Review

Cell PRESS

Faunal histories from Holocene ancient DNA

Mark de Bruyn[1], A. Rus Hoelzel[2], Gary R. Carvalho[1] and Michael Hofreiter[3]

[1] Molecular Ecology & Fisheries Genetics Laboratory, Environment Centre for Wales, School of Biological Sciences, Bangor University, Bangor, UK, LL57 2UW
[2] School of Biological and Biomedical Sciences, Durham University, Durham, UK, DH1 3LE
[3] Department of Biology, The University of York, Wentworth Way, Heslington, York, UK, YO10 5DD

Recent studies using ancient DNA have been instrumental in advancing understanding of the impact of Holocene climate change on biodiversity. Ancient DNA has been used to track demography, migration and diversity, and is providing new insights into the long-term dynamics of species and population distributions. The Holocene is key to understanding how the past has impacted on the present, as it bridges the gap between contemporary phylogeographic studies and those with inference on Pleistocene patterns, based on ancient DNA studies. Here, we examine the major patterns of Holocene faunal population dynamics and connectivity; highlighting the dynamic nature of species and population responses to Holocene climatic change, thereby providing an 'analogue' for understanding potential impacts of future change.

Climate change, migrations and extinctions: the neglected record of Holocene ancient DNA

We are presently witnessing what has been described as the 'sixth mass extinction' [1]. Several causes have been attributed to this phenomenon, including direct human persecution as well as habitat loss and degradation, but there is increasing evidence that implicates human-induced global warming as a further significant cause [2]. If we are to understand the impact of ongoing and future climate change on biodiversity, it is imperative that we determine how past climate change impacted the biota of Earth. Such studies provide a framework for informing understanding of the probable response of species to future climatic change, an approach that has been referred to as 'looking backwards to look forwards' [3]. One method of examining these questions is through the use of ancient DNA (aDNA; Box 1). Whereas the use of contemporary DNA requires extrapolations from historical species and population dynamics, aDNA provides a direct window on past patterns of population connectivity, size and distribution [4–6], and has been instrumental in advancing current knowledge regarding past faunal change (e.g. [7–14], Boxes 1,2,3). Studies of aDNA from Pleistocene fauna have revealed the dynamics of populations responding to habitat as it expanded or contracted through the glacial cycles, with some species successfully tracking habitat changes while others went extinct or were reduced in number and lost genetic diversity (reviewed in [4–6]). Similarly, Holocene aDNA has been used to examine species- and/or population-level dynamics directly, such as migration rates, effective population sizes (N_e) and rates of population growth or decline in the context of more recent environmental change.

Understanding the role of the Holocene is essential, as this period bridges the gap between contemporary patterns of faunal change and the major events of the Pleistocene, which included large-scale extinctions, migrations and changes in population size and connectivity, influenced by major glacials and interglacials [3–5]. Climate fluctuated considerably during the Holocene and, although not as dramatic as during the Pleistocene, this variability was greater than generally appreciated [15]. Indeed, periods of warming during the Holocene have been cited as an analogue for a future climate under current global warming trends [2]. Hence, Holocene faunal dynamics could also be regarded as an analogue under predicted scenarios of global warming.

For example, species that were able to track shifting habitats on millennial timescales probably require less direct intervention than species (and populations) unable to track such changes in habitat [16]. For the latter, assisted colonisation might be the most effective mitigation strategy [16], although such approaches are not without danger [17]. Such questions, crucial for informing conservation management strategies, are intractable based on contemporary samples, or (non-DNA based) fossil evidence alone.

Here, we review how aDNA has contributed to understanding of how the fauna responded to environmental change during the Holocene (i.e. the past ca 11 600 years). We explore the significance of these studies in light of ongoing and future climate change, highlighting priorities and promising directions for future research.

Glossary

Chronozone	a formal unit used to specify time strata.
Hybridisation capture	the use of a DNA probe that contains a known sequence of nucleotides to capture a corresponding region of DNA from a target organism.
Molecular barcoding	enables the parallel sequencing and subsequent identification of DNA from multiple samples using unique short (4–10 base pair) DNA tags.
Palaeoclimate	climate that predates direct weather observation and data collection, and is inferred from proxy data.
Phylogeography	the inference of historical processes that contributed to the present-day geographic distribution of species and populations, using contemporary DNA data.

Corresponding author: de Bruyn, M. (markus.debruyn@gmail.com)

0169-5347/$ – see front matter © 2011 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2011.03.021

Box 1. Ancient DNA: practise and pitfalls

Ancient DNA, defined loosely as any DNA recovered from biological samples that have not been preserved for later use, provides a direct approach to analysing the history of life. Examples include DNA recovered from archived bones and scales, preserved seeds and resting eggs, ice and permafrost samples, and so on. Ancient DNA might not only reveal insights into extinct populations and species, but can also inform about biological change across ecological timescales [71,72]. It provides a form of 'evolutionary time travel'; an opportunity to explore empirically how biota and species, including humans, have responded to environmental change. As such, it appeals to biologists, anthropologists, medical practitioners, climatologists and even those interested in economies of past civilisations [73]. Indeed, aDNA was recently hailed as one of the top-ten 'big ideas' of the decade [74], generating, for example, the draft nuclear sequence of Neanderthals [75] and even leading to the discovery of a new hominid form [76].

