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Forum communication

Rapid megafaunal extinction following human arrival throughout the New World

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ABSTRACT

Lima-Ribeiro and Diniz-Filho (2013) present a new compilation and analysis of the chronologies of human arrival and megafaunal extinction throughout the Americas. They find that in many places megafauna were apparently extinct before humans arrived; in many others, megafauna coexisted with humans for thousands of years before going extinct. They conclude that human impact made at most a minor and geographically restricted contribution to megafaunal extinction. We argue that Lima-Ribeiro and Diniz-Filho's (2013) conclusions are unreliable because they have not adequately accounted for uncertainties and biases that affect the estimation of extinction dates from fossil data and human-arrival dates from archeological data. We re-analyze their data taking these problems into account, and reach the opposite conclusion to theirs: extinction consistently followed human arrival with a delay of around one or two thousand years, in agreement with the overkill model of megafaunal extinction.

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1. Introduction

The cause of the Late Quaternary disappearance of megafauna from the Americas has been debated since Martin (1967, 1973) proposed the 'overkill' model, which envisaged newly arrived human populations hunting giant vertebrates rapidly to extinction. Credible tests of this hypothesis depend on establishing robust chronologies of human arrival and megafaunal extinction, to (i) show whether megafaunal taxa were present when humans arrived and if so, (ii) determine the duration of human–megafaunal overlap. Simulation models of hunter–prey interactions suggest that overkill could have caused extinction within only one or two thousand years (Mithen, 1993; Alroy, 2001; Brook and Bowman, 2002; Brook and Johnson, 2006). Given this, an ideal test would resolve these chronologies at local scales to allow for differences in time of arrival of people as they spread progressively over the vast land area of the Americas.

Lima-Ribeiro and Diniz-Filho (2013) attempt such a test in their new study. Using a new compilation of radiocarbon dates, they examine the evidence for temporal overlap of humans and megafauna throughout the New World. They analyze data at the site scale, using the youngest date on megafaunal fossils from a site to estimate the date of local megafaunal extinction, and the earliest dates of archaeological evidence at the same site (or the nearest archaeological site) to estimate time of human arrival. The difference between these dates measures the duration of local human–megafaunal overlap (or gap). Lima-Ribeiro and Diniz-Filho (2013) conclude from their analysis of these durations that in many parts of the New World megafauna were extinct before humans arrived, while in other places they persisted for 4000 years or more after human arrival. This suggests that if humans had any influence on megafaunal extinction, the effect was inconsistent and probably weak compared with other drivers of extinction.

Here we re-examine Lima-Ribeiro and Diniz-Filho's (2013) analysis, and show that their conclusions take insufficient account of the inherent biases and uncertainties that affect estimation of extinction and first-arrival dates from the incomplete data provided by the fossil and archaeological records. We present a re-analysis of their data that minimizes these problems, and leads to the opposite conclusion: megafaunal extinction followed soon after human arrival throughout the New World.

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2. Temporal bias

The latest fossil of an extinct taxon almost never records the true time of extinction. Instead, it represents the most recent date at which we have evidence that the taxon was *not* extinct. Extinction itself is not observed, and we can be certain only that it happened some time after the date of the latest fossil (assuming that the estimated date for that fossil is unbiased and sufficiently precise to allow such inferences). This delay constitutes a well-recognized bias that causes underestimation of the true duration of a taxon from last-appearance dates in the fossil record (Bradshaw et al., 2012). This bias is likely to be most severe when few dates are available, because in those cases most of the true history of the population will be unsampled. The same bias applies in reverse to estimation of time of arrival of people from presence data in the archaeological record: the true time of arrival is likely to have preceded the first dated evidence in the archaeological record, the more so as sample size is reduced.

These inherent sampling biases are especially relevant to Lima-Ribeiro and Diniz-Filho's study, for two reasons. First, if the true duration of overlap of megafauna and humans was brief, as expected from the overkill model, then even small biases in the estimation of extinction and arrival times could make it appear that megafauna went extinct before humans arrived. Second, Lima-Ribeiro and Diniz-Filho's decision to estimate an extinction and arrival time at each of their sites ensures that these estimates are based on small samples, a problem exacerbated by their choice to estimate overlaps separately for each megafaunal genus. Therefore, biases in their conclusions are potentially severe.

