Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions

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The late Quaternary period saw the rapid extinction of the majority of the world's terrestrial megafauna. The cause of these dramatic losses, especially the relative importance of climatic change and the impacts of newly arrived people, remains highly controversial, with geographically restricted analyses generating conflicting conclusions. By analyzing the distribution and timing of all megafaunal extinctions in relation to climatic variables and human arrival on five landmasses, we demonstrate that the observed pattern of extinctions is best explained by models that combine both human arrival and climatic variables. Our conclusions are robust to uncertainties in climate data and in the dates of megafaunal extinctions and human arrival on different landmasses, and strongly suggest that these extinctions were driven by both anthropogenic and climatic factors.

Most of the terrestrial megafauna present 100,000 years (100 ky) ago are now extinct (1). The extinctions were geologically rapid, and almost all occurred in the past 50 ky, but their exact timing varied among different parts of the world (2). Climatic change, and overhunting, habitat alteration, or the introduction of a novel disease by recently arrived people have been put forward as competing, and sometimes interacting, explanations (3). In addition to its enormous paleontological significance, this debate has drawn wide interest for its relevance to the relationship of humans with nature and to our understanding of the current anthropogenic extinction episode (4–8).

Attempts to explain megafaunal extinctions have, in addition to examining the effect of factors such as size and reproductive rate on extinction probability (9, 10), often focused on matching them in space and time with either climatic change or human arrival (11–13). However, most studies have been limited to single regions and limited numbers of taxa (e.g., 14–18), and have been beset by uncertainties in the accurate dating of human and/or megafaunal remains [e.g., the Cuddie Springs site in Australia (19–21)]. We believe that the problem is better approached by considering several landmasses simultaneously and dealing explicitly with uncertainty.

We did this by analyzing the relationship, across different areas and time periods, between variation in extinction rate and variations in human arrival and climatic conditions. Specifically, we compiled a dataset of human arrival (Table 1) and megafaunal extinction dates (Table S1) from the literature. We used the Antarctic Dome C core (22) as our main source of information on climatic variability; this dataset is the most complete among available time series and is well correlated with other time series at the scale used for our analysis (Tables S2–S4). We used generalized linear models (GLMs) with a binomial error structure and a logit link function to explore the role of human arrival (classified as either just arrived or not) and climatic variables in predicting the probability of extinction for a given landmass and time period (quantified as the proportion of taxa becoming extinct during a time period). We also allowed for landmasses to exhibit different background extinction rates (by including landmass as a block factor in the GLMs). To disentangle the roles of human arrival and climate, we compared the ability of models containing arrival or climate variables in isolation, or both of them simultaneously, to predict the pattern and severity of megafaunal extinctions. To explore the importance of uncertainty in extinction and human arrival dates, we reran the analysis for 10,000 combinations of first and last appearances of our taxa (for both the 700-ky and 100-ky time scales) and for the 32 most plausible combinations of human arrival dates for the 100-ky time scale only (Table S5).

Results and Discussion

We modeled megafaunal extinction rates on five landmasses (North America, South America, Palaearctic Eurasia, Australia, and New Zealand) during the past 700 ky at 100-ky resolution and during the past 100 ky at 10-ky resolution. Over the 700-ky time scale, both climatic variables and human arrival were important predictors of extinction rates. When considered in isolation, both climate and human arrival were informative in all our 10,000 extinction scenarios (Table 2) and predicted extinction very well. Predicted extinction rates were close to observed ones (Fig. 1), and a high percentage of deviance was explained by the models (92.5% and 91.4%, respectively; Fig. 2). Combining both climate and human arrival simultaneously led only to a marginal improvement in fit (Fig. 1): The deviance explained by models with all predictors increased little (to 93.0%) compared with models that only included either climate or human arrival (Fig. 2), even though climate improved the fit of models with human arrival alone in 28.8% of scenarios and human arrival improved models with climate alone in 33.4% of scenarios (Table 2). Of the climatic variables, the strongest predictor of extinction rate was the most rapid rate of temperature decrease within a time period, which had an effect almost double that of the SD and mean of temperature (Fig. 3; note that mean temperature has a negative coefficient, implying that extinctions were more likely to happen at lower temperatures). The maximum rate of temperature increase, on the other hand, had only a limited effect (Fig. 3). The effect of human arrival was of the same order of magnitude as that of mean temperature. Although both climate and human arrival are informative predictors of extinctions across the past 700 ky, the power of the analysis at this time scale to separate their effects is limited by the

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Table 1. Range of human arrival dates used in our analysis, with references

Landmass	Earliest proposed arrival, ky B.P.	Latest proposed arrival, ky B.P.
Australia	60–50 (33)	30–20 (34)
Eurasia	60–50 (34)	50–40 (35)
New Zealand	10–0 (36)	10–0 (36)
North America	30–20 (37)	20–10 (1)
South America	20–10 (1)	10–0 (38)

We tested all feasible combinations of these arrival dates (i.e., assuming that humans reached Eurasia before Australia and North America before South America). The details of all 32 extinction scenarios tested are provided in Table S5.

co-occurrence in all landmasses of peak extinction rate and human arrival in the past 100-ky time interval.

