Robust estimates of extinction time in the geological record

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ABSTRACT

The rate at which a once-abundant population declines in density prior to local or global extinction can strongly influence the precision of statistical estimates of extinction time. Here we report the development of a new, robust method of inference which accounts for these potential biases and uncertainties, and test it against known simulated data and dated Pleistocene fossil remains (mammoths, horses and Neanderthals). Our method is a Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) approach which weights observations inversely according to their temporal distance from the last observation of a species' confirmed occurrence, and for dates with associated radiometric errors, is able to sample individual dates from an underlying fossilization probability distribution. We show that this leads to less biased estimates of the 'true' extinction date. In general, our method provides a flexible tool for hypothesis testing, including inferring the probability that the extinctions of pairs or groups of species overlap, and for more robustly evaluating the relative likelihood of different extinction drivers such as climate perturbation and human exploitation.

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1. Introduction

The true point at which a species or a local population became extinct is a question commonly posed both by palaeontologists (Solow, 1993; Roberts and Solow, 2003; Solow et al., 2006) and modern ecologists (McInerny et al., 2006) because the timing of extinctions allows tests of the influence of hypothetical drivers such as human interference and climate change (Brook et al., 2008). Unfortunately, confirming the persistence of a species or a population in a given area becomes increasingly difficult as it declines to low densities (Fagan and Holmes, 2006), and pinpointing the timing of death of the last individual is virtually impossible. In the modern context, this makes estimates of extinction rate imprecise (Pimm and Raven, 2000) because most events are not observed (Bradshaw and Brook, 2009; Etienne and Apol, 2009). For palae-ontological questions, the additional uncertainty in radiometric dating, sampling rates, fossil preservation, and taphonomy, make inferring the final date of a species' demise highly problematic (Solow, 1993; Roberts and Solow, 2003; Solow et al., 2006).

To address these issues, various statistical models have been developed in an attempt to estimate extinction time – and its associated uncertainty – in a more robust manner, in both palae-ontology (Marshall, 1990, 1994, 1995, 1997; Solow, 1993; Weiss and Marshall, 1999; Alroy, 2000; Wang and Marshall, 2004; Solow et al., 2006) and modern extinction biology (Solow, 1993; Roberts and Solow, 2003; McInerny et al., 2006). Among these methods, Roberts and Solow (2003) developed an optimal linear estimation method based on the assumption that the records have an approximate Weibull form (a continuous probability distribution characterized by scale and shape parameters) (Weibull, 1951) of the parent distribution of the unsampled population. This approach was later extended using a maximum-likelihood framework to include uncertainty in radiometrically dated estimates (Solow et al., 2006). In a more modern context, McInerny et al. (2006) developed a statistical model derived from several methods for inferring recent extinctions based on sighting records (Solow, 1993).

Here we extensively modify the McInerny et al. (2006) method to take into account the influence of variation in the number of dates used to estimate extinction time. This problem is a major

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limitation of existing methods because they either assume independent and uniform dated fossil distributions (Solow et al., 2006) or fail to take sample size into account. Our approach is to weight inversely the contribution of each dated record to the estimated extinction time depending on its temporal distance from the most recent known record. We also incorporate Gaussian resampling to account for uncertainty in dating. Based on simulated data, we show that the full Gaussian-resampled, inverse-weighted McInerny et al. method (henceforth named the 'GRIWM' method) returns the 'true' date of extinction with less bias than any method applied thus far. We demonstrate real-world applications of the GRIWM method by re-analyzing three published palaeontological time series of radiometrically dated fossils and artefacts − late-Pleistocene mammoths and horses in Alaska (Guthrie, 2003, 2004; Solow et al., 2006), and Mousterian artefacts produced by Neanderthals and preserved in Gorham's Cave, Gibraltar (Finlayson et al., 2006; Tzedakis et al., 2007).

2. Materials and methods

2.1. Time series simulation

Given the exact dates of extinction are nearly always impossible to verify, especially for prehistorical extinctions, our first approach was to simulate a series of dated fossil specimens where the true date of extinction was set (and therefore known). We arbitrarily set the sampling interval between 15,000 and 20,000 years before present (YBP), to imitate a late-Pleistocene extinction event, and from this interval we randomly sampled 50 'dated' fossil specimens to represent the most recent remains of the model organism (cf. Solow et al., 2006).

