The Holocene

Linking modern pollen accumulation rates to biomass: Quantitative vegetation reconstruction in the western Klamath Mountains

Abstract:	Quantitative reconstructions of vegetation abundance from sediment-derived pollen systems provide insights into past ecological conditions. Recently, the use of pollen accumulation rates (PAR, grains cm-2 yr-1) has shown promise as a bioproxy for plant abundance. However, successfully reconstructing region-specific vegetation dynamics using PAR requires that accurate assessments of pollen deposition processes be quantitatively linked to spatially-explicit measures of plant abundance. Our study addressed these methodological challenges. Modern PAR and vegetation data were obtained from seven lakes in the western Klamath Mountains, California. To determine how to best calibrate our PAR-biomass model, we first calculated the spatial area of vegetation where vegetation composition and patterning is recorded by changes in the pollen signal using two metrics. These metrics were an assemblage-level relevant source area of pollen (aRSAP) derived from extended R-value analysis and a taxon-specific relevant source area of pollen (tRSAP) derived from PAR regression. To the best of our knowledge, aRSAP and tRSAP have not been directly compared. We found that the tRSAP estimated a smaller area for some taxa (e.g., a circular area with a 225 m radius for Pinus) than the aRSAP (a circular area with a 625 m radius). We fit linear models to relate PAR values from modern lake sediments with empirical, distance-weighted estimates of aboveground live biomass (AGLdw) for both the aRSAP and tRSAP distances. In both cases, we found that the PARs of major tree taxa – Pseudotsuga, Pinus, Notholithocarpus, and TCT – were statistically significant and reasonably precise estimators of contemporary AGLdw. However, predictions weighted by the distance defined by aRSAP tended

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

to be more precise. The relative root-mean squared error for the aRSAP biomass estimates was 9% compared to 12% for tRSAP. Our results demonstrate that calibrated PAR-biomass relationships provide a robust method to infer changes in past plant biomass.

SCHOLARONE™
Manuscripts

1   Title: Linking modern pollen accumulation rates to biomass: Quantitative vegetation

2   reconstruction in the western Klamath Mountains

3

4   Authors: Clarke A. Knight[1], Mark Baskaran[2], M. Jane Bunting[3], Marie Champagne[4], Matthew D.

5   Potts[1], David Wahl[4,5], James Wanket[6], John J. Battles[1]

6   [1] Department of Environmental Science, Policy, and Management, University of California,

7   Berkeley, Berkeley, California 94720 USA

8   [2] Department of Geology, Wayne State University, Detroit, Michigan 48202 USA

9   [3] Department of Geography, Geology and Environment, University of Hull, Cottingham Road,

10   Hull, HU6 7RX UK

11   [4] US Geological Survey, Menlo Park, California 94025 USA

12   [5] Department of Geography, University of California, Berkeley, Berkeley, California 94720 USA

13   [6] Department of Geography, California State University, Sacramento, Sacramento, California

14   95819 USA

15

16   Corresponding author: CAK, clarke.knight@berkeley.edu

1

Abstract

Quantitative reconstructions of vegetation abundance from sediment-derived pollen systems provide unique insights into past ecological conditions. Recently, the use of pollen accumulation rates (PAR, grains cm^{-2} yr^{-1}) has shown promise as a bioproxy for plant abundance. However, successfully reconstructing region-specific vegetation dynamics using PAR requires that accurate assessments of pollen deposition processes be ~~deterministically~~ quantitatively linked to spatially-explicit measures of plant abundance. Our study addressed these methodological challenges. Modern PAR and vegetation data were obtained from seven lakes in the western Klamath Mountains, California. To determine how to best calibrate our PAR-biomass model, we first calculated the spatial area of vegetation where vegetation composition and patterning is recorded by changes in the pollen signal using two metrics. These metrics were an assemblage-level relevant source area of pollen (aRSAP) derived from extended R-value analysis (*sensu* Sugita 1993) and a taxon-specific relevant source area of pollen (tRSAP) derived from PAR regression (*sensu* Jackson 1990). To the best of our knowledge, aRSAP and tRSAP have not been directly compared. We found that the tRSAP estimated a smaller area for some taxa (e.g., a circular area with a 225 m radius for *Pinus*) than the aRSAP (a circular area with a 625 m radius). We fit linear models to relate PAR values from modern lake sediments with empirical, distance-weighted estimates of aboveground live biomass (AGL_{dw}) for both the aRSAP and tRSAP distances. In both cases, we found that the PARs of major tree taxa – *Pseudotsuga*, *Pinus*, *Notholithocarpus*, and TCT (Taxodiaceae, Cupressaceae, and Taxaceae families) – were statistically significant and ~~reliable~~ reasonably precise estimators of contemporary AGL_{dw}. However, predictions weighted by the distance defined by aRSAP tended to be more precise. The relative root-mean squared error for the aRSAP biomass estimates was 9% compared to 12%

2

40   for tRSAP. Our results demonstrate that calibrated PAR-biomass relationships provide a robust

41   method to infer changes in past plant biomass.

42

43   **Key words:**

44   Pollen accumulation rate (PAR), quantitative reconstruction, biomass, source area of pollen,

45   Klamath Mountains, California

3

1
2
3
4
5
6
7
8
9
10
11
12

1. Introduction

46

47 Quantitative reconstruction of past plant abundance has been an important goal in paleoecology

48 since the field's inception (Von Post 1918) and a major research frontier spanning decades

49 (Davis and Deevey 1964, Likens and Davis 1975, Davis et al. 1984, Hicks 2001, Seppä et al.

50 2009, Matthias and Giesecke 2014, Marquer et al. 2014). ~~Currently, t~~The research community

51 lacks a complete understanding of how the pollen signal reflects plant population parameters

52 (e.g., biomass), and therefore past population change (Fagerlind 1952, Davis et al. 1984, Prentice

53 1988, Seppä et al. 2009). Developing methods to quantitatively reconstruct past plant

54 populations would aid climate science and restoration ecology. In climate science, for example,

55 quantitative reconstructions of past plant populations would allow better understanding of long-

56 term ecosystem dynamics (Galliard et al. 2000) and provide past analogues to test complex

57 climate models that account for the effects of landcover on the climate system (Galliard et al.

58 2010). Restoration ecology would benefit from an improved understanding of the impact of

59 disturbances (natural and anthropogenic) on landscapes and ecosystems (Broström et al. 1998,

60 Crawford et al. 2015) and from the increased participation by paleo-ecologists in the debates of

61 modern restoration ecology (Swetnam et al. 1999, Hellman et al. 2009).

62   Palynologists often use pollen percentage data in pollen-vegetation models to reconstruct

63 landcover and understand past plant populations, but this approach does not provide separate

64 reconstructions for each taxon's ~~plant~~ population change (Davis 1963, Prentice 1988). Relative

65 changes in abundance of species have been inferred form Bayesian hierarchical spatio-temporal

66 pollen-vegetation models (Dawson et al. 2019). In contrast, pollen accumulation rates (PAR) – a

67 measure of the rate of pollen deposition at the sediment surface per unit area during a given time

68 period (e.g., grains $cm^{-2}\,yr^{-1}$, Davis and Deevey 1964) – depend ~~solely~~ on the abundance of the

Commented [MOU1]: Added sentence for USGS reviewer.

4

69 plant taxa producing that pollen type around the collection site. That is, the PAR for each taxon

70 is independent of all other taxa. PAR allows results from different regions to be directly

71 compared, irrespective of other taxa in the investigations (Hicks and Hyvärinen 1999, Giesecke

72 and Fontana 2008). PAR has been used to reconstruct not only landcover, but also population

73 dynamics and plant biomass (Seppä et al. 2009, Theuerkauf et al. 2012, Matthias and Giesecke

74 2014). For example, PAR has been used to reconstruct past population growth rates (Bennett

75 1983, 1986, MacDonald 1993, Giesecke 2005) and to reconstruct Holocene biomass records in at

76 least two areas: the Finnish boreal zone (Seppä et al. 2009) and a sub-alpine forest in Utah

77 (Morris et al. 2015).

78 PAR is not a simple reflection of vegetation abundance because the pollen signal is a

79 distance-weighted measure of taxa abundance in the surrounding vegetation, responding to the

80 structure of the plant community as well as species abundance (Jackson 1990). Modern PAR

81 values must be quantitatively correlated with modern plant population data from the lake

82 surroundings in order to parameterize the PAR-population relationship before fossil PAR records

83 can be interpreted in terms of past plant population change. This correlation step requires

84 accurate vegetation data from forest inventories (Seppä et al. 2009, Matthias and Giesecke 2014),

85 careful field surveys (Bunting et al. 2013), or well-resolved spatial imagery coupled with

86 ground-truthing (Han et al. 2017) that encompasses the relevant source area of pollen ('RSAP',

87 discussed below and in section 2.3, *sensu* Sugita 1993). Previous work has shown a linear

88 relationship between PAR and distance-weighted biomass across a range of lake sites in

89 northeastern Germany (Matthias and Giesecke 2014).

90 In addition to quantitative vegetation data, reliable PAR data require a robust chronology

91 of the pollen system being studied. Ideally, a sedimentary core for PAR data collection has two

5

92   features: it is obtained from an undisturbed lake environment where sediment accumulates

93   evenly over time, and the resulting sediment is dated at high resolution. Where lakes are found to

94   have stable sedimentary conditions, reliable PAR datasets can be obtained (e.g., Ritchie 1969,

95   Hyvärinen 1975, Seppä and Hicks 2006) though there may still be channel funneling. The recent

96   development of Bayesian tools has improved the construction of chronologies from isotopic data

97   such as ^{210}Pb activity measurements, giving more reliable measures of uncertainty (Aquino-

98   López et al. 2018).

99   Lastly, all sedimentary basins have a relevant source area of pollen (RSAP), which is

100   sometimes referred to as the "pollenshed" of the basin (*sensu* Sugita 1993). The basic premise is

101   that vegetation within a certain area distance of the basin corresponds to the quantity and type of

102   pollen deposited at the site. With distance from the lake shore, Ccorrelations between plant

103   abundance and pollen loading are expected to improve close to the lake shore, then approach an

104   asymptote at some distance because source vegetation of pollen far from the basin should have

105   much less influence on the pollen representation than vegetation closer to the basin. Estimating

106   the RSAP is a key step for quantitative calibration because it provides information about the

107   spatial extent of any subsequent vegetation reconstruction (Sugita et al. 1999, Bunting et al.

108   2004, Hellman et al. 2009). To our knowledge, the distinction between an assemblage-level

109   pollenshed RSAP (aRRSAP, Sugita 1993) and taxa-specific RSAPpollensheds (tRRSAP, *sensu*

110   Jackson 1990, Matthias and Giesecke 2014) has not yet been drawn within the same basin (Table

111   X). Comparing these estimates provides insight about how pollen assemblages "sense"

112   vegetation, which is critical to the extraction of vegetation information from pollen data.

113   Given the methodological challenges, the application of calibrated PAR-biomass transfer

114   functions to any ecosystem is not routine. This paper develops PAR-biomass models using short

6

115 cores from seven small lakes in the western Klamath Mountains, California, and follows the

116 general approach used in previous studies (e.g., Seppä et al. 2009, Matthias and Giesecke 2014)

117 whilst critically evaluating each step in the process. The Klamath bioregion contains numerous

118 small lakes and is an area where Holocene-length paleoecological records have already provided

119 a portrait of ecological change (Fig. 1). We measured modern PAR from lake sediments and

120 acquired vegetation abundance data to achieve three goals: 1) to understand the spatial

121 relationship between pollen assemblages flux in small lakes and surrounding vegetation cover,

122 through modeling of the aRSAP and tRSAP, 2) to calibrate a PAR-biomass model using

123 distance-weighted biomass for major tree taxa, and 3) to assess the potential of this model to

124 reconstruct past changes in assemblage-wide biomass from the region.

125

126 **2. Background**

127 Below, we describe the study area's physical features (2.1), our pollen-vegetation modelling

128 approach (2.2), and the methodology used to estimate aRSAP and tRSAP (2.3).

129

130 *2.1 Study Area*

131 The Klamath bioregion, a physically and floristically diverse area in northwestern California

132 (Whittaker 1960, Cheng 2004), contains hundreds of small lakes. Many lakes are found at high

133 elevations and are glacial in origin, but there are also landslide-created lakes at low- and mid-

134 elevations in the western portion of the region (Wahrhaftig and Birman 1965). The landscape has

135 deep catchments and steep mountains (Irwin 1981)), and the climate is Mediterranean, consisting

136 of cool, wet winters and warm, dry summers (Skinner et al. 2006). Prior to 20th century fire

7

137 suppression, the landscape had a mixed-severity fire regime characterized by mostly small, low-

138 intensity, frequent fires, and infrequent large burns of mixed-severity (Taylor and Skinner 2003).

139   Our study focused on the western Klamath Mountains where low-elevation forests

140 (<600–800 m) are dominated by *Pseudotsuga menziesii* (Douglas-fir). Multiple *Pinus* (pine)

141 species including *Pinus lambertiana* (sugar pine), *Pinus jeffreyi* (Jeffrey pine), and *Pinus*

142 *ponderosa* (ponderosa pine) are also common but less frequent than Douglas-fir. The most

143 common broadleaf tree species in the low-elevation forests are *Notholithocarpus densiflorus*

144 (tanoak), followed by *Arbutus menziesii* (Pacific madrone), *Chrysolepis chrysophylla* (golden

145 chinquapin), and *Quercus kelloggii* (California black oak). *Chamaecyparis lawsoniana* (Port-

146 Orford-cedar) is mainly found in riparian areas but can be found on slopes. Higher-elevation

147 montane forests are dominated by *Abies concolor* (white fir) and *Abies magnifica* (red fir;

148 Sawyer and Thornburg, 1977), whereas sub-alpine (above ~1700 m) zones include *Tsuga*

149 *mertensiana* (mountain hemlock) and *Picea breweriana* (Brewer spruce) (Sawyer and Thornburg

150 1977). On areas of ultramafic soils derived from serpentinite and peridotite bedrock, Jeffrey pine,

151 *Pinus monticola* (western white pine) and *Calocedrus decurrens* (incense-cedar) are the

152 dominant forest taxa (Whittaker 1960; nomenclature follows Hickman 1993).

153   We selected seven small lakes in the Six Rivers National Forest with small basins, ~~and~~

154 minimal stream inputs, and shallow slopes (Table 1, Fig. 1). Vegetation around the lakes is

155 representative of the diverse mixed conifer forest of the Klamath bioregion (Hudiburg et al.

156 2009) although the dominant overstory varies at each lake site. Holocene-length pollen records

157 (percentage and PAR) already exist for three of the seven lakes and suggest that the modern

158 forest structure and composition have been relatively stable for the last 2,000 years (Wanket

8

159 2002) but also imply a 3,000-year historic high of Douglas-fir in the contemporary forest

160 (Crawford et al. 2015).

161 *2.2 Pollen-vegetation models*

162 Linear pollen-vegetation models (PVMs) have a long history of use in palynology (Davis 1963,

163 2000; Andersen 1970; Prentice 1985, 1988; Sugita 1993, 1994; Bunting and Middleton 2005,

164 Bunting et al. 2013). PVMs use the relationship between pollen assemblages and vegetation to

165 infer past vegetation composition or structure from fossil pollen data. The main strengths of

166 linear PVMs are: 1) they provide the means to reconstruct vegetation from landscapes with no

167 modern analogue; 2) they have been widely tested against empirical data in quantitative

168 reconstruction research (e.g., Davis 1963, Andersen 1970, Prentice 1985, Sugita 1993, Bunting

169 and Hjelle 2010); and 3) they have been successfully validated in at least one region (southern

170 Sweden, Sugita 2007a, b; Hellman et al. 2008a, b).

171 In this work, we used a version of Sutton's original PVM model (Sutton 1947, 1953)

172 inverted by Prentice (1985) and modified by Sugita (1994) for lake environments. This model's

173 form – called Prentice-Sugita-Sutton – assumes that pollen could land anywhere on the lake

174 surface and would be perfectly mixed in the water column before being deposited on the lakebed.

175 The Prentice-Sugita-Sutton model also assumes that pollen transport is largely via wind above

176 the canopy and gravity beneath the canopy, and that the sampling basin is circular with uniform

177 wind in every direction (Sugita 1994, full list of assumptions in the supplement). Under this

178 approach, we a) divide the vegetation into rings, b) distance-weight each ring, and c) compare

179 the PAR from the basin with the summed distance weighting from one or more rings, working

180 out from the edge of the basin. This model calculates the total pollen influx from each source

181 across the whole lake. Its simplest linear form is:

Commented [MOU2]: Addressed Reviewer 3 concern about "hidden assumptions."

9

1
2
3
4
5
6
7
8
9
10   182 $$Y_{ik} = \alpha_i \cdot \psi_{ik} \tag{1}$$
11
12   183   where,
13
14   184 $Y_{ik} = $ pollen influx for a taxon i at site k
15
16   185 $\alpha_i = $ pollen productivity of taxon i
17   186 $\psi_{ik} = $ the distance-weighted plant abundance (DWPA) of taxon i around site k with the
18
19   187   weighting term reflecting the pollen dispersal of taxon i (weighting term calculation shown in
20
21   188   Eqequation. 3).
22
23
24   189
25
26   190   DWPA (ψ_{ik}) is defined as:
27
28   191 $$\Psi_{ik} = \int_R^\infty X_{ik}(z) g_i(z) dz \tag{2}$$
29
30   192   where,
31
32   193 $R = $ the radius of the canopy opening in which the sample site is located
33
34   194 $X_{ik}(z) = $ the plant abundance measure consisting of the contribution of taxon i to the pollen
35   195   assemblage formed at site k from plants located distance z from sampling location k, and $g_i(z)$ is
36
37   196   the distance weighting term for taxon i at distance z from any sampling location.
38
39   197
40
41   198   The Prentice-Sugita-Sutton weighting term g_i for taxon i at distance z is calculated using:
42
43   199 $$g_i(z) = b_i \gamma z^{\gamma-1} e^{b_i z^\gamma} \tag{3}$$
44
45   200   where $b_i = \dfrac{4 v_g}{nu\sqrt{\pi}C_z}$ \tag{3a}
46
47   201   and,
48
49   202 $z = $ distance
50
51   203 $\gamma = $ a coefficient of 0.125 (Prentice 1985)
52
53   204 $v_g = $ approximated by v_s (fall speed, m sec^{-1})
54
55
56   10
57
58
59
60

205   C_z = the vertical diffusion coefficient ($m^{1/8}$)

206   n = a dimensionless turbulence parameter equal to 2

207   u = windspeed (m sec^{-1}), set equal to 3.

