but not local vegetation. Flr is the actual cumulative contribution of pollen from vegetation within different regional distances ($Flr = 100\%$ at 301 km), which was calculated from Fl , Fr , and the local contribution γ .

To compare the local contribution (γ) and the cumulative contribution Fr at 1 km predicted by regional pollen dispersal (denoted $\tilde{\gamma}$), we calculated the Localness Index (LI):

$$LI_{s,t} = \frac{\gamma_t}{\tilde{\gamma}_t} \quad (16)$$

$$\tilde{\gamma}_{s,t} = \frac{1 - e^{b_i (R_s^\theta - (1000 + R_s)^\theta)}}{1 - e^{b_i (R_s^\theta - (301 \times 10^3 + R_s)^\theta)}} \quad (17)$$

where $\tilde{\gamma}_{s,t}$ is similar to $Fr_{i,t}$, but also takes site-specific lake-radius (R_s) into consideration. An LI of 1 (one) would indicate that the regional dispersal pattern could predict local contribution and suggest similarities in dispersal between the local and regional scales. An LI higher (lower) than 1 would indicate that local populations are overrepresented or underrepresented by pollen deposited in the lake, after accounting for regional dispersal.

In Equations (9)–(12), we set $\theta = 0.1$ to represent an unstable “atmospheric condition” (temperature decreases with height at a faster rate than the adiabatic lapse rate, therefore representing a more turbulent atmosphere) (Jackson & Lyford, 1999). We explored other values, and $\theta = 0.1$ remained the most appropriate (Appendix S1: Section S1 Model Variant 1–2). For each taxon-specific b_i , rather than specifying fixed values based on pollen fall speeds (e.g., Hellman, Gaillard, et al., 2009; Prentice, 1985; Sugita, 2007a; Sugita et al., 1999), we estimated b_i and gave it a positive-valued, relatively non-informative exponential distribution prior:

$$b_i \sim \text{Exp}(0.1) \quad (18)$$

Similar to the original interpretation (Prentice, 1985), the taxon-specific b_i in our analysis can be viewed as a

composite parameter representing the overall effect of pollen-deposition velocities of each taxa and the atmospheric conditions operating to transport the pollen above the canopy.

To determine the robustness of our model specification related to the distance weighting of local and regional vegetation, Equations (9) and (10), we tested three additional models that explored different specifications for θ or wl (Appendix S1: Figures S2–S5). The model presented above was the most parsimonious (less risk of more than-parameterization compared with other models) and, therefore, we focused on this model throughout.

Model implementation

The model (Data S1; DOI: 10.5281/zenodo.5825842) was implemented in the Bayesian modeling software, JAGS version 4.2.0, using R version 3.4.2 and the *rjags* and *R2jags* (version 0.5-7) packages (Plummer, 2003). We ran three parallel Markov chain Monte Carlo (MCMC) for 3,000,000 iterations. For each chain, the starting values were generated from the prior distributions. All chains converged by iteration 2,000,000; we used the last 1,000,000 iterations, keeping every 200th sample to reduce within chain autocorrelation and to reduce the number of samples stored. Therefore, we obtained 5000 independent posterior samples per chain and, from these samples, we calculated the posterior median as a point estimate of each parameter, and the 2.5th and 97.5th percentiles to quantify the uncertainty in each parameter (i.e., 95% Bayesian credible interval [CI]).

RESULTS

These results describe the quantification of how pollen represents the surrounding vegetation. Posterior estimates from our model are summarized and presented in the following sections. Wherever suitable, we also discuss some specific, less expected results in relation to the model and the general understanding of pollen productivity and dispersal. By clarifying these points and interpretations in the section “Results,” we can focus on addressing the primary research questions in the section “Discussion.”

Model fit

The Bayesian statistical model captured the relationship between vegetation abundances and pollen assemblages,

as indicated by the observed versus predicted taxon-specific pollen relative abundances (proportions) at each site (Figure 2). The observed versus predicted correspondence was best ($R^2 > 0.81$) for the taxa that are abundant on the landscape and that produce a relatively large amount of pollen (*Betula*, *Fagus*, *Pinus*, *Quercus*, and *Tsuga*) compared with other taxa. In addition, *Larix*, which grows in low abundance and in highly localized populations, and *Acer saccharum*, which is an abundant

species but a low pollen-producer, also were associated with good fits ($R^2 = 0.81$ and 0.73 , respectively). The fit for Cupressaceae ($R^2 = 0.49$) was dominated by the pollen signal of *Thuja*, as Cupressaceae pollen higher than 0.25% is only found in EAD sites with substantial *Thuja* populations concentrated along some lake margins and no *Chamaecyparis* or *Juniperus*. The remaining taxa (*Abies*, *Acer rubrum*, *Fraxinus*, *Picea*, and *Populus*) displayed intermediate correspondence between observed

