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Abstract

Understanding megafaunal population dynamics is critical to testing and refining scenarios of how extinctions occurred during the terminal Pleistocene. Large-scale, collections-based, chronological, and taphonomic analyses of midwestern Proboscidea suggest divergent population histories in mammoths and mastodons after the Last Glacial Maximum (LGM). Although extinction of both taxa occurred in the very late Bølling-Allerød (B-A) or early Younger Dryas (YD), *Mammuthus* is dominant during the LGM with a decreasing presence in the region until extirpation. *Mammut americanum* however, is absent during the LGM but becomes the dominant taxon during the subsequent B-A. Trace and physical evidence of large carnivores in post-LGM proboscidean assemblages is extremely rare, suggesting apex predators had minimal impact on mammoth and mastodon populations at this time. The ultimate mechanism(s) of extinction remain unclear; however, the wide geographic distribution of late *Mammut* and an increase in the frequency of multi-animal death assemblages is consistent with a large, destabilized population experiencing periodic boom-bust cycling at the end of the B-A. We suggest this pattern is due to the collapse of trophic controls on proboscidean populations prior to the LGM and a subsequent system-wide shift from top-down to bottom-up regulatory mechanisms in Proboscidea.

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Late Pleistocene proboscidean population dynamics in the North American midcontinent

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Understanding megafaunal population dynamics is critical to testing and refining scenarios of how extinctions occurred during the terminal Pleistocene. Large-scale, collections-based, chronological, and taphonomic analyses of midwestern Proboscidea suggest divergent population histories in mammoths and mastodons after the Last Glacial Maximum (LGM). Although extinction of both taxa occurred in the very late Bølling-Allerød (B-A) or early Younger Dryas (YD), *Mammuthus* is dominant during the LGM with a decreasing presence in the region until extirpation. *Mammot americanum* however, is absent during the LGM but becomes the dominant taxon during the subsequent B-A. Trace and physical evidence of large carnivores in post-LGM proboscidean assemblages is extremely rare, suggesting apex predators had minimal impact on mammoth and mastodon populations at this time. The ultimate mechanism(s) of extinction

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remain unclear; however, the wide geographic distribution of late *Mammuthus* and an increase in the frequency of multi-animal death assemblages is consistent with a large, destabilized population experiencing periodic boom-bust cycling at the end of the B-A. We suggest this pattern is due to the collapse of trophic controls on proboscidean populations prior to the LGM and a subsequent system-wide shift from top-down to bottom-up regulatory mechanisms in Proboscidea.

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The factors underlying the extinction of 37 genera of North American mammals during the terminal Pleistocene have been debated for over a century (Grayson 1984). At issue are the relative impacts of climate change, human hunting, and other ecosystem changes on megafaunal populations (Martin & Klein 1984; MacPhee 1999; Koch & Barnosky 2006; Haynes 2009; Grayson & Meltzer 2015). These events occurred during a narrow window of time that, until recently, eluded efforts to establish a relative ordering of events. No clear consensus of the main drivers of megafaunal extinctions has emerged, despite extensive attention by researchers from many different disciplines. A persistent theme in this debate is ambiguity in the timing of events leading up to, and including, extinction. Although studies of megafaunal DNA have provided some insights into the late evolutionary dynamics of these populations (Nyström *et al.* 2012; Palkopoulou *et al.* 2015; Enk *et al.* 2016), geographic and temporal trends in megafaunal populations remain unclear across much of their range (Meltzer 2015). Considering the global scope of the current debate, there is a critical lack of chronometric data from temperate North America that can be used to improve models of proboscidean extinction dynamics.

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Assessing the relative importance of different drivers in proboscidean extinctions is not simply an academic exercise. The ultimate cause of these extinctions could have major implications for understanding the structure of modern ecosystems and the conservation of extant large mammals (Donlan *et al.* 2006; Barnosky *et al.* 2015). If indeed human hunting was responsible (or partly so) for these extinctions, then subsequent Holocene ecosystems were artificially depauperate in keystone herbivores and large carnivores, profoundly impacting the evolutionary trajectory of North American ecosystems over the last 12 ka (Martin 2005). Alternatively, if the impact of humans on the survival of megafauna was minimal, and climate-driven landscape changes were largely responsible for extinctions, then the processes leading up to extinction are important for understanding resilience in modern megafauna faced with unprecedented climate and environmental change over the next century (Bengtsson *et al.* 2003).

In recent years, researchers investigated the timing of extinctions in some of the taxa that went extinct during the terminal Pleistocene. The most successful of these studies focused on developing regional extinction chronologies of individual taxa (Mead *et al.* 1986; Stuart *et al.* 2004; Guthrie 2006; Solow *et al.* 2006; MacDonald *et al.* 2012; Stuart & Lister 2012; Zazula *et al.* 2014; Feranec & Kozłowski 2015). We approach this issue through radiocarbon-dated proboscidean remains in a region where the record of extinctions is particularly protracted (Woodman & Beavan Athfield 2009). By focusing on the Midcontinent we include some of the most recent proboscidean remains in North America (Agenbroad 2005). In modern threatened species, local to regional-scale population declines are seen as a “prelude” to extinction (Ceballos & Ehrlich 2002). However, in order to address long-term patterns in the evolution of proboscidean niches during the Late Pleistocene, we also include localities beyond the maximum extent of the last glaciation. The final dataset of newly dated individuals and properly vetted published data includes localities distributed from the Missouri Ozarks to Ontario, ranging in age from the last interglacial (Marine Isotope Stage (MIS) 5e) to the early Holocene. This dataset can be used to rigorously assess the timing of proboscidean extinctions as they relate to regional climate-driven landscape changes, human colonization, and extirpation of members of the midwestern large carnivore guild.