The underlying distribution determining the probability of remains being deposited, fossilized and recovered is generally unknown, but it is likely a combination of local abundance of live specimens, taphonomy and site-specific characteristics (Solow, 1993; Roberts and Solow, 2003; Solow et al., 2006). We therefore

used five hypothetical underlying distributions (Fig. 1) from which our simulated 50 fossil specimens were drawn (cumulative probabilities sum to 1): (*i*) uniform, indicating equal probability of recovering fossilized remains at any time during the interval; (*ii*) linear decline, representing a constant reduction to zero in the probability of recovering a specimen as extinction is approached; (*iii*) exponential decline, where the probability rises exponentially the earlier in time one searches; (*iv*) sigmoidal, where the probability rises exponentially throughout half of the period of investigation, after which point the probability eventually stabilizes; (*v*) logarithmic, where the probability is approximately constant during most of the sampling interval but declines precipitously nearer to extinction (Fig. 1).

Using these probability distributions, we iteratively simulated 1000 samples of 50 specimens based on each of the 5 distributions. To emulate error associated with radiometric dating, we ascribed a constant standard deviation of 5% of the sampled interval (i.e., 250 years) to all dates in each simulated series.

2.2. Estimating time of extinction

For each simulated time series we first applied Roberts and Solow's (2003) Weibull (Weibull, 1951) method, which assumes each date in the series is known with no error. Here, the k most-recent dated records are ordered $T_1 > T_2 > T_3... > T_k$, with the true extinction time θ estimated as $\hat{\theta} = \sum_{i=1}^{k} a_i T_i$ where the vector of weights $a = (e^t \Lambda^{-1} e)^{-1} \Lambda^{-1} e$ (e = a vector of k 1s) gives the symmetric k matrix with typical element $\lambda_{ij} = (\Gamma(2\hat{v}_i + i)\Gamma(2\hat{v}_i + j))/(\Gamma(\hat{v}_i + i)\Gamma(j))$, where $j \leq i$ and Γ is the standard gamma function. The shape of the joint Weibull distribution for the most-recent record dates is estimated as:

$$\hat{v} = \left(\sum_{i-1}^{k-2} \log(T_1 - T_k)/(T_1 - T_{i+1}) \right) \Big/ (k-1) \qquad (1)$$

Confidence intervals can also be estimated for $\hat{\theta}$ (Roberts and Solow, 2003).
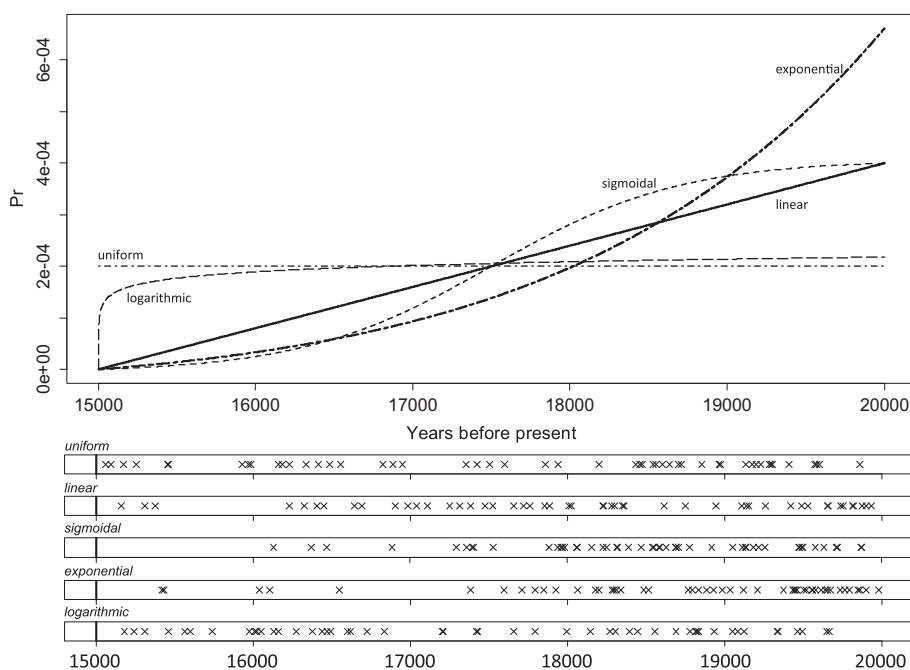
Fig. 1. Simulated time series distributions. (a) Five distributions (uniform, linear, sigmoidal, exponential and logarithmic) underlying the simulation of time series of 'dated fossils' between the hypothetical late-Pleistocene interval of 15,000–20,000 years before present (top). In all simulations, '15,000' was the date of 'true' extinction. Five example time series, each consisting of 50 dated specimens and sampled from each distribution, are also shown (bottom).