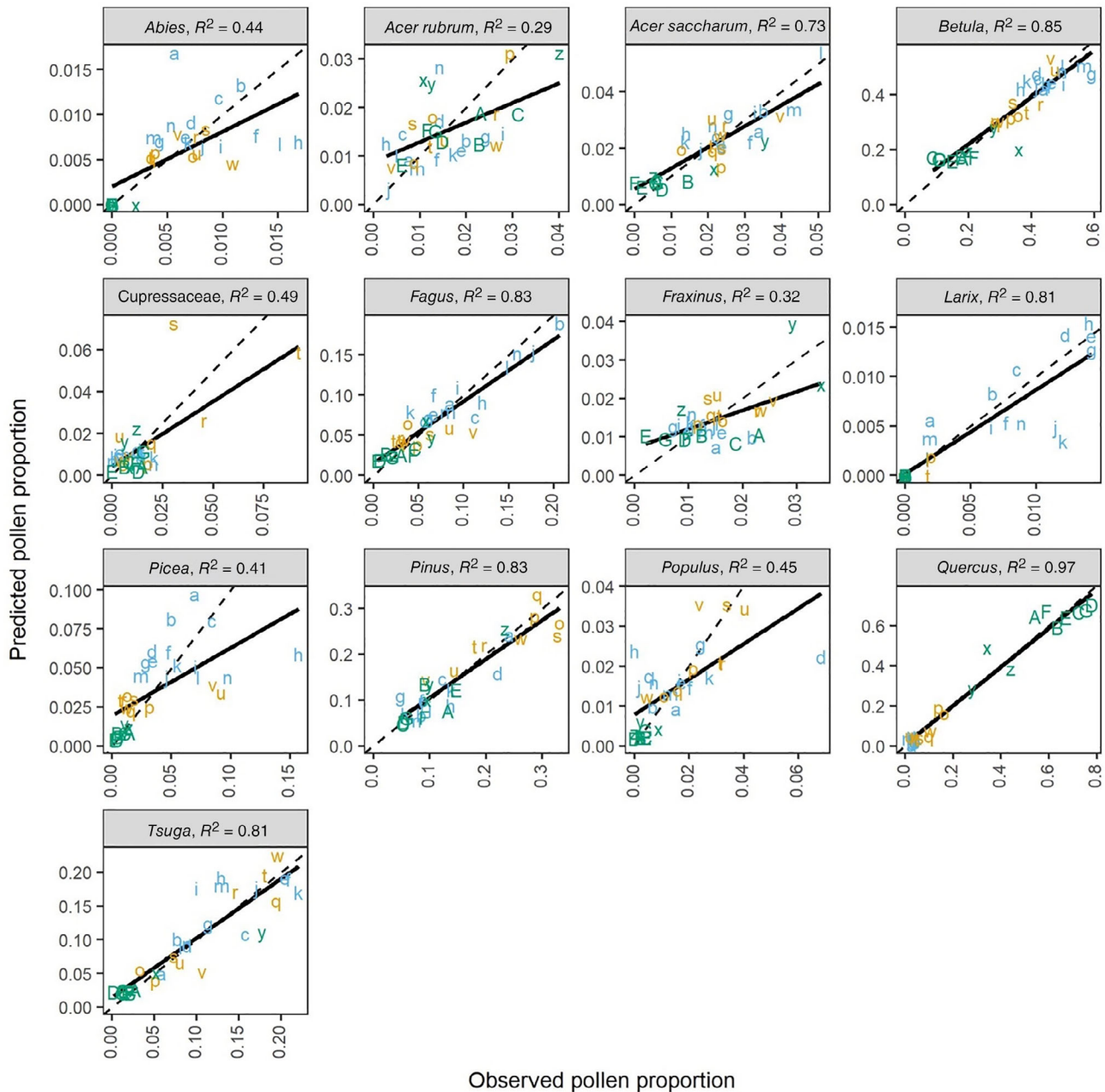


FIGURE 2 Observed versus predicted pollen relative abundances (proportions), where the predicted values are represented by the posterior means for $P_{s,t}$ (see Equations (1) and (2)). Taxon-specific coefficients of determination (R^2) are based on a linear regression (solid lines) of observed versus predicted values, overlaid with the 1:1 line (dashed lines). Site symbols (letters) are described in Appendix S1: Table S1 and the regions are color-coded: FC, blue symbols; EAD, yellow symbols; SNE, green symbols

versus predicted pollen relative abundances ($0.29 < R^2 < 0.45$, Figure 2). In general, the observed versus predicted pollen relative abundances varied about the 1:1 line without substantial systematic bias (Figure 2).

Pollen productivity

The taxon-specific relative pollen productivities at the regional (Φ_r) and population (overall) (Φ^*) scales are estimated with high confidence (narrow 95% Bayesian credible intervals [CIs]), distinguishing differences in pollen productivity among taxa (Figure 3). *Abies*, *Acer rubrum*, and *A. saccharum* are low pollen producers, with posterior medians for relative productivity of ~ 0.02 , significantly lower than any other taxa. In the other extreme, *Betula* produced significantly more pollen than all other taxa (posterior median of taxon-level estimate is ~ 0.28 , resulting in ~ 14 times higher productivity than the aforementioned low producers).

For most taxa, the posterior medians of the regional-level productivities (Φ_r) were similar within the taxon across the three regions of different forests, and are contained in the 95% CIs of the overall taxon-level productivity (Φ^*). The posterior estimate of the scaling parameter, α in Equations (3) and (4), for the regional variability in

pollen production was not clustered against the specified lower boundary of its prior (median and 95% CI: 91 [69, 126], compared with 20, the lower boundary for the prior of α), suggesting similar productivity among regions (higher α indicates more similarity across regions). For example, even though *Betula* populations were composed of *B. alleghaniensis* and *B. papyrifera* in FC and EAD, but dominated by the abundant populations of *B. lenta* and *B. populifolia* in SNE, the productivity estimates were still similar across these regions (Figure 3).

In several cases, however, regional-level pollen productivity (Φ_r) varied by a factor of two across regions (Figure 3). Here, intrataxon (species level or genus level) differences in productivity may play an important role. Notably, much lower productivity of *Picea* spp. was found in the SNE region (approximately half of the productivity of *Picea* in other regions). In this case, *P. abies* grew in scattered plantations in SNE, whereas *Picea* in the FC and EAD regions was represented by higher regional tree abundances of *P. mariana* and *P. rubens*. Moreover, Cupressaceae pollen productivity was 70% higher in the SNE compared with the EAD and FC regions. This variability may indicate genus-level differences: Cupressaceae is represented by *Chamaecyparis* and *Juniperus* in SNE, but by *Thuja* in EAD and FC. Finally, *Quercus* spp.

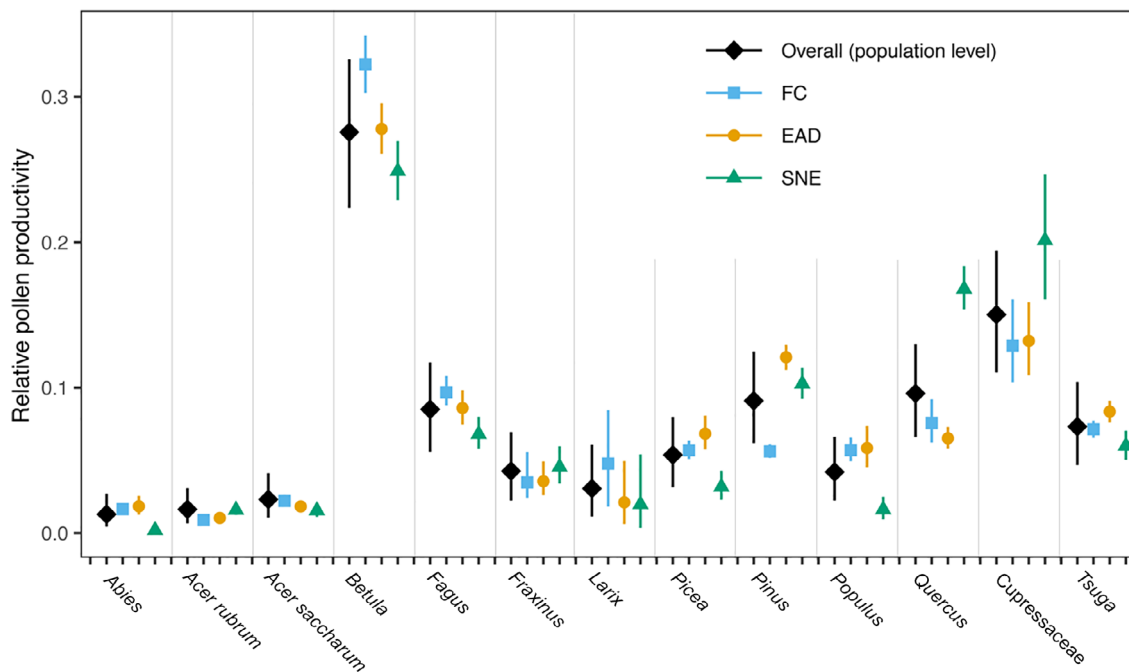


FIGURE 3 Posterior estimates (median and 95% credible interval [CI]) of the relative pollen productivity. Taxa are alphabetically ordered along the x-axis, and region-level productivity (Φ_r ; Equations (2) and (3); shown in blue, yellow, and green symbols) are shown in relation to the overall productivity (population-level, across all sites, Φ^* ; Equations (3) and (5); shown in black diamonds). The region-level productivities within each region and the population-level productivities all sum to one, respectively. For productivity scaled to reference taxa, see Appendix S1: Figures S2, S3

productivity was approximately two times higher in the SNE, where the dominant *Quercus* spp. (*Q. alba* and *Q. velutina*) and the climate differed from those of EAD and FC (*Q. rubra*). In contrast, pollen taxa comprising a single species in the study area (*Fagus grandifolia* and *Tsuga canadensis*) have more similar productivities across regions. However, pollen productivity of *Pinus* spp. in the densely forested FC region was significantly lower (approximately half) than in the other two regions, despite the similarity of dominant *Pinus* spp. (*P. strobus* and *P. resinosa*) in FC and EAD.