Methods

All materials, including previously published specimens, were physically examined during visits to regional museums and repositories (Tables S1, S2). Aspects of specimen context and condition were documented on-site, including location, taxonomic status, geologic context, taphonomic details, age and sex of the individual, specimen morphology, and an inventory of available elements.

Despite a long history of active radiocarbon laboratories in the region, prior to this study the record of proboscideans was poorly dated. This was primarily due to the effects of complex post-depositional processes (e.g., time averaged, disturbed, and mixed assemblages) and the use of associated materials (e.g., wood, charcoal) for radiocarbon analyses. Advances in dating bone collagen in recent decades have made it possible to obtain direct dates on proboscidean remains, vastly improving the accuracy of proboscidean dates.

Sample selection was not random. There is a significant preservation bias in the region due to extensive late Wisconsinan glaciation, so random sampling would have reflected this bias. Instead, most samples were selected according to criteria that were independent of postulated age. These specimens were chosen to sample the geography of the region (including unglaciated areas to the west and south of the Great Lakes) and to examine observed morphological variability (i.e., body-size and tooth morphology). Although localities that had previously yielded young or terminal ages (Dallman *et al.* 1996; Woodman & Beavan Athfield 2009) were re-dated, these make up a very small proportion of the overall dataset (N = 2).

For this project, all samples were removed from dense bone, tooth, or tusk dentin and submitted to the University of Arizona AMS laboratory. Radiocarbon dating was a multi-phase process. Collagen was extracted using standard acid-base-acid techniques, its quality evaluated both visually and through ancillary Carbon:Nitrogen (CN) analyses. Visually, well-preserved collagen had a white, fluffy appearance and CN ratios within the range of modern bones (2.9-3.6) (Tuross *et al.* 1988). Samples that had the potential to be terminal ages for Proboscidea within the study area were subjected to additional analyses. The ABA-extracted gelatin was ultra-filtered (UF) through >30 kD syringe filters to isolate relatively undegraded protein chains (Higham *et al.* 2006). This fraction was also dated. Typically, the UF fraction was decades to centuries older than the ABA fraction. In cases where the UF fraction was younger than the ABA fraction, contamination and preferential concentration of modern animal products was inferred

(e.g., animal glues used for consolidation). We consider ABA, ABA+UF, and XAD all appropriate pretreatment techniques in certain situations. However, terminal dates, especially outliers, should be accorded extra attention before communal acceptance. These samples should be routinely subjected to dating of multiple fractions by multiple labs, even using a variety of methods. By doing so, the degree and relative age of contamination can be rigorously assessed. Some of the samples we analyzed in this study were previously put forth as terminal dates (Woodman & Beavan Athfield 2009) however, we were unable to replicate published results. We report our dataset with the expectation that future, independent research in the region will review and potentially improve the chronology. However, because our interpretations draw from patterns in a large dataset, we believe our interpretations to be robust, even with improvements in dating technology.

Terminal ages on particular taxa have been the standard measure of when extinction occurs. However, this single metric can be problematic without an understanding of population dynamics or the inclusion of potentially flawed chronometric data. It is highly unlikely that a terminal age represents the last representative of a species (Signor & Lipps 1982).

An alternative method for estimating the timing of extinction is to model a terminal boundary (or extinction boundary) using OxCal (v4.2) software package (Bronk Ramsey 2009) and the IntCal13 calibration dataset (Reimer *et al.* 2013). The Bayesian statistical framework employed by OxCal is preferred for chronometric analyses because it allows prior information and/or assumptions about the dataset (e.g., stratigraphic relationships) to be incorporated directly into the model and used to constrain the calibrated results of the radiocarbon-based model (Manning *et al.* 2006; Bayliss & Whittle 2007; Buck & Bard 2007; Rawlence *et al.* 2015). The reliability of the model is indicated by how well the calibrated results of the model (i.e., the posterior probability distributions) agree with the calibrated results of the unmodeled input data, such that perfect agreement (i.e., no change imposed by the model) produces an agreement index (AI) of 100%. Empirical comparisons to χ^2 tests have shown that a threshold AI of 60% is roughly analogous to the 0.05 significance level of a χ^2 test (Bronk Ramsey 1995). For the purposes of this study, one of the most useful attributes of OxCal modeling is the ability to estimate the age of events that cannot be dated directly, such as the extinction of proboscidians in

the upper Midwest. This event, referred to as β_n elsewhere (Buck & Bard 2007), is modeled here as the terminal boundary of the distribution of available radiocarbon dates (Table 1).

In addition to chronological modeling, OxCal provides a series of analytical tools that can be used to query the model and perform operations on the results from the model. The Order function is one such tool and uses Markov Chain Monte-Carlo (MCMC) sampling to find the relative order of a series of events by calculating the probability that $A < B$, $A < C$, $B < C$, etc. Here, we used Order to test a series of hypotheses about the temporal relationship between the extinction of mastodons (12 790-12 520 cal. a BP) and three potential causal sources: shifts in climate, changes in vegetation, and human predation (Table 2). The small sample of post-LGM mammoths and poor chronological constraints on their extinction boundary precludes accurate ordering of events for this taxon.