That method does not, however, take into account the measurement error associated with each date in the k vector of radiometric date records. Thus, we also applied the maximum-likelihood method developed by Solow et al. (2006) to account for error where the estimated date X_j is the true date U_j plus ε_j error. Assuming the vector of U_j are independent and uniformly distributed (assumptions which might be difficult to meet) (Solow et al., 2006), the probability density function of X_j is estimated as:

$$f(x) = (\Phi((x - \beta_1)/\sigma_j) - \Phi((x - \gamma_1)/\sigma_j))/(\gamma_1 - \beta_1) \qquad (2)$$

The third method we applied to each simulated time series takes a completely different perspective for estimating extinction date. McInerny et al. (2006) developed a statistical model that was itself derived from several previously published methods for inferring extinction based on sighting records (Solow, 1993). Using the same format of k dated time series T as in the Solow et al. method (Solow, 1993), the McInerny et al. approach assumes that records are equally likely to occur during T such that the probability of a record is $p = (t_n/T)^n$, where n = the number of records and t_n = the initial period of observation. Low p indicate extinction or population decline because records are unlikely to have occurred in the period $0 \le t \le t_n$ given the magnitude of T and n (Solow, 1993; McInerny et al., 2006). However, because time to detection of extinction depends on t_n, the length of the period since the last record is potentially more informative than p for inferring the true extinction date (McInerny et al., 2006), since sample (record) density is assumed to be a proxy for population density. Therefore, the probability of finding another record (p) can be estimated from the previous sighting rate n/t_n and the time since last observation $T - t_n$ such that:

$$p = (1 - (n/t_n))^{(T-t_n)} \qquad (3)$$

The terminal record can be inferred by setting the threshold probability to a chosen value (i.e., $\alpha = 0.05$) and iterating until $p \le \alpha$, and adding the resulting time since observation to the last observed record to obtain $\hat{\theta}$.

The estimated time of extinction $\hat{\theta}$ is, however, sensitive to the number of dates (k) in the time series (Solow, 2005) (see Fig. 2). To account for this effect, we hypothesized that the most-recent records would be more influential on the sighting rate as extinction is approached, and thus $\hat{\theta}$, than earlier records in the time series. Accordingly, we modified the McInerny et al. method by inversely weighting the contribution of each dated record to $\hat{\theta}$ depending on its temporal distance from t_1 (i.e., the most recent record). For a particular k series of dates, the reciprocal of the differences (in years) between t_i and t_1 is $\partial_i = 1/(t_i - t_1)$ when $t_i > t_1$, and this becomes the weight ω for the time series composed of k records when expressed as a ratio to ∂_1. This is repeated iteratively for all possible time series lengths ($k = 2$ to $k = n$), with the total weighted $\hat{\theta}$ (Fig. 2) calculated as:

$$\hat{\theta}_w = \sum_{k=1}^{n} \omega_k \hat{\theta}_k \Big/ \sum_{k=1}^{n} \omega_k \qquad (4)$$