Our relative pollen productivities are subject to the “sum-to-one” constraint, whereas ERV-type models calculated productivities as relative to the reference taxa. This difference in methodology can potentially affect productivity estimates. However, we also found that the general patterns of high versus low pollen producers and regional variations in pollen productivity remained robust when relative pollen productivity was calculated in relation to a reference taxon (Appendix S1: Figures S2, S3), regardless of whether the reference was set to the productivity of *Fagus*, which is present at three regions, or *Tsuga*, which is present at the FC and EAD sites and a few SNE sites.

Local pollen contribution and dispersal

Taxon-specific local pollen contribution (γ_t , Equation 6), which we operationally defined as the proportion of pollen deposited in a lake that originated within 1 km from the lakeshore, is summarized in Figure 4. *Abies*, *Betula*,

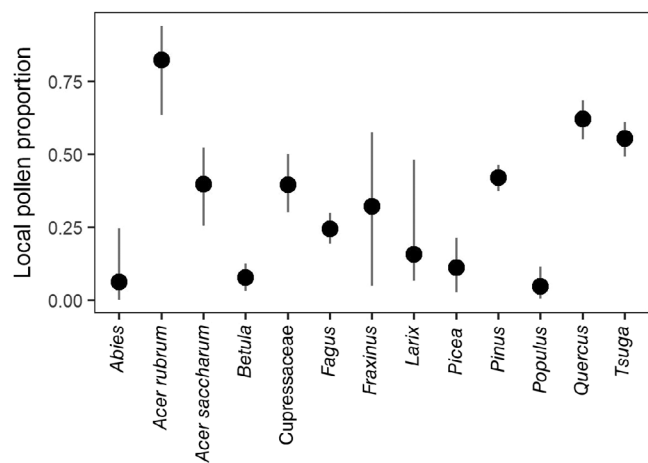


FIGURE 4 Posterior estimates (median and 95% credible interval [CI]) of the local contribution from within a 1 km radius, γ_t (see Equations (2) and (6)) of vegetation to pollen relative abundances. Taxon-specific γ_t is assumed to be the same across all sites

Picea, and *Populus* have the lowest local pollen contribution with medians <0.1 and upper CI limits <0.25 . *Acer rubrum*, the pollen of which has both anemophily and entomophily characteristics (Batra, 1985), showed the highest local contribution (median = 0.81). The local contributions for *Fraxinus* and *Larix* had comparatively large uncertainties, indicating that given the available data, our model cannot tightly resolve the local contributions for these taxa. However, there are many difficulties in quantifying the influence of taxa that are underrepresented in pollen (Parsons et al., 1983), so the true local influence may be very high for *Larix*, because all sites that have *Larix* pollen present have *Larix* trees near the lake. Similarly, the true local contribution of *Abies* may also be high. For the remaining taxa (*A. saccharum*, *Fagus*, *Pinus*, *Quercus*, Cupressaceae, and *Tsuga*), the local contribution is estimated with good confidence (width of CI less than the median posterior) and, overall, roughly less than half of the pollen originates locally (i.e., within 1 km of the lakeshore).

The local pollen contributions vary with distance from the lakeshore (outer boundaries of concentric rings at 20, 50, 100, 500, and 1000 m from the lakeshore) (Figure 5). For example, local pollen dispersal can be visualized as the estimated cumulative influences on pollen (Fl , Equation 13) from vegetation at different distances (Figure 5). We compared these estimated cumulative influences with those based on predefined functions typically used in distance weighting (Calcote, 1995; Gaillard et al., 2008; Jackson & Kearsley, 1998). For the majority of taxa, the estimated cumulative influences (Fl) are the most similar to the $1/\text{distance}^2$ weighting (steeper than the unweighted and $1/\text{distance}$ weighting, and generally less steep than weights based on the Prentice–Sutton equation). The uncertainty estimate (95% CI widths) for Fl was large for *Acer rubrum* and *Larix*, suggesting that it is possible that pollen grains of these two taxa mainly come from populations very close to the lakeshore (i.e., the upper boundary of the confidence interval reaches 80% of cumulative influence within 50 m).

We acknowledge that the “true” shape of cumulative influences of local pollen may be more complex than Fl . In this regard, despite potential pitfalls associated with the increased number of parameters, empirically estimating these weights (e.g., independent weights to be estimated at each distance for each taxon) allowed a more detailed perspective of cumulative influences and how they may have differed from those of distance-weighting functions (Appendix S1: Figure S4, Section S1 Model Variant 3). We found that the ultralocal (with 100 m of the lakeshore) populations of Cupressaceae, *Fagus*, and *Pinus* appeared to exert significantly greater influences than all