Results

The American Midwest has some of the highest densities of terminal Pleistocene proboscideans on the continent. Our census of proboscidean material includes 627 localities, >1600 specimens, curated in 45 repositories from 12 states (SD, NE, KS, MN, IA MO, AR, WI, IL, IN, KY, OH) and one province (ON) (Fig. 1, Tables 3, S1, S2). Although regionally dominated by the American Mastodont (*Mammut americanum*), two species of mammoths were also documented for the Midwest, *Mammuthus primigenius* and *M. jeffersonii*. Although morphologically distinct (Osborn 1942; Pasenko & Schubert 2004; Saunders *et al.* 2010), recent genomic work suggests all Late Pleistocene midwestern mammoths are part of a single North American meta-population (Enk *et al.* 2016). Single-animal localities are by far the most common, but multi-animal and multi-taxic assemblages are also present (Tables 3, S1, S2).

Mammut americanum is well-represented in the region (N = 281 localities), but *Mammuthus* spp. are also present in large numbers (N = 311 localities). Individuals that could not be identified beyond Proboscidea were recorded in 61 localities, as were the other proboscidean taxa *Cuvieronius* sp. (N = 1), *Zygodolophodon* (N = 2), *Stegomastodon* (N = 1), and *Pliomastodon* (N = 1). *Mammut americanum* and *Mammuthus* co-occur in seven localities.

Although 61% (N = 401) of the dataset consists of isolated teeth or teeth and attached bone elements, 15% (N = 101) of the localities contained partial or complete skeletons and 16

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sites were complex multi-animal bonebeds (Tables 3, S3). The recovery of well-preserved mammoths and mastodons (i.e., multi-animal bonebeds, partial or complete skeletons) is not limited to lacustrine taphonomic settings in the Great Lakes.

Within this dataset, sub-aerial and chemical weathering profiles were largely dependent on local depositional factors. The impact of these processes on proboscidean remains varies greatly within and between assemblages. Carnivore modification is extremely rare (present in only 12 localities) and consists almost exclusively of gnawing and furrowing of distal limb elements by small- to medium-sized carnivores.

We analyzed 134 ^{14}C samples of bone and tooth dentin to refine the chronology of 93 individuals from 79 localities. To this dataset, we added 38 published dates from 16 individuals that met our criteria for inclusion in the regional chronology (Tables S3, S4). 111 post-LGM samples were used to calculate a younger boundary in Oxcal (v4.2), which was used to assess the chronological relationship between regional extirpation and other landscape events.

During the LGM, *Mammuthus* was the dominant proboscidean in the midcontinent and *Mammut* was rare or absent from the region (Figure 1). The landscape at this time was more arid than the subsequent Bølling-Allerød (B-A), and vegetative communities have been characterized as a spruce forest tundra, spruce parkland, or taiga-like (Baker *et al.* 1989; Jackson *et al.* 2000; Gonzales & Grimm 2009; Saunders *et al.* 2010). Ice-marginal areas were considerably colder and dryer (Curry & Yansa 2004).

Mammut was widespread in the region during the post-LGM period, particularly the B-A (Fig. 1). Proportionally *Mammuthus* localities remained common in grassland habitats in the western part of the study area during the Oldest Dryas before declining in the B-A. Although *Mammuthus* retained a presence in forested areas of the Midwest, they were no longer the dominant proboscidean on the landscape (Fig. 1). This was a period of substantial warming with higher levels of effective precipitation (Voelker *et al.* 2015). These conditions promoted the growth of a non-analogue vegetative community in the southern Great Lakes which was dominated by spruce (*Picea*) and black ash (*Fraxinus nigra*). The formation of this habitat is variously attributed to regional climatic (Gonzales & Grimm 2009) (i.e., cold, wet conditions) or ecological factors due to the purported loss of keystone megafauna (Gill *et al.* 2009).

The youngest dated mammoth in this dataset is the Prillwitz mammoth, a relatively complete skeleton from Berrien Co., MI excavated by avocational archaeologists in the 1960s (Green 1963). This individual dates to 13 390-13 020 cal. a BP (11 300±100 ¹⁴C a BP), the end of the B-A as it is regionally expressed in the lake sediment record (Curry *et al.* 2007; Gonzales & Grimm 2009).

The youngest mastodon in the dataset is the Boaz mastodon (Richland Co., WI), now understood to be a small portion of a composite mount on display in the University of Wisconsin Geology Museum (Eaton & Slaughter 2015). This individual dates to 12 810-12 560 cal. a BP (10 780±80 ¹⁴C a BP), overlapping the boundary between the B-A and the Younger Dryas (YD) chronozones. Although some researchers have suggested a human association with this mastodon (Palmer 1976; Waguespack & Surovell 2003), recent historical research indicates this assertion should not be accepted uncritically (Eaton & Slaughter 2015).

These terminal ages represent the last documented occurrence of taxa; however, they are unlikely to record the last animal on the landscape. In order to estimate the age of extinction, we must account for sampling and preservation biases at a regional scale. In this case, the extinction boundary was modelled in the Bayesian calibration program OxCal. The calculated 95% probability extinction window for *Mammuthus* in the study area is 13 460-12 160 cal. a BP while the extinction window for *M. americanum* is 12 790-12 520 cal. a BP. The error associated with the *Mammut* extinction estimate is significantly smaller than that of mammoths due to their greater sample size during the late B-A.

