

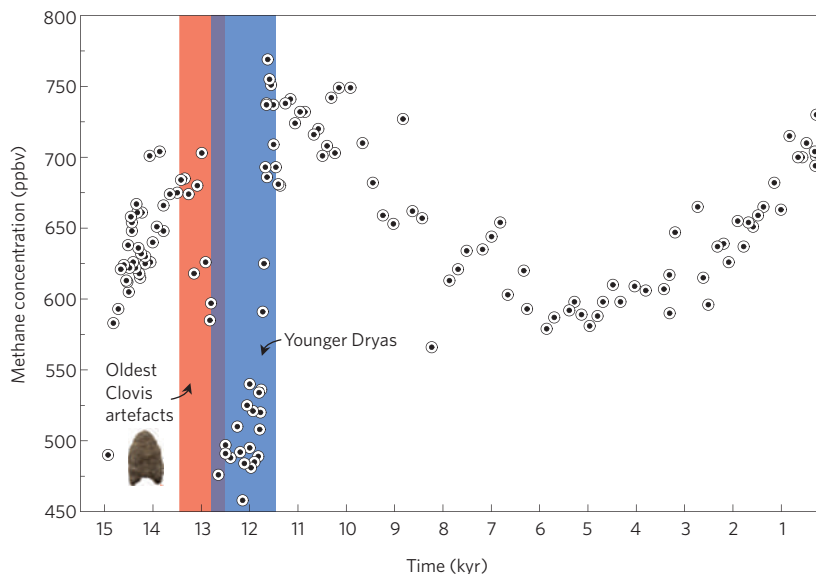
# Methane emissions from extinct megafauna

**To the Editor** — About 13,400 years ago, the Americas were heavily populated with large-bodied herbivores such as mammoths, camelids and giant ground sloths; the megaherbivore assemblage was richer than in present-day Africa. However, by 11,500 years ago and within 1,000 years of the arrival of humans in the New World, 80% of these large-bodied mammals were extinct<sup>1</sup>. The eradication of megafauna had marked effects on terrestrial communities, including changes in vegetative structure and reorganization of food webs<sup>1,2</sup>. Here, we suggest that the extinction also had profound effects on methane emissions and atmospheric methane concentrations, with potential implications for abrupt climate change during the Younger Dryas cold event.

Herbivores produce methane as a by-product of cellulolytic-microbial fermentation during digestion. Today, enteric emission by domestic livestock is an important contributor to greenhouse gas concentrations, representing ~20% of annual methane emissions<sup>3</sup>. This influence may have been greater in the Pleistocene epoch, when atmospheric methane concentrations were considerably lower, for example, ~680 compared with ~1,800 parts per billion by volume (ppbv) today<sup>4</sup> (Supplementary Information). To evaluate the potential influence on the global methane cycle of the geologically abrupt loss of millions of large-bodied herbivorous mammals, we estimated their likely annual enteric methane production.

We focus on the 114 herbivorous species extirpated from the Americas at the end of the Pleistocene epoch<sup>5</sup>, as the megafaunal extinction in Africa and Eurasia was comparatively minor. We have also ignored the extinction of carnivorous and omnivorous species, which have negligible rates of methane production. The annual enteric methane production by the extinct herbivores ( $P_H$ ) is dependent on the species-specific methane-emission factor ( $M$ ) in  $\text{kg yr}^{-1}$ , animal density ( $D$ ) per  $\text{km}^2$ , and the geographic range of the species ( $A$ ) in  $\text{km}^2$ . Our approach can be summarized as:

$$P_H = \sum_{h=1}^{114} M_h D_h A_h$$



**Figure 1** | Atmospheric methane concentrations over the past 15,000 years from the Greenland GISP2 core<sup>4</sup>. The extinction of megafauna (indicated by red shaded region) closely coincides with an abrupt drop in atmospheric methane concentration at the onset of the Younger Dryas (indicated by blue shaded region). Time is thousands of years (kyr) before present. We estimate that prior to the extinction event, large-bodied herbivores in the Americas released about 9.6 Tg of methane to the atmosphere annually. The loss of these species could be responsible for 12.5 to 100% of the overall methane decline.

where  $h$  is the extirpated herbivore. We then developed or employed allometric relationships between body mass and the relevant traits to compute overall methane production by megafauna (Supplementary Information).

Current Intergovernmental Panel on Climate Change (IPCC) guidelines for calculating herbivore methane emissions are derived from domestic ruminants and do not explicitly address the influence of body size or digestive-system type. We therefore compiled data from empirical studies for foregut and hindgut species spanning the extant size spectrum to assess any potential effects. We found a highly significant relationship that is influenced by both mass and type of herbivore (analysis of covariance (ANCOVA),  $N = 44$ ,  $P < 0.001$ ). Consequently, separate regressions were used for ruminant (foregut) and hindgut herbivores ( $N = 33$ ,  $P < 0.001$ ,  $r^2 = 0.949$ ;  $N = 11$ ,  $P < 0.001$ ,  $r^2 = 0.955$ , respectively;

Supplementary Information). Interestingly, these results suggest that methane production by non-domesticated animals is currently undervalued by the IPCC<sup>3,6</sup>.