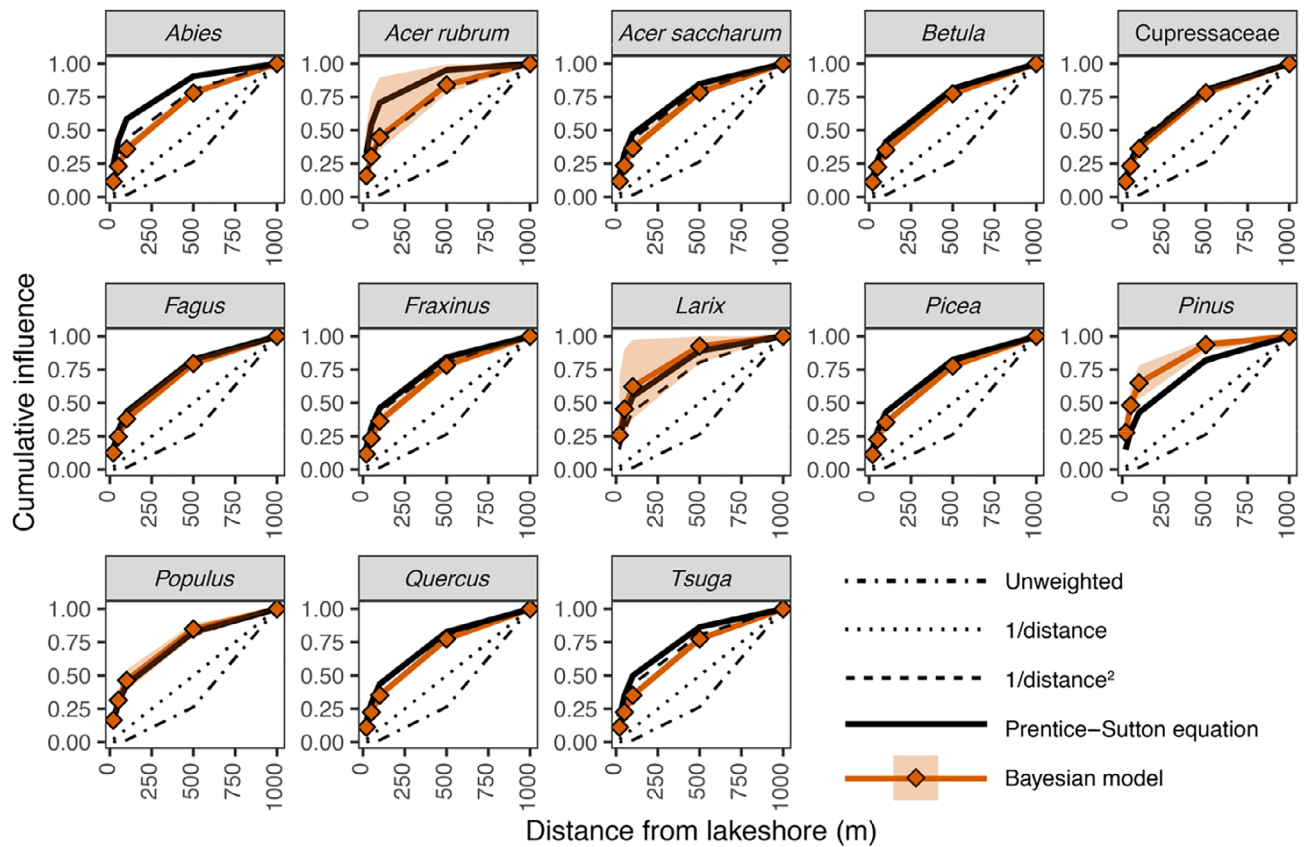


FIGURE 5 Posterior estimates for the cumulative influence of local vegetation at different distances from a lakeshore, Fl (Equation (13)), within 1 km of a typical, 30 m radius lake. Estimates from the model (orange points [median] and orange shaded areas [95% CI]) are compared with cumulative influences based on other widely used distance weighting. The weighting using the Prentice–Sutton equation (thick solid lines) is based on pollen fall speeds compiled in Jackson and Lyford (1999), with parameters corresponding to neutral atmospheric conditions. A cumulative influence of 1 (100%) represents the total influence of all pollen that originated locally, where the total local influence relative to local and regional combined is given by γ_l in Figure 4

distance-weighting methods (CIs higher and did not overlap with those based on distance weighting). In contrast, *Populus* had significantly smaller influences than all those of distance-weighting approaches at all distances. More generally, the influence of ultralocal populations may be noticeably strong for *Acer rubrum*, Cupressaceae, *Fagus*, and *Pinus*, as more than 50% of the local contribution of these taxa were attributed to populations occurring within 50 m of the lakeshore, which constituted only ~1.6% of the total area within the 1 km local radius (assuming a 30 m radius of the lake).

Regional pollen dispersal

The importance of regional pollen dispersal was visualized by the cumulative influence (Fl ; Equation 15) of vegetation at a range of different distances (Figure 6, cyan lines) and the distance at which the cumulative influence reached 75% (dashed line; influence at 300 km

is 100% by model design). *Betula* appeared to have the furthest regional dispersal, reaching the 75% influence at ~50 km (the lower CI limit corresponded to ~70 km). *Abies*, *Acer saccharum*, and *Fraxinus* also showed large pollen input from regional sources, reaching the 75% cumulative influence at 10–20 km. The 75% cumulative influence for Cupressaceae, *Fagus*, *Populus*, *Quercus*, and *Tsuga* was estimated to be only a few kilometers. For *Acer rubrum* and *Larix*, most pollen deposited in the lake came from within a couple of kilometers of the lakeshore, indicated by the steeply rising cumulative-influence curves, which confirmed the common notion that pollen from *Acer rubrum* and *Larix* were from nearby sources (Bradshaw & Webb, 1985; Jackson, 1990). However, the cumulative influence of *Pinus* also increased steeply with distance; a surprising finding because *Pinus* pollen is usually considered to be largely from regional sources (Bradshaw & Webb, 1985). Additional exploratory analysis (Appendix S1: Figures S4, S5, Section S1 Model Variant 3) also suggested a strong influence from

