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Human-vegetation interactions during the Holocene in North America

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38 **Abstract**

39 Between the initial colonization of North America and the European settlement period, Native
40 American land use practices shaped North American landscapes and ecosystems, but a critical
41 question is the extent of these impacts on the land, and how these influenced the distributions of
42 flora and fauna. The present study addresses this question by estimating the spatial correlation
43 between continental-scale records of fossil pollen and archaeological radiocarbon data, and
44 provides a detailed analysis of the spatiotemporal relationship between paleo-populations and ten
45 important North American pollen taxa. Maps of relative Native American population density,
46 based on the Canadian Archaeological Radiocarbon Database, are compared to maps of plant
47 abundance as estimated by pollen records from the Neotoma Paleoecology Database, using
48 nonparametric kernel estimators and cross-correlation techniques. Periods of high spatial cross-
49 correlation (either positive or negative) between population and plant abundance were identified,
50 but these associations were intermittent and did not increase towards the present. In many cases,
51 high values of population corresponded with high values of a particular taxon in one region, but
52 simultaneously corresponded with low values in other regions, lessening the overall correlation
53 between the two fields. This analysis suggests that human impacts were not significant enough to
54 be identified at a continental scale, either due to low populations or land use, implying significant
55 impacts of ancient human activities on the vegetation were regional rather than continental.

56

57

58 **Keywords:** Anthropocene, forest history, pollen, archaeology, spatio-temporal cross-correlation,
59 kernel smoother, Canadian Archaeological Radiocarbon Database, Neotoma Paleoecology
60 Database

61 1. INTRODUCTION

62 Historic human impacts on the vegetation in North America are well-understood. European
63 colonists deforested large areas of North America by the early 20th century, although the vegetation
64 has since regrown in many areas (e.g., Cronon, 1983; Williams, 1989; Whitney, 1994; Dyer 2006),
65 and these changes have been observed in fossil pollen studies (e.g., McAndrews, 1988). What is
66 less easily determined is the broad-scale impact of Indigenous American land use practices. In the
67 recent past it was generally assumed that the human footprint in North America prior to European
68 colonization was insignificant. Changes in human population numbers would have been primarily
69 driven by intrinsic factors and influenced by climate and environmental changes (e.g., Munoz et
70 al., 2010; Foster, 2012). This view assumed that the total population in the Americas was relatively
71 small and the impacts on the environment were minimal, or at best widely scattered (Denevan,
72 1992). Some authors have suggested between 2 and 18 million people may have occupied North
73 America during this time, although these numbers are controversial and questioned (Denevan,
74 1992; Warrick, 2008; Peros et al., 2010).

75
76 An alternative viewpoint based largely on archaeological and ethnohistoric research is that the
77 population in 1492CE was very high, particularly in coastal regions and temperate areas, and that
78 human impacts were extensive across many regions in North America (Denevan, 1992; Doolittle,
79 2000). Environmental historians have noted reports by the first European settlers of open forests,
80 of burning by Native Americans to encourage game and facilitate travel, and of active or
81 abandoned agricultural fields (e.g., Cronon, 1983; Silver, 1990; Krech, 2000; Kay and Simmons,
82 2002; McShea and Healy, 2002; Harkin and Lewis, 2007). These reports have been extrapolated
83 to suggest that much of the landscape was open parkland, although the extent is questioned

84 (Russell, 1983). Anthropologists have interviewed Native Americans about their lifestyles and
85 practices, and these studies indicate local adaptations to the vegetation, including burning of the
86 prairies or forests (e.g., Stewart, 2002; Courtwright, 2011). Ecologists Abrams and Nowacki
87 (2008) summarized studies of land survey records and concluded “... *that the vast majority of*
88 *vegetation in the eastern USA was managed directly or indirectly by Native Americans, especially*
89 *through the use of fire*” (pg. 1134). Similar conclusions have been made by many others, and this
90 viewpoint is becoming increasingly accepted (e.g., Pyne, 1982; Cronan, 1983; Silver, 1990; Krech,
91 2000; Kay and Simmons, 2002; Stewart, 2002; Harkin and Lewis, 2007; Courtwright, 2011).
92 Collectively, these studies suggest the North American landscape was a cultural or humanized
93 landscape millennia before 1492CE (Zelinsky, 1973; Orme, 1981; Delcourt, 1987; Delcourt and
94 Delcourt, 1987, 2004; Whitehead and Sheehan, 1985; Butzer, 1992; Silver, 1990; Doolittle, 1992;
95 Kay, 1994; Krech, 2000; Harkin and Lewis, 2007; Abrams and Nowacki, 2008; Munoz et al.,
96 2010, Courtwright, 2011; Denevan, 2011). The critical issue now is the quantification of the extent
97 of these impacts regardless of whether they were deliberate (e.g., setting fires, agriculture and
98 silviculture) or incidental (e.g., successional growth, changes in forest composition, extinctions).
99