Several statistical techniques are available to quantify uncertainties in the inference of extinction times from discontinuous records of occurrence (Alroy, 2000; McInerny et al., 2006; Solow et al., 2006; Bradshaw et al., 2012). These methods take account of the number and pattern of presence records through time to estimate the underlying sampling distribution, and infer the temporal range, beyond the last appearance date, within which it is possible to have a specified level of confidence (typically 95%) that extinction occurred. The more sophisticated of these methods (based on computer-intensive resampling) can also incorporate the additional uncertainty contributed by laboratory error ranges on radiocarbon dates; this is important because radiocarbon dates themselves are complex probability distributions, not single-point estimates. These methods cannot fix an exact date on the extinction of a population, but the date-ranges they specify as bounds for the time of extinction ought to be free of temporal bias. The same methods can be used to remove bias from the estimation of arrival times from archaeological data.

3. Ignoring uncertainty

Lima-Ribeiro and Diniz-Filho recognise that temporal biases have the potential to confound their analysis, but instead of removing these biases using the statistical methods described above, they attempt to derive exact estimates of the magnitudes of bias. They do this by experimenting with resampling of data from their most data-rich sites. For example, for megafauna in North America, they resample dates on mammoths *Mammuthus* sp. from Bechan Cave, where there are 20 dated remains younger than 19,000 years. They assume that the youngest of these (13,489 years) is the true date of extinction of mammoths at that site. Following Barnosky and Lindsey (2010), they sub-sample to construct a curve showing the relationship between sub-sample size and likely error in estimation of this youngest date. For example, they show that for 1000 random sub-samples of $n = 7$ taken from the full Bechan Cave *Mammuthus* dataset, the mean youngest date is 13,800 years ago. Therefore they conclude that a sample consisting of only 7 dates is likely to underestimate the true date of extinction by 13,800−13,489 ka = 311 years.

They then use the relationship between temporal bias and sub-sample size to arrive at a single value for that bias, which they apply as a correction factor to their estimates of duration of human−megafaunal overlap at other sites. For megafaunal extinction, they fix this value at the temporal offset associated with a sample size equal to the average number of radiocarbon dates for each genus across all sites. This procedure is used to find a bias value for North American sites, and (somewhat arbitrarily) a separate bias value for South America. They use a parallel approach to find bias values for estimates of human arrival from first-appearance dates in the archaeological record.

There are three serious problems with this approach. First, it assumes that times of extinction and human arrival are correctly determined by the end dates at the better-sampled sites used as test cases. This assumption is unsound because there is inevitably some uncertainty in the estimation of extinction or arrival dates from presence records. To illustrate the problem, we used the GRIWM (Gaussian-Resampled Inverse-Weighted McInerny) approach of Bradshaw et al. (2012) to estimate the 95% confidence range for the true extinction date of *Mammuthus* at Bechan Cave. This range was 12,365−13,608 years ago (median = 13,146 years). Although the errors associated with the radiocarbon dates mean that this range included the date of the youngest fossil in the series, the median extinction date based on the GRIWM modelling of the time series of all dates was 343 years later, and it is possible that true extinction could have been as much as 1124 years later.

Second, Lima-Ribeiro and Diniz-Filho's use of fixed values for temporal bias, which are applied uniformly to their summary data, does not adequately correct for the effects of sample size on bias. Most of their estimates of overlap duration are derived from small samples of dates (Fig. 1). The likelihood of underestimating duration of overlap increases greatly in small samples, as shown by Lima-Ribeiro and Diniz-Filho's own results from resampling. However, they derive their fixed bias estimates by assuming sample sizes larger than those used in most of their calculations of overlap duration. For example, to estimate the temporal bias in estimation of megafaunal extinction in North America, they assume a sample size of 11 dates (Fig. 1a). But most of their calculations of duration of overlap are based on much smaller samples − for megafauna, usually only a single date. Therefore, the actual biases would be much greater than the value of 95 years that Lima-Ribeiro and Diniz-Filho use to adjust their estimates of site-specific megafaunal extinction date in North American sites.

Third, and related to the second problem, Lima-Ribeiro and Diniz-Filho's use of fixed estimates of bias means they do not quantify uncertainty in the values of overlap duration that they use in subsequent meta-analysis. They do attach uncertainty ranges to overlap durations, but these refer only to laboratory error on the radiocarbon dates, not the additional uncertainty due to incomplete sampling. In other words, their approach ignores potentially most of the uncertainty that should be considered before inferences are drawn on the true duration of human−megafaunal overlap.

The combined effect of these problems is that Lima-Ribeiro and Diniz-Filho have a weak quantitative basis for their main conclusion: that in many parts of the New World megafauna went extinct before the arrival of humans. Almost certainly, systematic biases mean that they have consistently under-estimated the duration of human−megafaunal overlap. We demonstrate this with two re-analyses of their data.

