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Human–vegetation interactions during the Holocene in North America

Konrad Gajewski[1] · Björn Kriesche[2] · Michelle A. Chaput[1] · Rafal Kulik[3] · Volker Schmidt[2]

Abstract

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

Keywords Anthropocene · Forest history · Spatio-temporal cross-correlation · Kernel smoother · Canadian Archaeological Radiocarbon Database · Neotoma Paleoecology Database

Introduction

Environmental changes over the past 15 ka (15,000 years) in North America have been associated with cultural development and population growth and used to interpret the archaeological record of technological change. Sociocultural and technological transitions have been explained as a response to challenges and stresses resulting from climate changes (e.g. Fagan 2008; Foster 2012; Kehoe 2017) and early- to mid-Holocene cultural transitions have been correlated with environmental variability on multiple timescales (e.g. Anderson 2001; Kidder 2006). More examples are available from the past 2,000 years; for example, climate changes during the Medieval Warm Period had impacts across the continent, especially in the west where significant droughts were closely tied to cultural changes (e.g. Jones et al. 1999; Foster 2012; Arnold and Martin 2014; Schwindt et al. 2016; Comstock and Cook 2018). The impacts of climate changes hypothesized to have affected the regional archaeological record have been documented (Fiedel 2001; McWeeney and Kellogg 2001), where the palaeoclimate reconstructions were frequently derived from global-scale palaeoclimate syntheses. Indeed, many of the correlations are to ice core and ocean records or other non-local sources of palaeoclimate information. Recently, using radiocarbon

✉ Konrad Gajewski
  gajewski@uottawa.ca

[1] Laboratory for Paleoclimatology and Climatology, Department of Geography, Environment and Geomatics, University of Ottawa, Ottawa, ON K1N6N5, Canada

[2] Institute of Stochastics, Ulm University, 89069 Ulm, Germany

[3] Department of Mathematics and Statistics, University of Ottawa, Ottawa, ON K1N6N5, Canada

databases as indicators of demographic changes, regional scale associations between climate changes and population size have been shown (e.g. Munoz et al. 2010; Grayson 2011; Kelly et al. 2013).

At the same time, there is in interest in understanding how human activity may have affected the environment. Historic human impacts on the vegetation in North America are well-understood. European colonists deforested large areas of North America by the early 20th century, although the vegetation has since regrown in many regions (e.g. Cronon 1983; Williams 1989; Whitney 1994; Dyer 2006), and these changes have been observed in fossil pollen studies (e.g. McAndrews 1988; Kujawa et al. 2016). What is less easily determined is the broad-scale impact of Indigenous American land use practices. Through much of the 20th century it was generally assumed that the human footprint in North America prior to European colonization was insignificant. Changes in human population numbers would have been primarily driven by intrinsic factors and influenced by climate and environmental changes (e.g. Munoz et al. 2010; Foster 2012; Kelly et al. 2013). This view assumed that the total population in the Americas was relatively small and the impacts on the environment were minimal, or at best widely scattered (Denevan 1992). Some authors have suggested between 2 and 18 million people may have occupied North America during this time, although these numbers are controversial and questioned (Denevan 1992; Warrick 2008; Peros et al. 2010).

An alternative viewpoint based largely on archaeological and ethnohistoric research is that the population in 1492 CE was very high, particularly in coastal regions and temperate areas, and that human impacts were extensive across many regions in North America (Denevan 1992; Doolittle 2000). Environmental historians have noted reports by the first European settlers of open forests, of burning by Indigenous Americans to encourage game browse and facilitate travel, and of active or abandoned agricultural fields (e.g. Cronon 1983; Silver 1990; Krech 2000; Kay and Simmons 2002; McShea and Healy 2002; Harkin and Lewis 2007). These reports have been extrapolated to suggest that much of the landscape was open woodland, although the extent is questioned (Russell 1983; Abrams and Nowacki 2008). Ethnographic studies have documented the impacts of activities such as the burning of the prairies or forests (e.g. Stewart 2002; Courtwright 2011). Abrams and Nowacki (2008) summarized studies of land survey records and concluded "… *that the vast majority of vegetation in the eastern USA was managed directly or indirectly by Native Americans, especially through the use of fire*" (p 1134). Similar conclusions have been made by many others, and this viewpoint is becoming increasingly accepted (e.g. Pyne 1982; Cronon 1983; Silver 1990; Krech 2000; Kay and Simmons 2002; Stewart 2002; Harkin and Lewis 2007; Courtwright

2011). Collectively, these studies suggest that the eastern North American landscape was a cultural or humanized landscape millennia before 1492 CE (Zelinsky 1973; Orme 1981; Whitehead and Sheehan 1985; Delcourt 1987; Delcourt and Delcourt 1987, 2004; Silver 1990; Butzer 1992; Doolittle 1992; Kay 1994; Krech 2000; Harkin and Lewis 2007; Abrams and Nowacki 2008; Munoz et al. 2010; Courtwright 2011; Denevan 2011). The critical issue now is the quantification of the extent of these impacts regardless of whether they were deliberate (e.g. setting fires, agriculture and silviculture) or incidental (e.g. successional growth, changes in forest composition, extinctions).

