Since the inception of ancient environmental DNA (eDNA) research, considerable attention has been paid to the depositional and diagenetic processes of DNA molecules in different sediments and settings. Understanding those processes is critical to determine whether the recovered DNA is of the same age as the deposit in which it is found. It is therefore not unreasonable to ask, as Miller and Simpson have, in response to our recently published eDNA study of 50,000 years of Arctic ecosystem changes, whether remains of long-dead megafauna might have contributed older DNA to younger deposits. They propose that this may account for our finding that mammoths persisted into the Holocene epoch in the continental Arctic.

The basis for Miller and Simpson’s proposal is that mammoth remains could have persisted on the surface of cold Arctic landscapes for millennia after the species’ extinction, and while decomposing, released DNA into younger sediment layers. Their argument assumes that surface skeletal persistence is predominantly temperature-related, based on a correlation between mean annual temperature and the time unburied bones appear to persist. Leaving aside the limited sample size (n = 10) on which their correlation is derived, and the fact that not all the dated bones in the model have been on the surface since the animals’ death (for example, the Wrangel Island mammoths were evidently released from permafrost only a few years before their discovery), there can be little doubt that temperature is a factor in bone preservation in the Arctic. However, it is not the sole or even dominant factor. Instead, this is a region where multiple factors work against ubiquitous, millennia-long preservation, including carnivore and scavenger activity, moisture effects, seasonal freezing and thawing, strong ultraviolet radiation, and a range of biogeochemical processes that lead to enzyme digestion and organic matter decomposition. Mammoth individuals, being large, would require wide geographic ranges. The expected average density of mammoth fossils per unit area would therefore be extremely low, and so too would the likelihood that these rare remains contributed DNA to our sampling sites. Given that mammoth DNA was found in 23 Holocene samples from 14 different sites (Fig. 1a), these late survivals are highly unlikely to be a result of DNA released from dead remains.

Furthermore, the eDNA that we obtained from surface samples belonged solely to species present on the landscape presently, indicating that secondary contamination from fossil material is minor. However, it is well understood that some depositional settings (for example, riverbanks and thaw lakes) may be affected by complex processes, whereby older material (not only eDNA but the sediment strata) can be redeposited within younger sediments. This applied for one site (an actively eroding riverbank setting) of our original study that did not meet our criteria of an unmixed section with clear sedimentological and chronological contexts for eDNA sampling (described in the supplementary information of ref. 3), which was therefore excluded from the analysis. This reinforces the well-known caution that fluvial settings require particularly stringent sampling and dating protocols.

Although Miller and Simpson rightly note that there is a near-continuous record of dated mammoth fossils, that record is not a reliable estimator of extinction timing. The youngest dated fossil marks the last time a species was abundant on the landscape, rather than its last occurrence, which is highly likely to go undetected when a species is declining toward extinction, especially across the large geographic range of the vast Arctic landmass. Given the patchy nature of both the fossil and radiocarbon records, there can be centuries-long gaps between dated specimens (figure 1 in ref. 4). Those gaps would only increase as species declined and shifted their ranges to smaller portions of their former area. Mammoths may have survived in refugia—such as the last pockets of the steppe-tundra landscape to which they were adapted—long after the date of the last known fossils, and most probably also after their last recorded occurrence in eDNA. However, there is a greater chance of detecting the lingering presence of an animal with eDNA than with its fossils, because an animal releases millions of DNA molecules onto the landscape on a daily basis over the course of its lifetime, but only leaves one skeleton, which is far less likely to be preserved, found and dated.

Notwithstanding limitations in Miller and Simpson’s model and the lack of evidence for redeposition of DNA in our samples, it is reasonable to ask what we might expect to see if the slow decomposition of mammoth tissues on cold Arctic landscapes released DNA into sediments ubiquitously millennia after mammoth extinctions.

First, if redeposition of ancient DNA were widespread, we would expect to see mammoth eDNA in many sampling sites across the
indicating that it has not diffused through a horizontal layer. Herbaceous plants, and (3) palaeo-climate panels reconstructed independently from different climate models (figures 2 and 4 in ref. 3).

This finding instead conforms to a pattern of a species’ decline ubiquitously, we should not have seen spatiotemporal co-occurrences of mammoth, steppe vegetation, and the cold and dry Pleistocene-like climate conditions.

Finally, if redeposition of DNA in younger deposits was a problem, the eDNA of late-surviving mammoths ought to reflect the full range of clades present in mammoth populations in the late Pleistocene. They do not. Instead, we find a consistent decline of mammoth mitochondrial haplogroup diversity from the Pleistocene into the Holocene to the point where only Clade 1DE remained, both on isolated islands and on continental Siberia (figure 4 in ref. 3). It is highly unlikely that this reduction in genetic diversity was because individuals harbouring the same haplogroup were the only ones whose DNA was being released into younger sediments over time. This finding instead conforms to a pattern of a species’ decline towards extinction.

In sum, we find all evidence pointing to the validity of the eDNA identifications of late-surviving Arctic megafauna reported in our original study. However, we acknowledge the possibility that unburied or exhumed animal fossils can contribute DNA to younger sediment layers, and this should always be considered (along the lines we described in ref. 3). This is particularly important in cases in which the animal species targeted were abundant and widely distributed on the landscape, for fine-resolution reconstructions, and for studies relying primarily on fluvial sediments as the eDNA source.

**Reporting summary**

Further information on experimental design is available in the Nature Portfolio Reporting Summary linked to this Article.

**Online content**

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-022-05417-2.

**Data availability**

All data analysed in this study are included in this article or have been published previously.
The authors declare no competing interests.

Competing interests The authors declare no competing interests.

Additional information

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