208   Note that C_z and n depend on atmospheric stability.

209   Equation 2 can be re-written as a sum with two addends: 1) the unique contribution of the

210   vegetation close to site k where ζ is the pollen source area for site k, and 2) the long-distance

211   pollen transport ('background pollen,' which is uniform beyond ζ), giving:

212    $$\Psi_{ik} \ = \ \int_{R}^{\zeta} X_{ik}(z)g_i(z) \ dz + \int_{\zeta}^{\infty} X_{ik}(z)g_i(z)dz \qquad\qquad (4)$$

213   Which can be written as

214    $$Y_{ik} \ = \ \alpha_i \psi_{ik} \ + \ \omega_i \qquad\qquad (5)$$

215    $$\text{Where } \psi_{ik} = \int_{R}^{\zeta} X_{ik}(z)g_i(z)dz$$

216

217   *2.3 Spatial area represented by the pollen record*

218   We estimated the spatial extent of our sites' ~~pollensheds~~source area of pollen in two ways

219   (definitions in Table 2). We calculated the standard assemblage-specific metric – the relevant

220   source area of pollen (aRSAP) – which is defined as the area beyond which the correlation

221   between pollen and vegetation does not improve (Sugita 1993). Estimates of aRSAP can be

222   extracted from extended R-value (ERV) analysis using pollen percentage data (Parsons and

223   Prentice 1981). ERV analysis is the process of solving n equations for *2n* unknowns in order to

224   extract the parameter estimates, where ERV sub-models 1, 2 and 3 are the underlying vegetation-

225   pollen relationship models. The three sub-models define background pollen differently (Sugita

226   1994). Whereas models 1 and 2 use pollen data and vegetation percentages (Parsons and Prentice

227   1981), model 3 uses pollen percentages and plant abundance data in absolute units (e.g., biomass

11

228   per area) (Sugita 1994). Using the maximum likelihood method, ERV models iteratively fit the

229   relationship between pollen and vegetation percentages (Bunting and Hjelle 2010). Maximum

230   likelihood function scores measure the goodness of fit between pollen percentages and distance-

231   weighted plant abundance. The aRSAP can be estimated from visual inspection of the likelihood

232   function score plotted against distance; it is the point at which scores approach an asymptote

233   (Sugita et al. 1999, Bunting et al. 2005).

234   We then calculated a taxon-specific metric of the relevant source area (tRSAP) to

235   compare to the aRSAP. We call the tRSAP the distance beyond which the correlation between

236   PAR and DWPA summed to that distance does not improve (Jackson 1990). We fit a linear

237   equation (equation 5) for each individual taxon because both y and ψ are measured in

238   independent terms. We again used the ring source model, which converts the integral into a

239   summation. That is, we summed the value for each of the rings and $g_i(z)$ includes ring area in

240   this formulation. As with aRSAP, tRSAP can be estimated from visual inspection of the R^2 value

241   against the distance from the lake shore (m) (Matthias and Giesecke 2014).

242

243   **3. Methods**

244   Fitting PAR-biomass relationships requires a number of steps shown in a flowchart (Fig. 2) with

245   numbers matching the following sections.

246

247   *3.1 Lake selection and core sampling*

248   We used the following criteria to determine suitable lake sites: small size (radius approximately

249   100 m), no permanent outflow, simple basin, and core length greater than 25cm. Ten such lakes

250   were identified from topographical maps and satellite imagery as promising, but each were

12

251 assessed in the field. Out of this collection, seven lakes were viable and selected for ^{210}Pb dating.

252 During the summer of 2018, short cores (~50 cm) of 7 cm diameter were taken from each lake's

253 center using either a gravity corer (Ogaromtoc, Fish Lakes) or a piston corer (all other lakes).

254 The sediment-water interface was immobilized by sodium polyacrylate for transport. Cores were

255 later split and sectioned in the laboratory.

256 *3.2 Sediment dating, age-depth model, and sediment lithology*

257 We used lead-210 (^{210}Pb; 22.3 yr half-life) to assign ages to sediment deposited in the last 150

258 years. Surface bulk sediments from 0 cm to a maximum of 45 cm were taken from each core and

259 dried to 105°C (see Tables S1-S7). [210]Pb activity was determined by alpha spectrometry (see SI

260 for complete dating methodology)., via [210]Po. An aliquot of 0.2 to 1.0 g of dried and pulverized

261 sample was digested using concentrated HF, HNO_3, and HCl and a known amount of [209]Po spike

262 in an oven at 90°C for ~ 24 hours. The digested solution was dried, and the residue was mixed

263 with 1 M HCl until the pH was ~2. Auto-plating of Po was cold-plated onto an Ag disk for 24

264 hours at room temperature (Jweda and Baskaran 2011). The plated disk was assayed for Po using

265 Octete PC ORTEC alpha spectrometer. The reagent blanks were run simultaneously with each

266 batch of eight samples and were subtracted. Certified reference materials were periodically run.

267 For the determination of parent-supported (i.e., background) ^{210}Pb, several samples were run for

268 the activity of [226]Ra (using 352 and 609 keV) along with [137]Cs (661.6 keV) by Ge-well detector

269 (Baskaran et al. 2015). Small sample sizes prevented reliable ^{137}Cs from being obtained.

270 We used the Bayesian-based Plum software to develop age models from excess (unsupported)

271 ^{210}Pb data (Aquino-López et al. 2018). The Plum model is related to the constant rate of supply

272 (CRS) method (Appleby and Oldfield 1978) and retains two of the basic assumptions of CRS:

273 the rate of supply of ^{210}Pb is constant and there is no vertical mixing of radionuclides. Testing

13

274 ~~these assumptions requires independent validation using another marker, which is outside of this~~

275 ~~paper's scope. The Plum model is formulated within a robust statistical framework to quantify~~

276 ~~uncertainty (Aquino-López et al. 2018).~~ Plum uses a self-adjusting Markov Chain Monte Carlo

277 (MCMC) algorithm called the t-walk (Christen and Fox 2010). Plum uses millions of MCMC

278 iterations to model the accumulation of sediment, using a gamma autoregressive semiparametric

279 age-depth function (Blaauw and Christen 2011). This algorithm results in a probability envelope

280 around the mean age model. ~~The envelope allows the precision at any depth to be estimated~~

281 ~~explicitly. Plum makes use of prior information to determine the datable horizon, which is~~

282 ~~affected by two factors: the precision of methodology (alpha versus gamma counting) and the~~

283 ~~initial amount of excess lead. In Plum, the chronology limit is determined by the rate of supply~~

284 ~~of ^{210}Pb to the site and the equipment error, usually ~3 Bq/kg for a sample size of 1 g by alpha~~

285 ~~spectrometry for research laboratories.~~ Supported ^{210}Pb activities were determined from the

286 direct measurements of ^{226}Ra by gamma-ray spectrometry.

287

288 *3.3   Pollen analysis*

289 Pollen samples – one from each lake site – were extracted from 0.63 cm³ of wet sediment from

290 the top 0.5 cm of each core and were processed according to standard pollen preparation

291 procedures (Faegri and Iversen 1989) but modified to include two steps: 1) sieving with 5- and

292 153-micron mesh under vacuum and 2) swirling, with the less dense fractions retained. These

293 steps draw on~~current US Geological Survey protocol (Tom Sheehan, personal communication),~~

294 ~~which is based on D~~Doher's palynomorph methodology and current United States Geological

295 Survey procedures (Doher 1980). One *Lycopodium* spore tracer tablet~~s~~ containing 20,848 spores

296 ~~were~~as added to each sample to calculate pollen concentration (Stockmarr 1971, Faegri and

Commented [MOU3]: Clause added for USGS reviewer

14

297 Iversen 1989). Acetolysis and sieving steps were repeated for samples containing high amounts

298 of organic material. Pollen samples were mounted in silicone oil and examined at 500×

299 magnification. At least 400 terrestrial grains per sample were counted and identified using the

300 UC Berkeley Museum of Paleontology modern pollen reference collection, as well as pollen

301 atlases (Knapp 1969, Halbritter et al. 2018).

302   Seven wind-pollinated taxa were identified at all sites: *Pinus, Pseudotsuga, Quercus,*

303 *Notholithocarpus, Alnus,* TCT (Taxodiaceae, Cupressaceae, and Taxaceae families), and *Abies*.

304 The corresponding plant taxa from the study area were sugar pine, Jeffrey pine, ponderosa pine

305 (*Pinus*); Douglas-fir (*Pseudotsuga*); California black oak, canyon live oak (*Quercus*); tanoak,

306 golden chinquapin (*Notholithocarpus*); white alder (*Alnus*); Port-Orford-cedar, incense-cedar

307 (TCT); white fir, red fir (*Abies*). we only encountered Port-Orford-cedar and incense-cedar in the

308 vegetation survey at the study sites and assume all TCT originating within the surveyed

309 vegetation area came from these species. Counts of *Pinus*, *Quercus*, *Notholithocarpus* and *Abies*

310 reflect all the pollen grains from their respective genera (i.e., we report total *Pinus* which likely

311 contained sugar pine, Jeffrey pine, and ponderosa pine grains). *Pseudotsuga* and *Alnus* counts

312 represent the species *Pseudotsuga menziesii* (Douglas-fir) and *Alnus rhombifolia* (white alder).

313 Other wind-pollinated tree pollen present in trace amounts includes willow (*Salix*), buckthorn

314 (*Rhamnaceae)*, hazel (*Corylus*) and silk tassel (*Garrya*). This group of "other hardwoods"

315 accounted for only 0.35% of the woody species. Given their rarity, we omitted them from the

316 determination of pollen source area and subsequent PAR-biomass modeling.

317

318 *3.4 PAR determination*

319 Pollen concentrations (grains cm^{-3}) and PAR (grains cm^{-2} yr^{-1})were determined using the

15

320 *Lycopodium* marker grains, ~~pollen concentrations (C_i, grains cm^{-3}) were calculated for each~~

321 ~~pollen type i using the following equation:~~

322 $$C_i = \frac{A_i \times L_a}{L_e \times V_i} \tag{6}$$

323 ~~Where A_i is~~ the number of pollen grains counted for <u>each</u> taxon ~~i, L_a is the number of added~~

324 ~~marker grains, L_e is the number of counted marker grains in each slide, and V_i is~~ the volume of

325 the pollen sample (e.g., 0.63 cm^3) (Stockmarr 1971)<u>, and</u> ~~. Concentrations were used for PAR~~

326 ~~calculations by multiplying the concentration values by~~ the sediment accumula<u>tion</u> rate <u>(Davis</u>

327 <u>and Deevey 1964)</u>, which differed by lake site and was determined by the Plum age model in

328 increments of 0.5cm<u> (see SI for equations used).</u> ~~The equation used was:~~

329 ~~$PAR_i = C_i \times S \tag{7}$~~

330 ~~Where PAR$_i$ is the pollen accumulation rate for taxon i, C_i is the pollen concentration (grains cm^{-3})~~

331 ~~$^{-3}$) for taxon i, and S is the sedimentation rate (cm yr^{-1}) (Davis and Deevey 1964).~~

332

333 *3.5 Forest inventories*

334 We used cruising prisms (wedges of glass with a known size/angle) to determine the basal area

335 of the dominant pollen-producing taxa within 750 m from each lake's shoreline (USDA Forest

336 Service 2000). The prism method employs variable plot radius sampling at the stand level.

337 Transects in eight directions (N, S, E, W, NE, NW, SE, SW) from the lake shore were sampled.

338 The basal area of live trees was measured using the prisms ~~were taken~~ every 50m along the

339 transects, following Han et al. 2017 (Fig. 3).

340   We used aboveground live tree biomass (AGL) as the specific measure of abundance that

341 is distance weighted. To estimate AGL from basal area measurements, we developed species-

342 specific allometric equations using contemporary data from the US Forest Service Forest

16

343 Inventory and Analysis program (FIA). From the FIA plots inventoried in Six Rivers National

344 Forest between 2001 and 2017 (FIADB 2020), we calculated plot-level basal area (m^2 ha^{-1}) for

345 every species in the plot and linked it to the estimate of plot-level aboveground live biomass (Mg

346 ha^{-1}) for each species (n = 3,428 plot-by-species observations). AGL was estimated using the

347 regional model of tree biomass (Zhou and Hemstrom 2009). For every species, we predicted

348 AGL as a function of basal area using a linear log-log (natural) equation (*sensu* Knight et al.

349 2020).

350

351 Specifically,

$$\ln\left(AGL_{ij}\right) = \beta_{0_i} + \beta_{1_i} * \ln\left(Basal\ Area_{ij}\right) \tag{8}$$

353 where $\ln(AGL_{ij})$ is the natural log of aboveground live biomass for species i in plot j, $\ln$(Basal

354 Area$_{ij}$) is the natural log of tree basal area for species i in plot j, β_{0i} is the intercept for species i,

355 and β_{1i} is the slope coefficient for species i. For the six most abundant species that accounted for

356 90% of the basal area, fits ranged from a low of 0.85 for sugar pine to a high of 0.97 for Port-

357 Orford-cedar (Table S8). With these equations and field measurements of species basal area, we

358 calculated the AGL of each species in the prism sample.

359

360 *3.6 ERV analysis and estimation of aRSAP*

361 The aRSAP values were extracted from conventional ERV analysis using model 3. We used

362 PolERV from the software suite HUMPOL (Bunting and Middleton 2005) which has the same

363 core code (erv-v6.exe and polsim-v3.exe) as other ERV software, e.g. POLLSCAPE (Sugita

364 1994). In order to meet the requirement that the number of sites is at least twice the number of

365 taxa used in ERV analysis (Soepboer et al. 2007), we analyzed sub-sets of three taxa across the

17

366   seven sites using the same reference taxon (TCT) every time. For example, one such sub-set

367   combination was TCT, *Pseudotsuga*, and *Pinus*. We selected TCT as the reference taxon (i.e.,

368   specified that TCT has a relative pollen productivity of 1.0) for several reasons. First, a scatter

369   plot of TCT pollen values and unscaled distance weighted plant abundance is positive and linear

370   (Fig. S1). Second, TCT has an estimated relative pollen productivity in the middle of the dataset

371   upon ERV analysis with all seven taxa. Lastly, TCT is represented in pollen data at all sites

372   (unlike *Abies, Alnus,* or *Quercus*), and is present in vegetation close to the ~~sampling point~~coring

373   site. aRSAP was estimated by plotting the likelihood scores for each distance across all taxa

374   combinations and pooling the results.

375

376   *3.7 Distance weighting and estimation of tRSAP*

377   AGL results were first averaged by the number of plots in each concentric ring and then each

378   ring was weighted using the Prentice-Sugita weighting under stable conditions, which affect

379   parameters C_z and n (Eq. 3, 3a). We assumed stable atmospheric conditions because simulation

380   experiments comparing unstable and stable models demonstrate little difference in estimated

381   aRSAP and pollen productivity (Broström et al. 2004). The pollen-specific fall speeds (m sec^{-1})

382   of *Abies, Alnus, Pinus, Pseudotsuga,* and *Quercus* have been determined in previous work (Table

383   S9). For TCT, Stoke's Law (Gregory 1973) was used to calculate fall speed using the average

384   grain size of each taxon and weighted by relative abundance of the contributing species Port-

385   Orford-cedar and incense-cedar (both Cupressaceae family). For subprolate grain

386   *Notholithocarpus*, major and minor axes were measured from reference slides in UC Berkeley's

387   collections, and then Stoke's Law with Falck's (1927) correction was used. Lastly, we

388   determined the coefficient of determination (R^2) of the linear model predicted from AGL_{dw} at

18

389 distance z (AGL_{dw_z}) as a function of PAR. The R^2 between PAR and summed AGL_{dw} for each

390 ring distance was plotted against the distance. The tRSAP occurs where the line reaches an

391 asymptote.

392

393 *3.8 PAR-biomass transfer equations*

394 We developed transfer equations to predict taxon-specific contributions to the distance-weighted

395 AGL (AGL_{dw}) as a function of taxon-specific PAR. Although biomass "predicts" pollen

396 accumulation rates in a functional sense, our aim was to apply calibrated transfer functions to

397 predict biomass in the past. Consequently, we fitted regression lines with PAR values as the

398 independent variable. This reasoning has been used for needle accumulation rate as a predictor of

399 Holocene-era basal area (Blarquez et al. 2011).

400   In this analysis, each lake represented a sample with the ~~depositional~~ source area defined

401 by either aRSAP or tRSAP. We included seven pollen-producing taxa, namely *Pseudotsuga,*

402 *Pinus, Notholithocarpus,* TCT*, Alnus*, *Quercus,* and *Abies*, that collectively account for greater

403 than 99% of the pollen-producing trees present in the surrounding landscape. Using the assigned

> **Commented [MOU4]:** Added for USGS reviewer.

404 source area distances, we calculated AGL_{dw} for the taxa present at each lake and regressed it

405 against PAR using linear models (see Fig. 8a,b). Specifically, we evaluated three model forms: a

406 linear model with an intercept term and slope term, a linear model with only a slope term, and

407 segmented linear model with one breakpoint. In the linear models with intercepts, the intercept

408 represents the "background" pollen component; because we treated PAR values as the

409 independent variable, these intercepts are negative. So, we included an origin-forced model as an

410 option because negative-intercept models are not biologically meaningful for biomass

411 reconstruction given that very low PAR values would yield negative biomass. We included the

19

412 segmented model to potentially capture threshold responses in the relationship between AGL and

413 PAR (Muggeo 2008). We ranked the models by the Akaike Information Criterion for small

414 samples (AICc) in order to compare performance. AICc imposes a stronger penalty on model

415 complexity than AIC and was chosen in order to avoid fitting models which were overly

416 complex given the size of the dataset (Burnham and Anderson 2002).

417   To evaluate the uncertainty introduced by the PAR transfer functions, the AGL_{dw}

418 predicted from PAR at each lake (predicted AGL_{dw}) was compared to the AGL_{dw} calculated from

419 the observed AGL_{dw}. Error was propagated using a resampling method (Crowley et al. 1992).

420 Specifically, we estimated the error in predicted AGL_{dw} for each iteration as a random sample

421 from a normal distribution with the mean equal to zero and the standard deviation equal to the

422 standard error of the regression estimate (SEE) for each taxon. Results were based on 10,000

423 iterations and reported as means and standard errors of the predicted AGL_{dw} for each lake. Bias

424 between the predicted and observed AGL_{dw} was calculated as:

425 $$Bias = \frac{Predicted\ AGL_{dw} - Observed AGL_{dw}}{Observed\ AGL_{dw}} \tag{9}$$

426

427 **4. Results**

428 *4.1 Chronology*

429 The seven lakes' chronologies were established using at least 20 ^{210}Pb ~~dates~~ measurements at

430 each site (see Table S3-S9 for exact number of samples for each core). Blue Lake is shown as an

431 example (Fig. 4). The chronologies for Fish, North Twin, Ogaromtoc, Onion, Red Mountain, and

432 South Twin lakes followed the same procedure (Fig. S2). The lakes are characterized by rapid

433 sedimentation rates, with rates in the upper sediments in the range of 0.14-0.33 cm yr $^{-1}$ (3-7 yr

434 cm^{-1}). Therefore, surface samples (upper 0.5cm) contain pollen from 2018 (collection date) to

20

435 2011 at the oldest. Core lithology results are provided in the supplement (Figs. S3-4).

436

437 *4.2 PAR*

438 A group of highly abundant tree taxa contained *Pseudotsuga*, *Pinus*, *Notholithocarpus*, and TCT,

439 which were reflected in high (> 2,000 grains cm^{-2} yr^{-1}) PAR values in most samples (Fig. 5,

440 Table S10). For example, *Pseudotsuga* values were above 5,000 grains cm^{-2} yr^{-1} at all sites

441 except Onion Lake. The highest overall PAR value was *Pinus* at Onion Lake which exceeded

442 10,000 grains cm^{-2} yr^{-1}. High PAR values reflect the Douglas-fir and pine-dominant composition

443 of Six Rivers National Forest. Onion Lake is the only lake situated in the True Fir alliance zone

444 and, unsurprisingly, the *Abies* PAR value was the highest compared to all other sites (5,000

445 grains cm^{-2} yr^{-1}). PAR values for *Notholithocarpus* and TCT varied across sites and were

446 between 1,000-4,000 grains cm^{-2} yr^{-1}.

