



Using spatial analysis to estimate depopulation for Native American populations in northeastern North America, AD 1616–1645

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ABSTRACT

Eight years ago, [Ramenofsky et al. \(2003\)](#) characterized the discussion of the impact of Old World diseases on Native American populations as almost exclusively historical in nature. They specifically argued for the application of more evolutionary, genetic, and epidemiological theory to research into this topic. We agree with their assessment and further suggest that such research would greatly benefit from spatial analyses of disease spread as well. Using trend surface analysis of existing ethnohistorical and archaeological data pertaining to population sizes and disease events, we examine the spatiotemporal dimensions of 17th century depopulation in northeastern North America. The subsequent results allow us to predict possible depopulation rates for populations with very little demographic data. Further, our use of biological, historical, and cultural data to interpret the results represents an attempt to provide a more complex explanation for the variability in cultural survivability across the region and several possible avenues for productive future research. We believe research like this can significantly improve our understanding of how Old World diseases affected historic Native American populations and cultures and continue to impact them today.

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Introduction

Determining the magnitude of depopulation from the introduction of Old World diseases among Native American societies has many benefits, from helping us to understand cultural development, to providing information that may be helpful for understanding current demographic patterns in Native American communities, and to helping us understand disease transmission and effects among human populations. There currently exists a significant amount of data, albeit highly variable in accuracy and precision, on pre- and post-contact Native American population sizes, depopulation rates, and the timing of Old World disease events. However, large geographic, demographic, and temporal gaps exist in the data when viewed on regional scales. There is a need to fill in those gaps to better understand the variability of depopulation and the nature of disease spread. With more complete data, we may be able to synthesize and analyze population and disease patterns in more detail.

[Ramenofsky et al. \(2003\)](#) contended that discussions of pre-contact populations and the impact of Old World diseases on Native American populations have tended to focus on historical questions and have yet to adequately examine the complex set of cultural

and biological factors that were likely influencing depopulation rates. [Thornton \(1997\)](#) similarly critiqued the lack of demographic theory being applied to this area of research. We agree with these assessments and further suggest that this topic would benefit greatly from spatial analyses of existing population data in order to explore spatial trends in the data and even possibly predict population losses among groups with no current data.

Our first goal for this research is to simply map what we currently know about the population distributions and depopulation (i.e. percentage of population lost) for 17th-century Native American societies in northeastern North America. We will use this information to examine spatial trends in the depopulation—something that has yet to be done. Our second goal is to use spatial interpolation to determine depopulation for groups in northeastern North America with no current population information. This will fill in the gaps in our current information and help us to better understand the nature of depopulation in this region. To accomplish this goal, we map 17th-century population distributions and existing historic and archaeological depopulation data to examine simple spatial patterning in depopulation rates and analyze existing historic and archaeological data using kriging, a spatial interpolation method, in order to predict depopulation rates. Our final goal is to use our results and existing historic and archaeological population data to begin discussions about the cultural, biological, and historical factors that may have influenced depopulation rates among Native American groups. To accomplish the final goal, we

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use current hypotheses about host immune function and genetic variability, cultural information from these groups, and historical information from the region to explore possible causes of observed patterns of depopulation in the Northeast.

Background

The reduction of Native American populations during the sixteenth through nineteenth centuries was culturally and demographically devastating and has had lasting effects among Native American societies. As a result, numerous researchers, including archaeologists, paleodemographers, and historians, have been interested in gaining a better understanding of this phenomenon. Although warfare, slavery, and other mistreatments were causes, introduced Old World diseases were responsible for the overwhelming majority of deaths (Black, 1991). As such, these diseases have rightfully been the focus of research into the details of Native American depopulation. In this body of work, researchers have used numerous methods for estimating depopulation percentages and rates from disease. These have included the use of historical data (e.g. Dobyns, 1966, 1983; Kroeber, 1939; Palkovich, 1985; Thornton, 1987, 1997; Ubelaker, 1976, 1988), archaeological data (e.g. Jones, 2010a, 2010b; Snow, 1995a, 2001; Warrick, 2008), and combinations of both (Ramenofsky, 1987). To date, there have been almost no attempts to estimate depopulation figures or explore existing data using spatial analysis techniques.

Pre- and post-contact Native American populations in the Northeast present perhaps the best cases for examining existing depopulation patterns with new methods. Demographic archaeological research on Iroquoian-speaking populations, such as the Haudenosaunee and Wendat (Jones, 2010a, 2010b; Snow, 1995a, 1995b; Snow and Starna, 1989; Warrick, 2008), has produced an empirically based population dataset for several populations for the periods just prior to and around the time of the arrival of Europeans. For other groups in the region, population data in the form of total counts, warrior counts, and impacts of diseases come from historical texts dating to the very earliest 17th century interactions between Europeans and Native Americans through the 18th century (for examples see Jameson, 1909, p. 141; Thwaites, 1959, vol. 7: p. 87, vol. 8: p. 43, vol. 12: pp. 263–265; Winthrop, 1908, vol 1: pp. 111–114). However, there are a small but significant number of populations in the region that have little or no population data. These include the Erie, Wenro, Neutral, Susquehannock, Kennebec, Munsee, and Naragansett-Pokanoket. These gaps have made discussing large-scale patterns of disease spread and depopulation in the region difficult. However, this type of dataset with several reliable sources of population data and a few gaps is almost ideal for using spatial interpolation methods to estimate depopulation rates for those groups with no relevant data. Interpolation methods use trends in existing data to estimate values for holes in the dataset. Datasets with more data will produce more accurate estimated values. Once these gaps are filled, the depopulation data for the Northeast will be one of the more complete population datasets for the continent. Such a dataset would allow us to explore the biological, cultural, and historical factors behind the depopulation trends in much more detail than has been possible in the past.