At the 100-ky time scale, in which there was variation among landmasses in both human arrival and the timing of peak extinction rates, human arrival and climatic variables were both important predictors of extinction rate in the vast majority of cases. In all 320,000 extinction scenarios tested [10,000 for each of 32 human arrival scenarios (Table S5) designed to reflect uncertainty in human arrival dates], models forced to contain only climatic variables were improved by adding the effect of human arrival (Table 2). On the other hand, depending on which human arrival scenario was used, adding climatic variables improved human-only models in 92–100% of extinction scenarios (Table 2). Models including human arrival explained more deviance (Fig. 2) and generally gave more accurate predictions (Fig. 4) than climate-only models for most time intervals in all continents, with very few exceptions. Climate-only models, on the other hand, sometimes made inaccurate predictions for nonpeak extinction intervals (Fig. 4). This could be the result of assuming that climate covaried consistently, and had consistent effects, across all landmasses. The climate effect was almost completely attributable to the fastest rate of decrease in temperature, which had much larger coefficients than other climatic variables in almost all scenarios (Fig. 3), with steeper temperature declines being associated with greater extinction rates. Human arrival had an even stronger negative effect, which was consistent for all scenarios (Fig. 3).

Together, human arrival and climatic variables explained a large proportion of the deviance (93.0% and 65.4–85.0% for the 700-ky and 100-ky analyses, respectively; Fig. 2), especially for an ecological dataset with many inherent uncertainties. Our approach is conservative in attributing importance to human arrival because this forms one explanatory variable (compared with four climatic variables), which can only act in one (700-ky time scale) or two (100-ky time scale) time intervals, whereas climatic variables can act in all of them.

It would also be interesting to repeat the analysis with climatic records or reconstructions for each of the different areas. However, simulated reconstructions of climate covering the past 100 ky (23) are currently of insufficient resolution (i.e., fewer than 10 data points per 10-ky interval), especially in older time periods. Furthermore, there are no local climate records of sufficient length and resolution to cover our analysis, which is why we could only use the Antarctic Dome C ice core (22), which covers eight glacial cycles over the past 700 ky. However, it is possible to use the North Greenland Ice Core Project (NGRIP) record (24) for the past 100 ky. To ensure that our results were not biased by using only records from one hemisphere, we repeated the 100-ky analysis using the NGRIP record for all continents [note that it was not possible to use both records in the same analysis because they measure different climate proxies (Table S2) and there was insufficient power to treat the two hemispheres separately].

Table 2. Percentage of extinction scenarios in which climate and human arrival are informative predictors on their own ("climate only" and "human arrival only")

Analysis (ky)	Human arrival scenario	Climate only	Human arrival only	Climate on top of human arrival	Human arrival on top of climate
700	—	100	100	28.8	33.37
100	1	100	100	95.6	100
	2	100	100	100	100
	3	100	100	92.3	100
	4	100	100	100	100
	5	100	100	99.9	100
	6	100	100	100	100
	7	100	100	99.9	100
	8	100	100	100	100
	9	100	100	100	100
	10	100	100	100	100
	11	100	100	100	100
	12	100	100	100	100
	13	100	100	100	100
	14	100	100	100	100
	15	100	100	99.77	100
	16	100	100	100	100
	17	100	100	100	100
	18	100	100	100	100
	19	100	100	100	100
	20	100	100	100	100
	21	100	100	100	100
	22	100	100	100	100
	23	100	100	100	100
	24	100	100	100	100
	25	100	100	100	100
	26	100	100	100	100
	27	100	100	100	100
	28	100	100	100	100
	29	100	100	100	100
	30	100	100	100	100
	31	100	100	100	100
	32	100	100	100	100

The same figures are also obtained if climate is added to models forced to contain only human arrival ("climate on top of human arrival") and vice versa ("human arrival on top of climate"). For example, in the 700-ky analysis, adding climate improved a model forced to contain human arrival in only 28.8% of scenarios.