447 The group of less abundant arboreal taxa included *Alnus*, *Abies*, and *Quercus* which were

448 present in most samples with PARs of less than 2,000 grains cm^{-2} yr^{-1} (Fig. 5). *Alnus* values were

449 generally around 1,000 grains cm^{-2} yr^{-1}, although values above 2,000 grains cm^{-2} yr^{-1} were

450 observed at Ogaromtoc and Fish Lakes. *Abies* values were low (< 1,000 grains cm^{-2} yr^{-1}) at all

451 sites except North Twin and Onion Lakes. Although pollen from *Alnus*, *Abies*, and *Quercus* were

452 found at all sites, the taxa themselves were not recorded from the transect sampling at several

453 lakes. This could be due to low abundance such that they were not captured in the survey or due

454 to their absence in the ~~pollenshed~~ sedimentary basin in which case their PAR contributions are

455 background deposition. Pollen from the "other hardwood" category (defined as willows,

456 buckthorn, hazel, and silk tassel) was detected in trace amounts (< 100 grains cm^{-2} yr^{-1}).

457

21

458   *4.3 aRSAP and tRSAP*

459   Using the sub-setting approach for the aRSAP calculation, a coherent pattern was exhibited in

460   the likelihood function scores from model 3. The values were high at short distances and then

461   decreased rapidly until 175 m where they begin to flatten out. For all taxa combinations, we

462   inferred via visual inspection that the curves reached their asymptotes at a distance of 625 m and

463   thus the aRSAP of these lakes is 625 m from the lake shore. The likelihood function scores in

464   relation to the distance from the lake shore are shown for one of the three sub-set examples:

465   TCT, *Pseudotsuga*, and *Pinus* (Fig. 6).

466   Based on tRSAP calculations for the four dominant tree taxa, maximum R^2 values were

467   reached before the maximum distance surveyed (750 m) from the shoreline (Fig. 7). The R^2

468   values for *Pinus* and TCT were high (> 0.75) at only 25 m from the shore and stabilized around

469   225 m, the tRSAP. The R^2 values for *Pseudotsuga* and *Notholithocarpus* continued to improve

470   for some distance from the lake shore. For *Pseudotsuga,* the tRSAP was 625 m; for

471   *Notholithocarpus,* it was 525 m. Sample sizes were insufficient to estimate tRSAP values for the

472   minor taxa. For these taxa, we used the aRSAP value in AGL_{dw} calculations (i.e., 625 m).

473

474   *4.4 Transfer functions: PAR to AGL_{dw}*

475   PAR was a statistically meaningful and reasonably precise reliable estimator of contemporary

476   AGL_{dw} for most of the pollen taxa present (Fig. 8). Based on the aRSAP distances, the linear

477   model without intercept was the best performing model ($\Delta AIC_c > 4.0$) for the four most

478   abundant taxa (Fig. 8a). For these taxa, the no-intercept regressions were not only significantly

479   better than the null model ($p < 0.001$) but also explained most of the variation. R^2 ranged from

480   0.87 for TCT to 0.96 for *Pseudotsuga* (Table S11). The model results for the three less abundant

22

481 species (i.e., *Alnus*, *Abies* and *Quercus*) were more complex (Fig. 8b). Based on ΔAIC$_c$, the

482 segmented regression model best fit the *Alnus* and *Abies* data. However, both species were rare

483 and found in abundance at only one lake (Fig. 5). The existence of this one abundant point exerts

484 extraordinary leverage in the segmented regression. To avoid relying on a single point in these

485 two transfer functions, we used the second-best regression model. For *Alnus*, it was a linear

486 model; for *Abies*, it was a linear model without intercept (Table S11). For *Quercus*, none of the

487 regression models were superior to the null (Fig. 8b, Table S11), so we used the mean and

488 standard error to predict *Quercus* contribution to AGL$_{dw}$ estimates for each lake. We recalculated

489 the biomass transfer functions using the tRSAP weighted AGL$_{dw}$ estimates for all taxa. Both the

490 functional forms and fits were similar to aRSAP-based results (Table S12). However, the

491 coefficients varied with changes in the source area distance.

492   The transfer functions based on aRSAP distances provide robust means to estimate

493 contemporary AGL from PAR (Table 32). The coefficient of variation (COV) in predicted

494 AGL$_{dw}$ ranged from 13-17% for six lakes with Ogaromtoc being the exception with a COV =

495 24%. The standard error of the estimate varied little among lakes and averaged 32 Mg ha^{-1}. In

496 terms of accuracy the relative root mean squared error (rRMSE) between predicted and observed

497 AGL$_{dw}$ was 9.2%. There was a small tendency for predicted AGL$_{dw}$ to overestimate the

498 observed. The mean bias was 4.8% with two lakes, Red Mountain and South Twin, contributing

499 the most to the positive bias (Table 23). The predictions of AGL weighted using tRSAP

500 distances (Table 34) tended to less accurate (rRMSE = 12.7%) and more biased (10.1%).

501

502 **Discussion**

503 *5.1 Source areas of pollen: aRSAP and tRSAP*

23

504 Calibration of pollen-vegetation relationships is only effective when the scale of the vegetation

505 sampling is close to or exceeds the scale of the relevant source area of pollen (Bunting et al.

506 2004). Therefore, being able to specify the source area of pollen in a given basin is an important

507 step towards quantitative reconstruction of past vegetation (Sugita et al. 1999, Hellman et al.

508 2009). A primary aim of this work was to understand the spatial extent represented by the pollen

509 assemblage. We addressed this aim by determining the assemblage-level relevant source area of

510 pollen (aRSAP) obtained from pollen percentage data and ERV analysis and comparing those

511 estimates with the taxon-specific source area of pollen (tRSAP) for four main taxa. Both metrics

512 estimate the extent of vegetation that requires surveying for a subsequent reconstruction step but

513 are seldom compared.

514   aRSAP values have been estimated for lakes similar in size to those presented here (i.e.,

515 100 m radius), in different settings including simulated landscapes. Reported aRSAP values have

516 ranged from: 300 m in a simulation of a hemlock-hardwood forest in the US (Sugita 1994), to

517 800-1,000 m in a simulation of spruce forest in Sweden (Sugita et al. 1999), to 1,700 m in

518 varying landcover types in Denmark (Nielsen and Sugita 2005), to 1,500-2,000 m in semi-boreal

519 forests of Estonia (Poska et al. 2011), and to 2,200 m in the upper Tibetan Plateau (Wang and

520 Herzschuh 2011). Within this list, all aRSAP estimates were derived from Prentice-Sugita-Sutton

521 distance-weighted models and are thus comparable to our estimate. Our aRSAP value of 625 m

522 falls in the range (300-2,200 m), though on the small end.

523   The aRSAP is unique to a given set of lakes and is sensitive to numerous factors such as

524 lake size and basin shape (Sugita 1993), vegetation patch size (Sugita 1994, Broström et al.

525 2005), vegetation patterns (Bunting et al. 2004), and taxa spatial distribution (Hellman et al.

526 2009). For example, aRSAP values tend to increase with landscape openness defined as the

24

527 extent of the vegetation cover in the ~~pollenshed~~sedimentary basin. For example, the aRSAP for

528 small ponds in a closed forest was simulated to be 300 m (Sugita 1994) and empirically verified

529 by Calcote (1995), whereas the aRSAP for small ponds in an open Swedish landscape was 1,000

530 m (Sugita et al. 1999). However, expectations based on landscape openness can be complicated

531 by vegetation heterogeneity. Higher vegetation diversity and complex spatial distribution of taxa

532 are associated with larger aRSAPs (Hellman et al. 2009). The presence of rare taxa in a

533 landscape can also increase the aRSAP, other factors being held constant (Bunting et al. 2004).

534 For example, Commerford et al. (2013) observed the effect of rare taxa empirically: small lakes

535 in a 'very open' grassland in Kansas had a large aRSAP of 1,060 m, which they attributed to

536 scattered tree taxa in the tallgrass prairie.

537   The contemporary forests around our lake sites are dense, closed, and heavily dominated

538 by Douglas-fir (Skinner et al. 2018). Taxa like black oak (*Quercus*), white alder (*Alnus*), and

539 white fir (*Abies*) are present but not common. These rare taxa in the ~~pollenshed~~ area contributed

540 little to the overall biomass (2.3%) but make the landscape more heterogeneous. This

541 heterogeneity can result in a larger aRSAP than if there were no rare taxa present. All else being

542 equal, longer distances from each sampling site are required to get a sufficient cover of all taxa

543 within the landscape to reach the regional average. These greater distances produce larger

544 aRSAP estimates (Hellman et al. 2009).

545   tRSAPs have been estimated at small lakes and ponds. For example, the tRSAP for *Pinus*

546 was 200 m from the lakeshore in ~~southern~~ northeastern Germany (Matthias and Giesecke 2014),

547 and other tRSAP values in that study ranged from 50 m (*Quercus*) to 300 m (*Fagus*) to 1,000 m

548 (*Betula*). Jackson (1990) found small tRSAP estimates from ponds in New York: *Acer* (< 20 m),

549 *Betula* (> 1,000 m), *Fagus* (> 1,000 m), *Picea* (< 100 m), *Quercus* (> 1,000 m) and *Pinus*/*Tsuga*

25

550   (< 500 m). In this study, the tRSAP value for *Pinus* was 225 m, a near match to Matthias and

551   Giesecke (2014) and comparable to Jackson (1990). The other tRSAP values in this study ranged

552   from 225 m (TCT) to 525 m (*Notholithocarpus*) to 625 m (*Pseudotsuga*). Like Matthias and

553   Giesecke's results, the tRSAPs are inconsistent with expectations based solely on the respective

554   fall speeds of the taxa. For example, *Pinus* has one of the assemblage's lowest fall speeds and

555   was expected to travel longer distances and have a large tRSAP; in fact, it had one of the shortest

556   tRSAPs.

557   Unexpectedly small source areas of highly dispersible taxa have been observed in

558   simulated landscapes (e.g., *Betula*, Sugita 1994) and have been attributed to vegetation

559   patterning. The estimated RSAP reflects the minimum distance at which the regional vegetation

560   composition is attained. For example, if *Betula* is uniformly spread in a forest, the regional

561   distribution signal of *Betula* will be captured closer to the sampling point than in a forest where

562   *Betula* is heterogeneously spread across the forest~~When a taxon has a relatively homogeneous~~

563   ~~distribution across the landscape (e.g., found in all communities with small patch size, occurs~~

564   ~~frequently as individuals in all communities), the regional distribution of the taxon is attained~~

565   ~~relatively close to the sampling point (e.g., the lake); thus, the vegetation composition does not~~

566   ~~change with increasing distance beyond that point and the source area is small~~. In this case,

567   tRSAP reflects the distance at which regional vegetation composition is reached, instead of being

568   predominantly controlled by the taxon's pollen dispersal ability and depositional properties

569   (Sugita 1994). The vegetation patterns in the Klamath area are complex and heterogeneous

570   (Skinner et al. 2018). Within the sampling area, Douglas-fir (*Pseudotsuga*) is the dominant

571   species with large amounts of tanoak (*Notholithocarpus*) at most lake sites, with pines (*Pinus*)

572   intermixed and some cedars (TCT). The small "patches" of pines and cedars within a Douglas-fir

26

573 dominant overstory could effectively shrink the tRSAPs of *Pinus* and TCT, following the logic

574 presented in Sugita (1994). Thus, the finding of relatively small tRSAPs for *Pinus* and TCT,

575 despite their fall speeds, and relatively large tRSAPs for *Pseudotsuga* and *Notholithocarpus*,

576 aligns with the study area's vegetation patterning.

577   Our estimated aRSAP (625 m) and tRSAP values (all 625 m or less) suggest consistent,

578 though not identical, interpretations of the ~~pollenshed~~source area of pollen. Both estimates

579 indicate that the pollen record "senses" a local view of about the same area of the surrounding

580 vegetation. Given that vegetation surveying must meet or exceed the scale of the relevant source

581 area of pollen for quantitative reconstruction (Bunting et al. 2004), vastly different aRSAP and

582 tRSAP estimates would potentially be consequential. If, for example, we had estimated an

583 aRSAP << tRSAP, it would imply that our assemblage-level view was in some way blind to taxa

584 in the assemblage, and thus missing important landscape patterning or other features of the

585 ~~pollenshed~~area from which pollen originated. On the other hand, if we had estimated an aRSAP

586 >> tRSAP, it would imply the subsequent reconstruction represents a larger area than is

587 potentially being recorded by the pollen system.

588   This consistency between the aRSAP and tRSAP results was reflected in the similarity of

589 the AGL_{dw} reconstructions (Table 3~~2~~, Table 3~~4~~). On average, observed AGL_{dw} for each lake was

590 10.1 Mg ha^{-1} (5.2%) larger using aRSAP with the differences ranging from 2.6 Mg ha^{-1} (1.1%)

591 larger at North Twin Lake to 22.2 Mg ha^{-1} (10.3%) larger at Onion Lake. The differences in

592 terms of predictive ability were equally modest with aRSAP estimates producing somewhat more

593 accurate and less biased results.

594

595 *5.2 The potential of calibrated PAR as a bioproxy*

27

596   Establishing the relationship between contemporary biomass and modern PAR values is

597   contingent upon obtaining accurate sedimentation rates in cores. We are confident in our

598   estimated sedimentation rates for two key reasons. First, we used a state of the art, robust

599   Bayesian model to develop age models from ^{210}Pb dates (Aquino-López et al. 2018). Our results

600   showed low uncertainty in the modeled ages in all cores, particularly in the top 20cm. Second,

601   we were able to compare our upper sedimentation rates representing the last decade to estimates

602   from two of the same lakes (Ogaromtoc and Fish lakes) that were collected in 2008 and 2009

603   (Crawford et al. 2015). We found similar sedimentation rates in the upper sediments: 2.0-4.0 mm

604   yr^{-1} compared to 2.0-3.3 mm yr^{-1}. Our modern PAR values are also in agreement with PAR

605   values from the youngest sediments in Crawford et al. (2015).

606   The ultimate goal of this research was to assess whether PAR be used to predict distance-

607   weighted biomass for major tree taxa in the Klamath area, and therefore generate models suitable

608   for reconstruction of past biomass dynamics. The fact that contemporary pollen influx is a

609   reasonably reliableprecise predictor of contemporary distance-weighted AGL at these sites

610   suggests that PAR can be used to infer changes in plant biomass at for these sites. But even with

611   apparently statistically sound modern models, it may not be reasonable to apply the models for

612   reconstruction in all contexts.

613   In an ideal situation, the calibration dataset would include sites with a wide range of

614   population sizes of the main taxa to allow any time in the fossil record to be reconstructed. Our

615   model had less skill in estimating low levels of forest biomass because we were unable to find

616   lake sites that met our selection criteria and supported sparse forest cover. Other modern

617   quantitative vegetation reconstruction models have been restricted at the upper end of the

618   calibration. Trees growing in dense forest stands produce less pollen than an exposed tree in a

28

619 field, which suggests that increased forest density could result in reduced net pollen productivity

620 (Andersen 1970, Fægri and Iverson 1989, Feldman et al. 1999). For example, Blarquez et al.

621 (2011) found that the relationship between needle accumulation rate and forest basal area tended

622 to saturate above 40 $m^2 ha^{-1}$ for conifer-dominated sites. However, despite the high biomass-

623 density of the contemporary forest at our sites (Knight et al. 2020), there was no evidence of

624 saturation in the PAR-biomass functions for the major taxa. Even at the maximum PAR values,

625 the biomass values increase at pace following the log-linear fits (Fig. 8a).

626   Long-term PAR records from lakes in the area provide insight into time periods where

627 our calibrated models will be able to capture past conditions. Comparable taxa-specific PAR

628 values from lake sites in the region were only available for *Pinus*, and they suggest time periods

629 of agreement with our *Pinus* PAR measurements and our total *Pinus* PAR-AGL model, which

630 covers a range between 1,500 and 11,000 grains $cm^{-2} yr^{-1}$. For example, Briles et al. (2008)

631 reported *Pinus* PAR between 2,000 and 8,000 grains $cm^{-2} yr^{-1}$ at Sanger Lake in the western

632 Klamath Mountains over 15,000 years BP. Likewise, a 3,000-year PAR record from Fish Lake (a

633 lake also examined in this study) shows agreement with our total *Pinus* PAR range during some

634 time periods. Fish Lake's record shows temporal variability in~~total~~ *Pinus* PAR values between

635 2,000 to 9,000 grains $cm^{-2} yr^{-1}$ during the last two hundred years (Crawford et al. 2015), which

636 falls within our calibration. Lastly, total PAR values measured at eight lakes in the Klamath area

637 since 15,000 BP range from 2,000 to 15,000 grains $cm^{-2} yr^{-1}$ (Briles et al. 2011) and are similar

638 in size to lakes in this study and have a dense surrounding forest, although they are located in the

639 white-fir vegetation zone.

640   In addition to selecting a range of forest conditions, researchers undertaking similar

641 efforts will need to consider the number of lakes needed for statistical soundness for the

29

642   calibration. The seven lakes presented here appear to have been sufficient to build robust models

643   in terms of low coefficient of variation (Table 23), but it may be difficult in other locations to

644   find enough suitable lakes using consistent selection criteria. If reconstructions of continuous

645   Holocene-length biomass records are sought, using a high number of lakes has the downside of

646   great expense (from isotopic dating) and labor (from pollen counting), unless accurate automatic

647   classification systems become widespread (Sevillano et al. 2020).

648   The calibration step we undertook required modern biomass data, which may be difficult

649   to obtain empirically for a large number of lakes or in settings with challenging topography. For

650   example, transects in this study ran 750 m from the shoreline, but steep topography and scree

651   slopes occasionally prevented a complete survey. Because we studied small lakes and needed

652   finely resolved biomass data, sparse inventory data with large geographic extent (e.g., FIA data)

653   were not an appropriate substitute for field surveys. However, FIA data provided essential

654   information regarding the basal area to biomass relationships for the common tree species in the

655   region (Table S8).

656   *5.3 Limitations of PAR and PVMs*

657   Our results show the utility of calibrated PAR-AGL models for this study, and we have provided

658   a robust process for including uncertainty in PAR-AGL models. However, PAR itself may vary

659   in ways that reduce its value for pollen-based reconstructions in all landscapes. For instance, net

660   pollen deposition can vary spatially and temporally if sediment focusing or pollen redeposition

661   occurs. While studies investigating PAR from modern sedimentary records did not find that

662   redeposition and sediment focusing affected PAR (Seppä and Hicks, 2006; Giesecke and

663   Fontana, 2008), other studies have documented the influence of these factors on PAR (Davis et

664   al. 1984, Odgaard 1993, Matthias and Giesecke 2014). Additionally, between-lake differences in

30

665 PAR values can arise from differences in pollen taphonomy due to basin size or stream inflow

666 (Davis 1967b). Pollen monitoring studies have illustrated another known issue with PAR: the

667 amount of pollen produced can change year to year and is related to the weather conditions of the

668 preceding year (Hicks 2006). Lastly, one study has implied that PAR may depend on the net

669 primary production of the pollen-producing taxa as well as overall plant biomass (Matthias and

670 Giesecke 2014). Without long-term pollen monitoring studies across different biomes and

671 accompanying detailed biomass data, true data validation will not be possible.

672   Pollen transport in mountain environments has been studied in Europe through the European

673 Pollen Monitoring Programme, but, to our knowledge, has not been studied in the mountains of

674 western North America outside of the present work. Several pollen monitoring studies with

675 transects running through multiple vegetation zones in mountainous areas tend to show that

676 pollen from lower forest zones is quite abundant in upper zones, and this effect appears more

677 pronounced when high altitude zones have lower productivity (e.g., the Rila Mountains in

678 Bulgaria, Tonkov et al. 2001). Unlike mountain transect studies, our sites are all within one

679 vegetation zone, therefore reducing the significance of these effects, and we are not studying tree

680 line position. The Douglas-fir dominated conifer forest in the Klamath Mountain is a relatively

681 high productivity zone, and such zones typically show less of an "uphill" effect that impacts tree-

682 line pollen assemblages (e.g., Swiss Alps tree line study, Sjögren et al. 2008)."