While a great deal of research has gone into producing pre- and post-contact Native American population numbers, there have been far fewer attempts to explain the patterns of the diseases and other causes that gave rise to these numbers. In addition to generating new depopulation data, we attempt to build on the small number of influential studies that sought to explain the depopulation patterns. Black (1991) discussed the role of human genetic diversity in disease virulence, particularly within native

South American populations, which tend to be relatively homogeneous. Such host homogeneity can increase the virulence of a disease, because a pathogen that has infected and adapted to one host is thereafter preadapted to individuals who are genetically similar to the original host. There have been few attempts to apply Black's findings to other results.

Ramenofsky (1990) examined differential survivability as a result of Old World diseases for groups in the Southeast using a selectionist approach (i.e. Darwinian evolution). She developed a model based largely on settlement location and type and how characteristics, such as sedentism and distance to major waterways, would impact survivability of a group. Her work introduces several possible explanations for differential depopulation rates among groups in the same region. Like Black's work, little follow-up research has been done to test her hypotheses. Below, we discuss our results in reference to Ramenofsky's model.

Thornton et al. (1991) sought to bring a more complex demographic approach to the discussion of depopulation. They noted that it is an oversimplification to talk solely of mortality. We must take into account, in particular, fertility patterns before and after disease events in order to fully understand the overall depopulation rate that is observed. For example, they noted that a population with a 1% growth rate could completely recover from a 40% loss in population within 35 years (Thornton et al., 1991, p. 37). While we do not specifically address fertility below, it is important to keep their findings in mind when discussing depopulation rates.

Specifically in the Northeast where our research focuses (region and cultures shown in Fig. 1), it appears that Old World diseases had drastic negative impacts on Native American populations only after protracted contact with Europeans (Jones, 2010a, 2010b; Snow, 1995a, 1995b; Snow and Starna, 1989; Warrick, 2008). Snow and Lanphear (1988) sought to explain early results using modern knowledge of the virulence and vectors of transmission of smallpox, the most likely disease to have first struck Northeastern groups. They hypothesized that adults on the initial voyages to North America would have begun the journey with immunity to smallpox, as otherwise the disease would have burned itself out during the voyage. Only when a significant number of possible hosts (i.e. children) were present on boats could the disease infect and spread among susceptible individuals and thus be maintained on the long voyage. Although speculative, this is one of the only attempts to determine disease vectors and their role in the timing of diseases.

Using a different approach, Milner et al. (2001) and Milner and Chaplin (2010) sought to explain differential disease impacts and depopulation through first-level spatial analyses of the geographic ranges of Late Prehistoric cultures in eastern North America. First-level spatial statistics are the initial observations of patterns, and these two studies identified a clustered pattern of settlement that included significant areas of uninhabited space across the eastern portion of the continent. The authors proposed that these uninhabited areas acted as barriers to disease spread, preventing pandemics.

All of these studies were informative and represented the beginning of a wave of analyses that sought to move beyond numbers to explain the patterns of depopulation. Unfortunately, many of these studies (aside from Milner and associates' work) are over 20 years old. Few studies have sought to continue this approach over the last decade.

Methods

Information about the spatial distribution of early 17th-century Native American populations in the Northeast came from existing publications, which are listed in Table 1, and archaeological survey

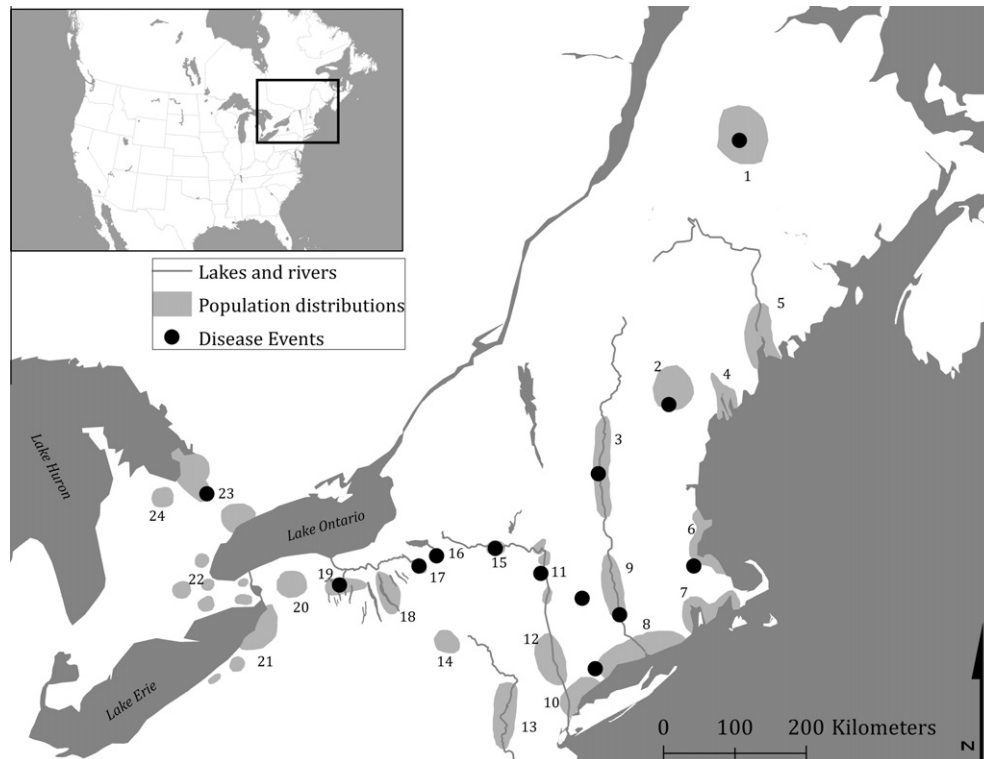


Fig. 1. The geographic distribution of 17th century Native American cultures of the Northeast used in the study. The populations are (1) Maliseet-Passamaquoddy, (2) Eastern Abenaki, (3) Western Abenaki, (4) Kennebec, (5) Penobscot, (6) Massachusetts, (7) Narragansett-Pokanoket, (8) Mohegan-Pequot, (9) Pocumtuc, (10) Quiripi-Unquachog, (11) Mahican, (12) Munsee, (13) Minisink, (14) Susquehannock, (15) Mohawk, (16) Oneida, (17) Onondaga, (18) Cayuga, (19) Seneca, (20) Wenro, (21) Erie, (22) Neutral, (23) Wendat, (24) Tionontaté.