4. Re-analysis

Lima-Ribeiro and Diniz-Filho (2013) calculate a total of 201 estimates of site-specific duration of overlap of megafaunal genera

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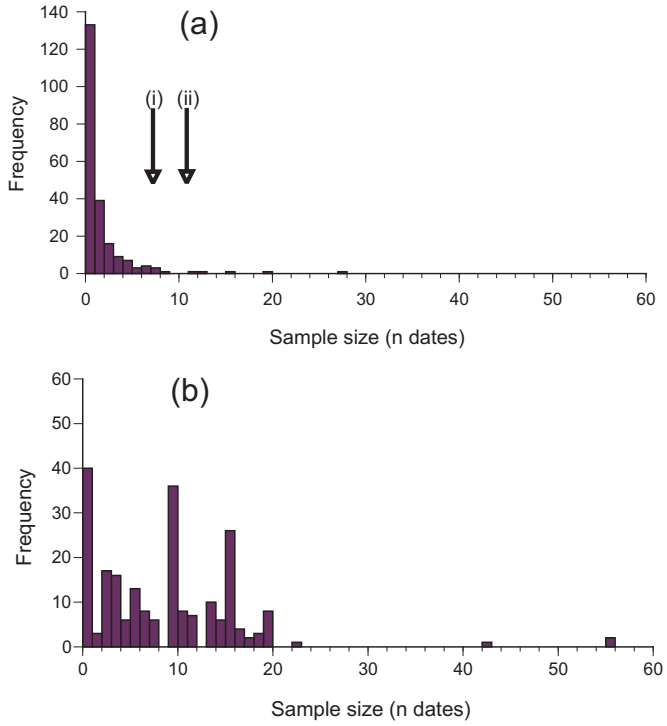

Fig. 1. Sample sizes of dates for (a) megafauna and (b) archaeology used by Lima-Ribeiro and Diniz-Filho (2013) to calculate estimates of duration of human–megafauna overlap throughout the Americas. The arrows on panel (a) show the sample sizes used for determination of temporal bias in the estimation of extinction from terminal youngest fossil dates for (i) South America and (ii) North America. These show that Lima-Ribeiro and Diniz-Filho (2013) determined bias in extinction date for samples of megafaunal dates larger than most of those actually used to estimate extinction date; they determined the equivalent archaeological biases at sample sizes of between six and ten dates.

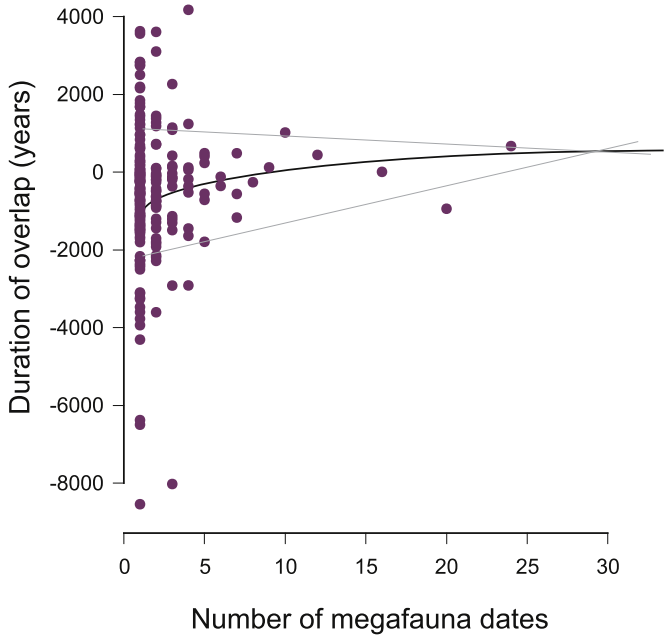

Fig. 2. Relationship between durations of human–megafauna overlap estimated by Lima-Ribeiro and Diniz-Filho (2013) and sample size of megafaunal dates. Similar patterns emerge for sample sizes of archeological dates, and combined sample sizes, but the pattern for megafaunal dates is shown because the generally small megafaunal samples contribute most to uncertainty and bias in estimation of overlap. The fits show a smooth spline (dark line; penalized log likelihood $\lambda = 0.142$), and quantile regression (light lines; fit to the 0.125 and 0.875 percentiles).

and humans in North and South America. These estimates vary from one extreme in which now-extinct megafauna persisted for up to 4176 years after first arrival of people, to the other in which megafauna were locally extinct 8543 years before people arrived. Across their North American sites, they find that megafauna were extinct on average 350 years before human arrival, and for South America extinction preceded human arrival by an average of 1235 years. However, these results are strongly affected by small sample size. This problem is clearly illustrated when Lima-Ribeiro and Diniz-Filho's (2013) effect sizes (i.e. years of human–megafauna overlap) are plotted against sample sizes (Fig. 2). Typically, a plot of this kind (which is a commonly used diagnostic tool for identifying biases in meta-analytical data) looks like a funnel lying on its side (Palmer, 2000). The flared end of the funnel is produced by high variance in estimates from small samples, while convergence on a robust estimate with increasing sample size gives the funnel its narrow neck.