100 The use of fire to encourage the growth of grasses, forbs and shrubs and to force prey out of densely
101 forested areas dates at least to the Paleoindian period (10,500 – 9,500 years BP), and this may have
102 encouraged the growth of pioneer and disturbance species such as *Pinus*, *Quercus* and *Populus*
103 (Bonnicksen, 2000). Several authors have suggested that Paleoindian fire use was a key driver of
104 past changes in vegetation and fire regime, particularly in biotas not prone to burning (e.g., Marlon
105 et al., 2013; Early Anthropocene Burning Hypothesis). The use of fires continued and intensified
106 into the Archaic period when Native Americans began using a more diverse group of foods that

107 included game, fish and a wide variety of plants, and burning larger patches of land to encourage
108 the growth of seed, nut and berry-producing species (Fowler and Konopik, 2007). During the
109 Woodland and Mississippian periods, North American cultures in the Midwest and the East
110 focused on building permanent settlements, plant cultivation and domestication (Fowler and
111 Konopik, 2007).

112

113 The demographic collapse of the Indigenous population associated with European colonization
114 coincides with the most significant decrease in CO₂ and CH₄ in the last 2,000 and 1,000 years,
115 respectively, suggesting a close association between Native American land use and the global
116 carbon cycle during the last several millennia (Ruddiman, 2003; 2014). Atmospheric greenhouse
117 gas levels may have decreased in response to the near cessation of human-induced biomass burning
118 and the regeneration of forests following this massive population decline (Ruddiman, 2003;
119 Ferretti et al., 2005; Faust et al., 2006; Abrams and Nowacki, 2008; Nevle et al., 2011; Ruddiman
120 et al., 2011), which may have amplified the global effects of the Little Ice Age (Dull et al., 2010).
121 Native American fire use could have doubled the number of fires that would have naturally-
122 occurred as a result of lightning strikes (Bonnicksen, 2000). Alternatively, it is possible that
123 population densities in North America may have been too low to have global implications
124 (Ubelaker, 1992; Steckel and Rose, 2005; Liebmann et al., 2016) and past changes in atmospheric
125 gas levels were not directly influenced by Native American land use (Bird et al., 2017).

126

127 At the other extreme, lower population numbers, perhaps combined with careful management of
128 the landscape, could have meant that Native Americans left a small footprint with only regional or
129 indications of impact (e.g., Vale, 2002; Munoz et al., 2014). This view seems to be held by

130 paleoecologists, whose studies emphasize the importance of climate variability on vegetation
131 composition (e.g., Williams et al., 2004). Paleoenvironmental studies at local or regional scales
132 have shown strong associations of tree species composition with human activity in time and space,
133 although the intensity of activity has been hard to estimate (e.g., Burden et al., 1986; Delcourt et
134 al., 1986; McAndrews and Boyko-Diakonow, 1989; Clark and Royall, 1995; Fuller et al., 1998;
135 Parshall and Foster, 2002; McLauchlan, 2003; Delcourt and Delcourt, 2004; Faison et al., 2006;
136 Munoz and Gajewski, 2010). Studies of the vegetation of mountainous western North America
137 concluded that human impact, including the setting of fires, was more local than regional (Vale,
138 2002), as did a study of the eastern deciduous forest (Munoz et al., 2014). There is difficulty in
139 separating climate-induced vegetation change from human impacts (Gajewski, 1987; Nordt et al.,
140 1994; Paquette and Gajewski, 2013; Lafontaine-Boyer and Gajewski, 2014).