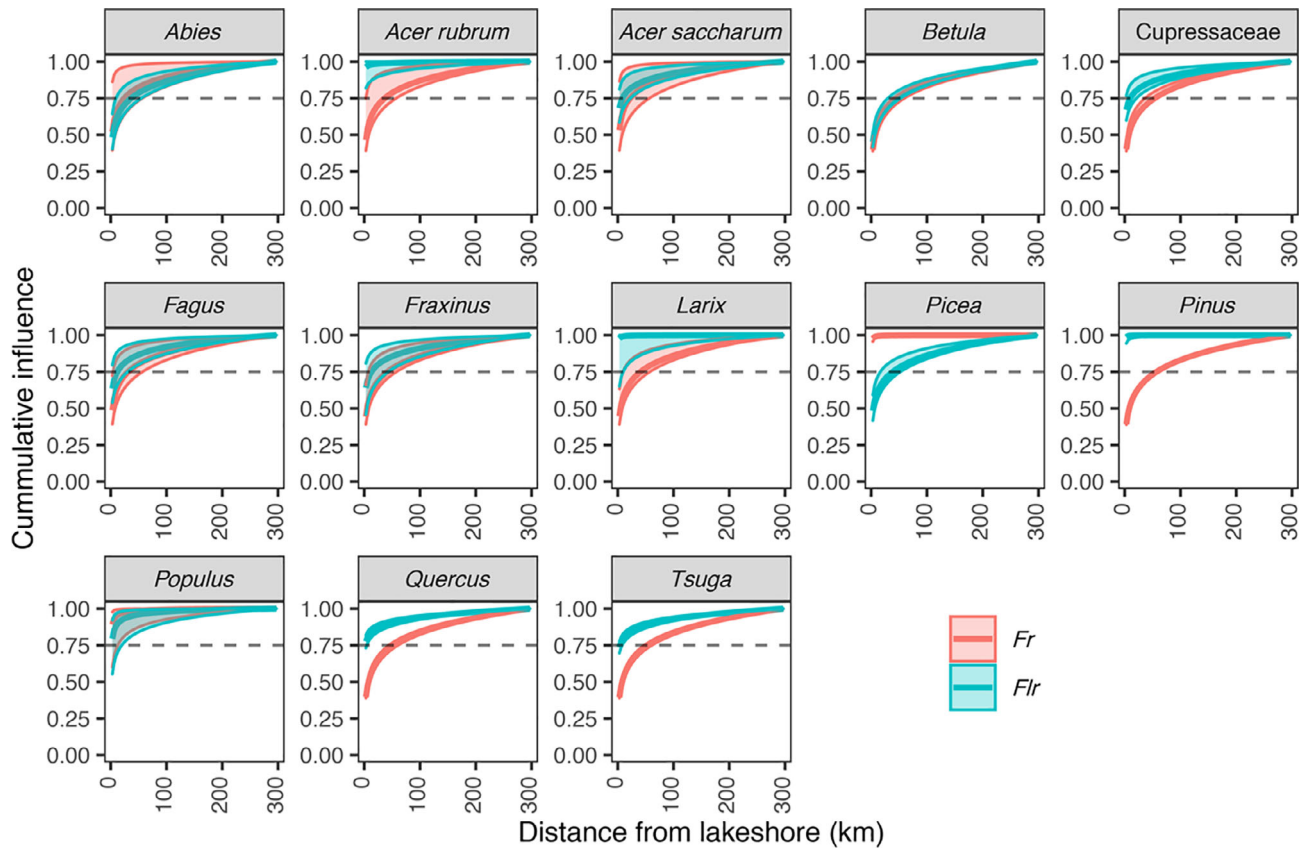


FIGURE 6 Posterior estimates for the cumulative influence of regional vegetation at different distances from a lakeshore, Flr (Equation (15)), from >1 to 300 km, for a typical, 30 m radius lake. Estimates (medians [solid lines] and the 95% CIs [colored shading]) are shown for regional distances from 3 km and up to 300 km, based on assuming no local vegetation contribution (Fr ; Equation (14); red lines) and based on including local vegetation contribution (Flr ; Equation (15); cyan lines) (Figures 4 and 5). The dashed horizontal line indicates 75% cumulative influence. A cumulative influence of 1 (100%) represents the total influence of all pollen that originated regionally, where the total regional influence relative to local and regional combined is given by $(1 - \gamma_l)$ in Figure 4

nearby vegetation: *Pinus* populations within 20 m from the lakeshore may exert strong influence on the pollen abundances retrieved from the lake (Appendix S1: Figure S4).

A comparison of the regional dispersal curves based on Flr (Equation 15, cyan lines in Figure 6) with those based on Fr (Equation 14, red lines in Figure 6) suggested the potential bias when regional dispersal was estimated solely with regional vegetation data (VFIA) and without considering local vegetation (VJCK). We found that, when local vegetation data were not used to inform dispersal, regional pollen dispersal of *Acer rubrum*, *Cupressaceae*, *Larix*, *Pinus*, *Quercus*, and *Tsuga* were notably overestimated relative to the scenario when such data were considered (Figure 6). For example, the estimated 75% cumulative influence of *Quercus* was reached at 3 km (local vegetation considered, Flr) versus 70 km (local vegetation not considered, Fr), respectively. In contrast, and expectedly based on posterior estimates of γ (Figure 4), the regional dispersal estimates for *Betula* (the

taxon with the furthest regional influence), and to a lesser extent, for *Abies* and *Fraxinus*, were not affected by the incorporation of local vegetation data.

Finally, our model estimated that the 75% cumulative influence of *Picea* was reached at ~50 km when local vegetation is considered, whereas the same cumulative influence was reached within a few kilometers when local vegetation was not considered (Figure 6). That is, *Picea* pollen percentage is well explained by vegetation within a few kilometers, but not by local vegetation within 1 km, which is counterintuitive. Exploratory analysis (Appendix S1: Section S1 Model Variant 3) provided a possible explanation for this seemingly confusing result: *Picea* pollen may be surprisingly insensitive to its population abundance within 50 m from the lakeshore (Appendix S1: Figure S4), but sensitive to other local populations further away (100–1000 m) and to those within a few kilometers (Appendix S1: Figures S4, S5). However, this level of flexibility of distance weighting was not allowed by the pollen dispersal function in our

original model, Equations (9) and (10); as a result, our original model may have misattributed observed *Picea* pollen to vegetation further away to minimize the influence of vegetation within 50 m from the lakeshore.

Comparing the local and regional dispersal

Localness Index is shown for all taxa in addition to *Acer rubrum* and *Larix*, which is likely to lack meaningful regional input (Figure 7). LI is defined as the ratio between the actual (i.e., empirically estimated) local contribution (γ , Figure 4) and the cumulative contribution at 1 km predicted by *Fr* (Equation 14, red lines in Figure 6). We found that many taxa have LI values significantly higher or lower than 1 (local populations of trees overrepresented or underrepresented, respectively), indicating that the dispersal patterns of these taxa differed between the local and regional scales. Notably, *Quercus* and *Tsuga*, which had local relative abundances typically higher than the regional ones (Appendix S1: Figure S6, also see descriptions in Jackson, 1990, 2019), had LI significantly greater than 1. In contrast, *Betula* and *Populus*,

which had lower abundances by the lakeshores (0–20 m) than further away, had LI significantly below 1.

The heterogeneous landscape

The spatial pattern of vegetation heterogeneity was quantified using SCD to reveal how much and how fast vegetation composition changed with distance for several “focal vegetation compositions” (Figure 8; Appendix S1: Figure S7). Two zones of high heterogeneity were revealed: the first zone was located at 0–20 m from the lakeshore, where the vegetation composition within this area is substantially different from adjacent vegetation at 20–50 m from lakeshore (especially at FC and EAD) and vegetation further away from the lakeshore (Figure 8a, SCDs increased sharply starting 20–50 m from lakeshore). The second zone was at 1–27 km from the lakeshore. Vegetation compositions within areas located 0.02, 0.1, 0.2, and 0.5 km from lakeshore, respectively, were all dissimilar from adjacent areas (Figure 8a–d) although, on average, vegetation composition within 27 km was similar to that occurring 27–100 km from the lakeshore