The results from the NGRIP 100-ky analysis were strikingly similar to those obtained using the Antarctic Dome C record (Figs. S1–S3). Human arrival always improved models forced to contain climatic variables; adding climate to human-only models improved them, on average, in 81.7% of extinction scenarios (ranging from 8.2–100%, depending on human arrival scenario; Table S6). Climate and human arrival together account for 55.9–78.8% of the deviance [depending on the extinction scenario, with 24.2–47.1% attributable solely to anthropogenic effects and 1.7–19.7% attributable solely to climate effects (Fig. S1)]. As with the analysis using the Antarctic record, human arrival was always associated with an increase in extinction rate and its effect had the strongest effect of all the predictors across all 32 human arrival scenarios (Fig. S2). Among the climatic variables, the maximum rate of temperature decrease was again often the most important factor (with large values associated with higher extinction rates), whereas the maximum rate of temperature increase had the smallest effect (Fig. S2). This suggests that our choice of the one hemisphere's climate record does not influence our conclusions. This result might appear surprising, given that temperature changes in the two hemispheres are known to be asynchronous. However, temperature increases in the Southern

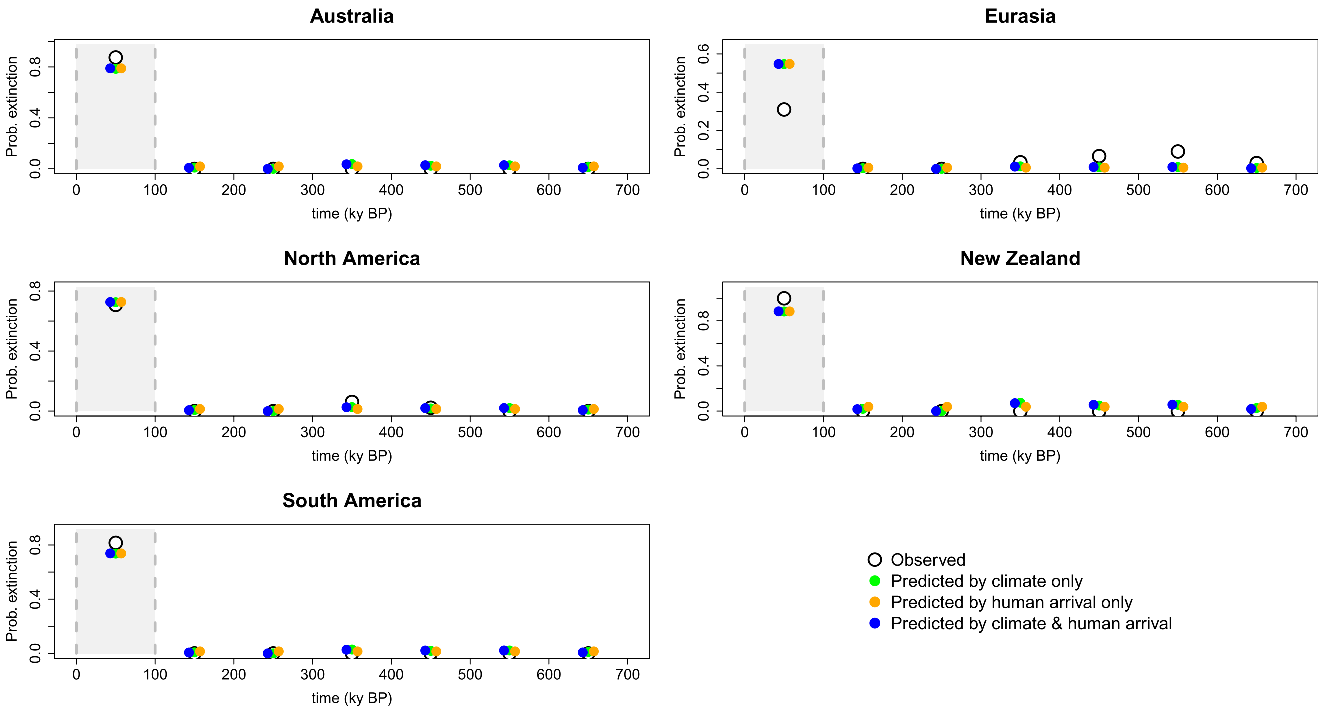

Fig. 1. Observed and predicted extinction rates (proportion of megafauna that become extinct) for each region and time interval in the 700-ky analysis. Observed extinctions (open circle) are the mean of the 10,000 extinction scenarios to take account of date uncertainties. Colored circles show the extinction rates predicted by models containing climate only (green), human arrival only (orange), or both human arrival and climate (blue). The time interval in which humans have an effect is shaded. Prob., probability.

Hemisphere only preceded those in the Northern Hemisphere by 1.5–3 ky (25), and the two climatic records are highly correlated (Table S2) at the resolution of our analysis (10-ky intervals).

In addition to being robust to the choice of climatic record, our results are robust to uncertainty over exact extinction and arrival dates, being remarkably consistent across different permutations. This is interesting in light of previous work in which the argument for the relative importance of climatic conditions or human arrival has hinged on the precise dating of megafaunal or human remains (21, 26). Although this may still hold true for specific taxa and locations, the analysis we have carried out suggests that arguments over precise dates are unlikely to affect the general result.