683   All PVMs, including PAR-biomass transfer functions, are based on assumptions that may not

684 hold in a changing landscape. It must be assumed, for example, that taphonomic processes

685 filtering pollen in lake sediments are constant over time and among lakes, unless taphonomic

686 biases are precisely quantified (Allison and Bottjer 2011). Using our method, quantitative

687 biomass reconstruction would also assume that the relevant source area of pollen is constant over

Commented [MOU5]: Added discussion of mountain pollen transport for Reviewer 2.

31

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

688   time. We estimated the aRSAP of our seven sites as well as the tRSAP of abundant taxa, but

689   these may apply to a landscape arrangement which is unique in the last 3,000 years. The present-

690   day high PAR values of *Pseudotsuga* are not replicated in the fossil pollen record at any other

691   time in three millennia (Crawford et al. 2015), suggesting that the dominance of shade tolerant

692   *Pseudotsuga* is also not found elsewhere in this time period. Deep-time reconstructions from

693   lakes in this study have shown large changes in vegetation composition due to climate, Native

694   land-use, fire disturbances, and, in the last century, fire suppression. In response, we anticipate

695   that the relevant source areas of pollen will expand and contract over time. Because the spatial

696   patterns of past vegetation are usually unknown, it is difficult to estimate past relevant pollen

697   sources areas. However, the Multiple Scenario Approach (MSA, Bunting and Middleton 2009)

698   offers insight on this issue. Under MSA, hypothetical landscapes are created via rules for plant

699   placement and environmental parameters, and then pollen assemblages are simulated and

700   compared to known pollen signals to identify probable past vegetation mosaics. Another

701   experimental method to estimate past relevant pollen source area has been explored through

702   modeling (Hellman et al. 2009) where regional vegetation composition and available pollen

703   productivity estimates are available for multiple sites (Sugita 2007b). Hellman et al.'s (2009)

704   simulations suggest relatively robust aRSAP estimates of 1,000 to 2,500 m for small lakes under

705   hypothetical landscapes from southern Sweden where natural and anthropogenic disturbances

706   have occurred during the Holocene. Such simulations provide a means to test the potential

707   robustness of aRSAP in the Klamath area.

708

709   **5. Conclusion**

32

710 Although methodologically challenging, calibrating PAR-biomass models is an important step

711 towards quantitative reconstruction of past vegetation. Our calibration steps included estimating

712 the spatial extent represented by the pollen system, comparing two estimates of the

713 ~~pollenshed~~RSAP, and evaluating PAR-AGL models. We found comparable aRSAP and tRSAP

714 estimates that aligned with expectations given the modern forest's dense, closed conditions. We

715 also demonstrated that PARs of major tree taxa derived from lake sediments are linearly related

716 to distance-weighted AGL, and our PAR-AGL$_{dw}$ models accurately reconstruct modern lake-

717 surrounding biomass. According to PAR values from local and regional lakes sites, our modern

718 models are broad enough to capture a range of forest structures over the last 15,000 years BP.

719 We therefore conclude that our results prove the utility of calibrated PAR-AGL models for

720 quantitative reconstruction of past vegetation.

33

References

Allison P and Bottjer DJ (2011) Taphonomy: Bias and process through time. In: Allison PA and

Bottjer DJ (eds) *Taphonomy*. Netherlands: Springer, pp.1–17.

Andersen ST (1970) The relative pollen productivity and pollen representation of north European

trees, and correction factors for tree pollen spectra. *Danmarks geologiske*

Undersogelse 96:1–99.

Appleby P and Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of

supply of unsupported 210Pb to the sediment. *Catena* 5:1–8.

Aquino-López MA, Blaauw J, Christen A, and Sanderson NK (2018) Bayesian Analysis of 210-

Pb Dating. *Journal of Agricultural, Biological, and Environmental Studies*

23:317-333.

Blaauw M and Christen JA (2011) Flexible paleoclimate age-depth models using an

autoregressive gamma process. *Bayesian Analysis* 6:457–474.

Baskaran M, Miller CJ, Kumar A et al. (2015) Sediment accumulation rates and sediment

dynamics using five different methods in a well-constrained impoundment: Case

study from Union Lake, Michigan. *Journal of Great Lakes Research* 41:607–617.

Bennett KD (1983) Postglacial population expansion of forest trees in Norfolk, UK. *Nature* 303:

164–67.

Bennett KD (1986) The rate of spread and population increase of forest trees during the

postglacial. *Philosophical Transactions of the Royal Society of London, Series B*

314:523–531.

34

743 Blarquez O, Carcaillet C, Elzein TM et al. (2011) Needle accumulation rate model-based

744   reconstruction of paleo-tree biomass in the western subalpine Alps. *The Holocene*

745   22:579–587.

746 Briles CE, Whitlock C, and Bartlein PJ (2005) Postglacial vegetation, fire, and climate history of

747   the Siskiyou Mountains, Oregon, USA. *Quaternary Research* 64:44–56.

748 Briles CE, Whitlock C, Bartlein PJ et al. (2008) Regional and local controls on postglacial

749   vegetation and fire in the Siskiyou Mountains, northern California, USA.

750   *Palaeogeography, Palaeoclimatology, Palaeoecology* 265:159–169.

751 Briles CE, Whitlock C, Skinner CN et al. (2011) Holocene forest development and maintenance

752   on different substrates in the Klamath Mountains northern California, USA.

753   *Ecology* 92:590–601.

754 Broström A, Gaillard M-J, Ihse M et al. (1998) Pollen–landscape relationships in modern

755   analogues of ancient cultural landscapes in southern Sweden — a first step

756   towards quantification of vegetation openness in the past. *Vegetation History and*

757   *Archaeobotany* 7:189–201.

758 Broström A, Sugita S and Gaillard M-J (2004) Pollen productivity estimates for the

759   reconstruction of past vegetation cover in the cultural landscape of southern

760   Sweden. *The Holocene* 14:368–381.

761 Broström A, Sugita S, Gaillard M-J et al. (2005) Estimating the spatial scale of pollen dispersal

762   in the cultural landscape of southern Sweden. *The Holocene* 15:252–262.

763 Bunting MJ, Gaillard M-J, Sugita S et al. (2004) Vegetation structure and pollen source area. *The*

764   *Holocene* 14:651–660.

35

765   Bunting MJ, Armitage R, Binney HA et al. (2005) Estimates of 'relative pollen productivity' and

766   'relevant source area of pollen' for major tree taxa in two Norfolk (UK)

767   woodlands. *The Holocene* 15:459–465.

768   Bunting MJ and Middleton R (2005) Modelling pollen dispersal and deposition using HUMPOL

769   software: simulating wind roses and irregular lakes. *Review of Palaeobotany and*

770   *Palynology* 134:185–196.

771   Bunting MJ and Middleton R (2009) The Multiple Scenario Approach: a pragmatic method for

772   past vegetation mosaic reconstruction. *The Holocene* 19:799–803.

773   Bunting MJ and Hjelle KL (2010) Effect of vegetation data collection strategies on estimates of

774   relevant source area of pollen (RSAP) and relative pollen productivity estimates

775   (relative PPE) for non-arboreal taxa. *Vegetation History and Archaeobotany*

776   19:365–374.

777   Bunting MJ, Farrell M, Broström A et al. (2013) Palynological perspectives on vegetation

778   survey: a critical step for model-based reconstruction of Quaternary land cover.

779   *Quaternary Science Reviews* 82:41–55.

780   Burnham KP and Anderson DR (2002) Model selection and multimodel inference: a practical

781   information-theoretic approach. New York: Springer-Verlag.

782   Calcote R (1995) Pollen source area and pollen productivity: evidence from forest hollows.

783   *Journal of Ecology* 83:591–602.

784   Cheng STE (2004) *Forest Service Research Natural Areas in California.* General Technical

785   Report PSW-GTR-188. Pacific Southwest Research Station, Forest Service, U.S.

786   Department of Agriculture, Albany, CA.

36

787   Christen JA and Fox C (2010) A general purpose sampling algorithm for continuous

788   distributions (the t-walk). *Bayesian Analysis* 5:263–281.

789   Colombaroli D and Gavin DG (2010) Highly episodic fire and erosion regime over the past

790   2,000 years in the Siskiyou Mountains, Oregon. *Proceedings of the National*

791   *Academy of Sciences* 107:18909–18914.

792   Commerford JL, McLauchlan KK and Sugita S (2013) Calibrating vegetation cover and

793   grassland pollen assemblages in the Flint Hills of Kansas, USA. *American*

794   *Journal of Plant Sciences* 4:1–10.

795   Crawford JN, Mensing SA, Lake FK et al. (2015) Late Holocene fire and vegetation

796   reconstruction from the western Klamath Mountains, California, USA: A

797   multidisciplinary approach for examining potential human land-use impacts. *The*

798   *Holocene* 25:1341–1357.

799   Crowley PH (1992) Resampling methods for computation-intensive data analysis in ecology and

800   evolution. *Annual Review of Ecological Systems* 23:405–447.

801   Daniels ML, Anderson RS and Whitlock C (2005) Vegetation and fire history since the Late

802   Pleistocene from the Trinity Mountains, northwestern California, USA. *The*

803   *Holocene* 15:1062–1071.

804   Davis MB (1963) On the theory of pollen analysis. *American Journal of Science* 261:897–912.

805   Davis MB (1967b) Pollen deposition in lakes as measured by sediment traps. *Geological Society*

806   *of America Bulletin* 78: 849–58.

807   Davis MB and Deevey ES (1964) Pollen accumulation rates: estimates from Late-Glacial

808   sediment Rogers Lake. *Science* 145:1293–1295.

37

809 Davis MB, Brubaker LB and Webb T (1973) Calibration of absolute pollen influx. In: Birks HJB

810 and West RG (eds) *Quaternary Plant Ecology*. Oxford: Blackwell Scientific

811 Publications, pp.9–25.

812 Davis MB, Moeller RE and Ford J (1984) Sediment focusing and pollen influx. In: Haworth EY

813 and Lund JWG (eds) *Lake sediments and environmental history.* Minneapolis:

814 University of Minnesota Press, pp.261–93.

815 Davis MB (2000) Palynology after Y2K: Understanding the source area of pollen in sediments.

816 *Annual Review of Earth Planetary Sciences* 28:1–18.

817 Dawson A, Paciorek CJ, Goring SJ, Jackson ST, McLachlan JS, Williams JW (2019)

818 Quantifying trends and uncertainty in prehistoric forest composition in the upper

819 Midwestern United States *Ecology* 100(12):1–18.

820 Doher LI (1980) Palynomorph preparation procedures currently used in the paleontology and

821 stratigraphy laboratories. *U.S. Geological Survey Circular* 830:1–28.

822 Fægri K and Iversen J (1989) *Textbook of Pollen Analysis*. New York: Haffner Press.

823 Fagerlind F (1952) The real significance of pollen diagrams. *Botaniska Notiser* 105:185–224.

824 Feldman R, Tomback DF and Koehler J (1999) Cost of mutualism: competition, tree

825 morphology, and pollen production in limber pine clusters. *Ecology* 80:324–329.

826 FIADB (2020) Forest Inventory and Analysis Database version 1.8.0.0.1.

827 https://apps.fs.usda.gov/fia/datamart/datamart.html

828 Gaillard M-J, Sugita S, Broström A et al. (2000) Long term land-cover changes on regional to

829 global scales inferred from fossil pollen — how to meet the challenges of climate

830 research? *Pages Newsletter* 8:30–32.

38

831 Gaillard M-J, Sugita S, Mazier F et al. (2010) Holocene land-cover reconstructions for studies on

832   land cover-climate feedbacks. *Climate of the Past* 6:483–499.

833 Giesecke T (2005) Moving front or population expansion: how did *Picea abies* (L.) Karst.

834   become frequent in central Sweden? *Quaternary Science Reviews* 24:2495–509.

835 Giesecke T, Fontana SL (2008) Revisiting pollen accumulation rates from Swedish lake

836   sediments. *The Holocene* 18:293-305.

837 Gregory PH (1973) *The Microbiology of the Atmosphere*. London: L. Hill Publishers.

838 Halbritter H, Ulrich S, Grímsson F et al. (2018) *Illustrated Pollen Terminology.* Vienna:

839   Springer International Publishing.

840 Han Y, Liu H, Hao Q et al. (2017) More reliable pollen productivity estimates and relative

841   source area of pollen in a forest-steppe ecotone with improved vegetation survey.

842   *The Holocene* 27:1567–1577.

843 Hellman S, Gaillard MJ, Broström A et al. (2008a) The REVEALS model, a new tool to estimate

844   past regional plant abundance from data in large lakes: validation in southern

845   Sweden. *Journal of Quaternary Science* 23:21–42.

846 Hellman S, Broström A, Gaillard MJ et al. (2008b) Effects of the sampling design and selection

847   of parameter values on pollen based quantitative reconstructions of regional

848   vegetation: a case study in southern Sweden using the REVEALS model.

849   *Vegetation Historical Archaeobotany* 17:445–460.

850 Hellman S, Bunting MJ and Gaillard M-J (2009) Relevant Source Area of Pollen in patchy

851   cultural landscapes and signals of anthropogenic landscape disturbance in the

852   pollen record: A simulation approach. *Review of Palaeobotany and Palynology*

853   153:245–258.

39

854   Hicks, S. and Hyvarinen, H. 1999: Pollen influx values measured in different sedimentary

855   environments and their palaeoecological implications. *Grana* 38:228–42.

856   Hicks S (2001) The use of annual arboreal pollen deposition values for delimiting tree-lines in

857   the landscape and exploring models of pollen dispersal. *Review of Palaeobotany*

858   *and Palynology* 117:1–29.

859   Hicks S (2006) When no pollen does not mean no trees. *Vegetation History and Archeobotany*

860   15:253–261.

861   Hickman JC (1993) *The Jepson manual: higher plants of California*. Berkeley: University of

862   California Press.

863   Hudiburg T, Law B, Turner DP et al. (2009) Carbon dynamics of Oregon and Northern

864   California forests and potential land-based carbon storage. *Ecological*

865   *Applications* 19:163–180.

866   Hyvärinen H (1975) Absolute and relative pollen diagrams from northernmost Fennoscandia.

867   *Fennia* 142:1–23.

868   Irwin WP (1981) Tectonic accretion of the Klamath Mountains. In: Ernst WG (ed) *The*

869   *Geotectonic Development of California*. Englewood Cliffs: Prentice Hall, pp.29–

870   49.

871   Jackson ST (1990) Pollen Source Area and Representation in Small Lakes of the Northeastern

872   United States. *Review of Palaeobotany and Palynology* 63:53–76.

873   Jweda J and Baskaran M (2011) Interconnected riverine-lacustrine systems as sedimentary

874   repositories: Case study in southeast Michigan using 210-Pb and 137-Cs sediment

875   accumulation and mixing models. *Journal of Great Lakes Research* 37:432–446.

876   Knapp RO (1969) *How to know pollen and spores*. Minneapolis: W.C. Brown Company.

40

877   Knight CA, Cogbill CV, Potts MD et al. (2020) Settlement-era forest structure and composition

878   in the Klamath Mountains: Reconstructing a historical baseline. *Ecosphere*

879   11:e03250.

880   Likens GE and Davis MB (1975) Post-glacial History of Mirror Lake and its Watershed in New

881   Hampshire: an Initial Report. *Internationale Vereinigung für Theoretische und*

882   *Angewandte Limnologie* 19:982–993.

883   MacDonald GM (1993) Fossil pollen analysis and the reconstruction of plant invasions.

884   *Advances in Ecological Research* 24:67–109.

885   Marquer L, Gaillard M-J, Sugita S et al. (2014) Holocene changes in vegetation composition in

886   northern Europe: why quantitative pollen-based vegetation reconstructions

887   matter. *Quaternary Science Reviews* 90:199–216.

888   Matthias I and Giesecke T (2014) Insights into pollen source area, transport and deposition from

889   modern pollen accumulation rates in lake sediments. *Quaternary Science Reviews*

890   87:12–23.

891   Mohr JA, Whitlock C and Skinner CN (2000) Postglacial vegetation and fire history, eastern

892   Klamath Mountains, California. *The Holocene* 10:587–601.

893   Morris JL, DeRose JR and Brunelle AR (2015) Long-term landscape changes in a subalpine

894   spruce-fir forest in central Utah, USA. *Forest Ecosystems* 2:1–12.

895   Muggeo VM (2008) Segmented: an R package to fit regression models with broken-line

896   relationships. *R News* 8:20–25.

897   Nielsen AB and Sugita S (2005) Estimating Relevant Source Area of Pollen for Small Danish

898   Lakes around AD 1800. *The Holocene* 15:1006–1020.

41

899   Odgaard BV (1993) Wind-determined sediment distribution and Holocene sediment yield in a

900   small, Danish kettle lake. *Journal of Paleolimnology* 8:3–13.

901   Parsons R and Prentice IC (1981) Statistical approaches to R-values and the pollen vegetation

902   relationship. *Review of Palaeobotany and Palynology* 32:127–152.

903   Poska A, Meltsov V, Sugita S et al. (2011) Relative pollen productivity estimates of major

904   anemophilous taxa and relevant source area of pollen in a cultural landscape of

905   the semi-boreal forest zone (Estonia). *Review of Palaeobotany and Palynology*

906   167:30–39.

907   Prentice IC (1985) Pollen representation, source area, and basin size: towards a unified theory of

908   pollen analysis. *Quaternary Research* 23:76–86.

909   Prentice IC (1988) Records of vegetation in time and space: the principles of pollen analysis. In:

910   Huntley B and Webb T III (eds) *Vegetation history*. Dordrecht: Kluwer Academic

911   Publishers, pp.17–42.

912   Ritchie JC (1969) Absolute pollen frequencies and carbon-14 age of Holocene lake sediment

913   from the Riding Mountain area of Manitoba. *Canadian Journal of Botany* 47:

914   1345–1349.

915   Sawyer JO and Thornburg DA (1977) Montane and subalpine vegetation of the Klamath

916   Mountains. In: Barbour MG and Major J (eds) *Terrestrial Vegetation of*

917   *California*. Berkeley: California Native Plant Society, pp.699–732.

918   Sevillano V, Holt K and Aznarte JL (2020) Precise automatic classification of 46 different pollen

919   types with convolutional neural networks. *PLoS ONE* 15:e0229751.

42

920 Seppä H and Hicks S (2006) Integration of modern and past pollen accumulation rate (PAR)

921 records across the arctic tree-line: a method for more precise vegetation

922 reconstructions. *Quaternary Science Review* 25:1501–1516.

923 Seppä H, Alenius T, Muukkonen P et al. (2009) Calibrated pollen accumulation rates as a basis

924 for quantitative tree biomass reconstructions. *The Holocene* 19:209–220.

925 Sjögren P, van der Knaap WO, Huuskoc A, van Leeuwen JFN (2008) Pollen productivity,

926 dispersal, and correction factors for major tree taxa in the Swiss Alps based on

927 pollen-trap results. *Review of Palaeobotany and Palynology* 152:200–210.

928 Skinner CN, Taylor AH and Agee JK (2006) Klamath Mountains Bioregion. In: Sugihara NG,

929 van Wagtendonk JW, Fites-Kaufmann J, Shaffer KE and Thode AE (eds) *Fire in*

930 *California's ecosystems*. Berkeley: University of California Press, pp.170–194.