In eastern United States, human-set fires may have encouraged the growth of pioneer and disturbance species such as *Pinus, Quercus* and *Populus* (Bonnicksen 2000) or thinned out closed forests. Several authors have suggested that Palaeoindian (10.5–9.5 ka) fire use may have been a key driver of past changes in vegetation and fire regime, particularly in biotas not prone to burning (e.g. Marlon et al. 2013). The use of fires continued and intensified into the Archaic period (~ 10.0 to 3.0 ka) when Indigenous Americans began using a more diverse group of foods that included game, fish and a wide variety of plants, and burning larger patches of land to encourage the growth of seed, nut and berry-producing species (Fowler and Konopik 2007). During the Woodland (~ 3.0 to 1.0 ka) and Mississippian (1.3–0.5 ka) periods, North American cultures in the Midwest and the East focused on building permanent settlements, plant cultivation and domestication (Fowler and Konopik 2007).

Thus, the environmental impacts of human activities over the course of the Holocene may have been significant. For example, Ruddiman (2003, 2014) suggested that the demographic collapse of the Indigenous population associated with European colonization coincided with the most significant decrease in CO_2 and CH_4 in the last 2,000 and 1,000 years, respectively, showing a close association between Indigenous American land use and the global carbon cycle during the last several millennia. Indigenous American fire use could have doubled the number of fires that would have occurred as a result of lightning strikes (Bonnicksen 2000). Atmospheric greenhouse gas levels may have decreased in response to the near cessation of human-induced biomass burning and the regeneration of forests following this population decline (Ruddiman 2003; Ferretti et al. 2005; Faust et al. 2006; Abrams and Nowacki 2008; Nevle et al. 2011; Ruddiman et al. 2011), which may have amplified the global effects of the Little Ice Age (1450–1850 CE; Dull et al. 2010; Koch et al. 2019).

Alternatively, it is possible that population densities in North America may have been too low to have global implications (Ubelaker 1992; Steckle and Rose 2005; Liebmann et al. 2016) and past changes in atmospheric gas levels were not directly influenced by Indigenous American land use

(Bird et al. 2017). More generally, lower population numbers, perhaps combined with careful management of the landscape, could have meant that Indigenous Americans left a small footprint with only regional or local impact (e.g. Vale 2002; Munoz et al. 2014). Continental-scale palaeoecological research has emphasized the importance of climate variability on vegetation composition (e.g. Williams et al. 2004). On the other hand, palaeoenvironmental studies at local or regional scales have shown strong associations of tree species composition with human activity in time and space, although the intensity of activity has been hard to estimate (e.g. Burden et al. 1986; Delcourt et al. 1986; McAndrews and Boyko-Diakonow 1989; Clark and Royall 1995; Fuller et al. 1998; Parshall and Foster 2002; McLauchlan 2003; Delcourt and Delcourt 2004; Faison et al. 2006; Munoz and Gajewski 2010). Studies of the vegetation of mountainous western North America concluded that human impact, including the setting of fires, was more local than regional (reviewed in Boyd 1999; Vale 2002; Lepofsky and Lertzman 2008), as did a study of the eastern deciduous forest (Munoz et al. 2014). Especially in the west, there is difficulty in separating climate-induced vegetation change from human impacts, given the topographic and ecosystem complexity in the mountain region, such that the spatial extent of the human impact is not clear (e.g. Boyd 1999; Lepofsky and Lertzman 2008). There is a need to understand traditional resource and environmental management (Lepofsky and Armstrong 2018), which to date has been approached through ethnographic and archaeological analysis, and most studies have concluded that impacts are local.

Quantitative estimates of population density are needed to investigate the extent of human impacts on the environment over the Holocene for North America (Day 1953), as well as to better understand how environmental changes may have caused a cultural response. Recently, these data have become available as a result of analyses using the Canadian Archaeological Radiocarbon Database (CARD; Gajewski et al. 2011; Chaput et al. 2015; Martindale et al. 2016). Although archaeological data provide only relative numbers, they have been used, for example, in a reconstruction of the time evolution of the population of North America for the past 15,000 years (Peros et al. 2008)(Fig. 1). These palaeodemographic estimates have also been mapped, depicting the time–space evolution of relative population density (Chaput et al. 2015). Fossil pollen data from sediment cores spanning the continent are available as part of the Neotoma Paleoecology Database (Williams et al. 2018), and it has been demonstrated that these are a proxy for past plant abundance (e.g. Davis 1981; Jacobson et al. 1987; Webb 1988; Webb et al. 1993; Williams et al. 2004). The availability of these databases provides an opportunity to study the question of the interaction of environmental change and human activity (Naudinot and Kelly 2017).

We approach the question of large-scale human-vegetation interactions by comparing estimates of Indigenous American populations over the past 13 ka (Chaput et al. 2015) to data on the distribution of trees during the same time period. We ask two alternative, although related questions. First, did changes in the vegetation affect human activity, including population growth? If tree populations that supported wildlife and produced consumables for Indigenous Americans, such as *Quercus* or *Castanea* (e.g. Wang et al. 2013) became more abundant, this could mean a more reliable food source, encouraging larger populations. For example, in the Pacific Northwest, Hebda and Mathewes (1984) have associated the development of large houses and wood use such as canoes with the arrival into the northwest of *Thuja plicata*, which was a preferred wood for these structures. Kelly et al. (2013) showed an association of population growth and climate variability in Wyoming over the Holocene using the kinds of data we use here. Alternatively, did Indigenous Americans and their activities affect the vegetation in a quantitative, measurable way at regional to continental scales? For example, if Indigenous Americans planted or encouraged the growth of particular tree species, such as *Carya* or *Juglans* (Wycoff 1991; Abrams and Nowacki 2008), then the abundance of these trees should increase after a population increase, if numbers are large enough. If there had been extensive burning or clearing through agriculture, as occurred in eastern North America, this should appear as an increase in disturbance taxa such as *Populus* or Poaceae, or a decrease in late successional taxa such as *Acer* or *Fagus*, as seen on a regional scale in Ontario in the late Holocene (Munoz and Gajewski 2010).