The body masses of extirpated species were obtained from a Quaternary mammal database<sup>5</sup>. We estimated  $D$  using a well-supported relationship:  $D = 103 \times (\text{body mass})^{-0.93}$ . We chose this equation because it was constructed using herbivores across a range of sizes (from 0.01 to 5,000 kg), included multiple habitats and continents, and had high predictive value<sup>7</sup> ( $N = 250$ ;  $r^2 = 0.71$ ;  $P < 0.001$ ). From historic range data<sup>8,9</sup>, we derived a relationship between body mass and  $A$  for extant large-bodied herbivores across the globe. A quartile regression allowed us to obtain a robust predictive equation relating median geographic range to body mass ( $N = 61$ ;  $r^2 = 0.756$ ;  $P < 0.025$ ).

Our calculations suggest that the late Pleistocene extinction resulted

in a decreased annual methane flux of ~9.6 teragrams (Tg) (range 2.3 to 25.5 Tg; Supplementary Tables T1 and T2). Interestingly, ice-core records of methane concentration reveal an abrupt drop of >180 ppbv at the onset of the Younger Dryas cold event, about 12,800 years ago (Fig. 1). The drop seems to be synchronous with the extinction of New World megafauna.

We can calculate the decline in methane emissions associated with this drop by relating the methane mass to an average or time-varying removal constant, for example,  $P(t) = M(\text{CH}_4)/\tau(t)$ ; where  $P(t)$  represents total production,  $M(\text{CH}_4)$ , atmospheric methane content in Tg, and  $\tau(t)$ , residence time in the atmosphere. The atmospheric lifetime of methane is currently approximately eight or nine years, but photochemical modelling suggests that it was somewhat shorter during cooler periods<sup>10,11</sup>. We used a Monte Carlo suite of coarse box-modelling exercises — conducted to explain isotope signature distributions<sup>12</sup> — to estimate the residence time of methane at the transition into the Younger Dryas event. We then computed reductions in global methane emissions at the transition using upper limits from the fifty-percent-likelihood category, which were consistent with multiple literature values. The calculations were then repeated for a pre-industrial time constant, thus bracketing likely values. Estimates of the decrease in the source pool were sensitive to the residence time employed (Supplementary Table T2).

We find that the loss of megafauna could explain 12.5 to 100% of the atmospheric decrease in methane observed at the onset of the Younger Dryas (Fig. 1; Supplementary Table T2). Moreover, the changes in methane concentration at this time seem to be unique. A comparison with the five

largest drops over the past 500,000 years shows that the Younger Dryas transition was characterized by a methane decrease that was two to four times more rapid than any other time interval (Supplementary Table T3,  $P < 0.01$  to  $P < 0.001$ ), which suggests that novel mechanisms may be responsible.

Methane is an important greenhouse gas<sup>3,6</sup> but the degree of radiative forcing resulting from fluctuations in atmospheric concentrations is unclear. Methane is often cited among the triggers or added factors in a cascade of effects leading to climate fluctuations<sup>3</sup>. The concentration of methane both influences and is influenced by temperature, but lead-lag and indirect relationships are not well characterized<sup>13</sup>. Ice-core records from Greenland suggest that the methane concentration change associated with a 1 °C temperature shift ranges from 10 to 30 ppbv, with a long-term mean of about 20 ppbv (ref. 13). Thus, empirically, the 185 to 245 ppbv methane drop observed at the Younger Dryas stadial is associated with a temperature shift of 9 to 12 °C. The attribution and magnitude of the Younger Dryas temperature shift, however, remain unclear. Nevertheless, our calculations suggest that decreased methane emissions caused by the extinction of the New World megafauna could have played a role in the Younger Dryas cooling event.

We are not the first to suggest that human-mediated activities influenced the planet prior to the industrial age<sup>14</sup>. Although still controversial, the megafaunal extinction is the earliest catastrophic event attributed to human activities. Thus, we propose that the onset of the 'Anthropocene' should be recalibrated to 13,400 years before present, coincident with the first large-scale migrations of humans into the Americas. □

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#### Author contributions

All authors contributed extensively to this work.

#### Additional information

Supplementary information accompanies this paper on [www.nature.com/naturegeoscience](http://www.nature.com/naturegeoscience).

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# African exception to drivers of deforestation

**To the Editor** — Today, tropical deforestation is thought to be driven by growing export demand for both agricultural and primary products, such as palm oil and timber<sup>1,2</sup>. DeFries *et al.*<sup>3</sup> build on this argument by correlating tropical deforestation with net agricultural trade and urban population growth. They conclude that local populations

and markets are no longer the dominant drivers of deforestation in many tropical regions. Here, we would like to highlight tropical Africa as an exception to this rule: as DeFries *et al.* acknowledge, but do not emphasize, deforestation in their African dataset is not significantly correlated with net agricultural trade.

Although export markets are probably strong drivers of deforestation in the neotropics<sup>4</sup> and southeast Asia<sup>5</sup>, much of sub-Saharan Africa still reveals old patterns of forest loss. Here, the slow expansion of subsistence or smallholder agriculture, and the extraction of primary products such as wood fuel, timber and charcoal for domestic use, are the