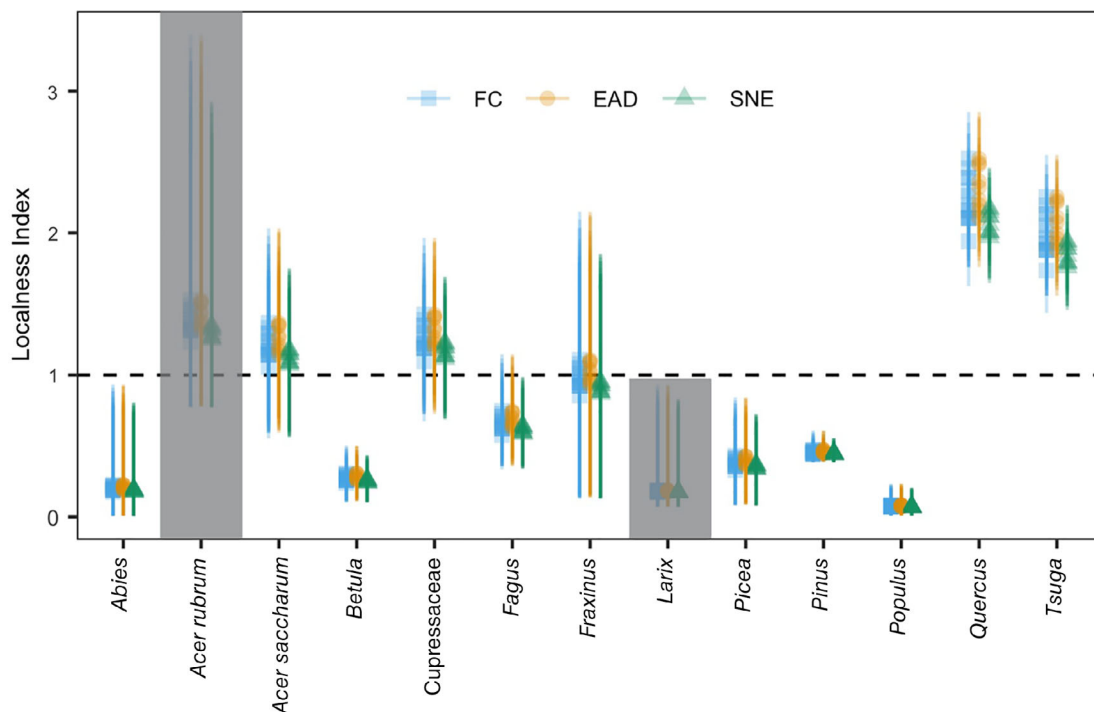


FIGURE 7 Localness Index (*LI*; Equation (16)) is defined and calculated as the ratio between the actual local contribution (γ_i ; Figure 4) and the cumulative influence at 1 km from the lakeshore predicted by regional pollen dispersal ($\bar{\gamma}_{s,t}$, Equation (17)). Horizontal dashed line indicates $LI = 1$; posterior medians (symbols) and 95% CIs for *LI* are overlaid for all sites within a region (14, 9, and 10 sites respectively for Fish Creek [FC], eastern Adirondack Mountains [EAD], and southern New England [SNE]). CIs that are significant higher (lower) than 1 would indicate that local populations are overrepresented or underrepresented by pollen deposited in the lake, after accounting for regional dispersal. Because *Acer rubrum* and *Larix* probably lack meaningful regional input (see “Results” section “Local pollen contribution and dispersal” and “Discussion” section “Comparing the local and regional dispersal”), their *LI* values cannot be accurately estimated and therefore were masked in gray

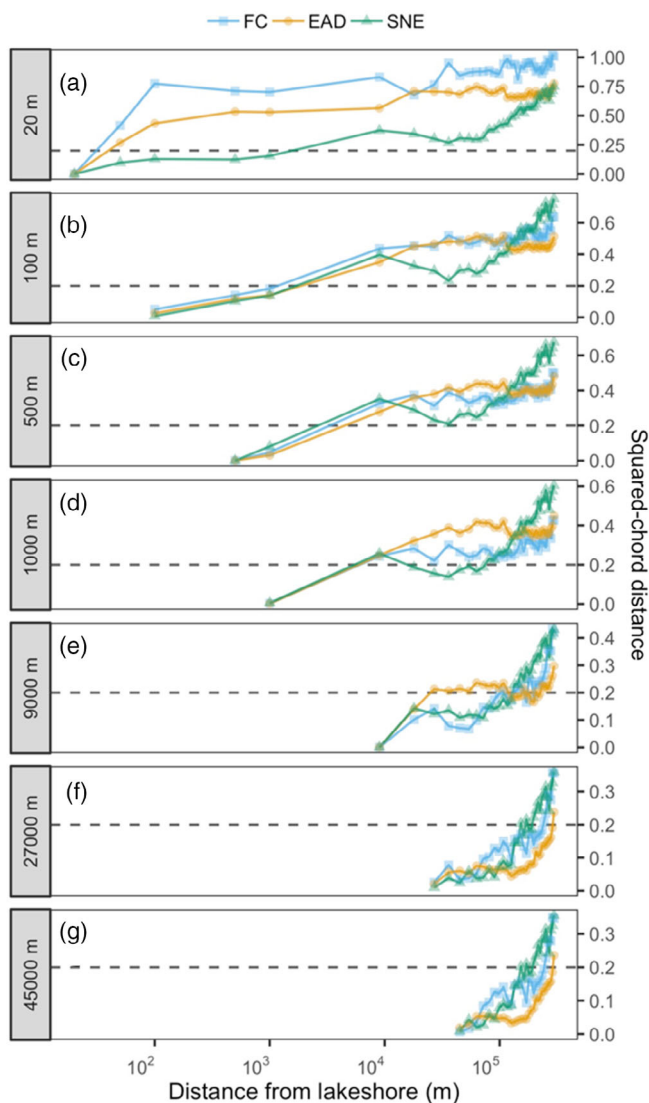


FIGURE 8 Spatial pattern of heterogeneous landscapes calculated from local and regional vegetation data. The dissimilarities, measured by the squared-chord distance (SCD), are shown for “focal vegetation” within (a) 20 m, (b) 100 m, (c) 500 m, (d) 1000 m, (e) 9 km, (f) 27 km, and (g) 45 km of a lakeshore. For focal vegetation within each of the aforementioned concentric ring, the dissimilarity between the its composition and the vegetation composition at a given distance from the lakeshore (x -axis) is calculate. Pollen records from different forest types typically have SCDs >0.2 (dashed lines). For clarity, we show the regional mean here; site-level dissimilarities can be found in Appendix S1: Figure S7. Lines are colored by region. EAD, eastern Adirondack Mountains; FC, Fish Creek; SNE, southern New England

(Figure 8f). By uniquely combining the finely resolved vegetation abundance data at the local scale (<1 km from the lakeshore) and the spatially coarse but extensive FIA information (~ 3 km resolution, extending up to ~ 300 km from the lakeshore), both zones of high heterogeneity were well represented in our study.

DISCUSSION

Our results allow the examination of currently contested notions of pollen productivity and dispersal, supporting some previous findings but contradicting others. First, regarding the intrataxon variability of pollen productivity (Q1), we found that pollen productivity is largely conserved within taxa across three regions with different forest composition and pattern (Figure 3). The greatest intrataxon difference we observed was less than three-fold. Second, regarding the overall pattern of pollen dispersal (Q2), the empirically estimated 75% cumulative influence of most taxa is reached within a few kilometers, yet the exceptions are distinct (e.g., *Betula* reaches its 75% cumulative influence ~ 50 km; Figure 6). More specifically, although local vegetation generally exerts a strong influence on pollen deposition in lakes (Figure 4), the dispersal patterns at the local scale may not be fully captured by the commonly used distance-weighting functions or mechanistic model of pollen dispersal (Figure 5; Appendix S1: Figure S4). Third, our results also examined the pattern of landscape heterogeneity and demonstrated that both detailed local vegetation and extended regional vegetation are needed to accurately estimate pollen productivity and dispersal (Q3). Based on these findings, in the following sections we suggest best practices for estimating pollen productivity and dispersal, highlight the importance of landscape heterogeneity, and identify key challenges.

Estimating pollen productivity and dispersal: Cautions and suggestions

Our results indicate that pollen productivity, pollen-dispersal processes, and the spatial arrangement of vegetation abundance (“landscape heterogeneity”) interact to influence how pollen assemblages in lake sediments represent surrounding vegetation. Therefore, inadequate vegetation information can hamper accurate estimation of both pollen productivity and dispersal. Furthermore, erroneous estimation of, or inappropriate assumptions of, dispersal processes can lead to inaccurate estimations of pollen productivity.

Knowledge of local vegetation composition is particularly important in estimating pollen productivity and dispersal. Our results indicated that, without finely resolved local vegetation abundances, pollen contributions of many taxa (*Cupressaceae*, *Pinus*, *Quercus*, *Tsuga*) from regional sources would be overestimated (Figure 6) and, consequently, lead to erroneous productivity estimates. When vegetation abundance is only available at coarse resolution (i.e., 3 km intervals in this case), variation in

pollen assemblages cannot be effectively attributed to spatial variation in vegetation composition at finer scales. Instead, variation in pollen assemblages is misattributed to differences in vegetation composition further away, biasing pollen productivity and dispersal estimates. This phenomenon may explain the large pollen-source areas, on the order of 10^2 km, estimated by STEPPS model studies using coarser vegetation data (Dawson et al., 2016; Kujawa et al., 2016; Paciorek & McLachlan, 2009).