Although the McInerny et al. (2006) approach does try to factor in the influence of sighting rate (but not a change in sighting rate over time), it suffers from the same problem as the Roberts and Solow (2003) method for radiometrically dated series, in that it does not take into account uncertainty in dating. We therefore modified the weighted McInerny et al. approach described above in order to resample each radiometric date in the series from a Gaussian distribution (radiometric errors are approximately normally distributed) (Walker, 2005) and recalculating $\hat{\theta}_w$ for 10,000 iterations (hence, 'GRIWM'). From the 10,000 resultant values of $\hat{\theta}_w$ we calculated the 95% confidence limits.
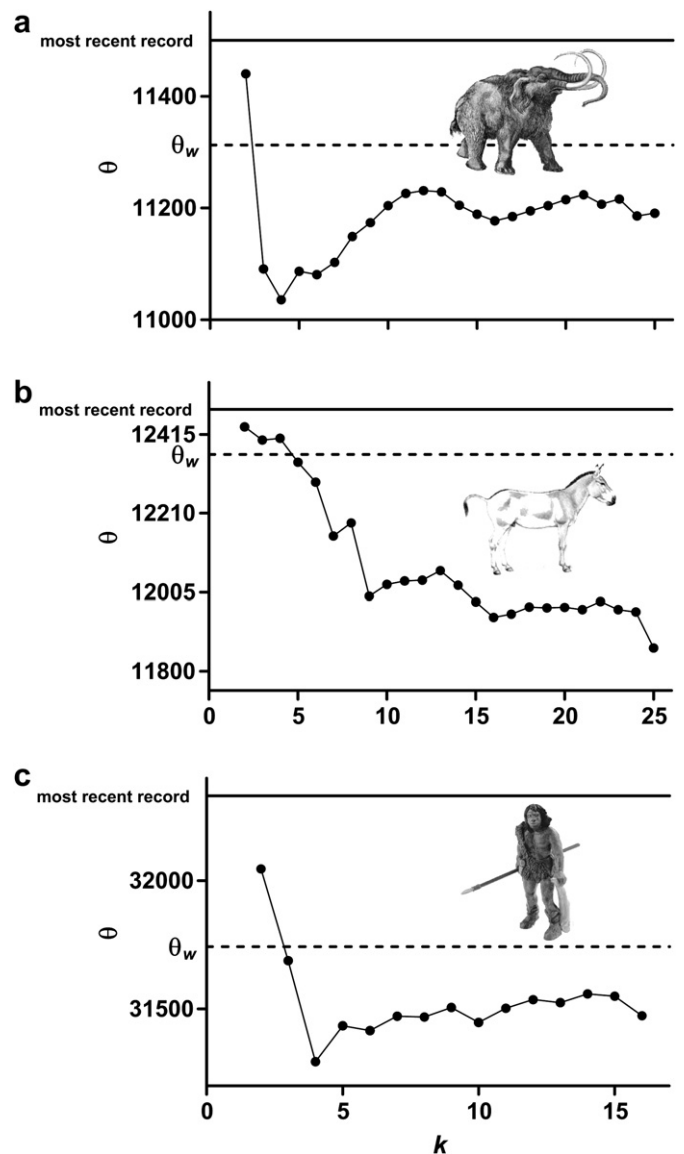
Fig. 2. Inverse weighting to estimate extinction time. Inversely weighting the McInerny et al. (2006) estimate of extinction date $\hat{\theta}$ by its temporal distance from t_1 (the most recent record). For a particular k series of dates, the reciprocal of the differences (in years) between t_i and t_1 is $\partial_i = 1/(t_i - t_1)$ when $t_i > t_1$, and this becomes the weight ω for the time series composed of k records when expressed as a ratio to ∂_1. This is repeated iteratively for all possible time series lengths ($k = 2$ to $k = n$), with the total weighted $\hat{\theta}$ calculated as $\hat{\theta}_w = \sum_{k=1}^{n} \omega_k \hat{\theta}_k / \sum_{k=1}^{n} \omega_k$. This inverse-weighted McInerny et al. method was applied to the 25 most recent mean Pleistocene (a) mammoth and (b) horse radiometric dates (i.e., ignoring dating error) from Guthrie (Guthrie, 2003, 2004) presented in Solow et al. (2006) for each value of k. Panel (c) shows the weighting for the Neanderthal data (Finlayson et al., 2006; Tzedakis et al., 2007). The final $\hat{\theta}_w$ and most recent radiometric dates are shown for each time series.