931 Skinner CN, Taylor AH, Agee JK et al. (2018) Klamath Mountains bioregion. In: van

932 Wagtendonk JW, Sugihara NS, Stephens SL, Thode A, Shaffer K, and Fites-

933 Kaufmann J (eds) *Fire in California's ecosystems*. Berkeley: University of

934 California Press, pp.171–193.

935 Soepboer W, Sugita S, Lotter AF et al. (2007) Pollen productivity estimates for quantitative

936 reconstruction of vegetation cover on the Swiss Plateau. *The Holocene* 17:65–77.

937 Stockmarr J (1971) Tablets with spores used in pollen analysis. *Pollen and Spores* 13:615–621.

938 Sugita S (1993) A model of pollen source area for an entire lake surface. *Quaternary Research*

939 39:239–244.

940 Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: Theory and method

941 in patchy vegetation. *Journal of Ecology* 82:881–897.

942 Sugita S (1998) Modelling pollen representation of vegetation. In: Gaillard M-J and Berglund

43

943   BE (eds) *Quantification of land surfaces cleared of forests during the Holocene –*

944   *modern pollen/vegetation/landscape relationships as an aid to the interpretation*

945   *of fossil pollen data*. Gustav Fischer Verlag, pp.1–18.

946   Sugita S, Gaillard M-J and Broström A (1999) Landscape openness and pollen records: a

947   simulation approach. *The Holocene* 9:409–421.

948   Sugita S (2007a) Theory of quantitative reconstruction of vegetation I: Pollen from large sites

949   REVEALS regional vegetation composition. *The Holocene* 17:229–241.

950   Sugita S (2007b) Theory of quantitative reconstruction of vegetation II: All you need is LOVE.

951   *The Holocene* 17:243–257.

952   Sutton OG (1947) The problem of diffusion in the lower atmosphere. *Quarterly Journal of the*

953   *Royal Meteorological Society* 73: 257–276.

954   Sutton OG (1953) Micrometeorology. New York: McGraw-Hill.

955   Swetnam TW, Allen CD and Betancourt JL (1999) Applied historical ecology: Using the past to

956   manage for the future. *Ecological Applications* 9:1189–1206.

957   Taylor AH and Skinner CN (2003) Spatial patterns and controls on historical fire regimes and

958   forest structure in the Klamath Mountains. *Ecological Applications* 13:704–719.

959   Theuerkauf M, Kuparinen A and Joosten H (2012) Pollen productivity estimates strongly depend

960   on assumed pollen dispersal. *The Holocene* 23: 14–24.

961   Tonkova S, Hicks S, Bozilovaa E, Atanassova J (2001) Pollen monitoring in the central Rila

962   Mountains, Southwestern Bulgaria: comparisons between pollen traps and surface

963   samples for the period 1993±1999. *Review of Palaeobotany and Palynology*

964   117:167–182.

44

965 United States Department of Agriculture, Forest Service (2000) *Timber Cruising Handbook and*

966 *Amendments.* Technical Report FSH 2409.12. Washington, DC, USA.

967 Von Post L (1918) Skogsträdpollen i sydsvenska torvmosselagerföljder. In: Forhandlinger ved de

968 skandinaviske naturforskeres 16. Møte i Kristiania den 10–15. Juli 1916.

969 Skandinaviska Naturforskaremöten, Kristiania, pp.432–465

970 Wahrhaftig C and Birman JH (1965) The Quaternary of the Pacific mountain system in

971 California. In: HE Wright and Frey DG (eds) *Quaternary of the United States*.

972 Princeton: Princeton University Press, pp.299–341.

973 Wang Y and Herzschuh U (2011) Reassessment of Holocene vegetation change on the upper

974 Tibetan Plateau using the pollen-based REVEALS model. *Review of*

975 *Palaeobotany and Palynology* 168:31–40.

976 Wanket J (2002) *Late Quaternary vegetation and climate of the Klamath Mountains.* PhD

977 Dissertation, University of California, Berkeley, USA.

978 Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*

979 *Monographs* 30:279–338.

980 Zhou X and Hemstrom MA (2009) *Estimating aboveground tree biomass on forest land in the*

981 *Pacific Northwest: a comparison of approaches*. PNW-RP-584. US Department

982 of Agriculture, Forest Service, Pacific Northwest Research Station.