141

142 One component that can help address this difficulty, and this was noted as far back as by Day
143 (1953), is consistently-derived and quantitative estimates of human population density over the
144 Holocene for North America. Recently, these data have become available as a result of analyses
145 using the Canadian Archaeological Radiocarbon Database (CARD; Gajewski et al., 2011; Chaput
146 et al., 2015; Martindale et al., 2016). Although archaeological data provide only relative numbers,
147 they have been used, for example, in a reconstruction of the time evolution of the population of
148 North America for the past 15000 years (Peros et al., 2008), and inferred changes in population
149 density are associated with climate variations (Fig. 1). These paleodemographic estimates have
150 also been mapped, depicting the time-space evolution of relative population density (Chaput et al.,
151 2015). Fossil pollen data from sediment cores spanning the continent are also now available as
152 part of the Neotoma Paleoecology Database (Williams et al., 2018), and a large literature has

153 demonstrated that these are a proxy for past populations of trees (e.g., Davis, 1981; Jacobson et
154 al., 1987; Webb, 1988; Webb et al., 1993; Williams et al., 2004). The availability of these databases
155 provides an opportunity to study the question of the extent of Indigenous American land use
156 impacts at a continental scale, and this forms the basis of the research presented here.

157

158 We approach the question of large-scale human-vegetation interactions by comparing estimates of
159 Native American populations over the past 13000 years (Chaput et al., 2015) to data on the
160 distribution of trees during the same time period. We ask two alternative questions. First, did
161 Native Americans and their activities affect the vegetation in a quantitative, measurable way at
162 regional to continental scales? For example, if Native Americans planted or encouraged the growth
163 of particular tree species, such as *Carya* or *Juglans* (Wycoff, 1991; Abrams and Nowacki 2008),
164 then the abundance of these trees should increase after a population increase. If there was extensive
165 burning or clearing through agriculture, this should appear as an increase in disturbance taxa such
166 as *Populus* or *Poaceae*, or a decrease in late successional taxa such as *Acer* or *Fagus*, as seen on a
167 regional scale in Ontario in the late Holocene (Munoz and Gajewski, 2010). Alternatively, did
168 changes in the vegetation affect human activity, including population growth? If tree populations
169 that supported wildlife and produced consumables for Native Americans, such as *Quercus* or
170 *Castanea* (e.g., Wang et al., 2013) became more abundant, this could mean a more reliable food
171 source, encouraging larger populations. Kriesche et al. (subm.) described a methodology
172 developed for this purpose, and briefly discussed the example of *Quercus*; here we investigate
173 these questions in greater detail.

174

175

176 2. METHODS

177 2.1 Data

178 For estimates of past vegetation, we used pollen data from the Neotoma Paleoecology Database
179 (Fig. 1a; www.neotomadb.org); all North American (north of Mexico) data were extracted. We
180 used estimates of human population in space and time (Chaput et al., 2015) based on the CARD
181 database (Fig. 1b; Gajewski et al., 2011; Martindale et al., 2016; www.canadianarchaeology.ca).
182 All radiocarbon and pollen data were calibrated (Chaput et al., 2015; Kriesche et al., *subm.*), and
183 ages are discussed in ka (1000 years before present). Details of data extraction and preparation of
184 the maps and figures are explained in Chaput et al. (2015; population) and Kriesche et al. (*subm.*;
185 pollen).

186

187 2.2 Methods

188 Spatial cross-correlations were computed to evaluate the relationship between population and ten
189 pollen taxa: boreal and widespread taxa (*Picea*, *Pinus*), major genera of the eastern deciduous
190 forests (*Quercus*, *Castanea*), important food sources (*Carya*, *Juglans*), important trees of closed
191 forests of the eastern deciduous forests (*Acer*, *Fagus*), and disturbance indicators (*Populus*,
192 Poaceae).

193

194 2.2.1 Population: Chaput et al. (2015) showed the spatial distribution of the human population of
195 North America through time in a series of maps based on a 500-year window, with subsequent
196 maps produced at overlapping intervals of 100 years: 0.5-1.0 ka, 0.6-1.1 ka, ..., 12.5-13.0 ka.
197 Smoothed population maps were prepared from the radiocarbon dates using a kernel density

198 estimator, which accounts for biases from inhomogeneous sampling strategies, taphonomic loss,
199 and boundary effects. This resulted in a total of 121 maps of population density.