Kriesche et al. (unpublished) described a methodology developed for this purpose, and briefly discussed the example of *Quercus*. In this study, as a next step, we apply this methodology and investigate the large-scale spatial associations in the North American archaeological and pollen records. These results are necessary before complete explanations of the regional intensities of human population-environment interactions, requiring case-specific models and accounting for changes in the associations over time, can be conceived (e.g. Anderson 2001).

Methods

Data

For estimates of past vegetation, we used pollen data from the Neotoma Paleoecology Database (http://www.neotomadb.org); all North American data were extracted. Because there are very few data from Mexico in the databases, we use North America in this paper to refer to the United States and Canada only. In total, there were 1,151 sites available

Fig. 1 a Map of the major biomes of North America (Olson et al. 2001) with locations of pollen records extracted from the Neotoma Paleoecology Database (http://www.neotomadb.org). Each point is one multivariate time series of pollen percentages (vegetation) at that site. Note that the record may vary in length. **b** Map of the major cultural regions of North America (Mooney 1928) with points from the CARD database (Gajewski et al. 2011; Martindale et al. 2016; http://www.canadianarchaeology.ca). Each point is one radiocarbon date from an archaeological site. Note there may be many points stacked at any location. **c** Mean July temperature anomaly of North America derived from the pollen records in **a** (Viau et al. 2006). This curve shows the complete record for the past 14 ka. **d** The same temperature data as in **c** but truncated at 10 ka and expanded to better show the variability in the Holocene. This is plotted against taphonomically-corrected human population (black curve) of North America for the past 14 ka, estimated using the data from **b**; see Peros et al. (2010) for details
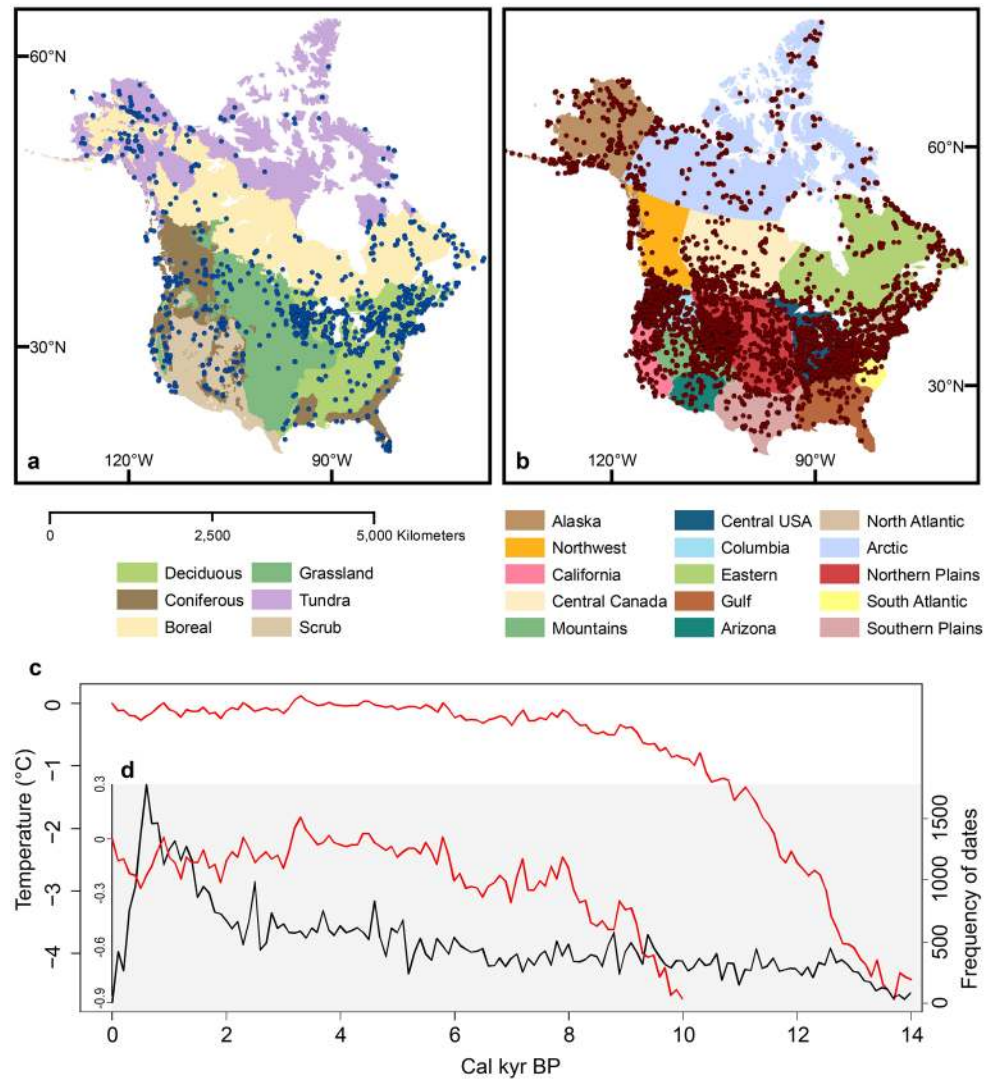
from across North America, although their distribution was uneven (Fig. 1a). The Great Lakes region and eastern North America are particularly well sampled, and sample density decreases to the southwest and far north. Chronology development was discussed in Kriesche et al. (unpublished). Sites vary greatly in temporal resolution of pollen samples and in number of radiocarbon dates, but are nevertheless appropriate for use in this study as shown in previous continental-scale studies at centennial to millennial-scale resolution (e.g. Williams et al. 2004; Viau et al. 2006; Gajewski 2008; Fig. 1c, d).