Hypothesis 1 assessed whether the extinction of mastodons occurred after the beginning of the Younger Dryas (YD; H1), as one might expect if shifts in climate played a role in extinction, or if extinction occurred prior to the YD (H1A). We used 12.9±0.125 ka as the age of the start of the YD, as defined globally in the NGRIP (Rasmussen *et al.* 2006; Steffensen *et al.* 2008) and supported by dendroclimatological work in the Midwest (Voelker *et al.* 2015). Although this boundary is precisely dated in ice core records, we use the more generous error in the regional dendroclimatological record due to unknown lag effects. The results from this test indicate that there is a high probability (0.9533) that extinction occurred after this event, not before (0.0467).

Gonzales & Grimm (2009) noted that there is a multi-century lag in regional response of vegetation to global cooling at the beginning of the YD. They use the well-dated sediment record from Crystal Lake, Kane Co., IL to place the start of this response at 12.4 ± 0.250 ka. Hypothesis 2 assesses whether mastodon extinction occurred after the vegetative response to a regional shift to cooler temperatures (H2), or if extinction predated this shift (H2A). Results from this test indicate that there is a greater probability of extinction occurring before the vegetation shift (0.8515), rather than after (0.1485).

Combining these two lines of inquiry to further constrain the relationship between extinction and regional changes to vegetation and climate lends further insight. Given the high likelihood that mastodons went extinct after climate began to change, Hypothesis 3 (H3) assesses the probability that these animals went extinct during the lag between the shift in climate (12.9 ± 0.125 ka) and the shift in vegetation (12.4 ± 0.250 ka), or if extinction occurred after both shifts (H3A). Not unexpectedly, the results from this test indicated that there is a very high likelihood (0.8099) that extinction occurred after the global climate shift, but before the regional response of midwestern vegetation is evident in the Crystal Lake sediment core. There is a low probability that extinction occurred after both events (0.1442).

The final causal scenario we examined centered on the temporal relationship between the extinction of mastodons and possible human predation in the greater Midwest. The extirpation of mastodons in the Midwest is not strongly related to human colonization because extinction postdates all pre-Clovis and Clovis localities in the region. There are few well-dated Clovis archaeological sites in the region so we modeled the late Clovis period boundary using the ^{14}C dataset published by Waters & Stafford (2007) and augmented by new dates on eastern Clovis sites (Shawnee-Minisink, Paleo-Crossing, Sheriden Cave) (Gingerich 2007; Miller & Gingerich 2013). The modeled boundary for the end of the Clovis period (12 720-12 620 cal. a BP) is roughly co-eval with the beginning of the YD. Hypothesis 4 assessed the likelihood that mastodon extinction occurred after the end of Clovis period in much of North America (H4), rather than before the end of the Clovis period (H4A). The results from this test place the probability of extinction occurring before the end of the Clovis period at 0.4855, and after Clovis at 0.5145, suggesting that the timing of extinction may have been roughly coeval with the end of

the Clovis period. However, we emphasize that the Clovis chronology is based almost entirely on localities outside the study area.

Over 90% of dated post-LGM mastodons date to the B-A chronozone (14.6-12.8 ka) (Fig. 2). Frequency diagrams, although commonly used to display chronological datasets, are highly sensitive to regional taphonomic and investigator bias and are unlikely to strictly reflect changes in proboscidean population size, so alternative lines of evidence are required to support population trends. The B-A mastodons are geographically widespread and morphologically variable (Fig. 1), which is consistent with the interpretation of a large regional population, not one that is decreasing in size and limited to refugia. Furthermore, localities with multiple individuals (3-31 individuals) are also more common during the B-A than during earlier climate periods.

Discussion

The regional extirpation of midwestern mammoths and mastodons occurs at the Allerød-Younger Dryas boundary. These are among latest occurrence dates for North American proboscideans (Agenbroad 2005; MacDonald *et al.* 2012; Feranec & Kozlowski 2015) and postdate the arrival of humans on the continent by centuries to millennia (Haynes 2015). Although we added significantly to the regional database of proboscidean records, we were unable to identify additional localities showing evidence of human involvement. Previously documented instances of human-proboscidean associations in the region were physically revisited to ensure consistent taphonomic and zooarchaeological data (Palmer 1976; Graham *et al.* 1981; Joyce 2006). Although human artifacts are, at times, strongly associated with proboscidean carcasses, we consider the specific behavioral role of human hunters in the formation of these sites to be ambiguous pending further investigation of potential zooarchaeological and taphonomic pathways. In any case, potentially hunted and butchered proboscideans make up a small proportion of the regional sample (0.5%, N = 3, show possible human association). Some authors (Mosimann *et al.* 1975; Surovell & Waguespack 2008) previously suggested that the scarcity of human/proboscidean sites in the Americas is due to the short period of overlap between the two species in the Americas. However, at the regional scale, >90% of dated mastodons overlapped with human occupation. Regionally, preservation of both natural and

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cultural death sites is ideal during this time, so we consider human factors to be only a minor contributor to the regional extirpation of mastodons.

Mammoth and mastodon extinction windows are co-eval with the beginning of the YD chronozone. Although often characterized as an abrupt return to glacial conditions, the YD in the Midwest manifests as a slightly cooler, but still humid period (Gonzales & Grimm 2009; Voelker *et al.* 2015). Regional pollen records show slightly elevated spruce concentrations occurring gradually over the first few centuries of the YD (Curry *et al.* 2007; Gonzales & Grimm 2009; Saunders *et al.* 2010). This shift in regional landscape conditions is neither abrupt nor as extreme as sometimes envisioned (Gonzales & Grimm 2009; Meltzer & Holliday 2010), so the role of regional climate shifts in midwestern proboscidean losses remains unclear.