200

201 *2.2.2 Vegetation:* A series of 121 comparable maps showing the pollen percentage distributions
202 was prepared for each taxon. As with population, an estimator from kernel regression (Kriesche et
203 al., *subm.*) was used to determine the spatial distribution of pollen percentages at the central age
204 of each 500-year time period. To enable comparability, the same configurations of the estimators
205 were used as for population, except that the population was illustrated on a logarithmic scale and
206 the pollen percentages on a linear scale (see Supplemental Data file). Only the values of population
207 within the range of the taxon were studied, and the range at a given year was determined where
208 pollen percentages had a value of at least 0.2 times the maximum of pollen percentages. These
209 estimated values were used in the following for correlation analyses.

210

211 *2.2.3 Correlations and cross-correlations:* Spatial correlation functions of both population and
212 pollen percentage maps (separately) were estimated for each time period. All of the 121 correlation
213 functions for each taxon within the range and for population were summarized in one graph, a heat
214 map that shows the spatial autocorrelation of the taxon or population through time (Supplemental
215 Data). Spatial cross-correlation functions were then computed showing the relationship between
216 estimates of population and pollen abundance of each taxon, restricted to the estimated taxon
217 range. The series of 121 functions for each taxon were summarized in one plot, which identify
218 times of strong spatial cross-correlation between population and taxa.

219

220 To determine if *changes* in population and taxon abundance were correlated, difference maps were
221 produced subtracting maps with a temporal distance of 500 years to provide 116 maps of 500-year
222 changes in population and taxon abundance (in 100-year steps). These correspond to the same 500-
223 year change interval and also to intervals that are shifted by the temporal lags +100, +200, ...,
224 +1000 years, and -100, -200, ..., -1000 years. A positive lag means that vegetation change
225 corresponds to a more recent 500-year change interval than change in population and a negative
226 lag means the opposite. Similar to the actual maps, spatial correlation functions were estimated for
227 the difference maps of vegetation abundance and population for each 500-year change interval,
228 and summarized as heat maps. Cross-correlations between the difference maps for vegetation
229 abundance and population were also prepared for lags of -1000, -900, ..., -100, 0, 100, ..., 900,
230 1000 years and the comparable summaries for all time periods are shown as heat maps
231 (Supplemental).

232

233 The final result depicts the mean cross-correlations between differences in taxon abundance and
234 population at small distances (between 30 and 200 km), summarized in a matrix plot. These
235 summarize all estimated statistical cross-correlations between changes in the considered taxon and
236 population (for all temporal lags) in one graph (Fig. 2).

237

238 Nonparametric resampling methods were used to assess the significance of the obtained correlation
239 results (Kriesche et al., *subm.*); correlations with higher absolute values are considered to indicate
240 a real signal: ca. 0.15 (*Picea*, *Pinus*), 0.2 (*Acer*, *Carya*, *Juglans*), 0.25 (*Fagus*), 0.3 (*Castanea*,
241 *Poaceae*, *Quercus*) and 0.4 (*Populus*). A more detailed methodology including an illustration of
242 each step mentioned above can be found in Kriesche et al (*subm.*) and in the Supplemental file.

243

244 **3. RESULTS**245 *3.1 Population*

246 The population maps were discussed in Chaput et al. (2015) so we briefly describe them here. Prior
247 to 10 ka, there were population maxima in the southern United States and northwestern North
248 America. Maxima remained in the south in the early Holocene, and population tended to increase
249 in the west over the course of the Holocene. Population increased across all of North America in
250 the past 2 ka.

251

252 *3.2 Boreal and widespread taxa: Picea and Pinus*

253 The range and abundance maps depicting the distribution of *Picea* through time closely resemble
254 those presented in Williams et al. (2004), suggesting that the differences in methodology are not
255 greatly influencing the results. There were no clear associations with population or changes in
256 population and these taxa. In the early Holocene, large increases in *Picea* occurred in the
257 northwestern part of range, but there were both positive and negative changes in population
258 depending on the region, reducing the cross-correlation of the difference maps of *Picea* and
259 population. In general, zones of increasing or decreasing values were sometimes in phase or not
260 with population, so the cross-correlation of *Picea* with population was low. During the period
261 between ~5.5-3.5 ka both *Picea* and population increased in the east, leading to a brief period of
262 high positive cross-correlations. In the past 1 ka, changes in *Picea* were relatively small, whereas
263 population was increasing across the entire range; the cross-correlation of the change maps
264 remained non-significant as a consequence. Again, our migration maps for *Pinus* look similar to
265 those of Williams et al. (2004) and there are no clear correlations with population change maps.