Table 1

The 17th-century Native American cultures of the Northeast used in this study and the source of their geographic information. Those in *italics* previously had no population information but have depopulation percentage estimates from our results below.

Culture	Sources on geographic distributions
Maliseet-Passamaquoddy	Snow (1980, p. 341)
Mohegan-Pequot	Dincauze (1990)
<i>Kennebec</i>	Piotrowski (2002)
Mahican	Bradley (2007)
Eastern Abenaki	Snow (1980, p. 62)
Western Abenaki	Snow (1980, p. 342)
Massachusetts	Dincauze (1990) and Bragdon (1996)
Pocumtuc	Dincauze (1990) and Piotrowski (2002)
Quiripi-Unquachog	Dincauze (1990)
<i>Narragansett-Pokanoket</i>	Dincauze (1990)
Mohawk	Snow (1995a)
Oneida	Jones (2010a, 2010c)
Onondaga	Jones (2010a, 2010c)
Cayuga	Jones (2010c)
Seneca	Wray et al. (1987) and Jones (2010c)
Wendat	Engelbrecht (2003) and Warrick (2008)
<i>Neutral</i>	Snow (1994) and Engelbrecht (2003)
<i>Wenro</i>	Snow (1994) and Engelbrecht (2003)
<i>Erie</i>	Snow (1994) and Engelbrecht (2003)
<i>Munsee</i>	Dincauze (1990)
<i>Susquehannock</i>	Snow (1994) and Engelbrecht (2003)
Minisink	Kraft (1991)

and mapping done by one of the authors (EEJ) during previous settlement and population research for the 16th- and 17th-century Haudenosaunee (Jones, 2006, 2010a, 2010b, 2010c). The information from existing publications comes from regional specialists who published detailed maps, from descriptions of the extent of

settlement of a group during the late sixteenth or early 17th century, and from published research that compiled geographic settlement data from unpublished regional sources. Using ESRI™ ArcInfo™ software, we digitized the information from these sources into a geographic information system (GIS). Previous research by EEJ produced regional settlement pattern data using pedestrian surveys and differential geographic positioning systems (GPS) technology. EEJ originally used these data to study the factors influencing settlement patterns (Jones, 2010c) as well as the relationship between settlement size and population size (Jones, 2010a, 2010b); our study here represents a new use of these existing data. Given our study period of 1616–1645, we used the locations of sites occupied during this period and within a GIS, simply created a shapefile of the geographic range that contained them. These data were combined with the aforementioned data from existing publications to create the total dataset for this research. Fig. 1 displays the geographic ranges for all of the groups.

Pre- and post-contact population estimates came from the same previous research (Jones, 2010a, 2010b) as well as published sources. All population numbers are estimates and carry varying levels of accuracy. The population numbers, depopulation percentages, and sources are listed in Table 2. The most accurate numbers are those of the included Haudenosaunee cultures (i.e. Mohawk, Oneida, Onondaga, and Seneca) and the Wendat-Tionontaté. These data were generated from long-term research projects that generated population sizes and changes over time using several lines of evidence, including archaeological settlement data and historic accounts. Population data for the other cultures come primarily from historic warrior counts or population counts by European traders and explorers. The sources from Snow and Lanphear (1988) are revised numbers from Snow (1980). Because they are based on a single line of evidence, the historic estimates are likely not as accurate

Table 2
Population data for the 17th-century Native American populations used in this study, including the year of the depopulation event being studied, beginning and ending populations for the depopulation event during the indicated year, percentage of total population that died, and sources.

Population	Date	Initial population	Resulting population	Percent lost	References
Maliseet-Passamaquoddy	1633	7600	2500	67	Snow and Lanphear (1988, p. 24)
Mohegan-Pequot	1633	16,000	3000	81	Bradford (1952, p. 260)
Mahican	1633	6400	500	92	Snow and Lanphear (1988, p. 24)
Eastern Abenaki	1633	13,800	3000	78	Snow and Lanphear (1988, p. 24)
Western Abenaki	1633	12,000	250	98	Snow and Lanphear (1988, p. 24)
Massachusetts	1633	44,000	6400	86	Snow and Lanphear (1988, p. 24)
Pocumtuc	1633	18,400	920	95	Snow and Lanphear (1988, p. 24)
Quiripi-Unquachog	1633	29,900	1500	95	Snow and Lanphear (1988, p. 24)
Mohawk	1633	8000	1750	78	Snow (1995a, 1995b), Jones (2010a), and Snow and Lanphear (1988, p. 24)
Seneca	1634	4850	3150	35	Jones (2010b)
Oneida	1635	1500	400	73	Jones (2010a)
Wendat	1639	20,000	10,000	50	Heidenreich (1976), Trigger (1976, pp. 588–589), and Warrick (2008)
Onondaga	1645	2700	1150	57	Jones (2010a)

as the Haudenosaunee and Wendat-Tionontaté numbers. However, they have sufficient reliability to use them to examine large-scale depopulation trends.

We calculated depopulation percentages from the initial and resulting population numbers. To georeference the depopulation data, we recorded each percentage as occurring at a single location and placed it at the center of the early 17th-century territory for the associated society. This created the spatial component necessary for accomplishing our first goal, which was to observe spatial patterns in the depopulation data.

To achieve our second goal of estimating depopulation rates for populations with no current data, we performed kriging analysis on the depopulation data to estimate the depopulation rates among groups with no population information. Kriging is a type of trend surface analysis, which in turn is an interpolation technique. Interpolation is “the prediction of exact values of attributes at unsampled locations from measurements made at control points within the same area” (O’Sullivan and Unwin, 2003, p. 220). It creates a continuous surface of values from a number of points within an area defined by the extent of those points. Interpolation is commonly used to predict climatological phenomena such as rainfall amounts or temperatures. In these cases, as it is with disease data, it can be very informative to have a continuous surface as opposed to a set of isolated points. It is important to note that kriging can only produce a surface that is an approximation of the spatial variation in the dataset (O’Sullivan and Unwin, 2003, p. 271). Unaccounted for anomalies will not be predicted.