Inaccurate assumptions about pollen dispersal can lead to biased pollen productivity estimates. Our analysis identified some complex and contextual features of pollen dispersal (e.g., the effects of ultralocal and local populations on pollen; Figures 5, 7; Appendix S1: Figure S4), which are not fully represented by the mechanistic models of pollen dispersal currently applied to pollen-vegetation calibration. Various studies have shown that, when the effects of dispersal are not properly taken into account, estimated pollen productivity is often entangled with dispersal and landscape heterogeneity (Bradshaw & Webb, 1985; Jackson, 1990; Jackson & Kearsley, 1998; Prentice, 1985). The estimates, rather than reflecting the productivity of pollen, only serve as highly contingent correction factors (Theuerkauf et al., 2016) and therefore lack predictive power across regions.

In particular, inaccurate dispersal assumptions, when combined with finely resolved local vegetation abundances, may misattribute pollen variation to vegetation variation at the wrong scale (i.e., overemphasizing influence of ultralocal vegetation with 100 m of the lakeshore and overlook the site-specific influence of regional vegetation) and cause errors in pollen productivity estimates. For example, we found that, although the relative abundances of *Betula* vary the most across sites and regions at the 0–50 m scale (Appendix S1: Figure S6), empirically the influence from this scale may be significantly smaller than predicted by widely used distance weightings (Appendix S1: Figure S4). In addition, *Betula* relative abundance at 100–500 m (often similar to abundance at 500–1000 m within each site; Appendix S1: Figure S6) explains most of the “local” influence—which amounts to less than 10% of cumulative influence (Figure 4)—and the majority of *Betula* pollen comes from regional sources, reaching 75% cumulative influence at ~50 km (relative to 100% influence at 300 km by model design; Figure 6). We also found highly similar relative productivities of *Betula* across the three study regions (medians at 0.30, 0.26, 0.23, respectively; for comparison, productivity of *Tsuga* is ~0.08), and strong correspondence ($R^2 = 0.85$) between predicted and observed *Betula* pollen relative abundances. Although many region-specific factors may be at play, our result contrasts with the large variation in *Betula* pollen productivity in Europe found

using ERV models; those from lake sites in Germany (Matthias et al., 2012) are approximately four times higher than those obtained from the Swiss Plateau (Soepboer et al., 2007) and Estonia (Poska et al., 2011). The difference between assumed and actual dispersal pattern may explain the anomaly.

To overcome these issues, we offer two general suggestions for estimating pollen productivity and dispersal from empirical data. First, the spatial resolution and areal extent of the vegetation survey must be adequate. For studies using small lakes, the survey resolution at the local scale should be adequate to distinguish populations in the immediate vicinity of the lake (<50 m) and those beyond (50 m to 1 km); This is not only because of the strong influence of ultralocal vegetation (Sugita, 1993), but also because vegetation composition and abundance at this scale is often notably variable within regions (Figure 8). This emphasis in resolution may be less important for larger lakes due to the non-linear relationship between circumference and area. The vegetation-survey area, regardless of lake size, should extend to span the other high-heterogeneity zones (Figure 8; see result in the section “The heterogeneous landscape”). For sites in this study, this heterogeneous zone spans to ~30 km. Future studies should consider the extent of this zone in developing models. Second, the effects of pollen productivity, dispersal, and landscape heterogeneity must be considered simultaneously. In particular, because current models may inadequately represent some important features of pollen dispersal (Jackson & Lyford, 1999), it may be desirable to estimate local and regional pollen dispersal using statistical models fitted to empirical data (Klein et al., 2003) rather than purely mechanistic pollen-transport models.

Complexity in the heterogeneous landscape

Our findings point to the important role of vegetation heterogeneity surrounding a lake in determining pollen-assemblage composition (Figure 8; Appendix S1: Figure S7), which provides a critical addition to previous studies. Here, landscape heterogeneity should not be confused with simple patchiness, in which different patches of vegetation are randomly distributed with constant probability or form a monotonic gradient with distance to the lake (Hellman, Bunting, et al., 2009; Hellman, Gaillard, et al., 2009; Sugita, 1994). Instead, we used landscape heterogeneity to refer to the observation that local and even regional populations of trees are, in general, distributed non-randomly with respect to proximity to lakes (Appendix S1: Figure S6), owing to at least two factors (Jackson, 1990, 1994, 2012). First, depositional basins

are often associated with microclimates and microenvironments unrepresentative of the broader landscape (e.g., cold-air drainage, wet margins, fire breaks). Second, lakes themselves are not randomly distributed on the landscape, but are often restricted to specific, and sometimes idiosyncratic, topographic, edaphic, hydrologic, and lithologic settings that may or may not be representative of the broader region. It is worth noting that these biasing factors do not necessarily affect studies using moss polsters, in which sites can be selected randomly (Bunting et al., 2013; Li et al., 2017).

The non-random distribution of vegetation interacts with pollen-transport processes to create complex patterns of pollen dispersal. First, we found that, depending on the taxon, ultralocal populations (e.g., within 50 m of the lakeshore; Appendix S1: Section S1 Model Variant 3) may exert influences significantly smaller or greater than those predicted by heuristic distance weighting or by Prentice's function (Appendix S1: Figure S4). In particular, considerable pollen contributions from populations of *Acer rubrum*, *Fagus*, and *Pinus* were estimated within 20, 50, and 20 m of the lakeshore, respectively. This phenomenon could be due to "gravity deposition" (i.e., anthers, microsporangia, and pollen falling from branches overhanging the lake surface; Jacobson & Bradshaw, 1981; Tauber, 1965), deposition of pollen clumps rather than individual grains (e.g., a tetrad of *Pinus* grains will fall four times faster than a single grain), or other physical processes of pollen transport that are not fully considered in current models (e.g., Theuerkauf et al., 2016; also see discussions in Jackson & Lyford, 1999; Theuerkauf et al., 2013). In contrast with the strong influence of ultralocal populations for some taxa, we found that *Picea* pollen is virtually unaltered by populations within 50 m of the lake, which is counterintuitive given its apparent high production, large grain size, and evidence from other regions (Jackson & Smith, 1994). This may be due to the local growth form of *Picea* on the lake margin at our sites, which often was comprised of stunted individuals on waterlogged histosols. Second, many taxa have an LI significantly different from 1 (Figure 7), indicating that local populations of many taxa are overrepresented or underrepresented relative to regional populations, after accounting for regional pollen dispersal. In general, taxa (e.g., *Quercus* and *Tsuga*) that are more abundant near the lakes than across the region (Appendix S1: Figure S6; also see descriptions in Jackson, 1990, 2019) tend to have $LI > 1$ (local population overrepresented in pollen), which are likely to allow additional pollen grains or pollen clumps to be transported to the lake. In contrast, *Betula* and *Populus* have $LI < 1$ (local population underrepresented in pollen), which may be driven by the low abundances (and lack of pollen input from ultralocal sources) of these taxa by the lakeshores (0–20 m) than further away. Together, these complexities

challenge our current understanding and representation of pollen-dispersal processes. Although pollen dispersal has been represented by a single function (known or to be estimated) in most previous studies, the actual pattern may be subject to multiple distinct processes and require more complex representations.