The pollen sum was based on 64 taxa (Williams and Shuman 2008) and ten were retained for analysis. Taxa were chosen for several reasons, but a first criterion was that they were abundant enough and found across a wide enough range to enable spatial analysis. Boreal and widespread taxa (*Picea, Pinus*) were included as indicators of late glacial and early Holocene environmental changes (Williams et al. 2004) and also due to interest in human-environment

interactions in Beringia (Mason et al. 2001), although we may expect little association with human populations which were at low density at those times (Peros et al. 2010; Chaput et al. 2015). These taxa were also chosen to verify our methodology, since they have previously been mapped on several occasions (discussed below). Several taxa represent major genera of the eastern deciduous forests (*Quercus, Castanea*; Abrams 1992) or important food sources from that region (*Carya, Juglans*) and were retained due to the associations that have been suggested in the literature (Wycoff 1991; Abrams and Nowacki 2008; Lepofsky and Armstrong 2018). Important trees of closed stands of the eastern deciduous forest (*Acer, Fagus*) were included as regional studies have indicated close associations of population and vegetation in the region coincident with their range (Munoz et al. 2010). Finally, two widespread taxa, *Populus* and Poaceae, were analyzed. Although the many species of *Populus* have different ranges and functional roles, Peros et al. (2008) have shown that the pollen record can be interpreted as an

indicator of continental-scale disturbance. Poaceae pollen could indicate possible burning along the prairie-forest border (Stewart 2002; Courtwright 2011), as well as disturbance by fire in forested regions of the east. The taxon selection is therefore biased towards eastern and northern forest regions for this first study, but these are also areas where our site density is greater, and where we could compare our results to previous mapping studies (e.g. Williams et al. 2004).

We used estimates of human population in space and time (Chaput et al. 2015) based on the CARD database (Fig. 1b, c; Gajewski et al. 2011; Martindale et al. 2016; http://www.canadianarchaeology.ca). This consists of over 29,000 radiocarbon dates from archaeological sites distributed across North America. All radiocarbon ages from the pollen and demographic databases were comparably calibrated (Chaput et al. 2015; Kriesche et al. unpublished), and ages are discussed in ka (1,000 years before present). Details of data extraction and preparation of the maps and figures are explained in Chaput et al. (2015, population) and Kriesche et al. (unpublished, pollen).

Methods

Population

Chaput et al. (2015) showed the spatial distribution of the human population of North America through time in a series of maps based on a 500-year time-spans, with subsequent maps produced at overlapping intervals of 100 years: 0.5–1.0 ka, 0.6–1.1 ka, …, 12.5–13.0 ka. These maps, interpreted as estimates of past population density, were prepared from the radiocarbon dates using a kernel density estimator, which accounts for biases from inhomogeneous sampling strategies, taphonomic loss and boundary effects. This resulted in a total of 121 maps of population density.

Vegetation

A series of 121 maps showing the pollen percentage distributions was prepared for each taxon. As with population, an estimator from kernel regression (Kriesche et al. unpublished) was used to determine the spatial distribution of pollen percentages at the central age of each 500-year time period. To enable comparability, the same configurations of the estimators were used as for population, except that the population was illustrated on a logarithmic scale and the pollen percentages on a linear scale. For each time period, the range of the taxon was used as a mask, and population values extracted from within this range. The range at a given year was that region where pollen percentages exceeded 0.2 times the maximum of pollen percentages. As a consequence, the analyses for several taxa

are restricted to eastern North America. These estimated values were used for correlation analyses.

Correlations and cross-correlations

Spatial correlation functions of both population and pollen percentage maps (separately) were estimated for each time period. All of the 121 correlation functions for population and for each taxon within the range were summarized in one graph, a heat map that shows the spatial autocorrelation of population or the taxon through time. Spatial cross-correlation functions were then computed showing the relationship between estimates of population and pollen abundance of each taxon, restricted to the estimated taxon range. The series of 121 functions for each taxon were summarized in one plot, which identify times of strong spatial cross-correlation between population and taxa.

To determine if changes in population and taxon abundance were correlated, difference maps were produced subtracting maps with a temporal distance of 500 years to provide 116 maps of 500-year changes in population and taxon abundance (in 100-year steps). These correspond to the same 500-year change interval and also to intervals that are shifted by the temporal lags + 100, + 200, …, + 1,000 years, and − 100, − 200, …, − 1,000 years. A positive lag means that vegetation change follows a change in population and a negative lag means the opposite. Similarly to the actual maps, spatial correlation functions were estimated for the difference maps of vegetation abundance and population for each 500-year change interval, and summarized as heat maps. Cross-correlations between the difference maps for vegetation abundance and population were also prepared for lags of − 1,000, − 900, …, − 100, 0, 100, …, 900, 1,000 years and the comparable summaries for all time periods are shown as heat maps.