Chronological hypothesis testing allows a probabilistic ordering of events occurring during the transition from B-A to YD (Table 2). The mastodon extinction boundary postdates the global temperature shift at the YD boundary ($p = 0.9533$), but predates the change in regional vegetation communities ($p = 0.8515$). It is likely that extinction occurred during the 4-5 century lag between the two events ($p = 0.8099$).

Although often considered synchronous, the underlying pattern of extinction in mammoths and mastodons is very different. Dated mammoth occurrences decrease gradually for millennia leading up to extirpation. The large extinction boundary reflects the low sample size of late mammoths, even though the terminal age of this taxon is similar to that of mastodons. Dated mastodon occurrences however, increase in number during the B-A, when they also reach their broadest spatial distribution. The frequency of multi-animal death assemblages also increases at this time (Fig. S1, Table S5). The largest portion of the mastodon chronological dataset comes from the B-A, contributing to the narrow *Mammut* extinction boundary.

At the ecosystem scale, a number of top-down and bottom-up processes could have impacted proboscidean populations. When present, large carnivores, parasites, and disease could have exerted top-down regulatory pressure on large herbivore populations (Cote & Poulin 1995; Terborgh & Estes 2010; Van Valkenburgh *et al.* 2015). Alternatively, bottom-up control of large herbivore populations would be susceptible to climate-driven changes to regional vegetation (Foley *et al.* 2008).

Large carnivores are rare in the Quaternary record of the Midcontinent. Terminal contexts for most large carnivores in the Midwest predate the LGM (Table 4). Trace evidence (e.g., gnawing) of carnivores does occur in proboscidean assemblages, but it is rare, appearing only as a minor component in 12 localities (<2% of the dataset). Although not directly comparable, much higher rates of carnivore damage have been documented in landscape scale, neo-taphonomic studies of large mammals (Faith *et al.* 2007), suggesting that the post-LGM midwestern large carnivore guild is depauperate compared to modern African ecosystems. If large carnivores are rare in the post-LGM Midwest, their ability to control recruitment in proboscidean populations (Van Valkenburgh *et al.* 2015) would have been reduced, leading to a population that was at or near carrying capacity. These large populations are typically unstable, characterized by boom-bust cycles, and more sensitive to even moderate, short-lived climate changes (Wilmers *et al.* 2007; Ripple *et al.* 2014). If this was the case with mastodons during the B-A, then the periodic occurrence of multi-animal death sites may represent “bust” cycles that were population responses to severe climate events such as drought or disease (Dudley *et al.* 2001; Moss 2001; Packer *et al.* 2003).

This shift from a three-level trophic system (carnivore-herbivore-vegetation) prior to the LGM to a post-LGM, two-level system (herbivore-vegetation) is important. Prior to the LGM, a smaller proboscidean population would have been kept in check by large predators. However, the reduction of large predators post-LGM could have encouraged the growth of proboscidean populations to sizes that were only controlled by bottom-up mechanisms such as forage availability.

Conclusions

It is difficult to reconcile the details of midcontinental proboscidean population dynamics with prevailing Pleistocene extinction scenarios. If humans were responsible for the extirpation of mammoths and mastodons in the Midwest, we would expect a larger proportion of proboscidean assemblages to be associated with cultural debris (e.g., artifacts, constructed features, or obviously butchered carcasses). Accommodating human overhunting would also require the Midwest to be colonized later than “classic” Clovis localities to the west. However, because the shift to the YD in the Midwest was neither abrupt nor extreme it is also unlikely that changing

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climates were the sole driver of midwestern proboscidean extinctions. Instead, we suggest that the regional extirpation of large carnivores during MIS 3 (at least in a functional sense) had major impacts on ecological complexity and biodiversity. As ecosystem biomass and complexity increased during the post-LGM period, the rarity of apex carnivores promoted larger, unstable herbivore populations. These systems were less resilient to climate or ecological changes due to decreased redundancy in trophic relationships (Laliberte & Ripple 2003; Wilmers *et al.* 2007; Ripple *et al.* 2014). The timing of these losses coincides with a moderate, climate-driven shift in regional landscapes, which may have been the final blow to increasingly unstable populations.

Although this model is broadly consistent with patterns in the taphonomy and chronology of midcontinental proboscidean extinctions, it is still in need of additional testing. Specifically, there is a need for further development of methods to assess the relative impact of predators on prey populations. At the regional scale, various methods for measuring predator pressure in herbivore populations are still in early stages of development. These include monitoring chronological changes in prey body size (Wolverton *et al.* 2007), population demography (Hill *et al.* 2008), and age at weaning (Fisher 2009). Regional isotopic studies of trophic organization (e.g. Fox-Dobbs *et al.* 2008) have yet to be developed. Along similar lines, this work highlights the difficulty palaeoecologists face in connecting meso-scale theoretical constructs borrowed from ecology to longer term chronological trends in the paleontological record. It is imperative that we bridge this gap if the discipline is to provide meaningful contributions to the conservation of modern animal populations.