To assess relative performance of each method to return the 'true' extinction date (15,000 years before present in all simulations), we calculated three separate metrics measuring relative precision and bias: (i) a χ^2 statistic calculated as the squared difference between the median estimated extinction year and the true extinction year divided by the true extinction year; (ii) the proportion of times the 'true' extinction date fell within the estimated confidence interval; and (iii) the coefficient of variation, estimated as half the width of the extinction date's confidence interval divided by the median date.

2.3. Real extinction data

Previously, Solow et al. (2006) re-assessed data presented by Guthrie (Guthrie, 2003, 2004) on the timing of Pleistocene mammoth and horse extinctions in Alaska. In that analysis, they challenged Guthrie's interpretation that horses survived over a millennium beyond the appearance of humans who arrived around 12,000 ^{14}C years before present. Solow et al. (2006) concluded that this assertion could not be supported because the horse's extinction date confidence interval substantially over-lapped with the arrival of humans. We applied our GRIWM method to the same dataset to re-assess this conclusion as a real-world example application.

To test the method using calibrated radiocarbon ages, we also re-assessed the time series of Mousterian artefacts produced by Neanderthals and preserved in Gorham's Cave, Gibraltar (Finlayson et al., 2006) to determine the range of plausible extinction time assuming the most realistic, final radiometrically determined date of 28,170 ± 240 ^{14}C years before present (1 standard deviation) as re-analyzed in Tzedakis et al. (2007). We first calibrated the 16 radiocarbon dates up to 28,170 ± 240 ^{14}C years before present using the Cariaco Basin sediment core calibration curve to provide calendar age estimates (Hughen et al., 2006) from the OxCal radiocarbon calibration tool Version 4.1 (Ramsey, 2010). We esti-mated three lower-bound (i.e., most recent) extinction dates using the calibrated earliest artefact date minus 2 standard deviations, the lower bound assessed using the Solow et al. (2006) method, and the lower bound produced using GRIWM.

3. Results

3.1. Simulations

A comparison of all five estimation methods − Roberts and Solow (2003), Solow et al. (2006), McInerny et al. (2006), inverse-weighted McInerny et al. (GRIWM) − showed that the GRIWM method returned the lowest average bias (as measured by the χ^2 statistic) when the underlying sample-generation distribution (Fig. 1) was linear, sigmoidal or exponential (Fig. 3a). For uniform and logarithmic distributions, where sampling was approximately constant through to extinction (or just prior to extinction), the simple (not resampled) weighted McInerny et al. method had the lowest bias (Fig. 3a).

When bias was assessed using the proportion of simulations where the estimated confidence interval overlapped the true extinction date, it was only possible to compare the three methods that provide confidence intervals (i.e., the original and inverse-weighted McInerny methods do not estimate confidence inter-vals). The Solow et al. (2006) method performed better for the uniform distribution (although all three methods performed consistently well, at around 0.9, based on this fossil-sampling distribution), but this method did considerably worse for all other underlying distributions (Fig. 3b). The Roberts and Solow (2003) method provided higher overlap probabilities for sigmoidal and exponential distributions (Fig. 3b); however, that method ignores uncertainty in radiometric sample dating. Thus, we conclude that based on methods incorporating full uncertainty, the GRIWM method provides highest overlap in the majority of plausible situations.