266

267 *3.3 Major taxa: Quercus & Castanea*268 *Quercus* was discussed in Kreische et al. (subm.) as an example of application of the methodology.269 At 12 ka there was abundant *Quercus* in the Gulf States, and by the mid-Holocene it was found

270 across the present-day range, with a maximum from Illinois to Virginia. Although there was some

271 association between *Quercus* and population (Fig. 2), it is probably because *Quercus* is

272 representative of the deciduous forest rather than through any kind of causal relation between

273 *Quercus* and population.

274

275 High values of the spatial autocorrelation and cross-correlation of population and *Castanea* prior

276 to ~5 ka are difficult to interpret as the pollen record is dominated by sites in Texas (Bryant and

277 Holloway, 1985), resulting in a discontinuous range. The cross-correlation between *Castanea* and

278 population abundances is relatively high and positive in the late Holocene, as both variables have

279 high values in the central portion of the range. In the past 2 ka, population maxima were found in

280 the western portion of the range, reducing the cross-correlation somewhat. *Castanea* is one taxon

281 where the positive and negative lag correlations differed (Fig. 2), but this is mostly in the older,

282 less reliable section of the graph. Between 5 ka and 4 ka, *Castanea* decreased or did not change

283 much as it moved northward, whereas population was increasing, and between 3.5 and 2.5 ka, both

284 pollen and population increased, especially in the southern part of the range. During the past 2 ka,

285 *Castanea* changed little, except in the northern part of the range (Paillet, 2002) where it increased,

286 whereas population was increasing greatly across the range, so there was little cross-correlation.

287

288 *3.4 Major mast trees: Juglans and Carya*

289 Shortly after 12 ka, the area mapped as high values of *Juglans* was located in a broad area from
290 Louisiana to the Great lakes, west of the Appalachians. By 9-10 ka, *Juglans* decreased in the south,
291 with maximum values centred over the Midwest. The range was at a minimum at this time and the
292 maximum values remained in this area until the present. In the early Holocene, the cross-
293 correlation of *Juglans* with population was relatively small, since the maximum population relative
294 density was in the south, whereas maximum *Juglans* was in the central part of the eastern United
295 States (Fig. 2). Similarly, the difference maps showed a complex sequence of changes that were
296 rarely aligned between populations and *Juglans* percentages. Through most of the mid- to late
297 Holocene, the range of *Juglans* changed little, and the population maxima were to the south and
298 east of that of *Juglans*. Since the trees seemed to increase first, this does not suggest that Native
299 populations caused an increase in abundance in this species, although the association may suggest
300 that it was exploited. In the late Holocene, population increased across the entire range of *Juglans*,
301 and maximum values were overlapping with the pollen maximum, displaced a bit to the west. High
302 values of population associated with high and low values of *Juglans* contributed to the lower
303 spatial autocorrelation. This preceded the major increase in agriculture in the region.

304

305 The range of *Carya* gradually extended northward in the early Holocene, especially west of
306 Appalachians, and extending to the Great Lakes by 9 ka. As *Carya* moved northward and was
307 found at moderate values across a large range, the maximum in population was also broadly
308 coincident, leading to high cross-correlations between 10-7.5 ka. In the mid-Holocene, high values
309 of population sometimes corresponded to high values of *Carya*, but in other regions to low values,
310 so the overall spatial correlation was around zero. The spatial cross-correlations of the difference
311 maps can be divided into three periods, the early Holocene, the mid-Holocene between 8-4 ka and

312 the late Holocene, with few consistent associations in the early or late Holocene. An alternation of
313 positive and negative cross-correlations in the mid-Holocene is driven in part by very large
314 increases in *Carya* from 7-5 ka in Texas, accompanied with increases or decreases in population,
315 and this may tend to overly affect the correlations. *Carya* decreased in abundance in the southern
316 part of the range at times when population did as well, leading to some periods of high cross-
317 correlation. Between 4.5-3.5 ka, *Carya* increased in the north-central part of the range, and large
318 population increases in the same area contribute to the band of high correlation in Figure 2. In the
319 past 2 ka, *Carya* changed less in the northern part of the range while at times decreasing in Texas;
320 during this time population was greatly increasing in the central portion of the range, leading to
321 overall low cross-correlations.