The complex patterns of vegetation distribution and dispersal also present implications and challenges for pollen-based vegetation reconstruction. Our productivity estimates may apply reliably to a range of lake sizes and the spatial extent of reconstruction because, unlike many other attempts, they are not entangled with factors such as dispersal and landscape heterogeneity. These productivity estimates can also serve as priors for multiscale reconstruction such as REVEALS/LOVE (Sugita, 2007a, 2007b) or large-scale efforts such as those using the STEPPS models (Dawson et al., 2016). In contrast, the empirically estimated dispersal is specific to lake size because it accounts for multiple pathways of pollen transport, ranging over scales from 1 m to 100 km, and the relative influence of these pathways may change with the size of the depositional basin. For example, gravity deposition is governed by trees along the lakeshore. As the radius of a lake increases, lake area increases more steeply than the length of its shoreline and, therefore, the influence of gravity deposition per unit lake area decreases rapidly. To gain a predictive understanding of how pollen dispersal scales with lake sizes for reconstruction, empirically estimated dispersal across different lake sizes and regions can be compared with developed qualitative insights that can be further tested by process-based models.

Addressing long-standing challenges

Our study revisits several long-standing, interlinked issues in the quantitative application of pollen percentages in vegetational inference: the intrataxon variability of pollen productivity, the physical processes governing pollen transport, and the role of landscape heterogeneity for understanding links between vegetation and pollen (Bradshaw & Webb, 1985; Davis, 2000; Jackson, 1994; Jacobson & Bradshaw, 1981; Prentice, 1985; Webb & McAndrews, 1976). Numerous solutions have been proposed to address these issues, and the understanding of pollen-vegetation relationships has advanced considerably over the past several decades. However, as our results have shown, the solutions developed to date are incomplete and are subject to ancillary assumptions (Oreskes et al., 1994). As efforts at reconstruction of past vegetation continue, it is important to be clear about the limitations of these partial solutions. Alternatively, there is an increasing danger

that untested assumptions embedded in these partial solutions over time are likely to be taken for granted, that is “ignorance creep” (Jackson, 2012).

Much remains unknown concerning the variability of pollen productivity and the nature of pollen dispersal. With regard to productivity, our analysis suggests that it may be much more conserved within pollen taxa than previously suggested, including in recent syntheses (Li et al., 2018; Mazier et al., 2012), and intrataxon variation (less than three-fold in our analysis) may be explained by differences in species and environmental conditions (Figure 3). To determine the influence of phylogeny versus environmental factors, future studies could integrate species characteristics and environmental information into the estimation of pollen productivity. For example, Equation (2) in our framework could be modified to estimate species-level productivity (as nested within taxon-level productivity) and the effect of environmental covariates such as temperature and precipitation. Comparative studies of pollen productivity similar to our analysis here need to be carried out across regions and vegetation types.

With regard to pollen dispersal, our results suggest that the widely used mechanistic pollen-transport models with a priori parameter values (e.g., the Prentice–Sutton model, Prentice, 1985) and distance-weighting function (Calcote, 1995; Gaillard et al., 2008; Jackson & Kearsley, 1998) may capture the general pattern of local dispersal (Figure 5), but with potential caveats suggested by Model Variant 3 (Appendix S1: Figure S4, Section S1). Also, pollen-dispersal patterns differ between local and regional scales (Figure 7; an LI value of 1 indicates the same dispersal pattern between local and regional scales). Advancing the understanding of pollen dispersal may require the dual application of deductive (i.e., mechanistic pollen-transport models) and inductive (i.e., semimechanistic and phenomenologic models in which dispersal patterns are statistically estimated using empirical data) approaches. Most dispersal studies to date are based on the Prentice–Sutton model (Prentice, 1985), which assumes that pollen grains are transported in the atmosphere in a similar way to ground-level Gaussian plumes. However, it has been suggested that a Lagrangian stochastic model may better capture the outcome of long-distance pollen dispersal (Kuparinen et al., 2007; Theuerkauf et al., 2013, 2016; although not everywhere, Wan et al., 2020); more tests on different regions and models are needed. Because multiple physical processes govern pollen transport, a single mechanistic model or dispersal kernel may ultimately be elusive (Jackson & Lyford, 1999). It is therefore important to develop semimechanistic (e.g., this study and Klein et al., 2003) and phenomenological models (Dawson et al., 2016; Kujawa et al., 2016) of pollen dispersal. In addition, statistically fitted semimechanistic and phenomenological models such as the STEPPS (Dawson et al., 2016)

can provide formal and coherent quantification of uncertainties.

Understanding and quantifying how pollen represents vegetation is at the heart of pollen analysis. Much has been learned since the initial proposals for quantitatively linking pollen and vegetation percentages (Davis, 1963), but some key questions may be better answered with alternative and emerging techniques. Manipulative experiments (e.g., isotope labeling of pollen grains; Colwell, 1951), experimental pollen release, and monitoring (Raynor et al., 1974, 1975), which have become uncommon in studies at this time, may effectively disentangle the relative importance of multiple pollen-transport processes operating at varying spatial scales. Although radioisotopic labeling is no longer feasible, genetic markers can be useful in tracing the dispersal of pollen (Dawson et al., 1997). Remote sensing techniques (e.g., using drones) could be leveraged to facilitate or even replace laborious vegetation survey (e.g., Williams et al., 2009, 2011), whereas machine learning approaches may be powerful for extracting vegetation information from remotely sensed images (Zanon et al., 2018). These approaches, together with iterative improvements to statistical and simulation models of pollen productivity and dispersal, will build toward a rigorous inferential basis, maximizing the unique potential of fossil pollen records in understanding and addressing global ecological and environmental challenges.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Yao Liu and Stephen T. Jackson designed the study; Stephen T. Jackson and Jeremy W. Lichstein provided data and advice; Yao Liu performed the data analysis with advice from Kiona Ogle and Stephen T. Jackson; Yao Liu wrote the paper with contributions from Stephen T. Jackson, Kiona Ogle, and Jeremy W. Lichstein.


DATA AVAILABILITY STATEMENT

All data used in our analyses are publicly available. Lake-pollen and local vegetation-survey data are freely available through Jackson (2019) at <https://doi.org/10.1002/ecy.2784>. Tree abundance in concentric rings from 1 to 300 km distance from each lake was estimated using data from the publicly available US FIA database version 5.1, downloaded in November 2012 from <https://www.fia.fs.fed.us/>. We used all available field-measured plot samples during the years 2000–2012. These plots were identified as follows: (1) at least one accessible forest condition present (FIA Condition table COND_STATUS_CD = 1); standard production plot (FIA Plot table QA_STATUS = 1 or QA_STATUS = No Data); and (2) plot was measured, as opposed to modeled (FIA Plot table KINDCD not = 4). The Bayesian statistical model was coded in R and is available in Data S1 (pollen_model.r) and also archived on Zenodo at <https://doi.org/10.5281/zenodo.5825842> (Liu, 2022).

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