45
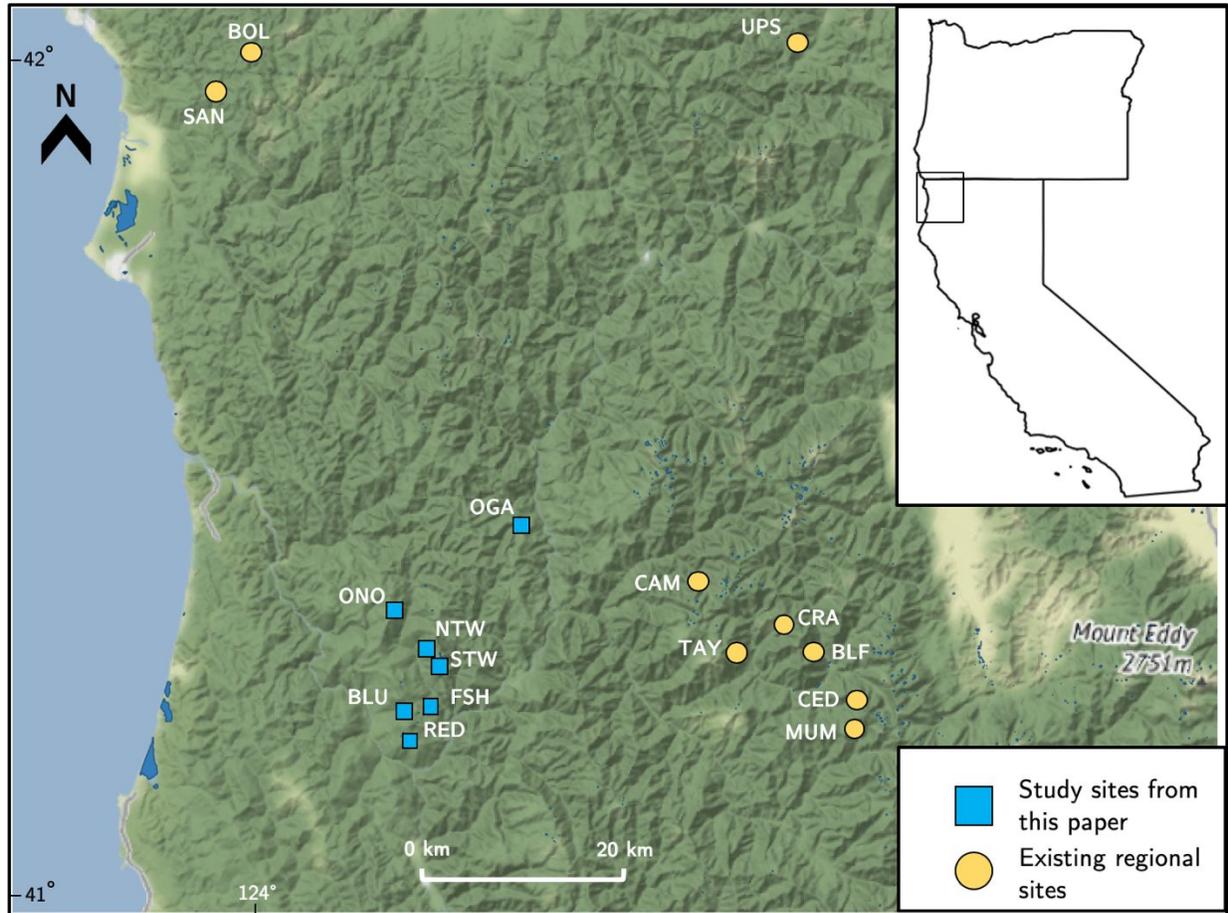
Figure 1. Map shows study sites (blue squares) in northwestern California: Blue Lake (BLU), Fish Lake (FSH), North Twin Lake (NTW), Lake Ogaromtoc (OGA), Onion Lake (ONO), Red Mountain Lake (RED), and South Twin Lake (STW). Note that Lake Ogaromtoc and Fish Lake were described in Crawford et al. (2015) and North and South Twin Lake were described in Wanket (2002) but were also studied in this project. Map also shows Holocene-era pollen records from other parts of the region (yellow circles): Bluff (BLF) and Crater (CRA) Lakes (Mohr et al. 2000); Sanger (SAN) and Bolan (BOL) Lakes (Briles et al. 2008); Upper Squaw Lake (USL; Colombaroli and Gavin 2010); Mumbo (MUM) Lake (Daniels et al. 2005); and Campbell (CAM), Taylor (TAY), and Cedar (CED) Lakes (Briles et al. 2011).
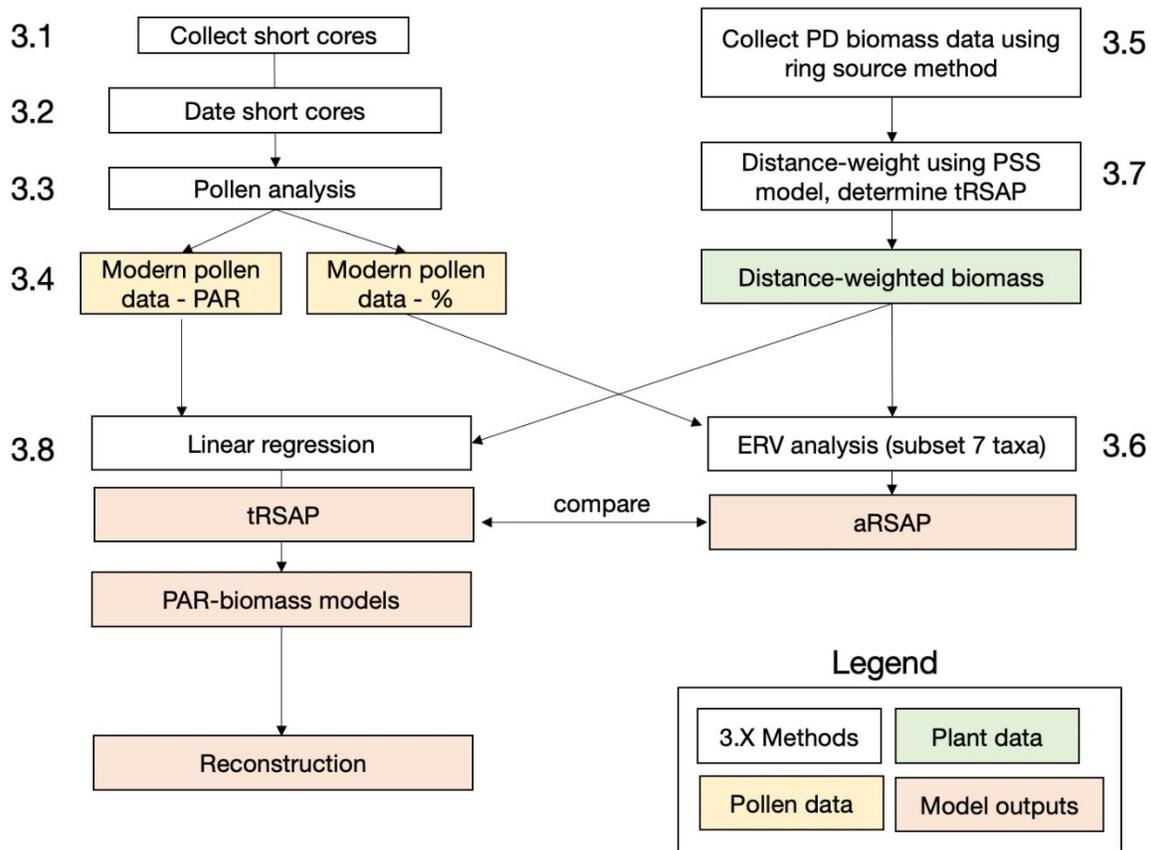
Figure 2. Flowchart of methodological steps leading to a calibrated PAR-biomass model.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
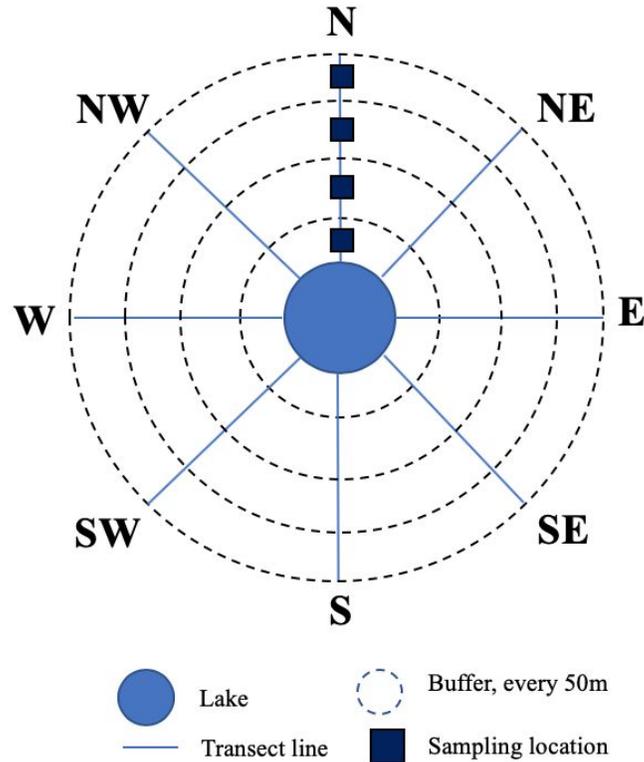
Figure 3. A schematic of the vegetation survey design (not to scale), following Han et al. (2017), that included eight transect lines along the cardinal and sub-cardinal directions where sampling occurred at the mid-point of each concentric ring (the schematic shows an example with only four rings). Sample locations (squares) are shown on the north transect for illustration.
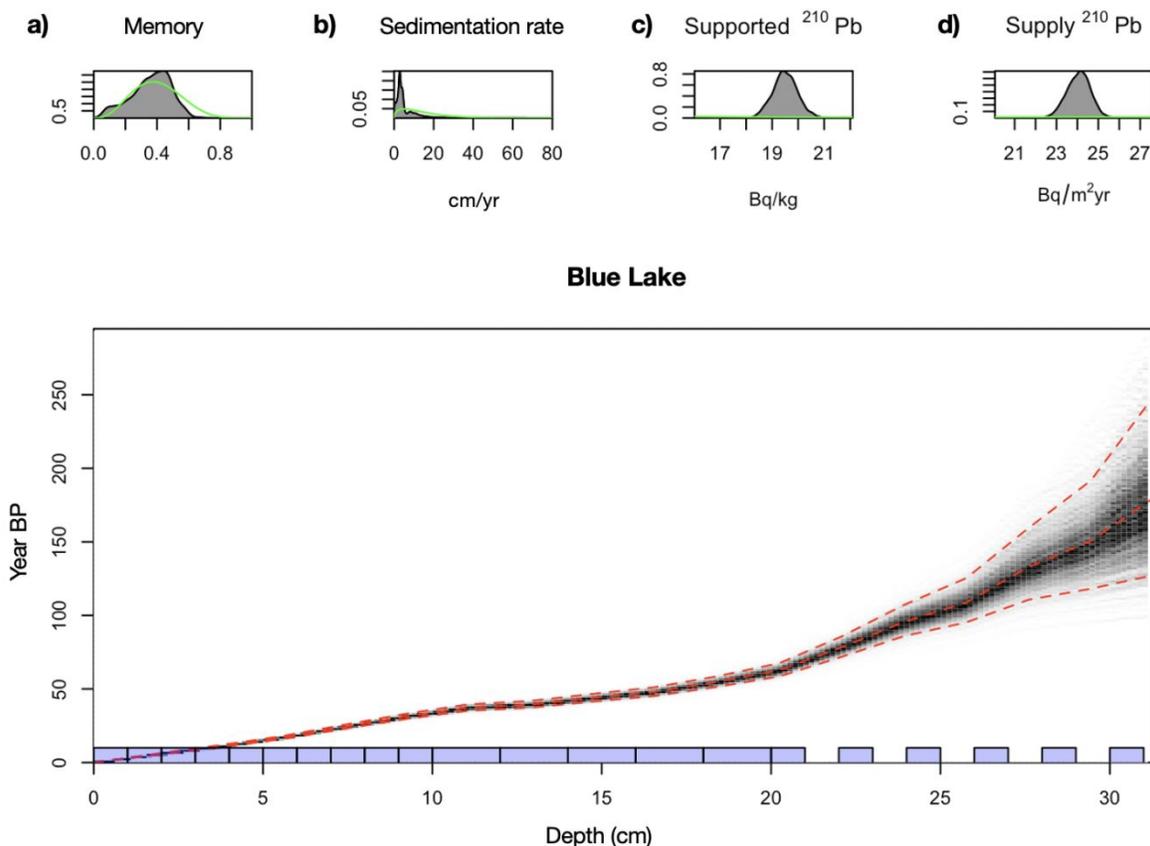
Figure 4. Example of Pb-210 age model construction. The age-to-depth results of the Plum modeling for Blue Lake. The grey lines are simulation from Plum and the dashed red lines represent the mean age and the 95% interval. The small panels at the top show the prior (green) and posterior (grey) distributions for **(a)** the memory (ω), which describes the coherence in sedimentation rates along the core **(b)** the sedimentation rate (α), **(c)** the supported ^{210}Pb (P^S), which is the background level of ^{210}Pb already present in the sediment, and **(d)** and the supply of ^{210}Pb (Φ). For other sites, see Supplementary Information.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
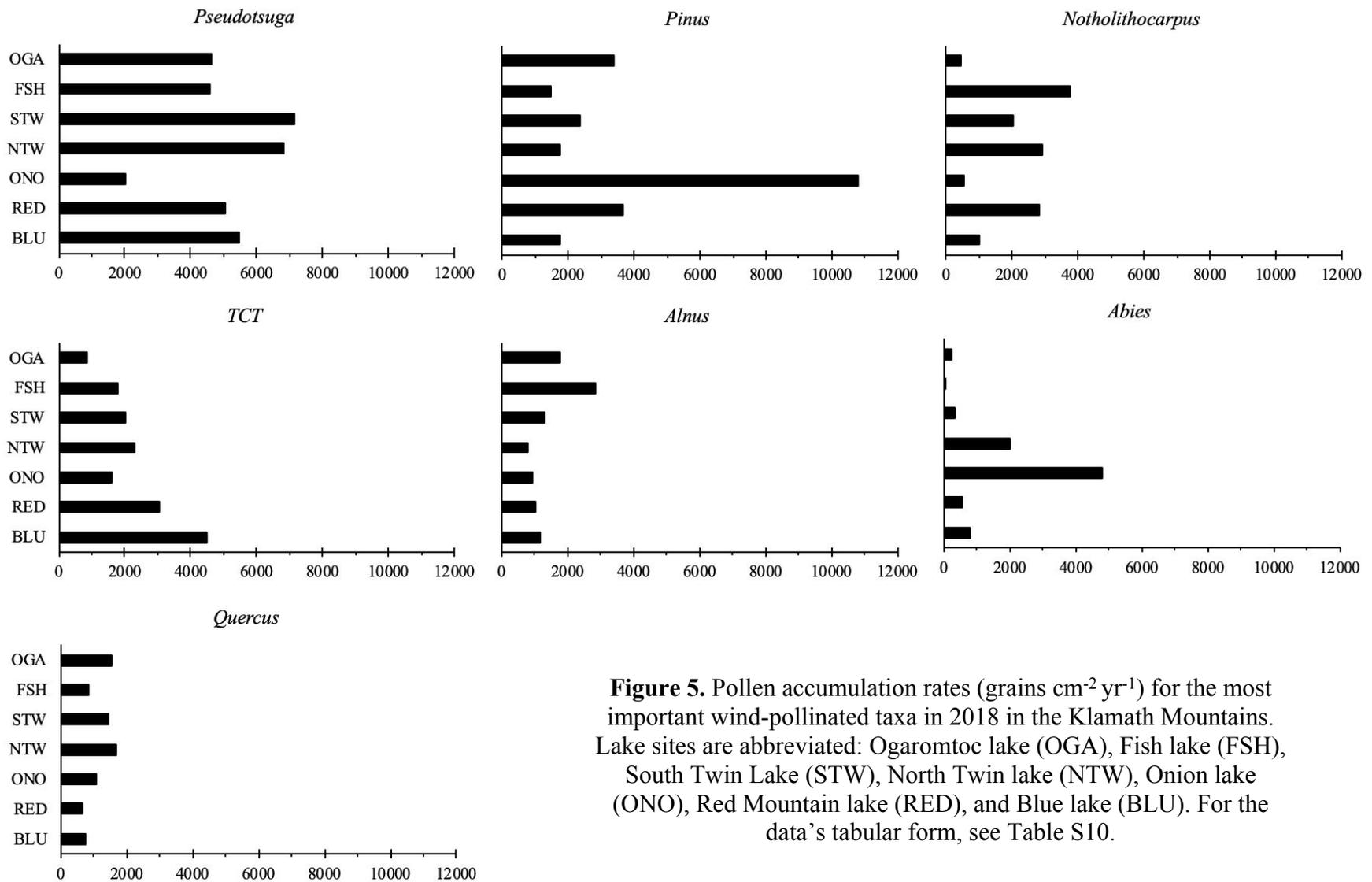
Figure 5. Pollen accumulation rates (grains cm^{-2} yr^{-1}) for the most important wind-pollinated taxa in 2018 in the Klamath Mountains. Lake sites are abbreviated: Ogaromtoc lake (OGA), Fish lake (FSH), South Twin Lake (STW), North Twin lake (NTW), Onion lake (ONO), Red Mountain lake (RED), and Blue lake (BLU). For the data's tabular form, see Table S10.
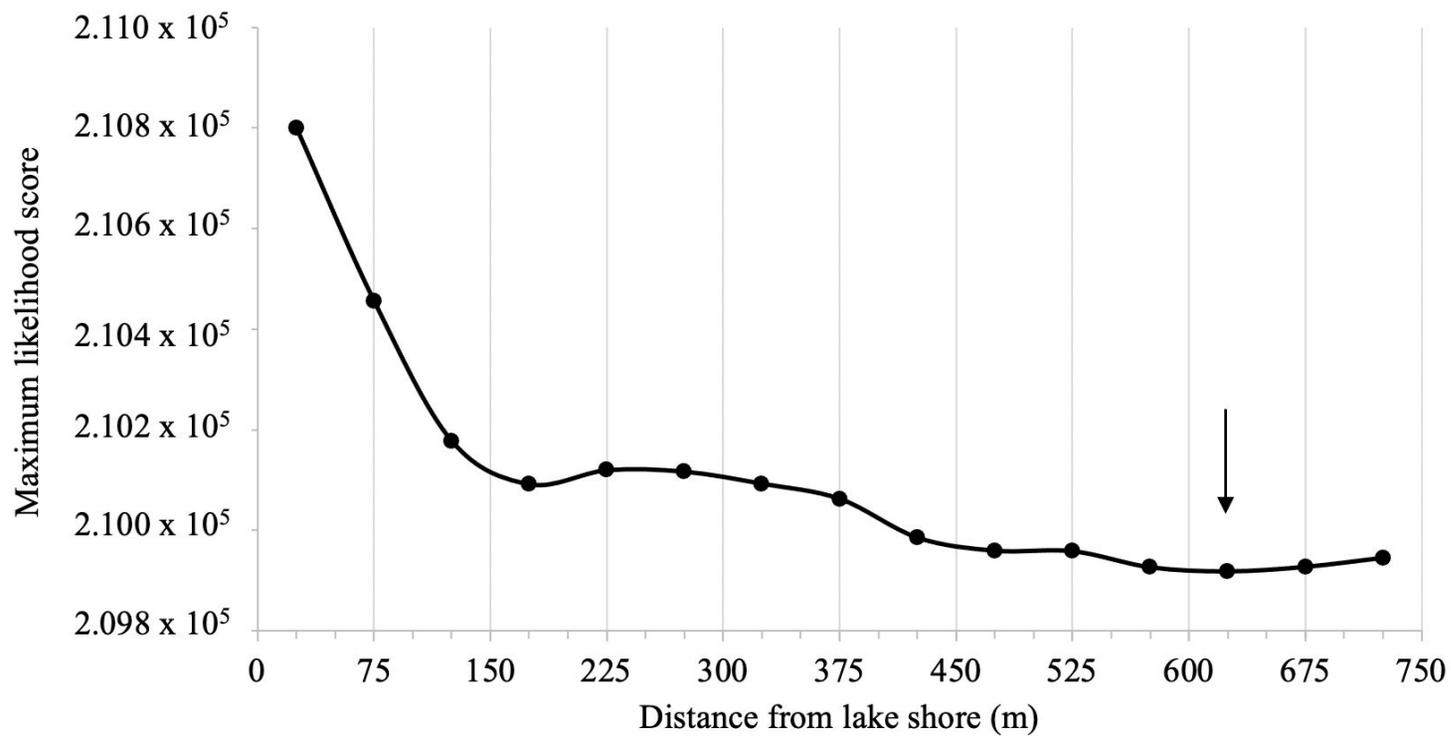
Figure 6. PolERV model 3 results of maximum likelihood scores compared to distance (m). Arrow indicates the aRSAP value (625m).
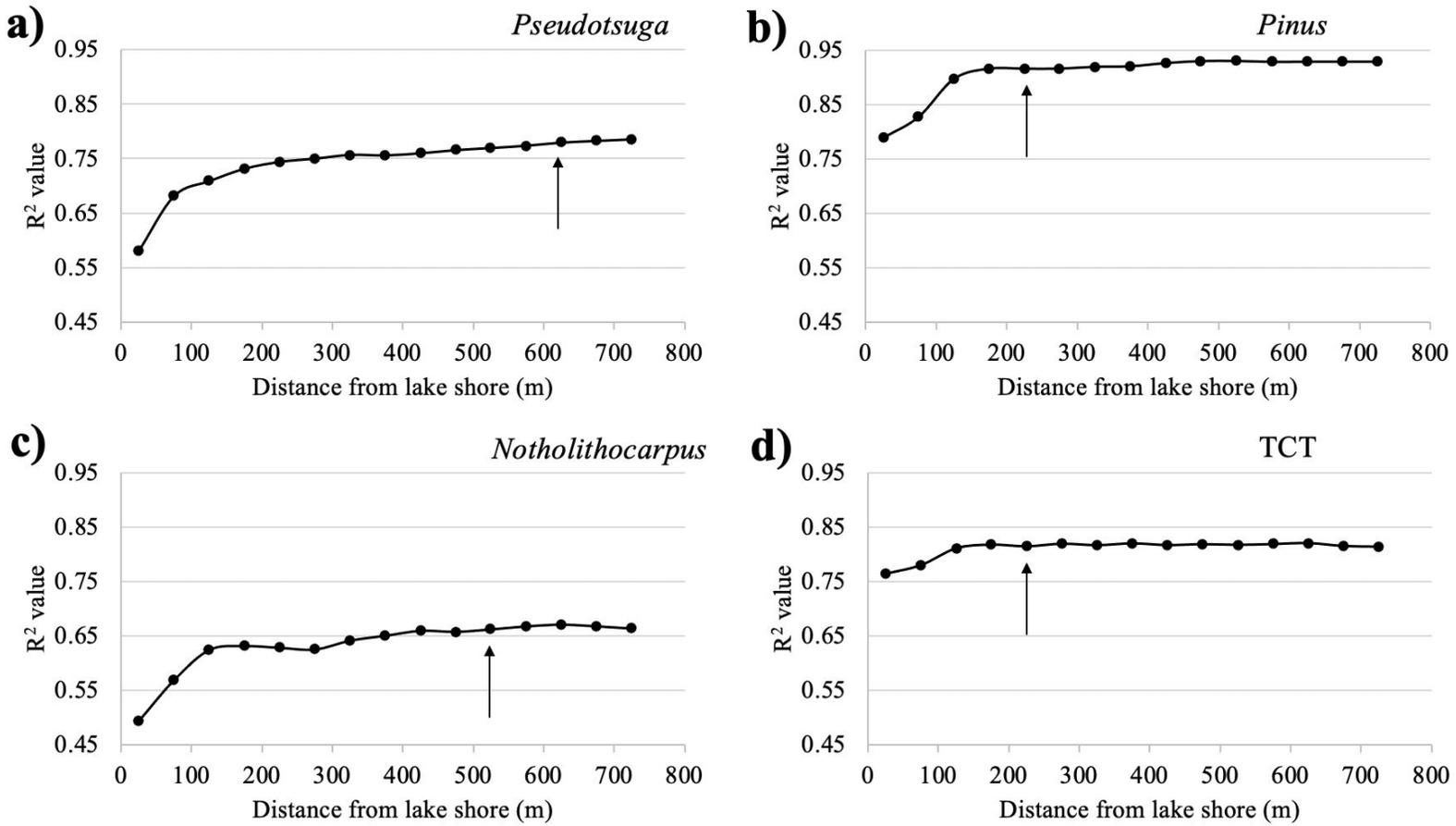
Figure 7. R^2 for regressions between AGL_{dw} and PAR at increasing distance from the lake shore to the furthest vegetation survey site. tRSAP is shown by the arrow: a) *Pseudotsuga* (625m), b) *Pinus* (225m), c) *Notholithocarpus* (525m), and d) TCT (225m).
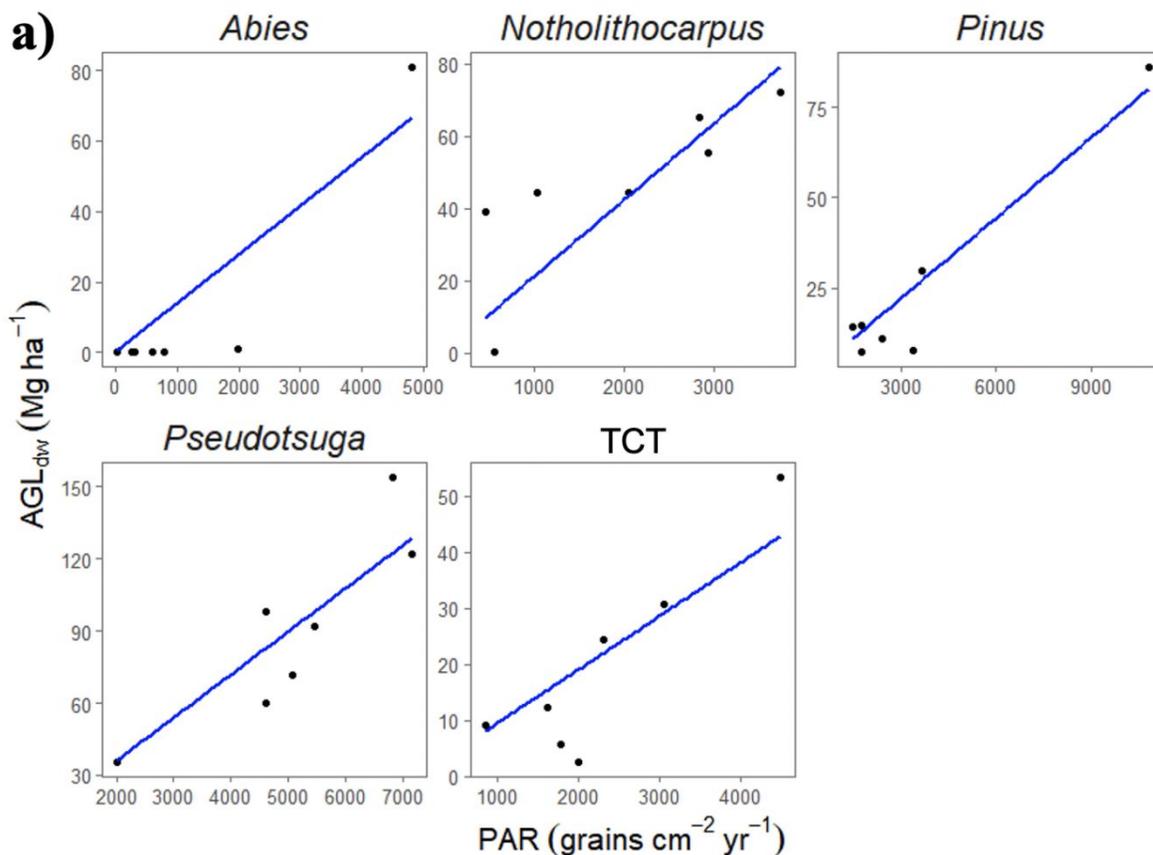
Figure 8a. The relationship between distance-weighted aboveground live biomass (AGL$_{DW}$) and pollen accumulation rate (PAR) for five of the pollen taxa present at the seven lake sites in the Klamath Mountains. Lines represent linear regressions forced through the origin. The relevant source area of pollen (aRSAP) was defined as a circle with a radius of 625 m from the centroid of the lake. Note that the scales change for each pollen taxa. For summaries of the linear models, see Table S11. (Note: Although biomass "predicts" pollen accumulation rates in a functional sense, our aim is to eventually apply calibrated transfer functions to predict biomass in the past; thus, we fitted regression lines with PAR values as the independent variable.)
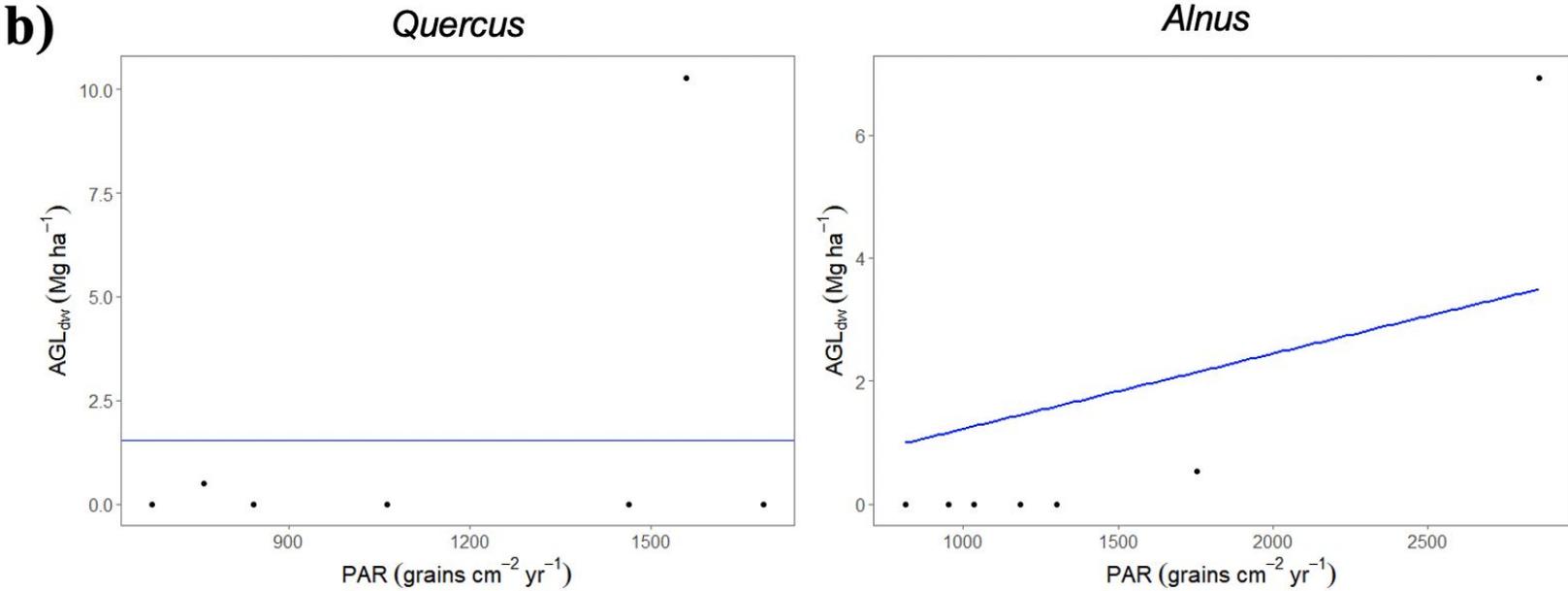
Figure 8b. The relationship between distance-weighted aboveground live biomass (AGL_{dw}) and pollen accumulation rate (PAR) for *Quercus* and *Alnus* at the seven lake sites in the Klamath Mountains. The line represents the intercept of the null model. The relevant source area of pollen was defined as a circle with a radius of 625 m from the centroid of the lake. For details on the linear model, see Table S11.

Table 1. Lake site characteristics and overstory vegetation at each site.

Lake site and code	Lat and long (dec. degrees)	Elevation (m)	Depth at deepest point/sample location (m)	Surface area (ha)	Mature overstory vegetation
Blue (BLU)	-123.69, 41.24	822	4.6	1.4	*C. lawsoniana, P. menziesii, C. chrysaphylla, N. densiflora, A. menziesii, A. rhombifolia, P. lambertiana, T. brevifolia*
Fish (FSH)	-123.68, 41.26	541	13	9.6	*C. lawsoniana, P. menziesii, P. lambertiana, N. densiflora, A. menziesii, A. rhombifolia, C. chrysaphylla*
North Twin (NTW)	-123.67, 41.32	1142	0.5	3.4	*P. menziesii, P. lambertiana, C. lawsoniana, C. chrysaphylla, P. jeffreyi, T. heterophylla, C. decurrens, N. densiflora, A. menziesii*
South Twin (STW)	-123.67, 41.31	1137	1.2	3.5	
Onion (ONO)	-123.75, 41.38	1356	1.5	0.66	*P. ponderosa, P. menziesii, A. magnifica, C. decurrens, A. concour, P. lambertiana, T. brevifolia*
Ogaromtoc (OGA)	-123.54, 41.49	600	6.3	1.74	*P. menziesii, N. densiflora, P. lambertiana, A. macrophylla, A. rhombifolia, A. menziesii, U. californica, C. decurrens, Q. kelloggii, Q. garryana*
Red Mountain (RED)	-123.69, 41.25	768	1.6	1.2	*C. lawsoniana, P. menziesii, P. lambertiana, N.densiflora, A. menziesii, A. rhombifolia, C. chrysaphylla*

Table 2. Definitions of RSAP, aRSAP, and tRSAP.

Term	Definitional basis and relevant literature
RSAP	Originally described by Sugita (1994) as the "smallest area within which reliable estimates of parameter values and asymptotic r^2 or likelihood function scores can be obtained." The definition was refined as the "distance from a pollen deposition point beyond which the relationship between vegetation composition and pollen assemblage does not improve" (Bunting et al. 2004, with Sugita). Estimates are derived for the overall assemblage from extended R-value analysis (Parsons and Prentice 1981) through inspection of the likelihood function score plot. RSAP varies depending on which taxa and which sites are included in the analysis, thus is dependent on the assemblage chosen for analysis.
aRSAP	Identical to the standard RSAP, but with the addition of an "a" to denote that it is an assemblage-specific metric, in contrast to the tRSAP.
tRSAP	The RSAP concept can be extended to single taxa where pollen taxa are measured independently (e.g., PAR values rather than percentage values). In this situation, we define a taxon-specific Relevant Source Area of Pollen, the tRSAP, as the distance beyond which the correlation between PAR (Y) and distance-weighted plant abundance (ψ) summed to that distance for a single taxon does not improve (Jackson 1990).