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

Nonparametric resampling methods were used to assess the significance of the obtained correlation results (Kriesche et al. unpublished). Correlations with higher absolute values are considered to indicate a real signal: ca. 0.15 (*Picea, Pinus*), 0.2 (*Acer, Carya, Juglans*), 0.25 (*Fagus*), 0.3 (*Castanea*, Poaceae, *Quercus*) and 0.4 (*Populus*). A more detailed methodology including an illustration of each step mentioned above can be found in Kriesche et al. (unpublished) and in ESM Appendix S1.

Fig. 2 Diagrams summarizing the cross-correlations between differences maps of taxon abundance and population density. For each of the spatial cross-correlation functions (121 for each taxon), the average correlation for distances between 30 and 200 km was extracted, for zero lag, ± 100 years, ± 200 years, …, ± 1,000 years, and these plotted on the one diagram. A positive lag means that vegetation change corresponds to a more recent 500-year change interval than change in population and a negative lag means the opposite
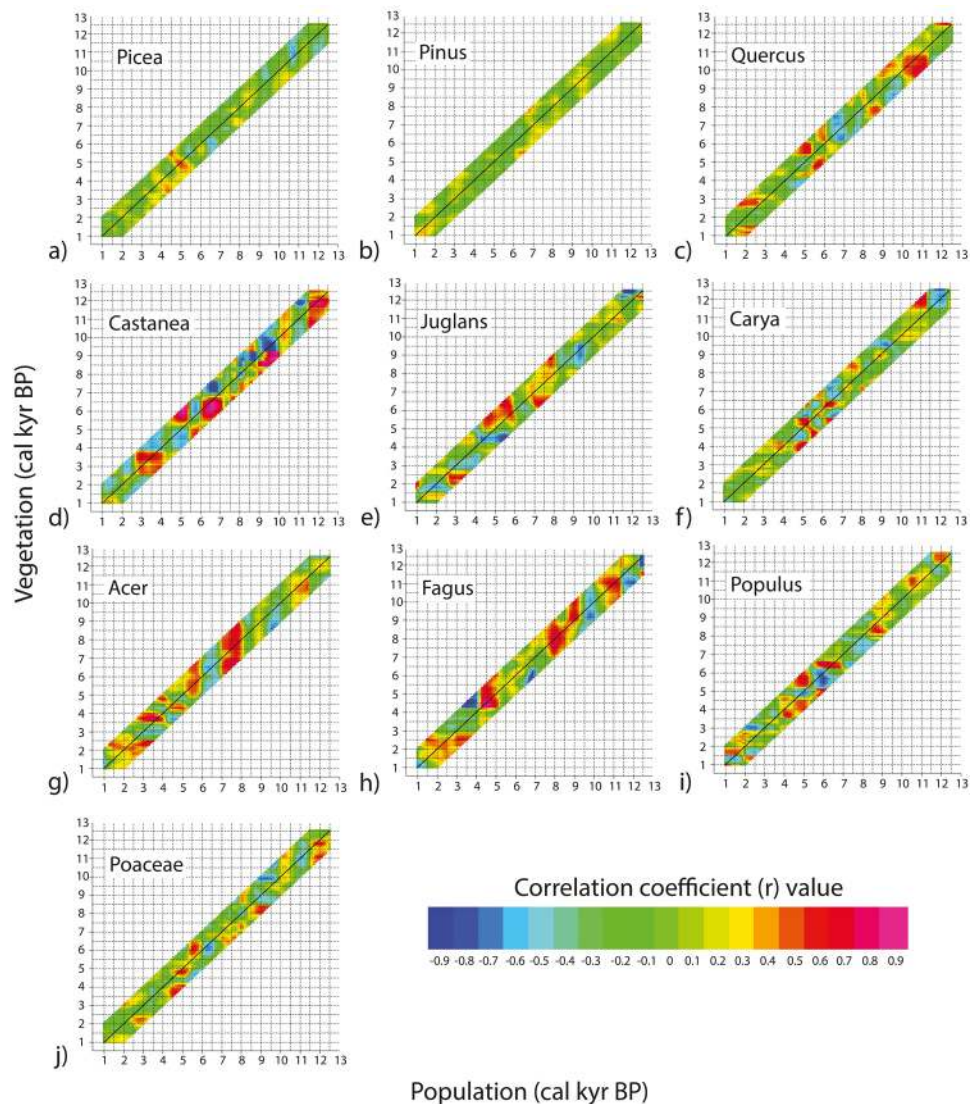
Results

Population

The population maps were discussed in detail in Chaput et al. (2015). Prior to 10 ka, there were population maxima in the southern United States and northwestern North America. Maxima remained in the south in the early Holocene, and population tended to increase in the west over the course of the Holocene. Population increased across all of North America in the past 2 ka. Our maps do not extend into the European contact period as they are based on radiocarbon dates which tend to be used less when historical information is available to date deposits. They therefore do not record the large Indigenous population decrease at that time.