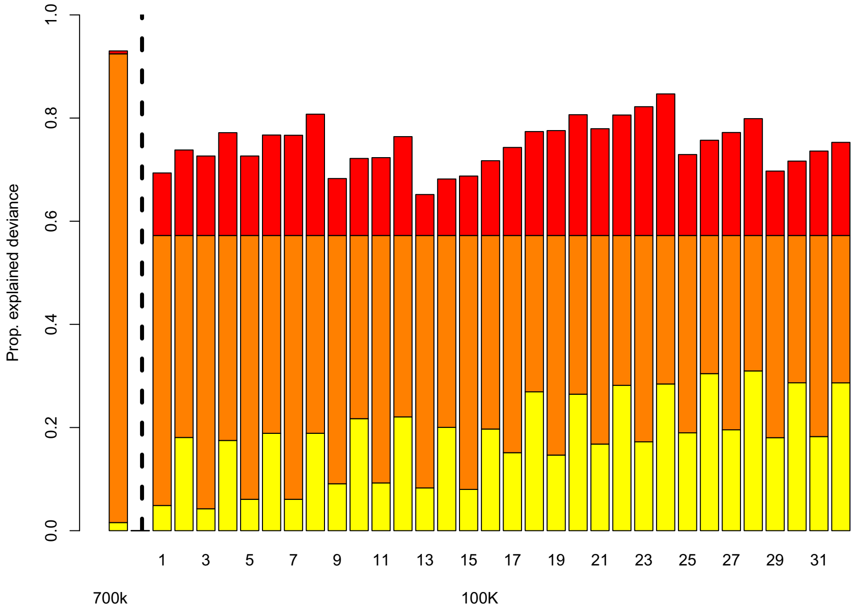

Fig. 2. Proportion (Prop.) of deviance explained by climate only (yellow), human arrival only (red), and shared deviance (orange) for the 700- and 100-ky analyses. For the 100-ky analysis, the results for each of the 32 human arrival scenarios are shown. The deviance explained by climate variables (yellow + orange combined) is independent of human arrival scenario.

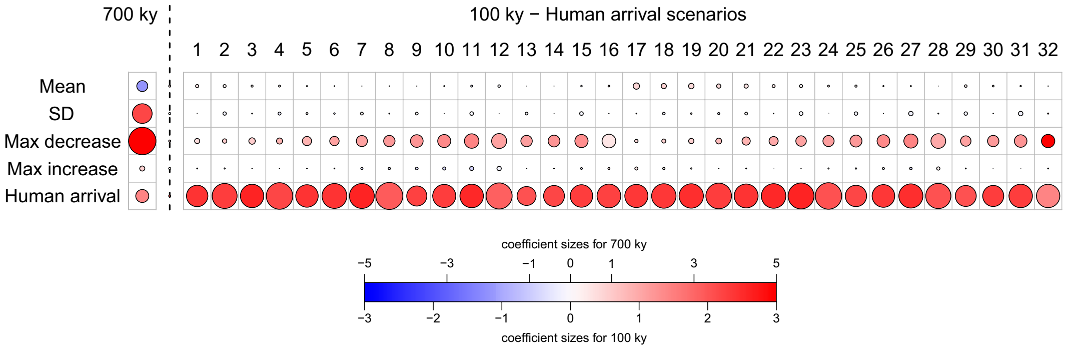

Fig. 3. Strength of the effect of four climatic variables and human arrival in predicting extinctions. The absolute magnitude of the median standardized coefficients for each scenario is given by the diameter of the circles, which are scaled such that the largest coefficient is represented by a circle filling a whole square in the grid. The sign and magnitude of the coefficients are given by the color of the circles, according to the scale at the bottom of the graph (positive coefficients represent increased extinctions, negative coefficients decreased extinctions). Note that the size and color scales differ between models covering the past 700 ky vs. the ones covering the last 100 ky. Max, maximum; SD, standard deviation.

We have demonstrated that extinctions were correlated in space and time with both certain climatic conditions and human arrival. There remains a debate as to the severity of the most recent glacial cycle in comparison to previous cycles, and to the extent to which this matters for climatic explanations of the extinctions (27). Our results show that for the 700-ky analysis in particular, the unique combination of a rapid period of cooling, high variance in temperature, and low mean temperature in the past 100 ky predicted higher levels of extinction than in previous periods. Such conditions are likely to have severe impacts on vegetation (28). For example, falling temperature and the expansion of the Scandinavian and Alpine ice sheets during the Last Glacial Maximum converted previously wooded areas into treeless "mammoth steppe," with severe impacts on species such as *Megaloceros giganteus* (the "Irish elk") (29). However, the strong and consistent effect of human arrival, particularly at the 100-ky scale, and the more accurate predictions made by combined models support the view that humans, either directly through overhunting (30) or indirectly by bringing disease (31) or altering habitat (32), also contributed to the extinctions.