Table 3. A comparison of observed to predicted distance-weighted aboveground live biomass (AGL$_{dw}$) for each lake site using the assemblage-level relevant source area pollen (aRSAP) estimates. Predicted AGL$_{dw}$ is the mean from 10,000 resampling iterations; Standard Error is the standard deviation of the 10,000 samples; COV is the coefficient of variation (Standard Error/Predicted AGL$_{dw}$); Bias is the percent difference between predicted and observed AGL$_{DW.}$

Lake	Observed AGL$_{dw}$ (Mg ha^{-1})	Predicted AGL$_{dw}$ (Mg ha^{-1})	Standard Error (Mg ha^{-1})	COV (%)	Bias (%)
Blue	205	189	31.5	17	-7.8
Fish	197	195	31.8	16	-1.1
North Twin	242	251	32.0	13	3.7
Ogaromtoc	127	134	31.6	24	5.7
Onion	215	212	32.1	15	-1.1
Red Mountain	197	218	31.4	14	10.5
South Twin	180	217	31.6	15	20.5

Table 4. A comparison of observed to predicted distance-weighted aboveground live biomass (AGL$_{dw}$) for each lake site using taxon-specific source area pollen estimates (tRSAP). Predicted AGL$_{dw}$ is the mean from 10,000 resampling iterations; Standard Error is the standard deviation of the 10,000 samples; COV is the coefficient of variation (Standard Error/Predicted AGL$_{DW}$); Bias is the percent difference between predicted and observed AGL$_{dw.}$

Lake	Observed AGL$_{dw}$ (Mg ha^{-1})	Predicted AGL$_{dw}$ (Mg ha^{-1})	Standard Error (Mg ha^{-1})	COV (%)	Bias (%)
Blue	196	189	31.5	17	-3.7
Fish	185	195	31.8	16	5.2
North Twin	239	251	32.0	13	4.9
Ogaromtoc	121	134	31.6	24	10.6
Onion	193	212	32.1	15	10.3
Red	184	218	31.4	14	18.4
South Twin	173	217	31.6	15	24.9

Supplemental Information

Title: Linking modern pollen accumulation rates to biomass: Quantitative vegetation reconstruction in the western Klamath Mountains

Authors: Clarke A. Knight, Mark Baskaran, M. Jane Bunting, Marie Champagne, Matthew D. Potts, David Wahl, James Wanket, John J. Battles

1

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
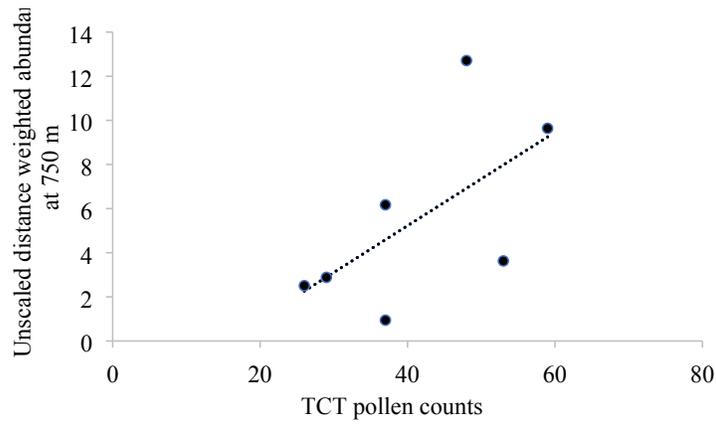
Figure S1. *TCT* pollen counts corrected to the same base sum plotted against unscaled distance weighted plant abundance at 750m to determine the reference taxon for the PolERV model.

2

Sediment dating and age-depth model

We used lead-210 (^{210}Pb; 22.3 yr half-life) to assign ages to sediment deposited in the last 150 years. Surface bulk sediments from 0 cm to a maximum of 45 cm were taken from each core and dried to 105°C (see Tables S1-S7). ^{210}Pb activity was determined by alpha spectrometry, via ^{210}Po. An aliquot of 0.2 to 1.0 g of dried and pulverized sample was digested using concentrated HF, HNO$_3$, and HCl and a known amount of ^{209}Po spike in an oven at 90°C for ~ 24 hours. The digested solution was dried, and the residue was mixed with 1 M HCl until the pH was ~2. Auto-plating of Po was cold-plated onto an Ag disk for 24 hours at room temperature (Jweda and Baskaran 2011). The plated disk was assayed for Po using Octete PC ORTEC alpha spectrometer. The reagent blanks were run simultaneously with each batch of eight samples and were subtracted. Certified reference materials were periodically run. For the determination of parent-supported (i.e., background) ^{210}Pb, several samples were run for the activity of ^{226}Ra (using 352 and 609 keV) along with ^{137}Cs (661.6 keV) by Ge-well detector (Baskaran et al. 2015). Small sample sizes prevented reliable ^{137}Cs from being obtained.

We used the Bayesian-based Plum software to develop age models from excess (unsupported) ^{210}Pb data (Aquino-López et al. 2018). The Plum model is related to the constant rate of supply (CRS) method (Appleby and Oldfield 1978) and retains two of the basic assumptions of CRS: the rate of supply of ^{210}Pb is constant and there is no vertical mixing of radionuclides. Testing these assumptions requires independent validation using another marker, which is outside of this paper's scope. The Plum model is formulated within a robust statistical framework to quantify uncertainty (Aquino-López et al. 2018). Plum uses a self-adjusting Markov Chain Monte Carlo (MCMC) algorithm called the t-walk (Christen and Fox 2010). Plum uses millions of MCMC iterations to model the accumulation of sediment, using a gamma

3

autoregressive semiparametric age-depth function (Blaauw and Christen 2011). This algorithm

results in a probability envelope around the mean age model. The envelope allows the precision

at any depth to be estimated explicitly. Plum makes use of prior information to determine the

datable horizon, which is affected by two factors: the precision of methodology (alpha versus

gamma counting) and the initial amount of excess lead. In Plum, the chronology limit is

determined by the rate of supply of ^{210}Pb to the site and the equipment error, usually ~3 Bq/kg

for a sample size of 1 g by alpha spectrometry for research laboratories. Supported ^{210}Pb

activities were determined from the direct measurements of ^{226}Ra by gamma-ray spectrometry.

4

Figure S2. The age-to-depth results of the Plum model for Fish, Ogaromtoc, Onion, North Twin, Red Mountain, and South Twin Lakes. The grey lines are simulation from Plum and the dashed red lines represent the mean age and the 95% interval. The small panels at the top show the prior (green) and posterior (grey) distributions for **(a)** the memory (ω), **(b)** the sedimentation rate (α), **(c)** the supported ^{210}Pb (P^S), which is the background level of ^{210}Pb already present in the sediment, and **(d)** and the supply of ^{210}Pb (Φ).

5
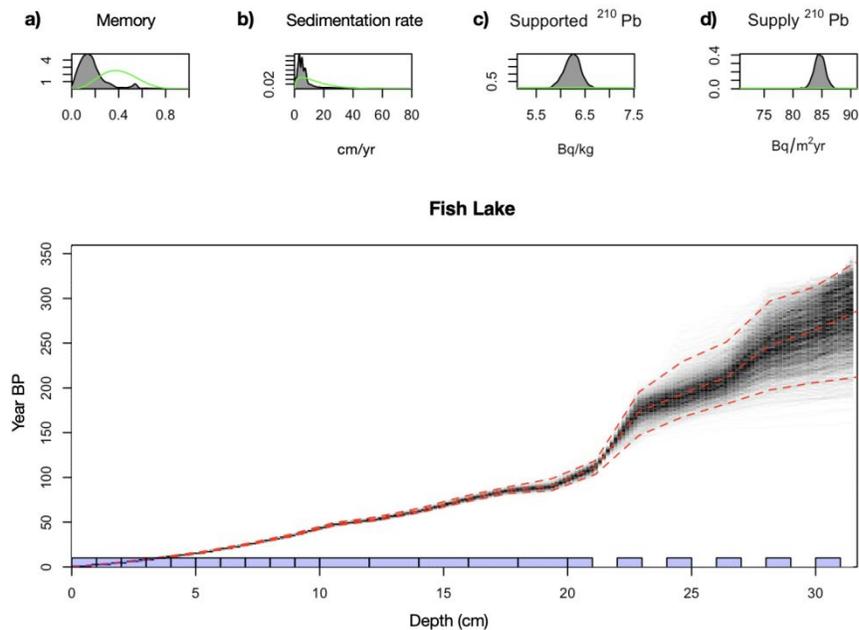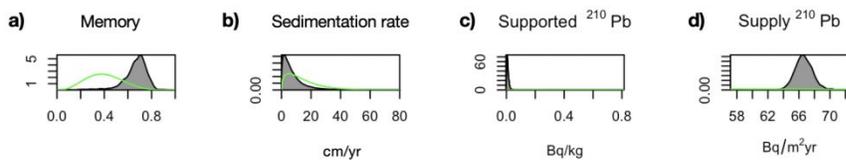
Ogaromtoc Lake

Onion Lake

6

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

a) Memory

b) Sedimentation rate

c) Supported 210 Pb

d) Supply 210 Pb

0.0   0.4   0.8

0   20   40   60   80

cm/yr

10.5   12.0   13.5

Bq/kg

40   44   48

Bq/m²yr

North Twin Lake

Year BP

Depth (cm)

a) Memory

b) Sedimentation rate

c) Supported 210 Pb

d) Supply 210 Pb

0.0   0.4   0.8

0   20   40   60   80

cm/yr

0.0   0.2   0.4

Bq/kg

14.0   15.5   17.0

Bq/m²yr

Red Mountain Lake

Year BP

Depth (cm)

7

a) Memory
b) Sedimentation rate
c) Supported ^{210}Pb
d) Supply ^{210}Pb

cm/yr

Bq/kg

Bq/m²yr

South Twin Lake

Year BP

Depth (cm)
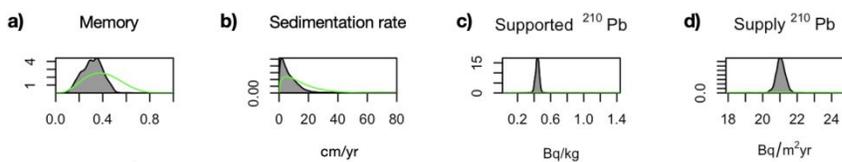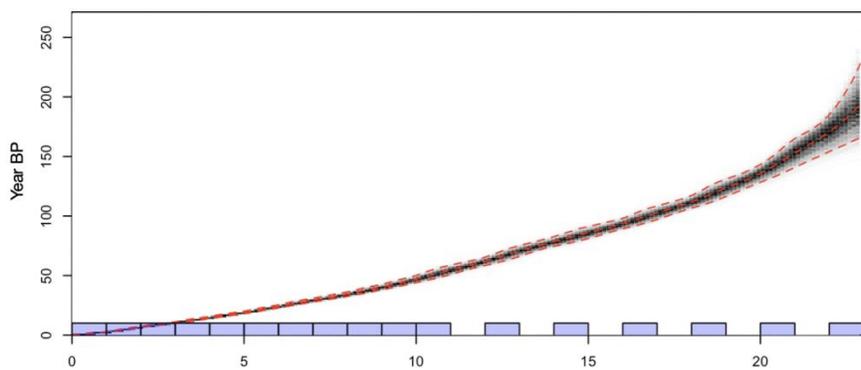
Lithology

Cores were split lengthwise and measured for magnetic susceptibility at every half

centimeter using a calibrated MS2E surface scanning point sensor (MS Bartsoft). Changes in

lithology were described and documented. The water content and dry bulk density were

determined for each core in 1 or 2 cm intervals (Tables S14-S20), matching the sampling pattern

for radioisotopic analysis (Table S1-S7).

Cores were composed of unlaminated gyttja. Occasional diatomaceous lenses (<1 cm

thick) were present in Blue and Ogaromtoc lakes. For the Onion lake core, pine needles were

visible in the top 3 cm, but needles were not seen in the other cores. Magnetic susceptibility was

near zero for Blue, North Twin, Red Mountain, and South Twin lakes, and although magnetic

susceptibility in Ogaromtoc lake was also generally low, Ogaromtoc had two distinct peaks (Fig.

S3). Fish and Onion lakes showed higher overall magnetic susceptibility than the other lakes, as

well as more variation across depths (Fig. S4). Peaks in magnetic susceptibility generally

corresponded to increases in dry bulk density (g cm^{-3}) for Ogaromtoc, Fish, and Onion lakes

(Tables S19, S17, S16, respectively). For example, two peaks at 14-15cm and 22-23cm in

Ogaromtoc matched the depths where dry bulk density tripled and doubled, respectively.

Ogaromtoc also had two light blue clay bands at 14-15cm and 22-23cm. Other cores did not

contain clear stratigraphic markers.

9
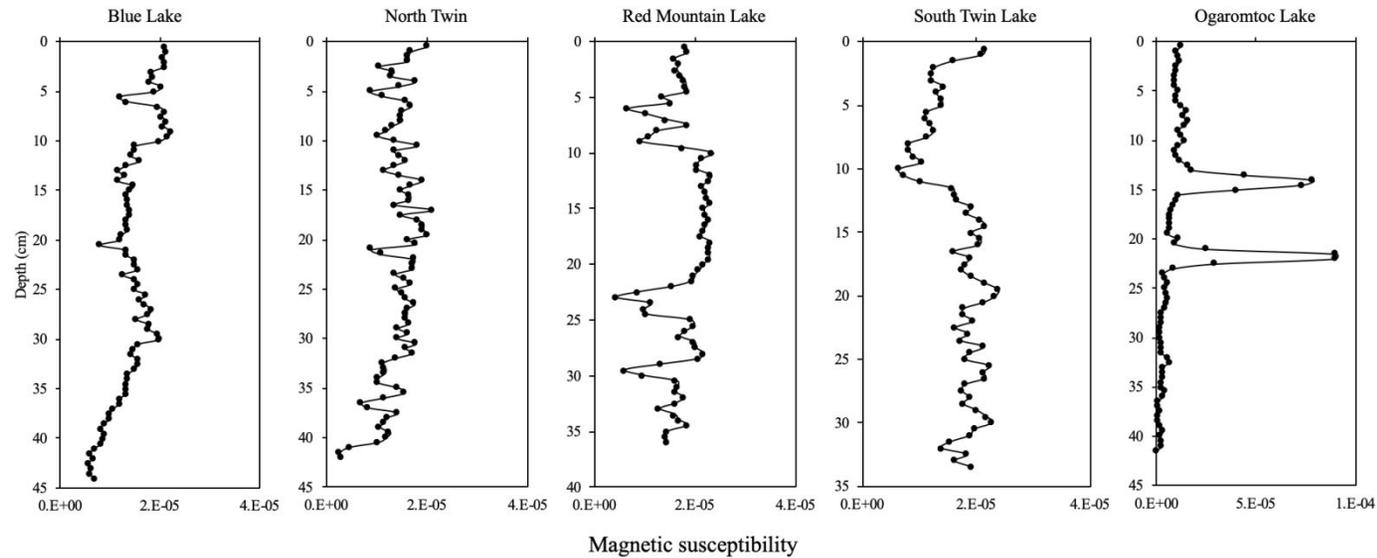
Figure S3. Magnetic susceptibility for the five study sites. The magnetic susceptibility was near zero with some variability for five lakes (note different x-axis for Ogaromtoc) – Blue, North Twin, Red Mountain, South Twin and Ogaromtoc Lakes.
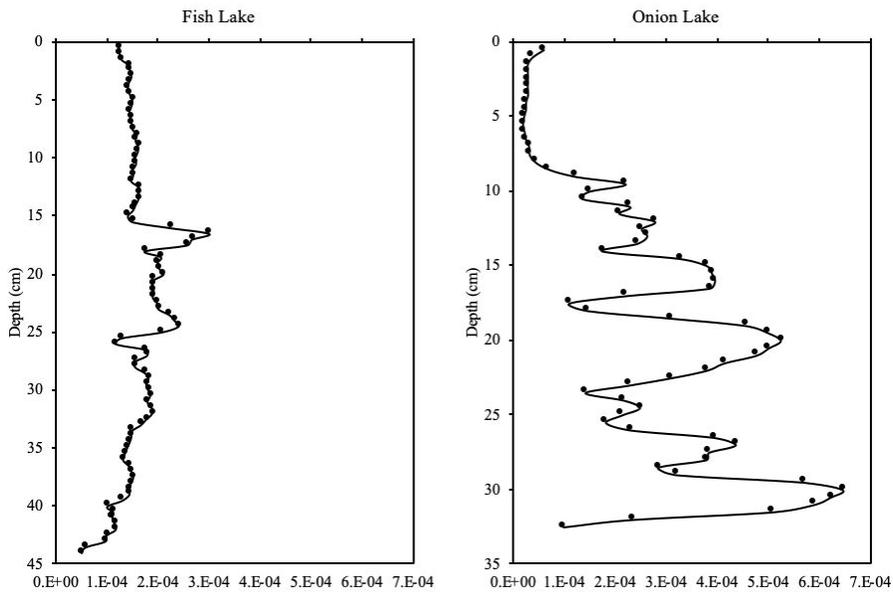
Figure S4. Magnetic susceptibility for the two study sites. Fish and Onion lakes (same x-axis) displayed higher overall magnetic susceptibility than the other five lake sites.

1

Table S1. ^{210}Pb dates used to create the Blue Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	3	0.3	210Pb_12	13.0	38	2
210Pb_2	1.5	6	0.5	210Pb_13	15.0	45	3
210Pb_3	2.5	9	0.6	210Pb_14	17.0	50	3
210Pb_4	3.5	12	0.7	210Pb_15	19.0	57	4
210Pb_5	4.5	15	0.9	210Pb_16	20.5	69	5
210Pb_6	5.5	19	1	210Pb_17	22.5	87	9
210Pb_7	6.5	23	1	210Pb_18	24.5	103	13
210Pb_8	7.5	27	2	210Pb_19	26.5	125	21
210Pb_9	8.5	31	2	210Pb_20	28.5	146	27
210Pb_10	9.5	34	2	210Pb_21	30.5	175	57
210Pb_11	11.0	37	2				

Table S2. ^{210}Pb dates used to create the Fish Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	2	0.2	210Pb_12	12.5	58	2
210Pb_2	1.5	5	0.4	210Pb_13	14.5	70	3
210Pb_3	2.5	8	0.5	210Pb_14	16.5	82	4
210Pb_4	3.5	12	0.6	210Pb_15	18.5	90	6
210Pb_5	4.5	15	0.7	210Pb_16	20.5	110	7
210Pb_6	5.5	20	0.8	210Pb_17	22.5	175	25
210Pb_7	6.5	25	1	210Pb_18	24.5	197	32
210Pb_8	7.5	30	1	210Pb_19	26.5	224	40
210Pb_9	8.5	36	1	210Pb_20	28.5	244	51
210Pb_10	9.5	44	2	210Pb_21	30.5	277	60
210Pb_11	10.5	49	2				

1.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S3. [210]Pb dates used to create the Ogaromtoc Lake age model. An outlier point at 6.5cm was excluded from the model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	3	0.2	210Pb_9	9.5	47	3
210Pb_2	1.5	7	0.4	210Pb_10	10.5	55	4
210Pb_3	2.5	11	0.6	210Pb_11	12.5	71	5
210Pb_4	3.5	15	0.8	210Pb_12	14.5	86	5
210Pb_5	4.5	19	1	210Pb_13	16.5	103	6
210Pb_6	5.5	24	1	210Pb_14	18.5	124	7
210Pb_7	7.5	34	2	210Pb_15	20.5	153	12
210Pb_8	8.5	40	2	210Pb_16	22.5	197	34

Table S4. [210]Pb dates used to create the Onion Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	8	0.6	210Pb_10	9.5	83	3
210Pb_2	1.5	15	0.7	210Pb_11	11.0	88	4
210Pb_3	2.5	24	0.9	210Pb_12	13.0	94	4
210Pb_4	3.5	32	1	210Pb_13	15.0	104	5
210Pb_5	4.5	44	1	210Pb_14	17.0	113	5
210Pb_6	5.5	54	2	210Pb_15	19.0	123	7
210Pb_7	6.5	63	2	210Pb_16	20.5	201	32
210Pb_8	7.5	68	2	210Pb_17	22.5	244	29
210Pb_9	8.5	77	2	210Pb_18	24.5	263	29

Table S5. [210]Pb dates used to create the North Twin Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	2	0.4	210Pb_7	6.5	112	4
210Pb_2	1.5	24	0.8	210Pb_8	7.5	128	5
210Pb_3	2.5	39	1	210Pb_9	8.5	147	6
210Pb_4	3.5	55	1	210Pb_10	9.5	173	10
210Pb_5	4.5	71	2	210Pb_11	11.0	197	18
210Pb_6	5.5	94	3	210Pb_12	13.0	229	30

1

Table S6. ^{210}Pb dates used to create the Red Mountain Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	5	0.3	210Pb_10	9.5	71	5
210Pb_2	1.5	10	0.2	210Pb_11	11.0	75	6
210Pb_3	2.5	16	0.8	210Pb_12	13.0	79	7
210Pb_4	3.5	23	1	210Pb_13	15.0	87	8
210Pb_5	4.5	30	2	210Pb_14	17.0	91	9
210Pb_6	5.5	37	2	210Pb_15	19.0	96	12
210Pb_7	6.5	45	2	210Pb_16	20.5	104	12
210Pb_8	7.5	53	3	210Pb_17	22.5	146	37
210Pb_9	8.5	62	4				

Table S7. ^{210}Pb dates used to create the South Twin Lake age model.

