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Implications of a Bayesian radiocarbon calibration of colonization ages for mammalian megafauna in glaciated New York State after the Last Glacial Maximum

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To understand what factors control species colonization and extirpation within specific paleoecosystems, we analyzed radiocarbon dates of megafaunal mammal species from New York State after the Last Glacial Maximum. We hypothesized that the timing of colonization and extirpation were both driven by access to preferred habitat types. Bayesian calibration of a database of 39 radiocarbon dates shows that caribou (*Rangifer tarandus*) were the first colonizers, then mammoth (*Mammuthus* sp.), and finally American mastodon (*Mammut americanum*). The timing of colonization cannot reject the hypothesis that colonizing megafauna tracked preferred habitats, as caribou and mammoth arrived when tundra was present, while mastodon arrived after boreal forest was prominent in the state. The timing of caribou colonization implies that ecosystems were developed in the state prior to 16,000 cal yr BP. The contemporaneous arrival of American mastodon with *Sporormiella* spore decline suggests the dung fungus spore is not an adequate indicator of American mastodon population size. The pattern in the timing of extirpation is opposite to that of colonization. The lack of environmental changes suspected to be ecologically detrimental to American mastodon and mammoth coupled with the arrival of humans shortly before extirpation suggests an anthropogenic cause in the loss of the analyzed species.

Introduction

Timing the colonization and extirpation of species within specific ecosystems is important for understanding how that ecosystem functions and evolves. Different factors, such as climate and competition are involved in determining when and whether particular species can colonize and establish in new geographic areas, which affects the ecological relationships that ultimately befall (Diamond, 1975; Lockwood et al., 1997; Weiher and Keddy, 2001; Young et al., 2001; Chase, 2003; Svenning and Skov, 2004; Ricklefs, 2008; Thibault and Brown, 2008; Lavergne et al., 2010; Chase and Myers, 2011; Weiher et al., 2011; Jackson and Blois, 2015). Establishment and loss of particular species in an ecosystem affects the ecological interactions involving not only the potential colonizing species but also incumbent species and possible future colonizers (Belyea and Lancaster, 1999; Young et al., 2001; Chase, 2003; Fukami et al., 2010; Weiher et al., 2011). This has important ecological and evolutionary implications regarding ecosystem composition and diversity.

Numerous studies examining species colonization and assembly within communities have focused on modern ecosystems (e.g., Cody and Diamond, 1975; Strong et al., 1984; Weiher and Keddy, 2001), and these necessarily concentrate on examining shorter-term factors that influence establishment within ecosystems (although see Jackson et al., 1997; Jackson and Blois, 2015; Webb, 1987; Williams et al., 2001, 2004). It is rare to have an opportunity to examine the timing of colonization and ecosystem assemblage at longer time scales. Many longer term studies have focused more on how species biogeographic ranges changed over time, and, particularly, how they react to climate change, than on determining the exact timing of colonization for species within a particular ecosystem (Wright, 1964; Ashworth et al., 1981; Davis, 1983; Schwert, 1992; Graham et al., 1996; Davis and Shaw, 2001; Lyons, 2003; Pearson and Dawson, 2003; Moritz et al., 2008; Chen et al., 2011).

Precisely identifying the timing of colonization within ancient ecosystems can be difficult. Dating is generally performed on a stratigraphic unit containing fossil specimens rather than on the individuals, and time averaging within the unit makes it largely impossible to determine whether one species arrived earlier or later than another within a specific paleoecosystem. Further, most dating techniques are generally not precise enough to determine whether a species arrived earlier or later than another. Knowing species colonization times within a particular ancient ecosystem permits comparison to the biotic and abiotic conditions present at the time. If the timing of extirpation can also be determined, additional ecological information such as how long species interacted and/or whether extirpation correlated to particular

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environmental conditions can be assessed. This information can help resolve what factors are involved in assembling and removing species in both modern and ancient communities (Jackson and Blois, 2015).

Radiocarbon dating of individual animals is a technique that provides enough precision to differentiate dates among species on shorter-term time scales. The use of accelerator mass spectrometry (AMS) in ^{14}C dating has led to increased precision on the scale needed to differentiate timing of colonization and/or extirpation for ancient species. Typically, individuals can be dated up to about the last 50–60,000 years (Linick et al., 1989; Bronk Ramsey et al., 2012; Aitken, 2014). Because of changes in the atmospheric concentration of ^{14}C, radiocarbon dates need to be calibrated, and calibration now also extends back over 50 ka cal yr BP (Bronk Ramsey et al., 2012; Reimer et al., 2013). Although the calibrated dates can provide an approximation of earliest and latest occurrences for species, because of preservation, it is not possible to be certain that the dated specimen represents the actual first or last occurring individual (Marshall, 1990). The use of Bayesian methods to calibrate radiocarbon dates has become a prominent technique to identify the timing of events, such as the age ranges of ruling dynasties, stratigraphic layers, or occurrence of species in particular geographic areas and can be used to provide posterior probabilities of age intervals for earliest and latest occurrences of species (Blockley et al., 2004; Bronk Ramsey et al., 2006, 2010; Bayliss, 2007, 2009; Buck and Bard, 2007; Bronk Ramsey, 2009; Kennett and Culleton, 2012).