Kriging involves three distinct steps. The first is the creation of a semivariogram, which is a description of the spatial variation in the dataset. The second is summarizing this data using a regular mathematical function. The final step is determining interpolation weights (O’Sullivan and Unwin, 2003, pp. 266–281). We performed all analyses using the Geostatistical Analyst tool in ArcGIS® 9.3.1. Unlike the Spatial Analyst tool, this tool allows the operator to choose from a wider array of mathematical functions, or models, based on the actual semivariogram. We chose ordinary kriging and a spherical model, which provided the best-fit line for the spatial variation of our dataset.

We chose kriging over other interpolation methods, such as inverse distance weighting, because other methods tend to determine the weight of interpolated points without consideration of the nature of the dataset being used (O’Sullivan and Unwin, 2003, p. 265). As such, these other methods are somewhat arbitrary, which can be problematic for irregular datasets. For example, kriging is preferred over inverse distance weighting in cases where positive autocorrelation is a factor and the density and distribution of points is irregular (Connolly and Lake, 2006, pp. 97–98). Positive

autocorrelation refers to situations where nearby events are likely to be similar to one another. In this case, disease events in close proximity to one another are likely to have similar depopulation rates and there is a large amount of variability in the depopulation rates at different locations (i.e. between different groups).

We used the locations and depopulation percentages as the input data for the analysis. Kriging created a surface from our data points that predicted the depopulation percentages for the areas between the points and represented different values with different shades. We then overlaid our map of the geographic ranges of 17th century cultures in the Northeast with the depopulation percentage surface. Next, we examined these overlaid layers focusing specifically on those groups with no existing depopulation data. The intersection of these layers provided us with a range of depopulation percentages for each of these groups.

Results

Fig. 2 displays the overlay of graduated depopulation severity markers and the location of Native American populations around AD 1600. Iroquoian-speaking and Algonquian-speaking populations are distinguished on the map. The map shows a correlation between high depopulation rates and Algonquian populations. This is also geographically correlated with cultures located in the central portion of the region (along the Connecticut and Hudson Rivers) experiencing greater overall depopulation.

Fig. 3 represents the results of kriging performed on the percentage of population lost for societies in the Northeast. This map represents 29 years of disease history; the earliest record is from AD 1616 among several groups in New England and the latest is AD 1645 among the Onondaga of modern-day central New York. Like Fig. 2, the surface shows the largest losses along the Connecticut River and in the area between there and the Hudson River. Mortality lessens as one moves away from this area. The trend surface overlaps with several groups, such as the Erie, Wenro, Neutral, Susquehannock, Kennebec, Munsee, and Naragansett-Pokanoket, for whom we previously did not have depopulation data. Estimated depopulation rates for these groups derived from the kriging results can be found in Table 3. It is important to reiterate that kriging does not predict anomalies.

Discussion

The depopulation rates in Tables 2 and 3 range from 35% to 98%. Most of these rates fall within the range of reliably estimated mortality rates associated with historic outbreaks of smallpox, measles

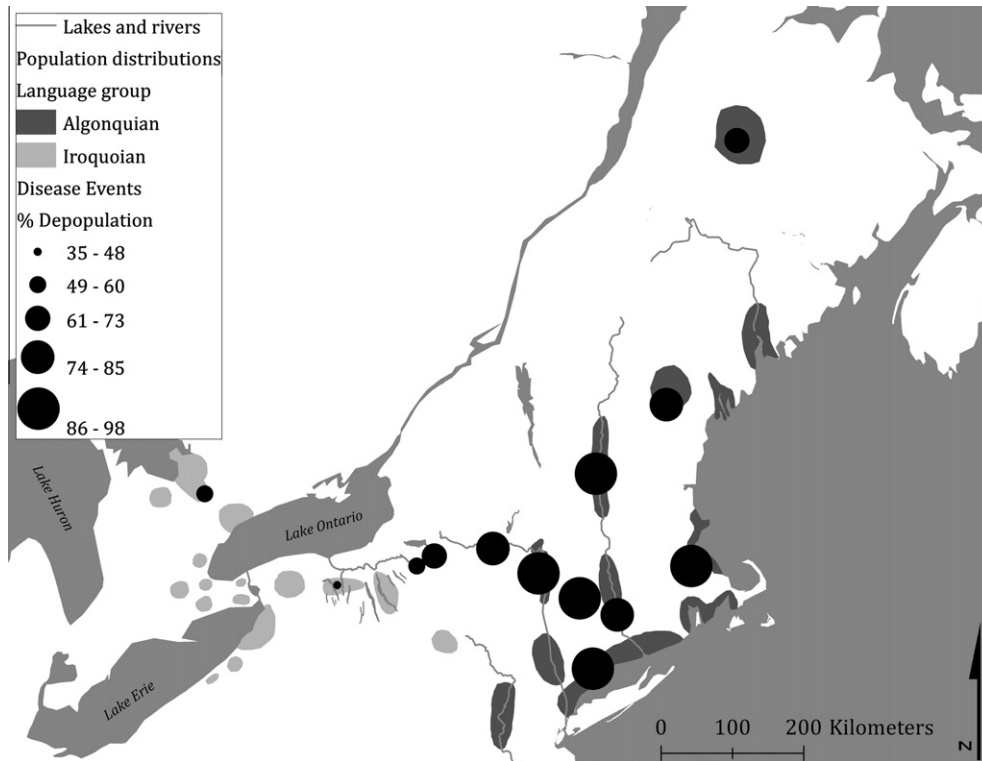


Fig. 2. The percentage of population lost in each disease event overlaid on the distribution of Iroquoian-speaking and Algonquian-speaking population distributions.