Sample	Depth (cm)	Age (yr)	Uncertainty (yr)	Sample	Depth (cm)	Age (yr)	Uncertainty (yr)
210Pb_1	0.5	3	0.3	210Pb_11	10.5	44	3
210Pb_2	1.5	7	0.4	210Pb_12	12.5	55	3
210Pb_3	2.5	12	0.6	210Pb_13	14.5	68	4
210Pb_4	3.5	17	0.8	210Pb_14	16.5	80	4
210Pb_5	4.5	22	1	210Pb_15	18.5	90	4
210Pb_6	5.5	26	1	210Pb_16	20.5	95	5
210Pb_7	6.5	29	1	210Pb_17	22.5	114	7
210Pb_8	7.5	33	2	210Pb_18	24.5	135	9
210Pb_9	8.5	36	2	210Pb_19	26.5	166	16
210Pb_10	9.5	40	2	210Pb_20	28.5	186	38

1

Assumptions of the Prentice-Sugita-Sutton PVM

As noted in section 2.2, the Prentice-Sugita-Sutton model has certain assumptions (Sugita 1994, Gaillard et al. 2008), which we describe in full here:

1) that there is a comprehendible and spatially and temporally consistent relationship between pollen loading and distance-weighted plant abundance

2) the vegetation surface where the pollen is derived from is flat

3) the sampling basin is a circular opening in the canopy

4) pollen productivity (the amount of pollen produced per vegetation cover unit) is a constant for a given pollen taxon

5) pollen is dispersed as single grains

6) pollen dispersal is largely via wind above the canopy and gravity beneath the canopy, and pollen transport into a basin (canopy opening) can be modelled by considering the canopy component only

7) wind is uniform in every direction therefore pollen dispersal is evenly distributed around the source

8) most pollen deposition takes place via sedimentation due to gravity and deposition by interception is negligible

9) the deposition of pollen at a specified distance from a plant can be approximated using a diffusion model of the dispersal of small particles from a ground level source (Sutton 1953)

10) inter-taxon pollen grain differences (e.g., grain size, weight, and density) affect pollen dispersal and can be quantitatively estimated, and use of a single value to represent each taxon is sufficient to capture

1.

11) atmospheric conditions during pollen deposition can be modelled as "stable" which

affects parameters C_z and n (Eq.3,3a)

12) all lake sites experience the same conditions

PAR calculation

After grains were counted, pollen concentrations and PAR were determined. Using the

Lycopodium marker grains, pollen concentrations (C_i, grains cm^{-3}) were calculated for each

pollen type i using the following equation:

$$C_i = \frac{A_i \times L_a}{L_c \times V_i}$$

(6)

Where A_i is the number of pollen grains counted for the taxon i, L_a is the number of added

marker grains, L_c is the number of counted marker grains in each slide, and V_i is the volume of

the pollen sample (e.g., 0.63 cm^3) (Stockmarr 1971). Concentrations were used for PAR

calculations by multiplying the concentration values by the sediment accumulate rate, which

differed by lake site and was determined by the Plum age model in increments of 0.5cm. The

equation used was:

$$PAR_i = C_i \times S$$

(7)

Where PAR$_i$ is the pollen accumulation rate for taxon i, C_i is the pollen concentration (grains cm^{-3}) for taxon i, and S is the sedimentation rate (cm yr^{-1}) (Davis and Deevey 1964).

Commented [MOU3]: Moved these equations, as requested by Reviewer 2.

1

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S8. Coefficients for the predicted aboveground live biomass (Mg ha^{-1}) of trees as a function of basal area (m^2 ha^{-1}) using a linear log-log (natural) equation. Results for all species encountered in the forest inventory conducted for the seven lakes in the Klamath Mountains. The p-value of the regression was < 0.0001 in all cases except for white alder where p = 0.034. B_0 is the intercept; B_1 is the slope coefficient; SEE = standard error of the estimate.

Genus	Species	Common name	B_o	B_1	R^2_{adj}	SEE (Mg ha^{-1})
Abies	*concolor*	white fir	1.65	1.07	0.95	0.40
Abies	*magnifica*	California red fir	1.47	1.19	0.92	0.46
Acer	*macrophyllum*	bigleaf maple	1.30	1.11	0.94	0.24
Alnus	*rhombifolia*	white alder	1.26	1.30	1.00	0.07
Arbutus	*menziesii*	Pacific madrone	1.55	1.12	0.94	0.29
Calocedrus	*decurrens*	incense-cedar	1.08	1.18	0.90	0.52
Chamaecyparis	*lawsoniana*	Port-Orford-cedar	1.16	1.19	0.97	0.37
Chrysolepis	*chrysophylla*	golden chinquapin	1.19	1.18	0.96	0.34
Cornus	*nuttallii*	Pacific dogwood	1.07	0.92	0.85	0.37
Notholithocarpus	*densiflorus*	tanoak	1.08	1.17	0.96	0.35
Pinus	*attenuata*	knobcone pine	1.18	1.06	0.96	0.21
Pinus	*jeffreyi*	Jeffrey pine	1.09	1.11	0.88	0.58
Pinus	*lambertiana*	sugar pine	1.67	1.22	0.85	0.59
Pinus	*ponderosa*	ponderosa pine	1.36	1.23	0.89	0.50
Pseudotsuga	*menziesii*	Douglas-fir	1.15	1.23	0.96	0.30
Quercus	*chrysolepis*	canyon live oak	1.47	1.12	0.92	0.43
Quercus	*kelloggii*	California black oak	1.62	1.11	0.96	0.27
Taxus	*brevifolia*	Pacific yew	0.83	0.82	0.94	0.21
Umbellularia	*californica*	California-laurel	0.95	1.30	0.95	0.38

1

Table S9. Fall speed (m/sec) for major taxa
used in the simulation runs of this study.

Taxa	Fall-speed (v_s) estimates (m s^{-1})
Abies	0.120 [a]
Alnus	0.021[b]
Pinus	0.031[a]
Pseudotsuga	0.126[a]
Quercus	0.035[a]
TCT	0.016[c]

[a] Eisenhut (1961); [b] Schober (1975);
[c] Calculated from empirical measurements using Stoke's Law
with Falck's (1927) correction

Table S10. PAR values of main taxa from 2018 (a modeled age) at each lake site.

Lake Site	*Pinus*	*Pseudotsuga*	*Quercus*	*TCT*	*Notholithocarpus*	*Alnus*	*Abies*
Blue	1760	5461	758	4490	1031	1183	789
Red Mt.	3672	5068	672	3051	2844	1034	569
Onion	10797	2014	1063	1622	559	951	4811
North Twin	1749	6808	1686	2311	2935	812	1999
South Twin	2384	7152	1463	2005	2059	1300	325
Fish	1479	4606	840	1782	3741	2858	34
Ogaromtoc	3376	4609	1558	844	454	1753	260

1

Table S11. Results from the linear regressions predicting distance-weighted aboveground live biomass (AGL$_{dw}$) as a function of pollen accumulation rate (PAR) for the pollen taxa present at the seven lake sites in the Klamath Mountains. The assemblage-level relevant source area of pollen (aRSAP) was defined as a circle with a radius of 625 m from centroid of the lake. Parameters provided the linear regression: AGL$_{DW}$ = B$_0$ + B$_1$ * PAR where AGL$_{dw}$ is measured in Mg ha^{-1}; PAR in grains cm^{-2} yr^{-1}; SEE = standard error of the estimate; ΔAICc = the difference in the Akaike Information Criterion for small samples between the top ranked model and the second ranked model.

Pollen Taxa	ΔAICc	B$_0$	B$_1$	SEE (Mg ha^{-1})	R$^2_{adj}$	P
Pseudotsuga	6.6	0	0.0180	19.1	0.96	< 0.001
Pinus	5.4	0	0.00740	8.42	0.94	<0.001
Notholithocarpus	4.2	0	0.0211	16.5	0.89	<0.001
TCT	4.0	0	0.00954	9.43	0.87	<0.001
Quercus[1]	--	--	--	--	--	--
Alnus	3.0	3.8	0.00341	1.05	0.84	0.002
Abies	4.2	0	0.0138	13.8	0.80	0.0018

[1]There was no evidence of a significant linear relationship for Quercus. For predicting AGL$_{dw,}$ a null model was used with the intercept = 1.54 and the standard error = 1.46.

Table S12. Results from the linear regressions predicting distance-weighted aboveground live biomass (AGL$_{dw}$) as a function of pollen accumulation rate (PAR) for the pollen taxa present at the seven lake sites in the Klamath Mountains. The taxon-specific source area of pollen (tRSAP) was defined as a circle with a radius determined by the strength of correlation (R^2) between plant abundance and PAR. Parameters provided the linear regression: AGL$_{dw}$ = B$_0$ + B$_1$ * PAR where AGL$_{DW}$ is measured in Mg ha^{-1}; PAR in grains cm^{-2} yr^{-1}; SEE = standard error of the estimate.

Pollen Taxa	B$_0$	B$_1$	SEE (Mg ha^{-1})	R$^2_{adj}$	P
Pseudotsuga	0	0.0180	19.1	0.96	< 0.001
Pinus	0	0.00558	6.78	0.95	<0.001
Notholithocarpus	0	0.0205	16.2	0.91	<0.001
TCT	0	0.00849	8.97	0.87	<0.001
Quercus[1]	--	--	--	--	--
Alnus	-3.8	0.00341	1.05	0.84	0.002
Abies	0	0.0138	13.8	0.83	0.0018

[1]There was no evidence of a significant linear relationship for *Quercus*. For predicting AGL$_{dw,}$ a null model was used with the intercept = 1.54 and the standard error = 1.46.

1

Table S13. Results from the linear regressions predicting distance-weighted aboveground live biomass (AGL_{dw}) as a function of pollen accumulation rate (PAR) for the pollen taxa present at the seven lake sites in the Klamath Mountains. These equations all include an intercept and slope term even if they were not the best fit. The relevant source area of pollen (aRSAP) was defined as a circle with a radius of 625 m from centroid of the lake. Parameters provided the linear regression: $AGL_{DW} = B_0 + B_1 * PAR$ where AGL_{dw} is measured in Mg ha^{-1}; PAR in grains cm^{-2} yr^{-1}; SEE = standard error of the estimate.

Pollen Taxa	B_0	B_1	SEE (Mg ha^{-1})	R^2_{adj}	P
Pseudotsuga	-14.7	0.0206	20.3	0.74	0.008
Pinus	-5.5	0.00829	8.23	0.92	<0.001
Notholithocarpus	16.8	0.0149	14.7	0.61	0.02
TCT	-12.1	0.0138	8.33	0.78	0.005
Quercus	-2.9	0.00386	3.84	0.0083	0.4
Alnus	-3.8	0.00341	1.05	0.84	0.002
Abies	-9.4	0.0168	12.35	0.84	0.002

2

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S14. Dry bulk density (g cm^{-3}) for Blue Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
Blue	0-1	0.102
Blue	1-2	0.093
Blue	2-3	0.085
Blue	3-4	0.095
Blue	4-5	0.088
Blue	5-6	0.087
Blue	6-7	0.089
Blue	7-8	0.085
Blue	8-9	0.084
Blue	9-10	0.078
Blue	10-12	0.087
Blue	12-14	0.096
Blue	14-16	0.102
Blue	16-18	0.093
Blue	18-20	0.095
Blue	20-21	0.095
Blue	22-23	0.104
Blue	24-25	0.089
Blue	26-27	0.090
Blue	28-29	0.090
Blue	30-31	0.093
Blue	40-42	0.124

2

Table S15. Dry bulk density (g cm^{-3}) for Red Mountain Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
Red Mt.	0-1	0.080
Red Mt.	1-2	0.090
Red Mt.	2-3	0.074
Red Mt.	3-4	0.078
Red Mt.	4-5	0.068
Red Mt.	5-6	0.068
Red Mt.	6-7	0.071
Red Mt.	7-8	0.074
Red Mt.	8-9	0.079
Red Mt.	9-10	0.074
Red Mt.	10-12	0.081
Red Mt.	12-14	0.090
Red Mt.	14-16	0.112
Red Mt.	16-18	0.098
Red Mt.	18-20	0.110
Red Mt.	20-21	0.100
Red Mt.	22-23	0.121
Red Mt.	24-25	0.141
Red Mt.	26-27	0.146
Red Mt.	28-29	0.144
Red Mt.	30-31	0.150
Red Mt.	35-37	0.158

2.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S16. Dry bulk density (g cm^{-3}) for Onion Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
Onion	0-1	0.084
Onion	1-2	0.093
Onion	2-3	0.082
Onion	3-4	0.074
Onion	4-5	0.073
Onion	5-6	0.065
Onion	6-7	0.049
Onion	7-8	0.047
Onion	8-9	0.061
Onion	9-10	0.082
Onion	10-12	0.128
Onion	12-14	0.140
Onion	14-16	0.157
Onion	16-18	0.195
Onion	18-20	0.224
Onion	20-21	0.235
Onion	22-23	0.227
Onion	24-25	0.228
Onion	26-27	0.246
Onion	28-29	0.189
Onion	30-31	0.223

2

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S17. Dry bulk density (g cm^{-3}) for Fish Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
Fish	0-1	0.101
Fish	1-2	0.099
Fish	2-3	0.101
Fish	3-4	0.100
Fish	4-5	0.101
Fish	5-6	0.100
Fish	6-7	0.107
Fish	7-8	0.101
Fish	8-9	0.115
Fish	9-10	0.120
Fish	10-11	0.117
Fish	12-13	0.142
Fish	14-15	0.149
Fish	16-17	0.541
Fish	18-19	0.198
Fish	20-21	0.222
Fish	22-23	0.286
Fish	24-25	0.494
Fish	26-27	0.198
Fish	28-29	0.187
Fish	30-31	0.203

2

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table S18. Dry bulk density (g cm^{-3}) for South Twin Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
South Twin	0-1	0.076
South Twin	1-2	0.073
South Twin	2-3	0.067
South Twin	3-4	0.059
South Twin	4-5	0.054
South Twin	5-6	0.050
South Twin	6-7	0.045
South Twin	7-8	0.047
South Twin	8-9	0.047
South Twin	9-10	0.050
South Twin	10-11	0.051
South Twin	12-13	0.060
South Twin	14-15	0.064
South Twin	16-17	0.073
South Twin	18-19	0.067
South Twin	20-21	0.075
South Twin	22-23	0.083
South Twin	24-25	0.110
South Twin	26-27	0.130
South Twin	28-29	0.130
South Twin	30-31	0.154

2

Table S19. Dry bulk density (g cm^{-3}) for Ogaromtoc Lake.

Lake	Depth (cm)	Dry Bulk Density (g cm^{-3})
Ogaromtoc	0-1	0.086
Ogaromtoc	1-2	0.083
Ogaromtoc	2-3	0.064
Ogaromtoc	3-4	0.064
Ogaromtoc	4-5	0.065
Ogaromtoc	5-6	0.068
Ogaromtoc	6-7	0.072
Ogaromtoc	7-8	0.074
Ogaromtoc	8-9	0.071
Ogaromtoc	9-10	0.066
Ogaromtoc	10-11	0.068
Ogaromtoc	12-13	0.081
Ogaromtoc	14-15	0.366
Ogaromtoc	16-17	0.116
Ogaromtoc	18-19	0.072
Ogaromtoc	20-21	0.096
Ogaromtoc	22-23	0.268
Ogaromtoc	24-25	0.147
Ogaromtoc	26-27	0.066
Ogaromtoc	28-29	0.061
Ogaromtoc	30-31	0.064

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

Table S20. Dry bulk density (g cm^{-3}) for North Twin Lake.

Lake	Depth (cm)	Dry Bulk Density (g/cm^3)
North Twin	0-1	0.099
North Twin	1-2	0.097
North Twin	2-3	0.101
North Twin	3-4	0.107
North Twin	4-5	0.108
North Twin	5-6	0.106
North Twin	6-7	0.092
North Twin	7-8	0.076
North Twin	8-9	0.076
North Twin	9-10	0.088
North Twin	10-12	0.132
North Twin	12-14	0.143
North Twin	14-16	0.145
North Twin	16-18	0.145
North Twin	18-20	0.141
North Twin	20-21	0.122
North Twin	22-23	0.133
North Twin	24-25	0.127
North Twin	26-27	0.137
North Twin	28-29	0.135
North Twin	30-31	0.137

2

References

Appleby P and Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. *Catena* 5:1–8.

Baskaran M, Miller CJ, Kumar A et al. (2015) Sediment accumulation rates and sediment dynamics using five different methods in a well-constrained impoundment: Case study from Union Lake, Michigan. *Journal of Great Lakes Research* 41:607–617.

Davis MB and Deevey ES (1964) Pollen accumulation rates: estimates from Late-Glacial sediment Rogers Lake. *Science* 145:1293–1295.

Eisenhut G (1961) Untersuchungen über die Morphologie und Ökologie der Pol- lenkörner heimischer und fremdländischer Waldbäume. Paul Parey, Hamburg.

Falck R (1927) Über die Größen, Fallgeschwindigkeit und Schwebewarte dcr Pilzsporen und ihre Gruppierung mit Bezug auf die zu ihre Verbreitung nötigen temperatuströmungs-Geschindigkeit. Berichte der Deutschen Botanischen Gesesellschaft 45:262–281.

Gaillard MJ, Sugita S, Bunting MJ et al. (2008) The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. *Vegetation History and Archaeobotany* 17:419-443.

Jweda J and Baskaran M (2011) Interconnected riverine-lacustrine systems as sedimentary repositories: Case study in southeast Michigan using 210-Pb and 137-Cs sediment accumulation and mixing models. *Journal of Great Lakes Research* 37:432–446.

Schober, R., 1975. Ertragstafeln wichtiger Baumarten bei verschiedener Durchfor- stung. Sauerländer, Frankfurt a. M.

Stockmarr J (1971) Tablets with spores used in pollen analysis. *Pollen and Spores* 13:615–621.

Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation. *Journal of Ecology* 82:881–897.

2