New York State, USA, provides a rare opportunity to examine colonization and extirpation for megafaunal (>45 kg) mammals. Except for a small area of western New York that now includes Allegany State Park (i.e., the Salamanca Re-entrant) and the southern-most part of Long Island all of NY was covered by the Laurentide Ice Sheet (LIS) at the last glacial maximum (LGM; Fig. 1). Plants and then animals, including Pleistocene megafauna (e.g., mammoth, mastodon), colonized the previously glaciated areas of NY as the ice receded. Interestingly, with the retreat of the LIS, the timing of megafaunal colonization in NY and the timing of the end-Pleistocene extinction of large mammals in North America occurred within only a few millennia (Dyke et al., 2002; Barnosky et al., 2004; Koch and Barnosky, 2006; Clark et al., 2009). There has been a well-studied, long-standing debate as to whether climate change or humans (e.g., overkill, habitat destruction) were the main reasons for the end-Pleistocene extinction (Martin and Wright, 1967; Martin and Klein, 1984; MacPhee, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006). While a few studies have pointed to a combination of humans and climate causing the extinction (Barnosky et al., 2004; Koch and Barnosky, 2006; Brook and Barnosky, 2012; Wroe et al., 2013), this is still a current topic of debate (e.g., Cooper et al., 2015; Surovell et al., 2015). Scrutinizing the causes for extirpation of megafaunal species from NY may help elucidate what causal factors were involved in the end-Pleistocene extinction.

In this study we use Bayesian calibration to model the timing of colonization and extirpation of mammalian megafauna in NY with the aim of assessing what conditions were present upon colonization, permitting establishment, as well as those conditions that effectuated extirpation. For this study, we hypothesize that the presence of favored environmental conditions (i.e., preferred habitats) controlled the timing of colonization of mammalian megafauna into NY, and similarly, that climate-induced habitat changes caused their extirpation.

Background

Few fossil assemblages containing mammalian megafauna of late Pleistocene age are known from NY. These assemblages include the Hiscock locality of Genesee County in western NY (Laub et al., 1988; Laub, 2003), the Dutchess Quarry Caves of Orange County in southeastern NY (Funk et al., 1994; Steadman et al., 1997), and Diddly and Joralemon's Caves of Albany County in eastern NY (Steadman et al., 1993a, 1993b). Although there are only a limited number of assemblage localities, single specimen localities are comparatively abundant. American mastodons (*Mammut americanum*) represent the most abundant Pleistocene megafaunal species in NY occurring at over 150 localities (Hartnagel and Bishop, 1922; Thompson et al., 2008). Mammoth, (i.e., *Mammuthus* sp., including *M. primigenius*, *M. columbi*, and *M. jeffersonii*) are known from over 20 specimens/localities (Hartnagel and Bishop, 1922; Feranec and Kozlowski, 2010, 2012). Caribou (*Rangifer tarandus*) specimens are less abundant but do range across the state (Hartnagel and Bishop, 1922; Laub et al., 1988; Laub, 2003). Other megafauna, including muskox (*Ovibos moscatus*), peccary (*Platygonus compressus*), giant beaver (*Castoroides ohioensis*), and

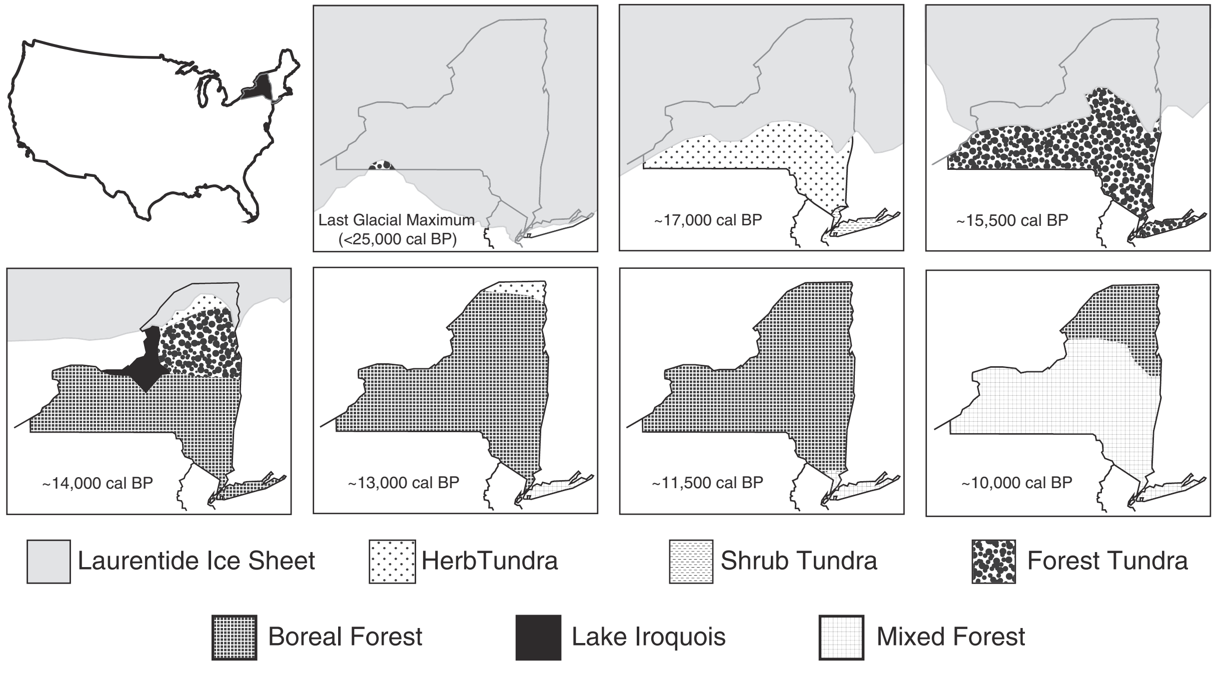

Fig. 1. Biomes present in New York State from the Late Glacial Maximum (LGM) into the early Holocene. Position of the Laurentide Ice Sheet and biome boundaries are modified from Dyke (2005) and Ridge (2003). Biomes shift northward as climate warms from the LGM.