Fig. 2 shows this classic funnel shape, making it clear that small sample sizes contribute the bulk of variability in estimates of duration of overlap, accounting for cases of apparent extinction before human arrival (that is, negative overlap) on the one hand and long persistence of megafauna with people on the other. Further, the asymmetry of the funnel – the lop-sided shape of the flared end with its preponderance of negative values, and the positive slope of the regression of mean effect size on sample size – indicates a tendency for small samples to be biased towards reduced or negative human–megafaunal overlap. This is expected, because with small samples it is more likely that the duration of overlap will be underestimated. We estimated the robust value of overlap duration implied by Lima-Ribeiro and Diniz-Filho's (2013) data, by using quantile regression to fit the upper and lower boundaries of the scatter on Fig. 2 and locating the point at which these boundary lines intersected. This intersection point, which lay on the flat portion of the regression of mean effect size on sample size, occurred at an estimated overlap of between 500 and 530 years. That is, the pattern of variation in Lima-Ribeiro and Diniz-Filho's (2013) data actually suggests that megafaunal extinction followed human arrival with a remarkably brief delay.

The indication in Fig. 2 of brief overlap of humans and megafauna is still likely to be affected by underestimation, because it is based only on last-appearance dates of fossils and first-appearance dates of archaeology. Even with relatively large samples, these dates are likely to suggest that megafauna went extinct earlier, and humans arrived later, than was truly the case (see estimates in Section 3, above). To test the effects of these temporal biases on estimates of overlap duration we recalculated dates for megafauna extinction and human arrival from data provided in Lima-Ribeiro and Diniz-Filho (2013), using the GRIWM method (Bradshaw et al., 2012) to overlay 95% confidence ranges on those events. This method requires a reasonable sample of dates to construct the sighting interval distribution, so we conservatively restricted ourselves to the 17 cases in which Lima-Ribeiro and Diniz-Filho's (2013) estimates of duration of overlap were based on at least four dates for both megafauna and people. Fig. 3 shows the median and 95% confidence ranges for megafaunal extinction and human arrival for these cases, in comparison with Lima-Ribeiro and Diniz-Filho's (2013) estimates of overlap duration derived from the ages of the youngest fossil and earliest archaeology in the same cases. Our analysis shows that megafaunal extinction either followed human arrival or that the confidence bounds for these events overlapped, with only one exception. This exceptional case (Cuevo Baño Nuevo in Chile, case 23 in Fig. 3) consisted of four dates on *Mylodon*, and 18 dates on archaeology. A strong feature of both sets

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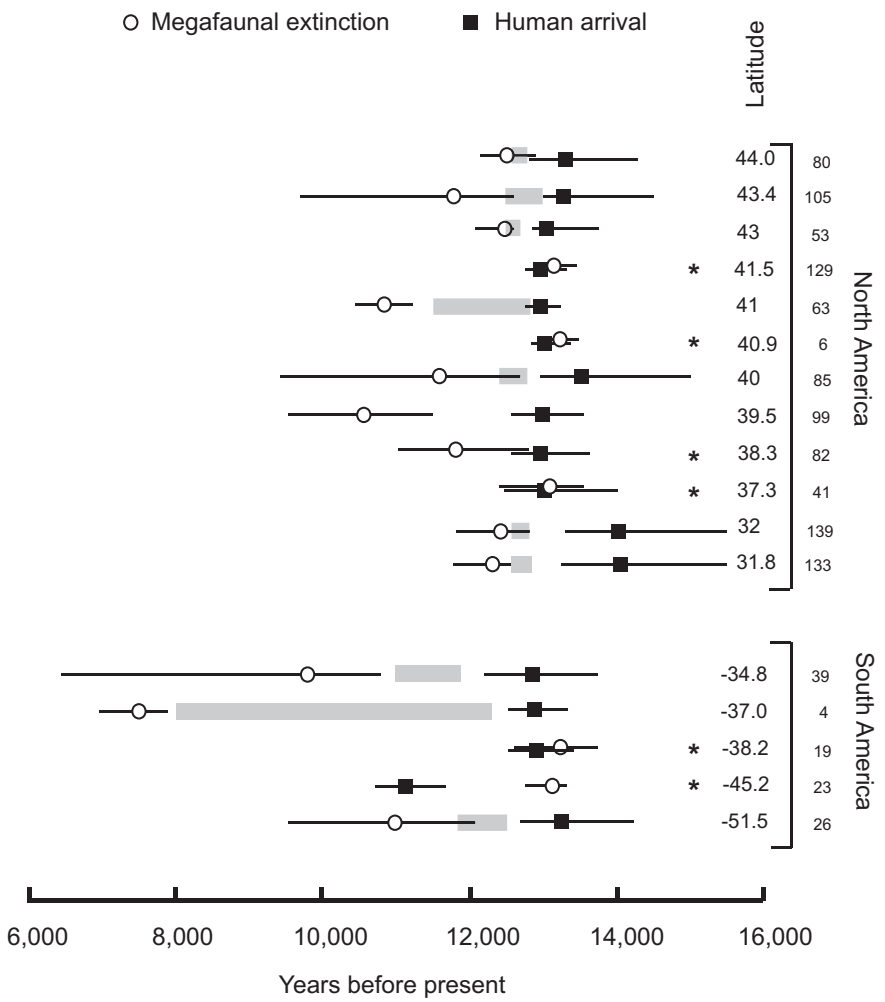