Finally, this study underscores the importance of regional extinction chronologies to understanding larger, continent-scale trends. As in previous work (e.g. Graham *et al.* 1996), taxa do not react to landscape changes as cohesive communities. The extinction of midwestern mammoths and mastodons are closely spaced in time. Despite a shared ecological niche, the underlying dynamics of the two meta-populations as they approached extinction were very different. Furthermore, the trajectory of extinctions occurring within a region precipitate ecological reorganization that may not be visible in larger scale analyses. In this case the retention of apex carnivores outside of the Midwest suggests that single-cause scenarios for the extinction of North American proboscideans simply do not accommodate continental-scale complexity.

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FIGURES AND TABLES

Fig. 1. Map showing all mammoth and mastodon localities in the database. Red = *Mammut americanum*; Blue = *Mammuthus* spp.; Black = Unspecified Proboscidean; Stars = multi-animal bonebeds; Glacial coverages from Dyke (2004).

Fig. 2. Weighted probability plot of *Mammuthus* spp. (blue) and *Mammut americanum* (red) dates compared to the Late glacial vegetation chronology from Crystal Lake, McHenry Co., IL (Gonzales & Grimm 2009). NGRIP event stratigraphy from Rasmussen *et al.* (2006). A total of 22 *Mammut* and 4 *Mammuthus* contribute to probability peaks during the B-A.

Table 1. Summary of terminal boundaries of proboscidean chronological datasets within the study area.

Table 2. Summary of tested chronological hypotheses. eM = Mastodon extinction; YDBGS1 = Younger Dryas Boundary defined as beginning of Glacial Stadial 1; YDBXL = Younger Dryas Boundary defined as shift in vegetation (Zone D/C transition) at Crystal Lake, IL; eC = end of Clovis period.

Table 3. Multi-Individual death assemblages. Assemblages from visibly time-averaged deposits (e.g., sand and gravel quarries) are excluded. MNI = Minimum number of individuals.

Table 4: Occurrence data for large (>40 kg) Rancholabrean carnivores in the study area.

Supporting Information

Table S1. All proboscidean localities, ordered by state.

Table S2. Institutions contributing to the midcontinental proboscidean database (N = 45).

Table S3. Dated individuals. CNratio refers to the Carbon:Nitrogen (atomic) of extracted bone collagen, Date type is a designation of how an age range for an individual was calculated, ie., as a single radiocarbon date, a combination of dates (OxCal combine function), or in one instance where we were unable to discard outliers on the basis of technical criteria alone, an age range was calculated using the OxCal phase function. Calibration dataset refers to the calibration curve used to create the calibrated age range. All dates in this dataset were calibrated using IntCal13 (Reimer *et al.* 2013).

Table S4. Raw ^{14}C dataset.

Table 1.

Taxon	Boundary range (95% probability)	Boundary width (years)
Mammuthus spp.	13 460-12 160 cal. a BP	1300
Mammut americanum	12 790-12 520 cal. a BP	270

Table 2.

Hypothesis		Probability
H1	Mastodon extinction (eM) occurred after YDB (12.9±125 ka) age of GS-1 (YDBGS1)	0.9533 $p(\text{YDBGS1} < \text{eM})$
H1A	Mastodon (eM) extinction occurred before YDB (12.9±125 ka) age of GS-1	0.0467 $p(\text{eM} < \text{YDBGS1})$
H2	Mastodon extinction (eM) occurred after the vegetation shift at YDB (12.4±250) age based on Crystal Lake core transition, Zone D/C (YDBXL)	0.1485 $p(\text{YDBXL} < \text{eM})$
H2A	Mastodon extinction (eM) occurred before the vegetation shift at YDB (12.4±250) age based on Crystal Lake core transition, Zone D/C (YDBXL)	0.8515 $p(\text{eM} < \text{YDBXL})$
H3	Mastodon extinction (eM) occurred after the climate shift, but before the vegetation shift at YDB (12.9-12.4 ka)	0.8099 $p(\text{YDBGS1} < \text{eM}) \times p(\text{eM} < \text{YDBXL})$
H3A	Mastodon extinction (eM) occurred after both the climate shift (YDBGS1) and the vegetation shift at YDB (YDBXL)	0.1442 $p(\text{YDBGS1} < \text{eM}) \times p(\text{YDBXL} < \text{eM})$
H4	Mastodon extinction (eM) occurred after the end of the Clovis period (eC)	0.5145 $p(\text{eC} < \text{eM})$
H4A	Mastodon extinction (eM) occurred before the end of the Clovis period (eC)	0.4855 $p(\text{eM} < \text{eC})$

Table 3.

Locality Name	State	Repository	MNI	Taxon	Chronozone
Aurora	IL	PPMG	4	Mammut americanum	Allerød
Bamford Farm	IL	FMNH/SMM	8	Mammut americanum	Allerød
Benedict	IN	InSM	5	Mammut americanum	Allerød
Boney Spring	MO	ISM	31	Mammut americanum	Allerød
Bothwell Farm	IN	InSM	13	Mammut americanum	Allerød
Schimelphfenig Bog	WI	UWZP	3	Mammut americanum	Allerød
Trolinger Spring I	MO	ISM	5	Mammuthus	Illinoian
Bogges Farm	IA	SUI	3	Mammuthus	LGM II
Jones Spring, c2	MO	ISM	5	Multi-Taxic	Mid-Wisconsinan
Jones Spring, e	MO	ISM	19	Multi-Taxic	Mid-Wisconsinan
Trolinger Spring II	MO	ISM	15	Mammut americanum	Mid-Wisconsinan
Big Bone Lick ¹	KY	UNSM/ISM/CMC	>8 ²	Multi-Taxic	Postglacial
Couch Cave	IL	FMNH	15	Mammut americanum	Pre-LGM
Jones Spring, c1	MO	ISM	4	Multi-Taxic	Sangamonian
Barnhart	MO	ISM/MSHS	>6	Mammut americanum	undated
Kimmswick	MO	ISM/MSHS	>3 ²	Mammut americanum	undated

¹Big Bone Lick is the subject of ongoing chronological and geomorphological research (Tankersley et al. 2015), therefore it is difficult to assess the age of previously excavated materials.