Materials and Methods

Following an extensive literature review, we estimated the extinction rates of megafaunal genera for five landmasses (North America, South America, Palaearctic Eurasia, Australia, and New Zealand) on two time scales: (*i*) the past 700 ky, split into intervals of 100 ky, and (*ii*) the past 100 ky, split into intervals of 10 ky (*SI Materials and Methods*). All first and last appearance dates were

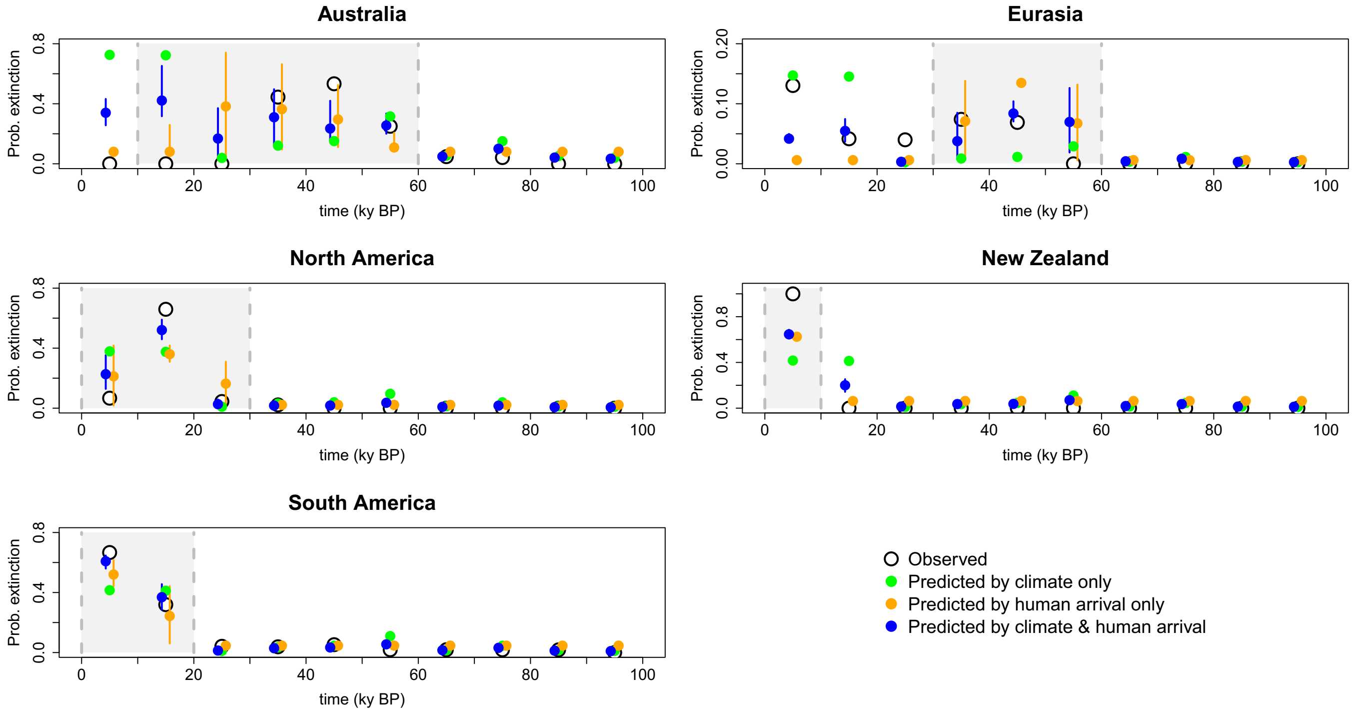

Fig. 4. Observed and predicted extinction rates (proportion of megafauna that become extinct) for each region and time interval in the 100-ky analysis. Observed extinctions (open circle) are the means of the 10,000 extinction scenarios. Colored circles show the extinction rates predicted by models containing climate only (green), human arrival only (orange), or both human arrival and climate (blue). For time intervals in which there is uncertainty over the timing of human arrival, the interquartile range of predicted values is shown, with the circle representing the median of these predictions. The ranges of time intervals in which humans may have had an effect are shaded. Prob, probability.

taken from the published literature (a list of dates and the relevant references is provided in Table S1). Because of the uncertainty in the exact timing of the first and last appearances of many genera, we generated 10,000 datasets (which we term "extinction scenarios") for each time scale by randomly sampling dates from the ranges of first and last appearances available from the literature. We then modeled the extinction rate (in each time interval) in each extinction scenario by building GLMs with four climatic variables (mean temperature, its SD, and the fastest decreasing and increasing rates of change in temperature) derived from ice core data from Dome C in Antarctica (22) (Tables S3 and S4) and the occurrence of human arrival (presence/absence) during the time interval as explanatory variables. We used the Antarctic ice record because it remains the longest record of adequate resolution, allowing us to investigate the effects of several glacial cycles, and we used only the presence/absence of humans because there are insufficient data on prehistoric human densities. We also repeated the 100-ky analysis using an ice record from Greenland (24) to ensure that our conclusions were not biased by using only a Southern Hemisphere climatic record.