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

The range and abundance maps depicting the distribution of *Picea* through time closely resemble those presented in Williams et al. (2004), suggesting that the differences in methodology are not greatly influencing the results. There were no clear associations with population or changes in population and these taxa. In the early Holocene (> ~ 8 ka), large increases in *Picea* occurred in the northwestern part of range, but there were both positive and negative changes in population density depending on the region, reducing the cross-correlation of the difference maps of *Picea* and population (Fig. 2a). In general, zones of increasing or decreasing values were sometimes in phase or not with population (ESM Appendix S2), so the cross-correlation of *Picea* with population was low. During the period between ~ 5.5

to 3.5 ka both *Picea* and population increased in the east, leading to a brief period of high positive cross-correlations (ESM Appendix S3). In the past 1 ka, changes in *Picea* were relatively small, whereas population was increasing across the entire range; the cross-correlation of the change maps remained non-significant as a consequence. Again, our migration maps for *Pinus* look similar to those of Williams et al. (2004) and there are no clear correlations with population change maps (Fig. 2b). Occasional associations between population and *Pinus* in the southern, eastern or western regions are masked by a lack of association in others.

Major taxa of the eastern deciduous forest: *Quercus* and *Castanea*

Quercus was discussed in Kriesche et al. (unpublished) as an example of application of the methodology. At 12 ka there was abundant *Quercus* in the Gulf States, and by the mid-Holocene it was found across the present-day range, with a maximum from Illinois to Virginia. There was some association between *Quercus* and population (Fig. 2c), probably because *Quercus* is representative of the deciduous forest rather than through any kind of causal relation between *Quercus* and population.

High values of the spatial autocorrelation and cross-correlation of population and *Castanea* prior to ~ 5 ka are difficult to interpret as the pollen record is dominated by sites in Texas (Bryant and Holloway 1985), resulting in a discontinuous range (ESM Appendix S2). The cross-correlation between *Castanea* and population density is relatively high and positive in the late Holocene (most recent ~ 4 ka), as both variables have high values in the central portion of the range (Fig. 2d). In the past 2 ka, population maxima were found in the western portion of the range, reducing the cross-correlation (ESM Appendix S3). *Castanea* is one taxon where the positive and negative lag correlations differed (Fig. 2d), but this is mostly prior to 7 ka. Between 5 ka and 4 ka, the range of *Castanea* decreased as it moved northward, whereas population was increasing. Between 3.5 and 2.5 ka, both pollen and population increased, especially in the southern part of the range. During the past 2 ka, the *Castanea* range changed little, except in the north (Paillet 2002) where it increased, whereas population was increasing across the range, so there was little cross-correlation.

Major mast trees of the eastern deciduous forest: *Juglans* and *Carya*

Shortly after 12 ka, the range of *Juglans* was located in a broad area from Louisiana to the Great lakes, west of the Appalachians (ESM Appendix S2). By 9–10 ka, *Juglans* decreased in the south, so the range was at a minimum. Maximum pollen percentages were centred over the Midwest and

remained in this area until the present. In the early Holocene, the cross-correlation of *Juglans* with population was relatively small, since the maximum population relative density was in the south, whereas maximum *Juglans* was in the central part of the eastern United States (Fig. 2e). Similarly, the difference maps showed a complex sequence of changes that were rarely aligned between population density and *Juglans* pollen percentages. Through most of the mid- to late Holocene, the range of *Juglans* changed little, and the population maxima were to the south and east of that of *Juglans*. Since the trees seemed to increase first, this does not suggest that Indigenous populations caused an increase in abundance in this species, although the association may suggest that it was exploited. In the late Holocene, population increased across the entire range of *Juglans*, and maximum values were overlapping with the pollen maximum, displaced to the west. High values of population associated with high and low values of *Juglans* contributed to the lower spatial autocorrelation. This preceded the major increase in agriculture in the region.

The range of *Carya* gradually extended northward in the early Holocene, especially west of Appalachians, and extending to the Great Lakes by 9 ka (ESM Appendix S2). As *Carya* moved northward and was found at moderate values across a large range, the maximum in population density was also broadly coincident (ESM Appendix S3), leading to high cross-correlations between 10 and 7.5 ka (Fig. 2f). In the mid-Holocene (~ 8 to 4 ka), high values of population sometimes corresponded to high values of *Carya*, but in other regions to low values, so the overall spatial correlation was around zero. The spatial cross-correlations of the difference maps showed few consistent associations in the early or late Holocene (Fig. 2f). An alternation of positive and negative cross-correlations in the mid-Holocene was driven in part by very large increases in *Carya* from 7 to 5 ka in Texas, which were accompanied with increases or decreases in population. *Carya* decreased in abundance in the southern part of the range at times when population did as well, leading to some periods of high cross-correlation. Between 4.5 and 3.5 ka, *Carya* increased in the north-central part of the range, and large population increases in the same area contributed to the band of high correlation in Fig. 2f. In the past 2 ka, *Carya* changed less in the northern part of the range while at times decreasing in Texas; during this time population was greatly increasing in the central portion of the range, leading to overall low cross-correlations.

Northern deciduous forest: *Fagus* and *Acer*

Acer and *Fagus* were found in the northern part of the eastern deciduous forest in the mid- to late Holocene (ESM Appendix S2). At 13 ka, the range of *Acer* was extensive, with maximum values in south-central United States. *Acer*

moved north quickly, present even up to the retreating ice sheet. By the mid-Holocene until the present, maximum values were centred on Ontario. The stability of the range in the mid- to late Holocene, and general increase in abundance led to relatively high cross-correlations with population at certain times, but population maxima also shifted, leading to alternating periods of positive and negative correlation (Fig. 2g; ESM Appendix S3). For example, in the mid-Holocene, there was a minimum in population density in the area centred over Ontario where *Acer* was most abundant, leading to weak cross-correlations. Generally, the maximum in population was found to the south of the region of most abundant *Acer*. The period of large positive cross-correlations in the difference maps from 8 to 9 ka (*Acer*) and 7–8 ka (population) occurred when *Acer* was increasing greatly in Ontario, and population was relatively constant across all of its range. In the past 2 ka, *Acer* increased in the southwest portion of its range, when population was also increasing, leading to positive correlation. Given the stability of a large maximum in *Acer* centred over southern Ontario through much of the Holocene in both the absolute and difference maps, the lack of a comparable feature in population density (in either a negative or positive sense) reduces the correlation between these two variables.