²An accurate estimate of the Minimum Number of Individuals is not possible due to the dispersal of collections materials across multiple institutions.

Table 4.

Family	Species	N/Dated ¹	Distribution ²	Terminal Age	Source
Canidae	<i>Canis dirus</i>	15/1	AR, IA, IL, IN, KS, KY, MO, NE, WI	28.8-28.2 ka ²	(Dundas 1999)
	<i>Canis lupus</i>	2 ⁴	Present	Extant	neotomadb.org
Felidae	<i>Smilodon fatalis</i>	4/3	AR, IN, MO	Sangamonian ⁵	(Saunders 1988)
	<i>Homotherium serum</i>	1/1	MN	27.6-26.2 ka	(Widga et al. 2012)
	<i>Panthera onca</i>	3/0	IN, MO	Unknown	neotomadb.org
	<i>Panthera atrox</i>	--	Absent	--	(Kurtén & Anderson 1980)
	<i>Felis concolor</i>	-- ⁴	Absent	Extant	(Culver et al. 2000), neotomadb.org
	<i>Miracinonyx trumani</i>	--	Absent	--	(Van Valkenburgh et al. 1990)
Ursidae	<i>Arctodus simus</i>	9/3	IN, KS, MO, OH	12.9-12.7 ka	(Schubert 2010), neotomadb.org
	cf. <i>Tremarctos</i>	1/1 ⁶	IL	Sangamonian	This study
	<i>Ursus</i> spp.	2 ⁴	KY, OH, MO	Extant	(Scheick & McCown 2014)

¹N is the number of known localities from the study area. “Dated” refers to the number of localities for which reliable chronological information is available.

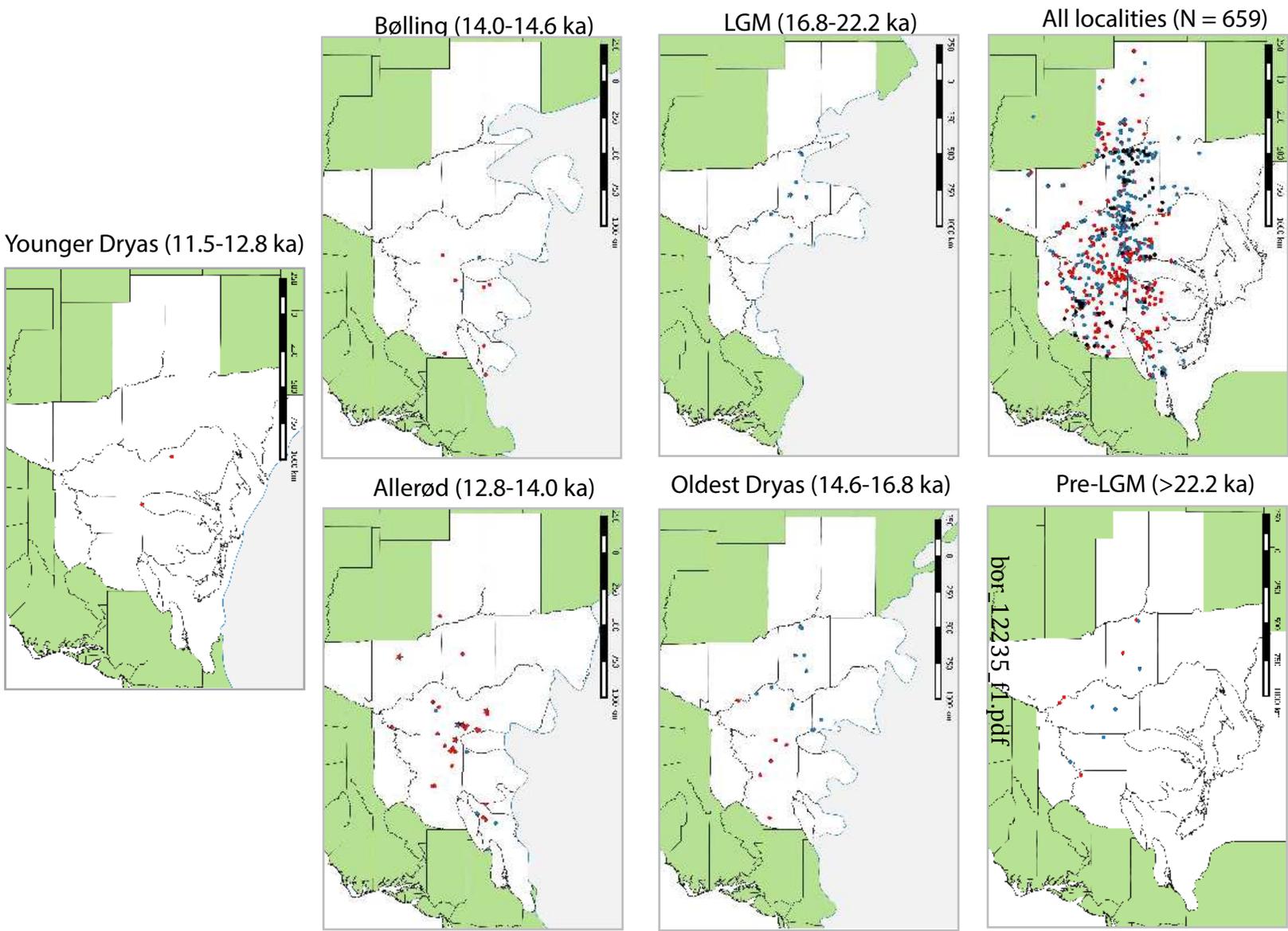
²AR = Arkansas; IA = Iowa; IL = Illinois; IN = Indiana; KY = Kentucky; KS = Kansas; MO = Missouri; MN = Minnesota; NE = Nebraska; OH = Ohio; WI = Wisconsin.