322

323 *3.5 Northern deciduous forest: Fagus and Acer*

324 *Acer* and *Fagus* were found in the northern part of the deciduous forest in the mid- to late
325 Holocene. At 13 ka, the range of *Acer* was extensive, with maximum values in south-central United
326 States. *Acer* moved north quickly, with significant values even up to the retreating ice sheet. By
327 the mid-Holocene until the present, maximum values were centred on Ontario. The stability of the
328 range in the mid- to late Holocene, and general increase in abundance led to relatively high cross-
329 correlations with population at certain times, but human population maxima also shifted, leading
330 to alternating periods of positive and negative correlation. For example, in the mid-Holocene, there
331 was a minimum in population in the area where *Acer* was most abundant, leading to weak cross-
332 correlations. Generally, the maximum in population was found to the south of the region of most
333 abundant *Acer*. The period of large positive cross-correlations in the difference maps from 8-9 ka
334 (*Acer*) and 7-8 ka (population) occurred when *Acer* was increasing greatly in Ontario, and

335 population was quite constant across all of range. In the past 2 ka, *Acer* increased in the southwest
336 portion of its range, when population was also increasing, leading to positive correlation. Given
337 the stability of a large maximum in *Acer* centred over southern Ontario through much of the
338 Holocene in both the absolute and difference maps, the lack of a comparable feature in population
339 (in either a negative or positive sense) suggests little relation of these two variables.

340

341 By 10 ka there were high values of *Fagus* in western Pennsylvania; this remained until the present.
342 In the past 8.5 ka, large values of *Fagus* pollen were restricted to the north of Virginia, with most
343 abundant values in Pennsylvania and New York. In the oldest part of the record, when *Fagus* was
344 restricted to the south, there was little association of *Fagus* and population intensity, and this
345 continued in the period between 11-8.5 ka as it migrated rapidly northward. In the period around
346 8 ka, *Fagus* difference maps were positive, centred on the range for long time periods, whereas
347 population increased or decreased in various portions of the range. Large positive values of cross-
348 correlation occurred with large increases in *Fagus* and small but smooth values of population. The
349 large positive association between 4.5-6 ka (*Fagus*) and 4-5 ka (population) occurred when both
350 were increasing in the northeastern portion of the range. After 4 ka, *Fagus* increased in Ontario
351 and Quebec, at times when population was decreasing and at other times when increasing.
352 Increases in *Fagus* and population in the past 3 ka in the western part of the range lead to positive
353 cross-correlations.

354

355 *3.6 Disturbance indicators: Populus & Poaceae*

356 The range of significant values of *Populus* decreased rapidly between 10-8 ka, and almost no
357 pollen was found in sediment subsequently (Peros et al., 2008). Cross-correlations of *Populus* and

358 population were high in the early Holocene, as both were abundant in Beringia and Alberta. After
359 8 ka, when the range of *Populus* was very small and broken into disjunct regions, the
360 autocorrelation functions decreased substantially, as did the cross-correlation with population. In
361 the mid Holocene, during periods of strong cross-correlation of the difference maps, *Populus* was
362 restricted to a small area of the Southwest.

363

364 Before 9 ka, Poaceae pollen was found above the threshold in several areas from the Arctic to
365 Florida. Over the course of the Holocene, it increased in abundance in the present-day prairie
366 region, as this biome developed after 8 ka. High values of Poaceae and population, especially in
367 the southern plains, and low values elsewhere led to some high spatial cross-correlations. The
368 cross-correlation of the maps as well as the differences decreased after 5 ka, as maximum Poaceae
369 values were found in the central portion of the range, whereas the maximum population was around
370 the edges of the range.

371

372 4. DISCUSSION

373 Although periods of high spatial cross-correlation between population and pollen abundance were
374 identified, these are not consistent, nor do they concur with expected interpretation. We should
375 expect increasing cross-correlations in the recent past, with increasing populations (Peros et al.,
376 2008) and expansion of agriculture, but in fact, this was not observed. If extensive human-caused
377 fires did push the forests of eastern North America toward more *Quercus* and disturbance taxa
378 across a large area, we would not expect high positive correlations with *Acer* and *Fagus*. Given
379 the importance of mast species as a food source, we would have expected a higher correlation of
380 *Juglans* and *Carya* with population than was seen. The increase of *Populus*, as agriculture

381 developed in Ontario (Munoz and Gajewski, 2010) does not seem to scale upwards to the
382 continental scale.