Although human arrival is known to have occurred only during the past 100 ky, the exact dates of human arrival are less certain when expressed in the 10-ky intervals of our shorter time scale. We therefore considered 32 different human arrival scenarios (Table S5), covering all plausible permutations of arrival dates proposed in the literature, and fitted models for each of them (*SI Materials and Methods* and Table S5). In these shorter time scale models, the effect of human arrival was considered to last for two time intervals (i.e., 20 ky) to ensure that humans had enough time to colonize the whole landmass. Important predictors of extinction rates were determined by comparing models using Akaike's information criterion. Additional details are provided in *SI Materials and Methods*.

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Supporting Information

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Supporting Information Corrected April 13, 2012

SI Materials and Methods

First and Last Appearance Dates for Megafauna. We built a database of the first and last recorded appearances of terrestrial megafaunal genera over the past 700 ky. We focused on genera to avoid taxonomic problems (e.g., whether disappearance of a species represents extinction or evolution into a different one) and used Martin's definition of megafauna as terrestrial animals with a mean adult mass greater than 44 kg (1), using mass data from Smith et al. (2) where possible. We restricted our analysis to North America, South America, Australia (including New Guinea and Tasmania, which were connected to Australia during the Pleistocene), New Zealand, and Eurasia (Palaearctic only: west of the Indus and north of the Himalaya and the Yangtze).

We searched for the first and last recorded appearance dates of megafaunal genera in each region (Table S1). Although mindful of the Signor–Lipps effect (3), we treated the two dates as first appearance and extinction dates, respectively, and assumed the genera were present between them. We used data from books and reviews (especially 4–6), and searched online databases (7, 8) and search engines (9, 10) using the following search terms (where GN is genus name): GN, GN start date, GN Pleistocene, GN Pliocene, GN fossil record, GN first appearance, GN terminal date, and GN extinction date. All records were derived from the primary literature; search engines and databases were simply a means to access primary sources. Where we used a database (7, 8) to find a record, we have cited the primary source underlying the record.

The primary sources comprise a variety of different authors and methods, and some dates will inevitably be more reliable than others. For genera where the extinction date was unknown or disputed, we used the full range of proposed dates. Our aim in this study was not to provide new data on the timing of extinctions but to see what conclusions could be drawn from what has already been published.

For the purposes of the analysis, we split the past 700 ky into intervals of 100 ky and the past 100 ky into intervals of 10 ky. For both time scales of analysis, we scored the presence and/or extinction of each genus in each time interval. In cases where the dates could not be definitively placed into one time interval, we recorded the range of possible time intervals for the dates.

To investigate the importance of individual dates, we generated 10,000 random datasets where first and last dates for each genus were picked randomly from the list of possible dates. We ran this process separately for the 700-ky and 100-ky datasets.

Climatic Records. We used the fluctuations in δD (the deuterium/hydrogen ratio in ice, a proxy for temperature) measured in a deep ice core from Dome C, Antarctica (11) as our record of global climatic change in the past 700 ky. We used this record because it was the only available climate record of sufficient resolution that covered the entire time interval in which we were interested. Other records, such as the NGRIP record (12), were of sufficient resolution but insufficient length, whereas others were of sufficient length but insufficient resolution (Table S2). We tested how this covaried with climate records from different regions by performing Pearson's correlation tests, matching data points of the same age. When local records did not have data points of the same age as Dome C, we interpolated approximate values for the matched age. Dome C correlated positively with some of but not all the local records (Table S2).

We used the Dome C record for both the 700-ky and 100-ky analysis. We also replicated the 100-ky analysis using the NGRIP record from Greenland. For each time interval, we calculated the mean value of the climate proxy, its SD, and the minimum and maximum rates of change with time between successive values (i.e., the minimum and maximum slopes; Tables S3 and S4). To account for differences in the number of data points in each interval (which could affect the slope measures), we filtered the data to have the same number of points in each interval by selecting a subset of data points to give even spacing.

Human Arrival. We searched the literature for the first arrival date of anatomically modern humans (references in Table 1) in each of the five landmasses. As with megafauna, where we judged there to be reasonable disagreement in the literature over the dates, we considered the range of possible time intervals in which human arrival could have occurred.

To allow for this uncertainty, we considered all feasible combinations (assuming humans reached Eurasia before Australia and North America before South America) of arrival dates (32 possible scenarios; Table S5) and repeated the analysis for each scenario (this only affects the shorter scale analysis of the past 100 ky because, in the 700-ky time scale, human arrival always occurs during the last time interval).

Because no reliable data are available on prehistoric human densities, we considered only the presence or absence of human arrival.