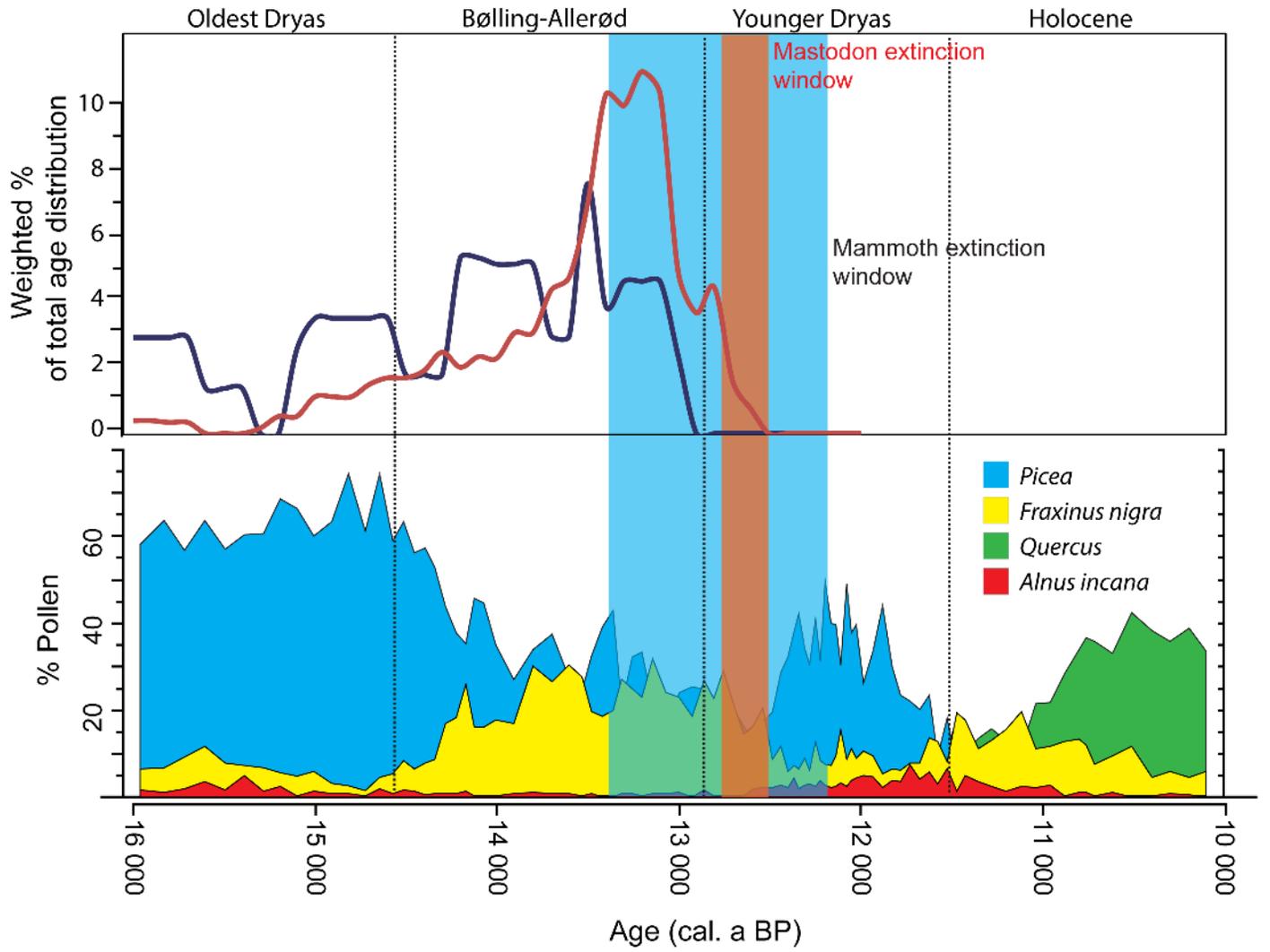
³Terminal age is on *C. dirus* from Crawford Co., IA; SANF 140-59-Z (24 460±110 ¹⁴C a BP AEON 1381).

⁴Wisconsin-aged localities for extant taxa.

⁵Although the published age of *Smilodon* at Hurricane River Cave (HRC), AR is 12 500 ¹⁴C a BP, these analyses predate the implementation of standardized radiocarbon techniques to improve the accuracy of bone dates. Therefore, the HRC date is discarded. Subsequent efforts to isolate collagen from the HRC specimens have been unsuccessful.

⁶*Tremarctos* is recorded from the Hopwood Farm locality, Montgomery Co., IL





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