Precision, assessed using the coefficient of variation, was rela-tively constant among the fossilization distributions tested for the GRIWM method, but GRIWM's precision was slightly lower in most cases compared to the Roberts & Solow and Solow et al. methods (Fig. 3c); this probably results from a the more conservative accounting of uncertainty using Gaussian resampling.
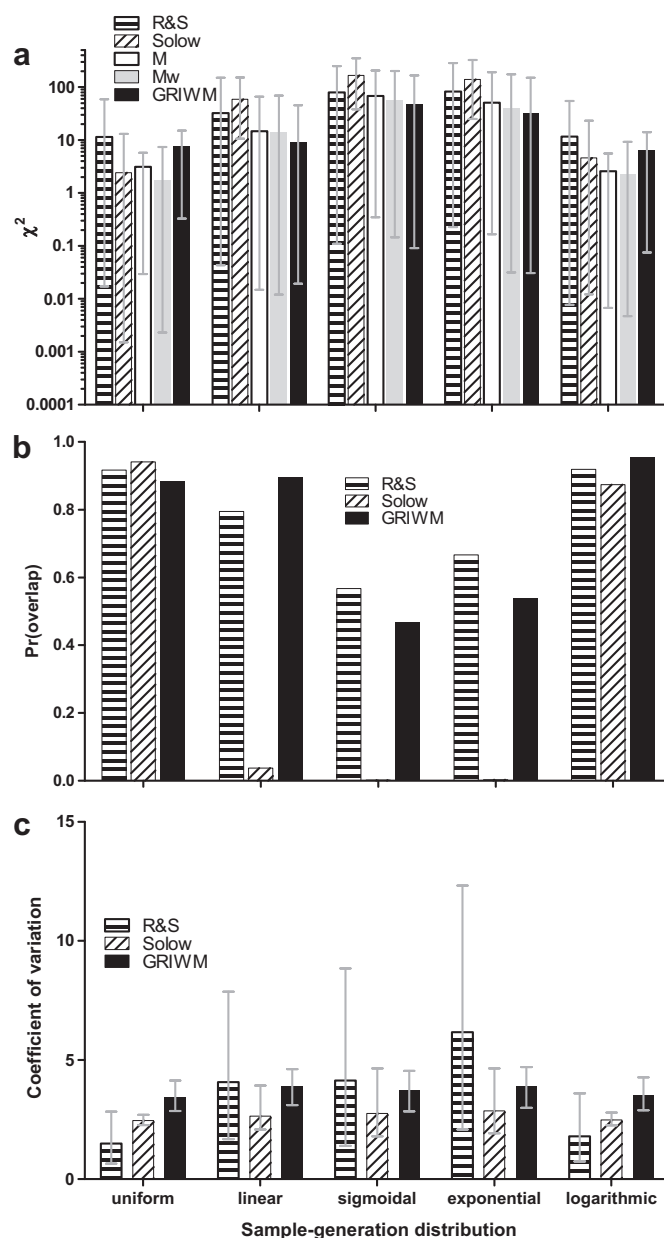
Fig. 3. Method bias and precision. (a) Bias of the five extinction date-estimating methods compared, based on a χ^2 statistic (smaller χ^2 = less bias) over 1000 itera-tions and generated using five different underlying distributions (uniform, linear, sigmoidal, exponential and logarithmic). Extinction-estimating methods include R&S = Roberts and Solow (2003), Solow = Solow et al. (2006), M = McInerny et al. (2006), and the new methods developed here: Mw = time series length-weighted McInerny, and GRIWM = Gaussian-resampled and inverse-weighted McInerny. See Methods for details. (b) Proportion of simulated series where the estimated extinction date's confidence interval overlapped with the 'true' extinction date (greater proba-bility of overlap = less bias). (c) Coefficient of variation of the estimated confidence intervals of extinction date (lower coefficient of variation = greater precision).

3.2. Pleistocene mammoth and horse extinctions

The late-Pleistocene extinction of North American mammoths and horses appears to have been broadly coincident with both the termination of the last glacial period (the onset of the current interglacial, the Holocene, has been dated to 11,650 calendar years before present) (Walker et al., 2009) and the arrival of modern humans (Waters and Stafford, 2007). When the GRIWM method is applied to the data on Pleistocene mammoth and horse extinctions (Guthrie, 2003, 2004), it upholds the conclusion that humans cannot

be ruled out as a cause for the horse extinction event (Solow et al., 2006). However, the re-analysis considerably increases the width of the confidence interval for the estimated date of mammoth extinction, and yet provides more compelling evidence that the horse and mammoth extinction events were not synchronous, being centred on 12,200 and 11,150 ^{14}C years before present, respectively (with a minimum separation of 300 ^{14}C years between events; Fig. 4).