Statistical Analysis. The relative roles of human arrival and climate were estimated using GLMs with logit link and a binomial error structure, where, for each time interval, the response variable was the number of genera that went extinct out of the total number of genera that were present at the beginning of the time interval. The four climatic variables (mean and SD of δD as a proxy for temperature and the maximum and minimum gradients between consecutive data points) were used as predictors, together with human arrival [for the shorter time scale, we considered human arrival to affect the first 2 time steps after the reported date (i.e., to span 20 ky)]. The climatic variables were each centered on 0 and scaled to have a SD of 1, such that coefficients from linear models would be "standardized," and thus directly comparable. The effect of landmass was modeled as a blocking factor and was included in all models. No interaction term between predictor variables and continent was used, forcing the effect of predictors to be consistent across landmasses. We considered four possible models: a "combined" model that included all variables; a "climate-only" model and a "human-only" model that included either climatic variables or human arrival, respectively; and a "null" model that did not include any predictor (except for continent as a blocking factor). Comparisons between the appropriate models, based on the Akaike Information Criterion, allowed us to determine the effect of one predictor when another predictor was forced to be in the model (e.g., comparing a model with only climate variables with a model with both climate and human arrival to determine the importance of human arrival above and beyond climate).

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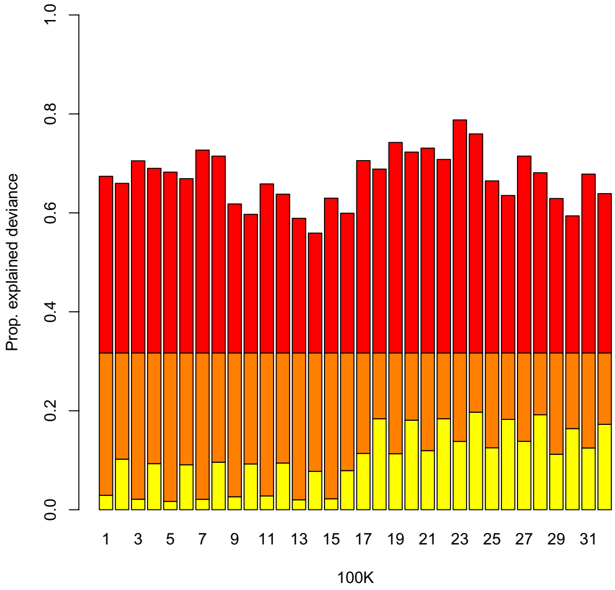

Fig. S1. Proportion (Prop.) of deviance explained by climate only (yellow), human arrival only (red), and shared deviance (orange) for the 100-ky analysis, using the Greenland NGRIP record (instead of the Antarctic Dome C record as in Fig. 2) for climate data. For the 100-ky analysis, the results for each of the 32 human arrival scenarios are shown. The deviance explained by climate variables (yellow + orange combined) is independent of the human arrival scenario.

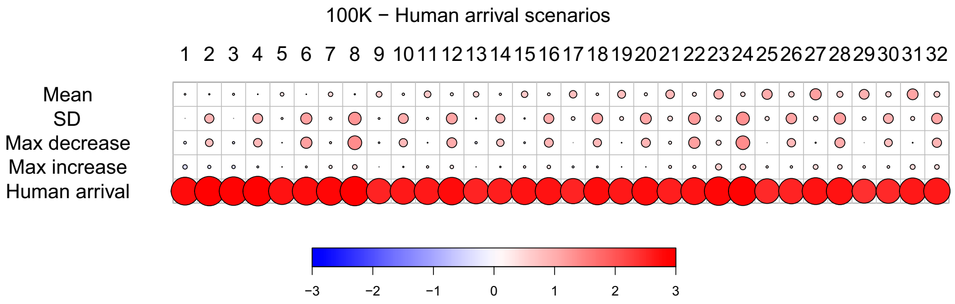

Fig. S2. Strength of the effect of four climatic variables and human arrival in predicting extinctions, using the Greenland NGRIP record (instead of the Antarctic Dome C record as in Fig. 3) for climate data. The absolute magnitude of the median standardized coefficients for each scenario is given by the diameter of the circles, which are scaled such that the largest coefficient is represented by a circle filling a whole square in the grid. The sign and magnitude of the coefficients are given by the color of the circles, according to the scale at the bottom of the graph (positive coefficients represent increased extinctions, and negative coefficients decreased extinctions. Max, maximum; SD, standard deviation.