By 10 ka there were high values of *Fagus* in western Pennsylvania; this remained until the present. In the past 8.5 ka, large values of *Fagus* pollen were restricted to the north of Virginia, with most abundant values in Pennsylvania and New York. In the oldest part of the record, when *Fagus* was restricted to the south, there was little association of *Fagus* and population density, and this continued in the period between 11 and 8.5 ka as it migrated rapidly northward (Fig. 2h). In the period around 8 ka, *Fagus* difference maps were positive, centred on the range for long time periods, whereas population increased or decreased in various portions of the range. Large positive values of cross-correlation occurred with large increases in *Fagus* and small but smooth values of population density. The large positive association between 4.5 and 6 ka (*Fagus*) and 4–5 ka (population) occurred when both were increasing in the northeastern portion of the range. After 4 ka, *Fagus* increased in Ontario and Quebec, at times when population was decreasing and at other times when increasing. Increases in *Fagus* and population in the past 3 ka in the western part of the range led to positive cross-correlations.

Disturbance and prairie indicators: *Populus* and Poaceae

The range of significant values of *Populus* decreased rapidly between 10 and 8 ka, and almost no pollen was found in sediments subsequently (Peros et al. 2008, ESM Appendix S2). Cross-correlations of *Populus* and population were high in the early Holocene, as both were abundant in Beringia and Alberta (Fig. 2i, ESM Appendix S3). After 8 ka, when the range of *Populus* was very small and broken into disjunct regions, the autocorrelation functions decreased substantially, as did the cross-correlation with population. In the mid-Holocene, during periods of strong cross-correlation of the difference maps, *Populus* was restricted to a small area of the Southwestern US.

Before 9 ka, Poaceae pollen was found in several areas from the Arctic to Florida. Over the course of the Holocene, it increased in abundance in the present-day prairie region, as this biome developed after 8 ka. High values of Poaceae and population, especially in the southern plains, and low values elsewhere led to high spatial cross-correlations between 6.5 and 3.5 ka (Fig. 2j). The cross-correlation of the maps as well as the differences decreased after 5 ka, as maximum Poaceae values were found in the central portion of the range, whereas the maximum population was around the edges of the range.

Discussion

Periods of high spatial cross-correlation between population density and pollen abundance were identified, although they were limited in extent in time and space. However, the correlations did not consistently increase across all taxa, although there was a large increase in population in the late Holocene, and the plants had mostly become established in their respective ranges. Frequently, maxima in population and a plant taxon were displaced, which may be associated with site density and the estimation of the intensity surfaces, but is more likely due to a limited association between population density and abundance of the plant taxon. This suggests that the associations are sub-regional in extent. The clear associations between population density and environmental change seen at a regional scale (e.g. Munoz et al. 2010; Kelly et al. 2013) do not appear to scale up to the continent either because spatial differences lower overall correlations, or impacts always remain regional. These results justify the need for regional-scale studies, such as Munoz et al. (2010) and Kelly et al. (2013), to identify and quantify human-environment associations.

We do not see evidence of the converse: biome-scale impacts of human activity on the vegetation, as hypothesized by numerous authors (see Introduction), especially for eastern United States. We should expect increasing cross-correlations in the recent past with increasing populations (Peros et al. 2008) and expansion of agriculture in the eastern deciduous forest, but in fact, this was not observed. If extensive human-caused fires did push the forests of eastern North America toward more *Quercus* and other disturbance taxa across a large area, we would not expect high positive

correlations with *Acer* and *Fagus*. Given the importance of mast species as a food source, we would have expected a higher correlation of *Juglans* and *Carya* with population than was seen. The increase of *Populus*, as agriculture developed in Ontario (Munoz and Gajewski 2010), does not seem to scale upwards to the biome scale. Several possibilities can be proposed as explanation for this lack of association.

a. Associations were minimal: human impact was not great enough to have a significant influence on the vegetation, either due to low human population density or the intensity of the activities. Our conclusion is that there is presently little indication of continental-scale impacts of human activities on the vegetation of North America over the course of the Holocene, but rather that it was local and regional. Vale (2002) provided a classification of land use by Indigenous Americans useful for this discussion, and more work at regional scales, as discussed in the Introduction, could document this interaction.

b. Alternatively, the impact of Indigenous American activity on the vegetation may have been widespread, but not associated with changes in the human population density. Although this is a possibility, it cannot be investigated at present. Ongoing work attempting to estimate vegetation density (Chaput and Gajewski 2018), and new data on charcoal and pollen from more sites may help resolve this question.

c. We did not see the associations since our method is too insensitive, or results are highly determined by aspects of the data such as a low signal-to-noise ratio. We identified some taxa, especially those that are underrepresented in the pollen rain, where problems with estimating the spatial fields for part of the time period may make interpretation more difficult. Inadequacies with the databases, especially low site density or incomplete archaeological data in some regions may be reducing the sensitivity of the study. However, for many taxa and time periods, the maps resemble previous versions (Davis 1981; Jacobson et al. 1987; Webb 1988; Webb et al. 1993; Williams et al. 2004) and associations should be observable. The population maps are consistent with archaeological knowledge (Chaput et al. 2015). Future work at regional scales, or using different averaging periods, could determine the robustness of these results.