Fig. 3. Median dates with 95% uncertainty ranges for human arrival and megafaunal extinction in different locations in the Americas estimated by the GRIWM method of Bradshaw et al. (2012) for the 17 cases from Lima-Ribeiro and Diniz-Filho's (2013) study with sample sizes ≥4 for both archaeology and fossils. The grey bars show Lima-Ribeiro and Diniz-Filho's (2013) estimates of overlap duration, determined by dates of first archaeology and last megafauna. Cases marked by * indicate their inference that megafauna were extinct before human arrival. The latitude of the megafaunal site used in each case is shown, with sites arranged from north to south through the Americas. Numbers to the right of each comparison are identifiers that allow cross-referencing of these summary results to the full details of each case provided by Lima-Ribeiro and Diniz-Filho (see the file mmc2.xls in the Supplementary Information to their paper; the identifying numbers on our figures are the IDs in column one of this file).

of dates is that they cluster tightly around a modal value. For the megafauna, there are three dates all within 100 years of 13,250 and one date 1500 older. For the archaeology, 13 of the 18 dates fall between 10,000 and 10,500 years ago, and only two are older (at 10,655 and 10,898). This clumping of dates suggests there may be some physical feature of the site that resulted in dateable material not being retrieved for much of the true history of human occupation and megafaunal presence, perhaps leading to errors in estimation of extinction and arrival dates and underestimation of the uncertainty ranges on this dates. Across all cases, there is no strong evidence of major geographic variation in timing of human arrival or megafaunal extinction, with no clear latitudinal gradient in these dates (Fig. 3).

Our estimates of the time of megafaunal extinction are consistently later than those inferred by Lima-Ribeiro and Diniz-Filho (2013) from latest fossil dates, and estimates for human arrival are consistently earlier (Fig. 3). This means that probable durations of overlap were consistently longer than inferred by Lima-Ribeiro and Diniz-Filho's (2013). We estimated durations of overlap for the 17 cases shown in Fig. 3 as the median of 10,000 pairs of simulated first-human/last-megafauna dates, derived using GRIWM. Across all of these estimates, the mean duration of overlap (weighted by sample size) was 1570 years. The mean difference in our overlap estimates and those calculated by Lima-Ribeiro and Diniz-Filho (2013) was 1316 years. That is, our analysis suggests that Lima-Ribeiro and Diniz-Filho (2013) under-estimated overlap by more than 1000 years even in cases with relatively large samples.

5. Conclusions

Our re-analysis of Lima-Ribeiro and Diniz-Filho's (2013) data shows that their conclusions are not supported by their data. Our more explicit handling of bias and uncertainty in the estimation of the duration of human–megafaunal overlap leads to a reversal of their conclusions. We find that human arrival in the Americas was consistently followed by megafaunal extinction, typically with a lag of between 1000 and 2000 years. This sequence of events agrees with demographic modelling of the impacts of hunting by early humans on megafaunal populations (Mithen, 1993; Alroy, 2001; Brook and Bowman, 2002; Brook and Johnson, 2006), and therefore supports the hypothesis that overkill was the predominant cause of megafaunal extinction throughout the Americas.

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