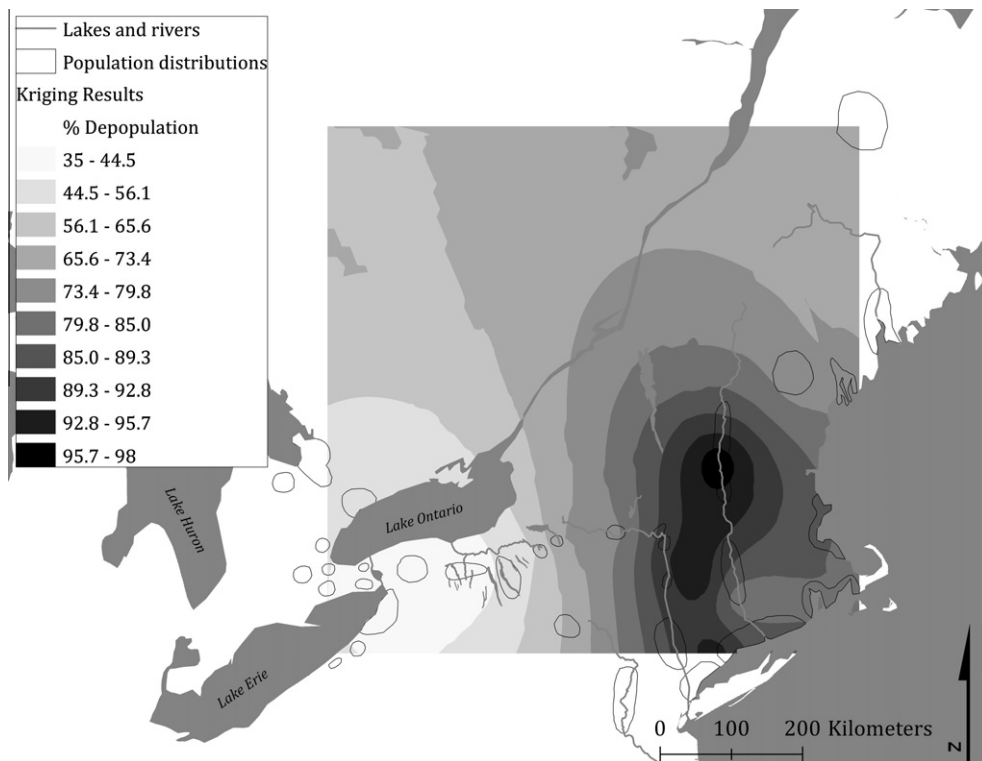


Fig. 3. Results of kriging based on existing depopulation data.

and influenza (i.e. several suspected causes of the 17th century epidemics in the Northeast) among other Native American populations. For example, over 50% of people in several Northern Plains groups were killed during an epidemic of smallpox in 1782 (Decker, 1991).

Haida villages lost about 81% of their populations between 1839 and 1884, and Boyd (1992) attributes this precipitous drop to a smallpox epidemic in 1862–1863. During this same smallpox epidemic, mortality among groups living along the

Table 3
Estimated depopulation rates based on the Kriging results.

Culture	Depopulation (% loss)
Wenro	35–44.5
Neutral	35–56.1
Erie	35–56.1
Cayuga	44.5–56.1
Susquehannock	56.1–73.4
Kennebec	65.6–73.4
Munsee	85–92.8
Narragansett-Pokanoket	79.8–85

coast of Washington ranged from 22% to 83% (Boyd, 1990). A measles epidemic in 1819 killed 25–50% of people in several Northern Plains groups (Decker, 1991). In 1900, measles and influenza epidemics killed an estimated 22% of native Alaskans at St. Lawrence Island (and other, though less reliable, estimates place mortality from these two diseases at nearly 75% in other native Alaskan villages) (Wolfe, 1982). Influenza alone killed 25–50% of Woodland Cree during an epidemic in 1835 (Decker, 1991), and nearly 80% of people in an Inuit community died during the 1918 epidemic (Markham, 1986).

The kriging results, when overlapped with prehistoric culture ranges, produce new population information for several groups in the Northeast. This has the potential to help us understanding historical and cultural developments among these cultures as well as explain differential cultural survivability in the region. We can be fairly certain that every Iroquoian culture in the Northeast underwent significant demographic and cultural changes during the mid-17th century (Bradley, 1987; Fitzgerald, 2001; Jones, 2010a, 2010b; Snow, 1995a, 1995b; Trigger, 1976; Warrick, 2008). However, we have very little information on Iroquoian population estimates outside of the Haudenosaunee and Wendat-Tionontaté. In addition, we are certain about the reasons why some groups survived while others did not. Demographic stress almost certainly played a significant role in cultural survivability, so our population data provide us with a starting point for exploring this topic.

We know that depopulation during the 17th century had significant impacts on cultural and historical developments in the region. The Mohawk suffered the greatest losses from disease during this period compared to other Haudenosaunee cultures. (We must exclude the Cayuga from this discussion because we do not have reliable population data.) Of the Mohawk, Onondaga, Oneida, and Seneca, the Mohawk are the only group that did not retain some portion of their traditional homeland (Snow, 1994, p. 199). Although we also have to consider the high religious conversion rates and subsequent migration to Canada and the comparatively frequent participation in warfare by the Mohawks (Snow, 1994), their severe depopulation likely played a significant role in their dispersal and migration.

Given the Mohawk situation, it is productive to examine our depopulation estimates with respect to the cultural survivability of groups in the Northeast. The Neutral Iroquoians were dispersed during the 1650s, and while individuals almost certainly survived, the Neutral ceased to exist as a discreet cultural unit thereafter (Fitzgerald, 2001). There is some historic documentation of the timing of diseases among the Neutral (Fitzgerald, 2001, p. 37), but no data exists on the actual numbers lost. Our results here offer a possible explanation for their dispersal. They show that groups like the Neutral and Erie, both of whom did not survive culturally, may have experienced higher depopulation rates, as much as 56%, compared to their closest surviving neighbor, the Seneca, who experienced a 35% depopulation. This would have offered the Seneca a distinct advantage over the Neutral Iroquoians, similar to the advantage they had over the Wendat.