Overall, there was little relation between changes in *Picea* or *Pinus* and changes in population. This is not surprising, as even in the recent past, the human population density of boreal regions was low and agriculture was not possible. In the mountains of the west, the density of available pollen records is still relatively low, given the topographic and ecological complexity of the region, and thus it is difficult to find associations. The wide range of these taxa,

extending over many different cultures and climates can lead to regional positive and negative correlations between population density and the taxon cancelling and leaving little correlation. We also saw little relation between *Populus* and population. Although local and regional palaeoecological studies have shown the impact of agriculture on long-term vegetation dynamics (Delcourt 1987; McAndrews and Boyko-Diakonow 1989; Clark and Royall 1995; Delcourt and Delcourt 2004; Munoz and Gajewski 2010), these impacts apparently do not scale to the entire forest region.

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

In the eastern deciduous forest, we have the most data, an extensive historical literature and several regions of extensive palaeoecological study on the interaction of Indigenous populations with the environment (Delcourt and Delcourt 1979; Delcourt et al. 1986; Delcourt 1987; Foster et al. 2002; Munoz and Gajewski 2010). The importance of human-caused fires has been emphasized by many authors but whether or not the pre-European eastern forests were continuous or open parklands is not resolved (Pyne 1982; Cronon 1983; Silver 1990; Krech 2000; Kay and Simmons 2002; Stewart 2002; Harkin and Lewis 2007; Abrams and Nowacki 2008; Courtwright 2011). The continual clearing of land, abandoning and moving to new locations, especially after the introduction of maize, could have had a significant impact on the vegetation, especially if fire was used to aid in clearing the forests, although Doolittle (1992) has questioned some of the assumptions about this aspect. We would expect an increase in grasses and other herbaceous plants after the introduction of agriculture, or as a consequence of extensive burning. There are many historical reports of Indigenous American ground fires in the forests of eastern North America and this is supposed to have affected the large-scale nature of the forests (e.g. Silver 1990; Stewart 2002). However, palaeoecological studies find little evidence for fires in the region (e.g. Clark and Royall 1996; Lafontaine-Boyer and Gajewski 2014), although there are few available records. *Quercus* would be favoured by fires caused by human activity (Abrams 1992; McShea and Healy 2002; Black et al. 2006; Tulowiecki and Larsen 2015), however, we did not see an association. Due to its ability to sprout, *Castanea* increased after European settlement (Southgate 2006) and there is speculation that it may have been favoured by fires associated with Indigenous American populations in New England (Foster et al. 2002), but we see little evidence in our results. We might expect *Acer* and *Fagus* to

decrease if growth of mast trees were being encouraged by Indigenous American activities such as fire or planting, as these are late successional canopy trees and can reproduce in the shade, whereas positive correlations of these two taxa with population density would be expected if populations were having little impact on the forests. The overall positive association of *Fagus* and *Acer* abundances with population may suggest that any human disturbance was insufficient for wide-scale conversion of the forest into earlier successional states, as shown, for example in southern Ontario (Munoz and Gajewski 2010). The alternative interpretation is that factors that favoured the maintenance of these taxa also maintained populations of Indigenous Americans, and this seems to be the nature of the association of population and vegetation in this region.

An extensive literature has noted the importance of acorns and nuts for human consumption as well as for animal populations they would have hunted (e.g. Delcourt and Delcourt 1979; Silver 1990; Wycoff 1991; Anderson 2001; Scarry 2003). There is a possibility of Indigenous American dispersal of nut trees either deliberately or at least more rapidly than would have occurred naturally (Dorney 1981; Wycoff 1991; MacDougall 2003; Smith 2007). There are also reports of large populations of mast-producing trees in association with villages, due to intentional or accidental growth of trees planted or discarded (Silver 1990; Black et al. 2006). Today, *Carya* is not regenerating across large areas in eastern North America (Cowden et al. 2014). *Carya* would increase in abundance within the range not only at times of appropriate temperature and moisture, but also with sufficient canopy disturbance, and we may expect an increase when population increased. However, increased drought or other factors could also increase canopy disturbance, and the lack of a clear association with population (Fig. 2f) may indicate a lack of such disturbances. The clearest signal of a potential association between these two taxa and population is found in the northeastern United States in the middle Holocene, and a regional study could help determine its significance.

Studies in Eurasia have suggested increasingly intense impacts of human activity as the Holocene progressed, and in extreme cases, have led to ideas of an "early Anthropocene" (Ruddiman 2014), which proposes that human impacts on the global climate (carbon cycle) began to be measurable thousands of years ago. We attempted to determine if the impacts of Indigenous North Americans contributed to this early Anthropocene. The results of our study do not suggest a significant impact; if they had occurred, we could not identify these at a continental scale. Rather, we identified regional-scale associations between changes in human population density and vegetation change, perhaps due to increasing human adaptation as the forests developed, which led to periods of positive association. Further regional studies may illustrate the complex interactions of humans and their environment on long timescales, and better identify the spatial extent of impacts.

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