3.3. European Neanderthal extinction

The Neanderthal Mousterian artefacts at Gorham's Cave, Gibraltar record the last-known sites of *Homo neanderthalensis* occupation in Europe. The most recent level confidently associated with Neanderthal occupation has been dated to 28,170 ± 240 ^{14}C years before present (Finlayson et al., 2006; Tzedakis et al., 2007), which was translated to 32,350 ± 450 calendar years before present using the Cariaco Basin calibration (Meese et al., 1997). Using two standard deviations from this mean value gives a final plausible extinction of 31,450 calendar years before present (Fig. 5). The Solow et al. method provided a nearly equivalent lower bound of 31,400 years before present when applied to the calibrated time series. However, the GRIWM provided a considerably later lower bound of 29,950 calendar years before present (Fig. 5), a date consistent with estimates of around 30,000 calendar years before present often used for the extinction of Neanderthals in Europe (Stringer et al., 2003; Roebroeks, 2008; Herrera et al., 2009).

4. Discussion

We contend that the Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) method is the most robust and simplest means to estimate extinction events when (*i*) the event itself is not observed and (*ii*) when there is considerable uncertainty in the dating of confirmed presences (e.g., dated fossils). We have demonstrated, using simulations in which the 'true' extinction date is set (and therefore known), that for most underlying probability distributions driving the deposition of retrievable fossils (Fig. 1), GRIWM outperforms existing methods. GRIWM does particularly well in circumstances where the sampling rate declines linearly, exponentially or sigmoidally prior to extinction. This is important because species do not always go extinct abruptly (as the uniform or logarithmic distributions imply) − the usual precursor to

extinction is a systematic reduction in range-wide population density, often followed by an extended lag period prior to final extinction (Brook et al., 2008).

The GRIWM method might still over-estimate the uncertainty associated with the final extinction estimate under some conditions. In the case of late-Pleistocene megafauna extinctions, for example, the rapid disappearance of certain dated fossils in conjunction with evidence for rapid human expansion, followed by the apparent replacement by different clades and/or species (e.g., Barnes et al., 2002; Hofreiter et al., 2007), seems to suggest that extinction was more abrupt than estimated by GRIWM. Even when assuming an underlying logarithmic distribution, additional genetic or fossil evidence for a clade/species shift at the same site could be used to constrain the confidence interval of the estimated extinction date. Alternatively, more formalised statistical approaches could be developed to incorporate *a priori* knowledge of such transitions using, for example, a Bayesian inference framework for the underlying model estimating extinction times to set a prior based on sighting probability or population dynamics from demographic models.