Such whole-scale enthusiasm was, however, not always the case: even aDNA molecules from recent material are characteristically degraded into short pieces, and present only in trace quantities. Such attributes render contamination of specimens and reagents, and the synthesis of spurious DNA sequences via PCR, a major risk [77,78]. Early unfounded claims during the 1980s, such as the presumed 80-million-year-old dinosaur DNA, which turned out to be human, and frequent bacterial or human contamination of proposed aDNA samples led to many flawed studies [79]. Over the past 10 years, however, investment in aDNA studies has been revitalised by new methods developed for analysing the human genome, most notably the advent of next-generation high throughput sequencing that works most efficiently on short DNA sequences. Moreover, new robust statistical tools for generating reliable estimates of sequence damage in aDNA are now available [80].

In an effort to enhance the quality control of aDNA studies further, there have been attempts to use standardised criteria in their design, the so-called 'nine criteria for authenticity' [81]. Although whole-scale adherence to such a check-list might be laudable and tractable [82], it often proves impractical for certain studies and material [78] and, in practice, many aDNA studies incorporate only a subset of the criteria initially recommended. Using a 'common-sense approach', such as being aware of the severe contamination issues when working with human DNA, for example, appears to be more feasible and meaningful (see [78] for details). 'Taphonomic bias' should also be taken into account in aDNA studies; that is, the differential preservation (and success of recovering DNA) and, hence, representation of remains preserved under differing environmental conditions and timeframes.

The Holocene climate was dynamic, not stable

Pioneering geological work on glacier fluctuations [18] provided an initial framework for more recent palaeoclimate research (see Glossary), which has demonstrated that the Holocene climate was characterised by considerable fluctuations in temperature (Figure 1), impacted significantly on biodiversity, and even caused human societal collapse (reviewed in e.g. [2,15,19]). Although less extreme than the Pleistocene fluctuations, major climatic shifts occurred, particularly at the Pleistocene–Holocene boundary, when the temperature in Greenland increased by 15 °C between the Younger Dryas [approximately 12 800–11 600 years before present (YBP)] and the early Holocene [20], and at various periods throughout the Holocene, such as the so-called '8.2k event', the 'Little Ice Age' and the 'Medieval Warm Period'. During the Holocene proper, three broad phases comprising distinct chronozones have been recognised [19]. The first phase (~11 600–9000 YBP) coincided with the 'Preboreal' and 'Boreal' chronozones, and was characterised by cooler temperatures as the vast northern ice-sheets melted.

The second, the 'hypsithermal' phase (referring to warm temperatures in northern mid- to high-latitudes) coincided with the 'Atlantic' chronozone (approximately 9000–5000 YBP). This period is also known as the 'Holocene Climatic Optimum', owing to temperatures that were significantly warmer than before. In fact, temperatures were probably as warm, if not warmer, than at present [2,21]. The Holocene Climatic Optimum was punctuated by a notable anomaly, the '8.2k', or '8k event' [21]. Temperatures declined rapidly by up to 10 °C in the North Atlantic Ocean around this time, with changes of 7.4 °C in Greenland, and of 2 °C extending well across Europe. These cooler temperatures probably lasted some 200–400 years [2,21]. The probable cause of this event was an extremely large flood of cold freshwater from Lake Agassiz (formed by the melting Laurentide ice-sheet) into the North Atlantic [21]. A simultaneous increase in sea surface temperature is indicated from proxy records in the South Atlantic [22]. This southern warming event is not well supported at present, but both aDNA and palaeoclimate proxy data are consistent with this timing of a warming event in the far south [22,23]. A second 'rapid climate change' event occurred around 6000–5000 YBP, marked by cooler temperatures at high latitudes and drier conditions in the tropics (Figure 1) [15].

The final phase, or 'Neoglacial', coincided with the 'SubBoreal' and 'SubAtlantic' chronozones, covering the period from 5000 YBP to pre-industrial times. Four significant cooling events, including the 'Little Ice Age' (approximately 1350–1850 AD), probably occurred during this period (Figure 1), punctuated by anomalies such as the warming event of the 'Medieval Warm Period' or 'Medieval Climate Anomaly' (approximately 950–1200 AD) [19]. It is unclear to what extent the temperature fluctuated, and whether these events were restricted to the Northern Hemisphere alone, although it is unlikely that mean annual temperatures varied by more than 1–2 °C [2,15,19].

A key feature of the Holocene, particularly the mid- to late-Holocene, is a lack of vast northern ice-sheets, which means that this period was, in terms of both geography and climate, more similar to the present than was the Pleistocene [19]. Although these characteristics make comparisons of faunal change between the present and the Holocene easier to interpret, the Holocene climate data have a low signal:noise ratio compared with those from the Pleistocene [24]. The range of temperature fluctuations through the Holocene varies considerably by region and, as such, there is geographic variability among other complexities in the climate record (see [2,15,19]) and also, therefore, in environmental pressures and evolutionary response. Nonetheless, common Holocene climatic patterns, such as those mentioned above, have emerged, thereby providing a framework within which to examine faunal change in relation to a rapidly changing climate and environment (Figure 1).

Causes of lost Holocene faunal diversity illuminated by ancient DNA analyses

The Holocene is conspicuous by its lack of many taxa that were driven to extinction during the Pleistocene [e.g. cave bears (*Ursus spelaeus*) [25]; Neanderthals [26]; and sabre-