383

384 Several possibilities can be proposed as explanation: (a) there was little or no relation; human
385 impact was not great enough to have an influence at this scale, either due to low populations or the
386 kinds of activities, and any large impact of human activity on vegetation was regional rather than
387 continental; (b) the impact of Native American activity on the vegetation was ubiquitous, but not
388 associated with changes in the population; (c) we did not see the associations since our method is
389 too insensitive, or results are too much determined by aspects of the data such as a low signal to
390 noise ratio;

391 a) Our conclusion is that there is presently little indication of continental-scale impacts of human
392 activities on the vegetation of North America over the course of the Holocene, but rather that
393 it was local and regional. Vale (2002) provided a classification of land use by Native
394 Americans useful for this discussion, and more work at regional scales, as discussed in the
395 Introduction, could document this interaction.

396 b) Although this is a possibility, it cannot be investigated at present. Ongoing work attempting to
397 estimate vegetation density (Chaput and Gajewski, 2018), and new data on charcoal and pollen
398 from more sites may help resolve this question.

399 c) We identified some taxa, especially those that are underrepresented in the pollen rain, where
400 problems with estimating the spatial fields for part of the time period may make interpretation
401 more difficult. Inadequacies with the databases, especially low site density or incomplete
402 archaeological data in some regions may be reducing the sensitivity of the study. However, for
403 many taxa and time periods, the fields are coherent with a large body of previous work (Davis,

404 1981; Jacobson et al., 1987; Webb, 1988; Webb et al., 1993; Williams et al., 2004) and
405 associations should be observable. Future work at regional scales, or using different averaging
406 periods, could determine the robustness of these results.

407

408 Overall, there was little relation between changes in *Picea* or *Pinus* and changes in population.
409 This is not surprising, as even in the recent past, the human population density of boreal regions
410 was low and agriculture was not possible. The wide range of these taxa, extending over many
411 different cultures and climates can lead to regional positive and negative correlations between
412 population and the taxon cancelling and leaving little correlation. We also saw little relation
413 between the disturbance indicators and population. Although local and regional paleoecological
414 studies have shown the impact of agriculture on long term vegetation dynamics (Delcourt, 1987;
415 McAndrews and Boyko-Diakonow, 1989; Clark and Royall, 1995; Delcourt and Delcourt, 2004;
416 Munoz and Gajewski, 2010), these impacts apparently do not scale to the entire forest region.

417

418 It is widely claimed that the prairie or especially the prairie-forest border was maintained by fires
419 (e.g., Gleason, 1913; Pyne, 1982; Abrams, 1992; Pyne, 2007; Courtwright, 2011) and that these
420 were augmented, if not almost entirely caused, by humans. Again, we could not identify a clear
421 association of population with the extent of the prairie, and more work is needed to understand the
422 human role in prairie fires.

423

424 In the eastern deciduous forest region, we have the most data, an extensive historical literature and
425 several regions of extensive paleoecological study. The importance of human-caused fires has been
426 emphasized by many authors but whether or not the pre-European forests were continuous or open

427 parklands is not resolved at a continental scale (Pyne, 1982; Cronan, 1983; Silver, 1990; Krech,
428 2000; Kay and Simmons, 2002; Stewart, 2002; Harkin and Lewis, 2007; Abrams and Nowacki,
429 2008; Courtwright, 2011). The continual clearing of land and abandoning and moving to new
430 locations, especially after the introduction of maize, could have had an significant impact on the
431 vegetation, especially if fire was used to aid in clearing the forests, although Doolittle (1992) has
432 questioned some of the assumptions about this aspect. We would expect an increase in grasses and
433 other herbaceous plants after the introduction of agriculture, or as a consequence of extensive
434 burning. *Quercus* would be favoured by fires caused by human activity (Abrams, 1992; McShea
435 and Healy, 2002; Black et al., 2006; Tulowiecki and Larsen, 2015), however, we did not see an
436 association. Due to the ability to sprout, *Castanea* increased after European settlement (Southgate,
437 2006) and there is speculation that it may have been favoured by fires associated with Native
438 American populations in New England (Foster et al., 2002), but we see little evidence in our
439 results.