Wendat history offers an analogy for the fate of the Neutral and Erie. The Wendat also did not survive the century culturally intact; they experienced a 50% decline in population. Historical documents and archaeological data indicate that the Seneca adopted a large number of Wendat people in the mid-17th century after several decades of sustained warfare (Jones, 2010b; Thwaites, 1959, vol. 52: pp. 52–55). The Wendat people survived biologically, but their geographic dispersal and adoption by other groups led to the destruction of their traditional culture. The same may have happened with the Neutral (and the Erie) given the similarities in rates of depopulation among these two groups and the Wendat. Below we further discuss these adoption practices and the genetic implications thereof for Haudenosaunee people.

Similarly, the Susquehannocks did not survive the 17th century culturally intact and may have experienced greater depopulation than neighboring groups. Most historic evidence indicates that the migration and eventual extinction of the Susquehannocks as a culture was the direct result of European actions (Jennings, 1968). Their possible comparatively heavy loss of population during the 17th century may have expedited this unfortunate result.

Conversely, the Wenro may not have had a depopulation rate significantly different from that of the Seneca, but they also did not survive the 16th century culturally intact. This may have been more of a factor of their original population size than mortality rates *per se* (i.e. if their original population was small, they may have been at an initial disadvantage). However, we do not currently have the pre-contact population data to know the size of the Wenro population. The Munsee may have experienced one of the highest depopulation percentages in the region, but they survived biologically and culturally intact. Clearly other factors outside of demography were at play with these two cultures.

Kriging appears to be a viable method for producing demographic data for Native populations in regions where reliable data already exists. More generally, looking at depopulation data from a spatial perspective allows us to explore topics like differential survivability. For several cultures in the Northeast, depopulation percentages appear to have been indirectly correlated with survivability. However, there are exceptions. Several other factors certainly played a role in determining which cultures survived this tumultuous time, such as alliances with European nations and original population sizes, but in many cases depopulation from disease almost certainly was the primary contributor to cultural extinctions. In addition, this dataset, which is now even more robust, is a good place to revive discussions of the complex interaction of demography, genetics, cultural practices, and historical events that shaped historic Native American populations in the Northeast.

Explaining the patterns of depopulation in the Northeast

Multiple diseases and their impact on immune competence

There are several possible explanations for the variable mortality rates observed across the Northeast. The groups living along the New England coast were impacted by two waves of diseases, in 1616 and 1633, compared to one wave over this span of time for the other populations further north and to the west (Snow and Lanphear, 1988, p. 23). By most historic accounts, the 1616 epidemic did not spread far inland (Snow and Lanphear, 1988). Interestingly, of the four groups with the highest depopulation percentages, Western Abenaki, Massachusetts, Quiripi-Unquachog, and Pocumtuc, only two, Massachusetts and Quiripi-Unquachog, were coastal groups. Groups like the Western Abenaki and Pocumtuc actually had similar or higher depopulation percentages even though they did not live along the coast. The Pocumtuc, however,

did live along the Connecticut River and not very far inland. It is not a stretch to assume that they also contracted the unidentified 1616 disease. The Western Abenaki, however, were located much farther up the Connecticut River—farther from the coast than several other groups who experienced much less population loss.

It is not surprising that groups that experienced two disease events had higher rates of depopulation than many of those that experienced just one. However, disease dynamics are more complex than simple mathematics; other factors likely further increased risks of severe depopulation. Researchers studying modern disease dynamics have found that infection with some diseases can have deleterious effects on the immune system's ability to respond to subsequent disease exposure. Infection with numerous viruses, such as measles, influenza, chickenpox, human immunodeficiency virus (HIV), Epstein-Barr, and respiratory syncytial virus (RSV) can cause immunosuppression through a variety of mechanisms (Beadling and Slifka, 2004; Louie et al., 1995; Manchester et al., 2002; McChesney and Oldstone, 1987; Mims, 1986; Notkins et al., 1970; Roberts, 1982; Wolfe, 1982). For example, people infected with measles virus have reduced immunity and thus increased susceptibility to secondary infections; measles infection is associated with increased risks of morbidity and mortality from such pathogens as *Mycobacterium tuberculosis* and *Staphylococcus aureus* (Casali et al., 1984; Manchester et al., 2002; Shaheen et al., 1996; Slifka et al., 2003). Researchers have observed that people who survive acute measles have reduced cell-mediated immunity and are more likely to die during the subsequent months from secondary infections than their vaccinated peers, and there is evidence that this suppression of immunity can last for years following the initial measles infection (i.e. after viral clearance) (Shaheen et al., 1996). Infection with influenza and RSV can lead to changes in immunity that increase an individual's susceptibility to and risk of mortality from bacterial pneumonia long after the initial infection has ended (Didierlaurent et al., 2008). Thus, not only were groups like the Massachusett and Quiripi-Unquachog inflicted with two separate diseases, but also the diseases were less than a generation apart. Thus, impacts from the first disease could have led to even higher mortality during the second event than the second disease would have normally inflicted. These two factors combined might partly explain the large disparity in depopulation rates.

Although we are not entirely certain of the identity of the diseases that impacted these populations during the early 17th century, several diseases including smallpox, measles, influenza, yellow fever, and leptospirosis have been cited as possible causes (Bratton, 1988; Carter, 1931; Crosby, 1976; Duffy, 1953; Jackes, 1983; Marr and Cathey, 2010; Snow and Lanphear, 1988; Spiess and Spiess, 1987; Talbot, 1956). These diseases could have negatively affected immune function as described above. Further, several studies (Allison et al., 1973; Arriaza et al., 1995; Buikstra and Cook, 1981; Mackowiak et al., 2005; Owsley and Bass, 1979; Powell, 1991; Rieder, 1989; Stone et al., 2009) suggest that tuberculosis and other bacterial diseases could have been present in North America prior to contact. Thus, the introduction of Old World viruses could have made people more susceptible to bacterial infections that were already present in these populations, thereby increasing infectious disease mortality rates.