We contend that the GRIWM method will provide reasonable estimates of extinction time when applied to relatively precise and numerous dates in a fossil time series, and that the discovery of younger specimens should fall within the estimated window of uncertainty for the inferred extinction date. Further, the GRIWM method's higher estimated uncertainty in the final extinction date compared to previous methods is more realistic because it takes into account full dating uncertainty and it corrects simultaneously for bias associated with the different patterns and frequencies of dated records among time series. Thus, poor-quality time series (i.e., high date uncertainty and few records) will necessarily result in wider confidence intervals for GRIWM-estimated extinction dates. The relatively lower precision does not necessarily reduce bias as measured by overlap (Fig. 3b) merely because of wider confidence intervals; indeed, for many underlying probability distributions (linear, sigmoidal, exponential), the Solow et al. (2006) method in particular was nearly always too biased to overlap the true extinction date regardless of confidence interval width. Indeed, the Solow et al. (2006) method cannot return known extinction dates reliably in most circumstances tested. Solow et al. (2006) themselves stated that their method "assume[s] that the true ages U_1, U_2, ..., U_m are independent and uniformly distributed... The uniform assumption is a strong one and should be
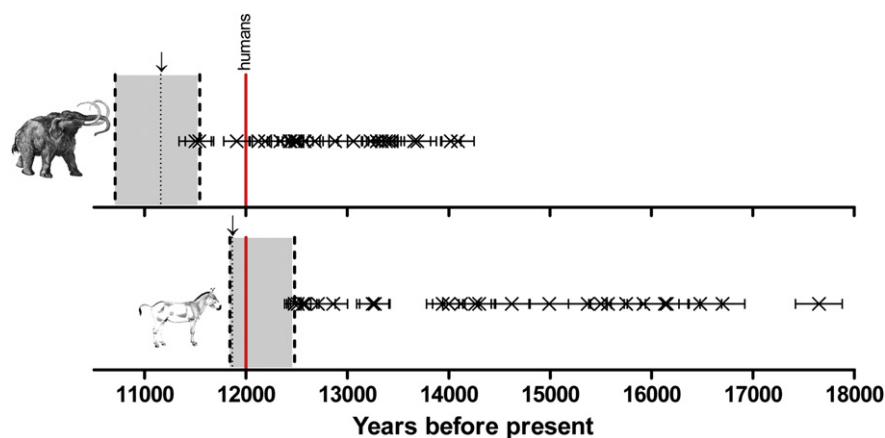
Fig. 4. Pleistocene mammoth and horse extinction estimates. Estimated extinction date confidence intervals (grey-shaded area) based on the GRIWM method for Pleistocene dated fossil time series of mammoths (top) and horses (bottom) in Alaska (data from Guthrie, 2003, 2004). Dates are shown as 'x' along the *x*-axis with their corresponding radiometric date (^{14}C years before present) standard deviation. Also shown with arrows are the most recent confidence bounds of extinction date for each time series as estimated by Solow et al. (2006). Humans are estimated to have arrived in the area around 12,000 years before present (red line) (Guthrie, 2003, 2004; Solow et al., 2006; Waters and Stafford, 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
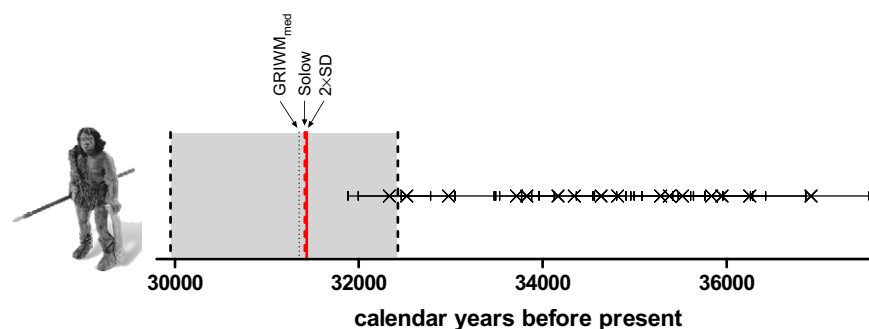
Fig. 5. Gorham's Cave Neanderthal extinction estimates. Estimated extinction date confidence intervals (grey-shaded area) based on the GRIWM method for Mousterian artefacts produced by Neanderthals in Gorham's Cave, Gibraltar (data from Finlayson et al., 2006; Tzedakis et al., 2007). Dates are shown as 'x' along the *x*-axis with their corresponding calibrated radiometric date (calendar years before present) standard deviation. Also shown with arrows are the earliest possible extinction dates as estimated by 2 standard deviations below the mean calibrated most recent fossil date (2 × SD: solid red line), the most recent confidence bound of extinction date as estimated by Solow et al. (2006) (dashed red line) and the median GRIWM (GRIWM$_{med}$) extinction date (light dotted black line). The shaded area represents the 95% confidence interval of estimated extinction date using GRIWM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

checked". It appears obvious that fossil dates are not independent and uniformly distributed, which could explain the lower overall accuracy and over-estimated precision of that method.

Finally, it should be noted that our approach can also be applied to time series where the goal is to estimate the first appearance of a species at a site (e.g., the invasion or evolution of a new species). The true date of first appearance likely precedes the earliest dated record in any fossil time series for the same reasons the most recent fossil probably does not represent the true extinction date. Thus, GRIWM could also be applied reciprocally to estimate the time of true first appearance in relevant dated fossil series.

Acknowledgements

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