440

441 There are many reports of Native American ground fires and this is supposed to have affected the
442 large-scale nature of the forests (e.g., Silver, 1990; Stewart, 2002). Paleoecological studies find
443 little evidence for fires (e.g., Clark and Royall, 1996; Lafontaine-Boyer and Gajewski, 2014),
444 although there are few available records, especially to the south. We might expect *Acer* and *Fagus*
445 to decrease if growth of mast trees were being encouraged by Native American activities such as
446 fire or planting, as these are late successional canopy trees and can reproduce in the shade. Positive
447 correlations of these two taxa with population would be expected if populations were having little
448 impact on the forests. The overall positive association of *Fagus* and *Acer* abundances with
449 population may suggest that any human disturbance was insufficient for wide-scale conversion of

450 the forest into earlier successional states, as shown, for example in southern Ontario (Munoz and
451 Gajewski, 2010). An alternative interpretation is that factors that favoured the maintenance of these
452 taxa also maintained populations of Native Americans.

453

454 An extensive literature has noted the importance of acorns and nuts for human consumption as
455 well as for animal populations they would have hunted (e.g., Delcourt and Delcourt, 1979; Silver,
456 1990; Wycoff, 1991; Scarry, 2003). There is a possibility of Native American dispersal of nut trees
457 either deliberately or at least more rapidly than would have occurred naturally (Dorney, 1981;
458 Wycoff, 1991; MacDougall, 2003; Smith, 2007). There are also reports of large populations of
459 mast-producing trees in association with villages, due to intentional or accidental growth of trees
460 planted or discarded (Silver, 1990; Black et al., 2006). Today, *Carya* is not regenerating across
461 large areas in eastern North America (Cowden et al., 2014). *Carya* would increase in abundance
462 within the range not only at times of appropriate temperature and moisture, but also with sufficient
463 canopy disturbance, and we may expect an increase when population increased. However,
464 increased drought or other factors could also increase canopy disturbance. The lack of a clear
465 association with population (Fig. 2) may indicate a lack of such disturbances. The clearest signal
466 of a potential association between these two taxa and population is found in the northeast in the
467 middle Holocene, and a regional study could help determine its significance.

468

469 Ruddiman (2014) has suggested that human impacts on the global climate (carbon cycle) began to
470 be measurable thousands of years ago, the Early Anthropocene Hypothesis. One question related
471 to the research presented here is: did the impacts of Indigenous Americans contribute to this early
472 Anthropocene? The results of our study do not suggest a significant impact; if they had occurred,

473 we could not identify these at a continental scale. Further regional studies may illustrate the
474 complex interactions of humans and their environment on long timescales, and better identify the
475 spatial extent of impacts.

476

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484

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711

FIGURE CAPTIONS

712 Figure 1. a) Map of the major biomes of North America (Olson et al., 2001) with locations of
713 pollen records extracted from the Neotoma Paleoecology Database (www.neotomadb.org). Each
714 point is one multivariate time series of pollen percentages (vegetation) at that site. Note that the
715 record may vary in length. b) Map of the major cultural regions of North America (Mooney, 1928)
716 with points from the CARD database (Gajewski et al., 2011; Martindale et al., 2016;
717 www.canadianarchaeology.ca). Each point is one radiocarbon date from an archaeological site.
718 Note there may be many points stacked at any location. c) Mean July temperature anomaly of
719 North America derived from the pollen records in Figure 1a (Viau et al., 2006). This curve shows
720 the complete record for the past 14 ka. d) The same temperature data as in Figure 1c but truncated
721 at 10 ka and expanded to better show the variability in the Holocene. This is plotted against
722 taphonomically-corrected human population (black curve) of North America for the past 14 ka,
723 estimated using the data from Figure 1b; see Peros et al., 2010, for details.

724

725 Figure 2. Diagrams summarizing the cross-correlations between differences maps of taxon
726 abundance and population. For each of the spatial cross-correlation functions (121 for each taxon),
727 the average correlation for distances between 30 and 200 km was extracted, for zero lag, +/-100
728 years, +/-200 years, ..., +/-1000 years, and these plotted on the one diagram. A positive lag means
729 that vegetation change corresponds to a more recent 500-year change interval than change in
730 population and a negative lag means the opposite.