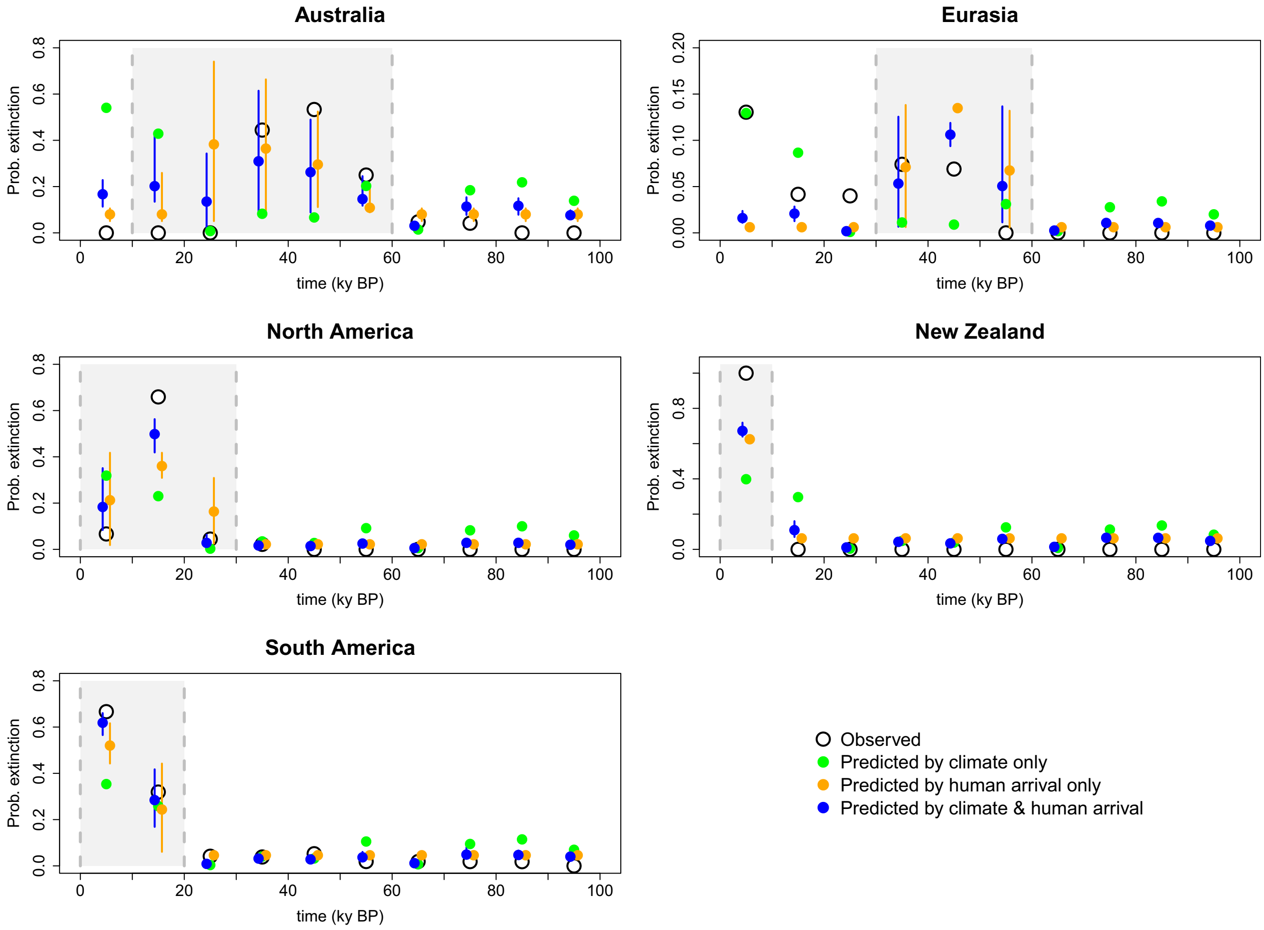

Fig. S3. Observed and predicted extinction rates (proportion of megafauna that become extinct) for each region and time interval in the 100-ky analysis, using the Greenland NGRIP record (instead of the Antarctic Dome C record as in Fig. 4) for climate data. Observed extinctions (open circle) are the means of the 10,000 extinction scenarios. Colored circles show the extinction rates predicted by models containing climate only (green), human arrival only (orange), or both human arrival and climate (blue). For time intervals in which there is uncertainty over the timing of human arrival, the interquartile range of predicted values is shown, with the circle representing the median of these predictions. The ranges of time intervals in which humans may have had an effect are shaded. Prob., probability.

Table S1. Megafaunal genera from Australia, Eurasia, New Zealand, North America, and South America used in our analyses

Table S1 (DOC)

Dates shown are regarded as the earliest and latest reliable dates in the fossil record.

Table S2. Climate records from each landmass and their correlation with the Antarctic Dome C ice core record

Table S2 (DOC)

Table S3. Climate proxy variables taken from the Antarctic Dome C ice core for past 700 ky

Table S3 (DOC)

Table S4. Climate proxy variables taken from the Antarctic Dome C ice core for past 100 ky

Table S4 (DOC)

Table S5. Human arrival scenarios used in analysis

Table S5 (DOC)

Table S6. Percentage of extinction scenarios in which climate and human arrival are informative predictors on their own (“climate only” and “human arrival only”), using the Greenland NGRIP record for climatic variables

Table S6 (DOC)

The same figures are also obtained if climate is added to models forced to contain only human arrival (“climate on top of human arrival”) and vice versa (“human arrival on top of climate”). The details of the different human arrival scenarios are provided in Table S5.