Settlement location and type

We are still left with the interesting case of the Western Abenaki and the fact that they experienced the highest depopulation percentage of any group in the Northeast. Although they differ geographically from the other three groups with the highest depopulation percentages, their position along the Connecticut River may explain their high depopulation percentage. As previously

mentioned, Ramenofsky (1990, p. 42) developed a model that predicted disease impacts based on geographic location and settlement. In her model, sedentary groups living along navigable waterways were at the highest risk of being severely affected by disease because they would have had consistent and frequent contact with Europeans, who were the primary vectors. The Western Abenaki were semi-sedentary (Carson, 2002; Snow, 1980) and lived along a major waterway in the region, so they meet the qualifications described by Ramenofsky. Although most accounts state that the 1616 epidemic did not travel very far inland, it is very possible that it traveled longer distances with Europeans along major waterways like the Connecticut River. The most likely explanation for the high depopulation percentage among the Western Abenaki is that they were one of the few inland groups that experienced both the 1616 and 1633 disease events because of their degree of sedentism and location along a major waterway.

In addition to the Western Abenaki, Fig. 2 shows that other groups that settled along major rivers tend to have depopulation percentages in the highest two categories (74–85% and 86–98%). Groups along secondary drainages tend to have lower depopulation percentages. These data also fit Ramenofsky's model. In addition, the kriging results suggest that the Munsee, Susquehannock and Kennebec had the highest depopulation percentages among the groups with no data. The Munsee and Susquehannock resided along major rivers and the Kennebec settled along the coast.

Genetic variability

As mentioned, the data used in this study also reveal a pattern of depopulation percentages varying by language group (i.e. Iroquoian or Algonquian). As explained, the highest rates do occur among Algonquian populations in western New England, and Iroquoian populations have lower mortality figures than these groups. The only exception is the Maliseet-Passamaquoddy. In addition to the geographic factors discussed above, there are several possible genetic explanations that could explain why Algonquian populations suffered higher mortality rates.

One possibility is that the Iroquoian people had genetic variants that conferred immunity to certain diseases, and these variants did not exist in Algonquian-speaking peoples. This topic is worth investigating further because numerous genes associated with susceptibility or resistance to disease have been identified in human populations, such as mutations of the *G6PD* gene, which are associated with resistance to malaria, and the *CCR5-delta32* allele, which confers resistance to HIV in homozygotes and slows progression to AIDS in heterozygotes (Dean et al., 1996; Libert et al., 1998; Novembre et al., 2005; Stephens et al., 1998). Some human major histocompatibility complex (MHC, also often referred to as human leukocyte antigen, or HLA) haplotypes are associated with resistance to specific diseases (e.g. DRB1*1302 is associated with reduced risks of malaria) whereas other haplotypes result in increased susceptibility to certain diseases (e.g. HLA-DR2 is associated with increased risks of both leprosy and tuberculosis); there are also haplotypes that simultaneously confer resistance to some diseases while increasing susceptibility to others (Apanius et al., 1997). Further, the genetic background of hosts can affect MHC-dependent pathogen resistance, so even if the same MHC haplotype exists in two populations, immune responses might differ if there are differences between the two populations with respect to other genetic loci.

Genetically, Iroquoian-speaking peoples are different from Algonquian-speaking peoples (Malhi et al., 2004). Malhi et al. (2004) examined mitochondrial DNA haplotype diversity among living Iroquoian and Algonquian populations and found significant differences between the haplotype frequency distributions of the two groups. They also found that the Iroquoian and Algonquian

groups are the most genetically divergent of all the groups included in their study with respect to the hypervariable segment I (Malhi et al., 2004). Given that there are modern genetic differences between the two groups, there might have been genetic factors that affected disease susceptibility and mortality in these populations at the time of 17th-century disease events. To date, however, no data have been published on differences between Iroquoian and Algonquian populations with respect to genes associated with immune function or susceptibility to particular infectious diseases. Furthermore, the patterns of genetic diversity that exist among living populations do not necessarily directly reflect the genetic diversity of their ancestral populations. The modern genetic diversity of populations in the Northeast has been shaped not only by the diseases themselves but also by the combined effects of selection, mutation, admixture, and genetic drift during the intervening years since the 17th-century disease events.

Differences in mortality rates between Haudenosaunee and their Algonquin neighbors might also have been the result of population differences in levels of heterozygosity. This line of thinking is similar to Black's (1991) work but examines the role of genetic diversity on a smaller scale. Studies have found that genetic homozygosity, at least in vertebrates, is associated with reduced immune competence and increased susceptibility to pathogens, whereas heterozygosity is associated with immune advantages (e.g. Acevedo-Whitehouse et al., 2005; Keller and Waller, 2002; Lie et al., 2009; Lyons et al., 2009a; MacDougall-Shackleton et al., 2005). In humans, for example, homozygosity is associated with elevated risks of tuberculosis, hepatitis, and bacterial meningitis (Lyons et al., 2009a, 2009b). The health advantages of genetic heterozygosity are apparently not just limited to infectious diseases, as several studies have demonstrated an association between homozygosity and increased susceptibility to degenerative diseases in humans such as hypertension, high cholesterol, and cancer (Lie et al., 2009; Bener et al., 2007; Rudan et al., 2003).

The genes of the major histocompatibility complex (MHC) are among the most highly polymorphic genes in vertebrates, and they have been the focus of extensive study because of their role in immunity (Lenz et al., 2009). MHC genes encode cell-surface molecules that play a vital role in the immune system's recognition of pathogens (Lenz et al., 2009). MHC-heterozygotes have immune systems that can respond to and thus confer resistance to a much wider array of pathogens than is true of homozygotes (Apanius et al., 1997; Doherty and Zinkernagel, 1975; Grob et al., 1998; Woelfling et al., 2009). Studies indicate that MHC heterozygotes have faster virus clearance rates (Rapin et al., 2010), lower parasite loads and better overall body condition (Lenz et al., 2009) than homozygotes. The immune benefits associated with genetic diversity are not unique to the MHC; Lie et al. (2009) found that greater genetic diversity at non-MHC loci was associated with fewer reported symptoms of infectious disease in humans.

Levels of heterozygosity might have been affected by the cultural practices of Northeast populations. As mentioned, the Haudenosaunee had a long-standing cultural practice of replacing lost community members through capture and adoption of enemies. This practice had spiritual importance as well as economic, social, and kinship functions (Richter, 1992, p. 32). During the 17th century when large numbers of people were dying from diseases and warfare, adoption increased in scale to the point where entire communities of outside people were adopted into Haudenosaunee cultures (Snow, 1995a, pp. 364, 403; Thwaites, 1959, vol. 52: pp. 52–55). Although these two large-scale cases occurred after the disease events in question, the practice was likely long-standing in Haudenosaunee culture (see Wray et al. (1987) for evidence of pre-contact adoption of outsiders). In addition to bolstering dwindling population sizes, adoption among the Haudenosaunee might have also have inadvertently served to increase their genetic

diversity, which could have enhanced their immune functions relative to groups that did not practice adoption to the same extent.

There is some evidence that rates of adoption may have affected genetic heterozygosity among Northeast native populations. Langdon's (1995) analysis of anthropometric data (which are informative about genetic relationships), collected between 1891 and 1893, revealed that among the Haudenosaunee, the Seneca and Onondaga have the highest mean phenotypic variance, which might indicate that they experienced relatively high levels of external gene flow, at least some of which might have resulted from adoption of people from other groups. Historical accounts of the Seneca detail their adoption of an entire Wendat village during the 17th century (Thwaites, 1959, vol. 52: pp. 52–55), and previous archaeological research suggests that adoption of Wenro and other outside women was common prior to contact (Wray et al., 1987, pp. 242–248; Wray et al., 1991, p. 396). In addition, several studies (Bradley, 1987; Jones, 2010a) provide evidence for the adoption of Hochelagan and Stadaconan Iroquoians into Onondaga society during the late 16th century. Further, as the information in Table 1 displays, the Seneca and Onondaga had the lowest depopulation rates of the four Haudenosaunee groups with population estimates. Patterns of genetic diversity offer one possible explanation for this pattern.

Despite the corroborating historical and archaeological data for these two groups, there are currently few published data available to further test hypotheses about the possible relationships between levels of genetic heterozygosity and disease resistance/susceptibility among historic Northeastern populations. Further, Langdon's (1995) study uses late 20th century anthropometric data, and like modern haplotype diversity data (Malhi et al., 2004), such relatively modern data may not accurately reflect the phenotypic and genetic diversity that existed in the ancestral populations at the time of disease events in 17th century. Examination of genetic diversity between Iroquoian and Algonquian populations, particularly in regions of the genome associated with immune function, would be helpful in fully examining the variable depopulation rates among Native American populations.

Other possible explanations

Although we have provided several explanations for the patterns of depopulation in the Northeast, we must remain open to the possibility of other factors. First, we must be aware that the largest depopulation rates occurred among the groups for which only historic data are available. It is possible that these data are less reliable because they are based on a single line of evidence. While unlikely, this could account for the higher depopulation percentages. We believe this is unlikely because historic data were used, at least in part, to estimate population sizes for all of the groups included in our study. Such historic data were simply combined with archaeological data when available for many of the Iroquoian cultures.

In addition to possible biases in the data, there are other possible biological and cultural factors that affected variation in depopulation rates among Northeast groups. As mentioned, adoption processes among the Haudenosaunee undoubtedly would have masked some of the population loss (Jones, 2010a), and that is a likely explanation for lower depopulation rates among them. The adoptees were also coming from surrounding populations and these emigrants could be counting toward some of the other depopulation rates elsewhere. However, at this time we have no way of confirming such migratory activity. Conversely, the Wendat had a much lower depopulation rate than groups in New England, and they did not adopt large numbers of outsiders during this period. Thus, the differences in depopulation rates between Iroquoian and Algonquian groups is not solely due to adoption practices and

is in need of investigation. Wars and other mistreatments at the hands of Europeans cannot be discredited as causes either. For example, serious conflicts between New England Algonquian groups and settlers occurred throughout the early 1600s, while major conflicts between Iroquoian groups and Europeans did not begin until later in the 1600s. A full understanding of the depopulation rates and subsequent effects on these cultures requires a comprehensive analysis combining demographic, archaeological, epidemiological, and historical factors.

Conclusions

Researchers interested in the health effects of contact between Europeans and Native American populations have, for the most part, been content with reporting estimates of populations losses derived primarily from historic sources. However, other methods for estimating depopulation numbers and rates should be explored. Through spatial analyses of archaeological and historical data, this new research reveals clear differences in mortality rates between populations in the Northeast. The results also allowed us to predict depopulation rates for groups that previously lacked sufficient population data with which to do so.

Further, only a small number of studies have gone beyond estimates to explore the possible genetic, demographic, environmental, cultural, and historical reasons for observed patterns in depopulation. We suggest several possible reasons for the observed variation in depopulation: prior disease exposure resulting in compromised immune function, genetic variants that increase or decrease disease susceptibility, and cultural practices (particularly adoption among the Haudenosaunee) that may have increased genetic diversity in beneficial ways. This portion of our research is certainly a very early step and somewhat speculative. However, we hope that these questions will encourage future collaborative research between archaeologists and biological anthropologists focusing on demographic archaeology and genetic data. In particular, research into regions of the genome associated with immune function, from modern consenting Native American populations, might reveal which potential factors most likely influenced mortality rates among Northeast populations (and those in other regions) and how the observed patterns of depopulation impacted historic and modern Native American peoples and cultures.

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