RESEARCH PAPER

Population dynamics and range shifts of moose (*Alces alces*) during the Late Quaternary

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Abstract

Aim: Late Quaternary climate oscillations had major impacts on species distributions and abundances across the northern Holarctic. While many large mammals in this region went extinct towards the end of the Quaternary, some species survived and flourished. Here, we examine population dynamics and range shifts of one of the most widely distributed of these, the moose (*Alces alces*).

Location: Northern Holarctic.

Taxon: Moose (*A. alces*).

Methods: We collected samples of modern and ancient moose from across their present and former range. We assessed their phylogeographical relations using part of the mitochondrial DNA in conjunction with radiocarbon dating to investigate the history of *A. alces* during the last glacial.

Results: This species has a relatively shallow history, with the most recent common ancestor estimated at ca. 150–50 kyr. Ancient samples corroborate that its region of greatest diversity is in east Asia, supporting proposals that this is the region of origin of all extant moose. Both eastern and western haplogroups occur in the Ural Mountains during the last glacial period, implying a broader contact zone than previously proposed. It seems that this species went extinct over much of its northern range during the last glacial maximum (LGM) and recolonized the region with climate warming beginning around 15,000 yr BP. The post-LGM expansion included a movement from northeast Siberia to North America via Beringia, although the northeast Siberian source population is not the one currently occupying that area.

Main conclusions: Moose are a relatively recently evolved species but have had a dynamic history. As a large-bodied subarctic browsing species, they were seemingly confined to refugia during full-glacial periods and expanded their range northwards when the boreal forest returned after the LGM. The main modern phylogeographical division is ancient, though its boundary has not remained constant. Moose population expansion into America was roughly synchronous with human and red deer expansion.

KEYWORDS
Alces alces, ancient DNA, last glacial maximum, mitochondrial DNA, moose, Quaternary

1 | INTRODUCTION

The large-scale, climatically driven environmental changes of the Pleistocene influenced the evolution of many terrestrial species, and drove dramatic changes in species' biogeography, including changes in both range size and position, through a combination of migration, expansion and local extinction (extirpation) events (e.g. Hewitt, 1996, 2004; Lister, 2004). However, the exact nature of these effects has long been debated. One recent focus has been on range contraction and extinction in the Northern Holarctic, with an emphasis on ecological differences between species as a determinant of their individual histories (Lorenzen et al., 2011). Most of the focus has been on Europe, northern Asia and North America (e.g. Brace et al., 2012; Cooper et al., 2015; Rey-Iglesia et al., 2017; Stuart & Lister, 2012; Valdiosera et al., 2007), while relatively little work has been conducted on mammalian species that survived the Pleistocene extinction event elsewhere in Asia (e.g. Barnes, Matheus, Shapiro, Jensen, & Cooper, 2002; Campos et al., 2010; Meiri et al., 2013; Turvey, Tong, Stuart, & Lister, 2013).

In this study, we examine population dynamics and range shifts of moose (*Alces alces*), the largest extant member of the Cervidae (Geist, 1999), across its Holarctic range with a particular focus on eastern Asia. While many northern Holarctic large mammals went extinct towards the late Quaternary, moose survived and flourished (Geist, 1999). At present, moose are widely distributed across the boreal zone, from Scandinavia through Siberia to eastern North America, between latitudes 40–50° and 70°N, and even further northward due to warming climates (Flerov, 1960; Geist, 1999; Lister, 2005; Tape, Gustine, Ruess, Adams, & Clark, 2016; Trense, 1989; Whitehead, 1972). However, during the last glacial maximum (LGM; ca. 27,000–20,000 yr BP; Clark et al., 2009), they were found further south in Asia including central Japan, and as far south in Europe as the Italian Peninsula, the Balkans and the Carpathians. By the early Holocene, they reached as far west as Britain (Geist, 1999; Sommer & Nadachowski, 2006).

Moose are the only extant species in the genus *Alces*. They are usually considered to have evolved from the broad-fronted moose *Cervalces* (or *Alces*) *latifrons* (Lister, 1993). *C. latifrons* had a wide Holarctic range, and was replaced by *A. alces* in Europe and Asia in the late Middle or early Late Pleistocene, and gave rise to the stag-moose *Cervalces scotti* in North America (Churcher & Pinsof, 1987; Lister, 1993). Late Pleistocene moose (*A. alces*) fossils cover almost the entire range of living moose in Asia (Sher, 1987). However, they are somewhat inconsistently distributed and findings are scarce (Sher, 1987). There was a single radiocarbon date available on a moose fossil from Asia (MacPhee et al., 2002), and it was thus unclear whether they inhabited northeast Siberia during the LGM (Clark et al., 2009). Sher (1987) proposed that moose were present in the region, but in small numbers, while Guthrie (1995) claimed they only reached the region after the LGM. Some data have suggested that moose (*Alces*) entered North America only in the late-glacial, although this has not been conclusively demonstrated (Guthrie, 1995, 1996, 2006). Alceine remains of unknown species (*Cervalces/Alces*) are present in the Alaskan record between 30,000 and 10,000 yr BP (Churcher & Pinsof, 1987; Geist, 1999). The lack of complete antlers makes it difficult to determine whether these represent *C. scotti* that had advanced northwards from the unglaciated mid-continent of N. America, or whether *A. alces* crossed the Bering Isthmus before the late glacial (Churcher & Pinsof, 1987; Geist, 1999).

Guthrie (2006) radiocarbon dated dozens of alceine remains from Alaska, most of which were identifiable as *Alces* and were younger than 15,000 yr BP. Only a handful were older (all older than 40,000 calendar yr BP; Guthrie, 2006; Table S1). These older dates were apparently not firmly identified as *A. alces* (Guthrie, 2006; Figure 1), and may either represent *C. scotti* or *C. latifrons*, or point to earlier migration to Alaska by *A. alces*. Alceine fossils south of the ice sheet are mostly from sites of unknown age or dated indirectly (e.g. on associated charcoal); the few direct radiocarbon dates are either identifiable as *Cervalces* or are late-glacial in age (Churcher & Pinsof, 1987). Some caution attaches to these radiocarbon dates in any case, many of which were performed in the 1960s and 1970s and could be erroneous due to methodological problems or potential contamination of the bone samples from adhesives and consolidants, as has been demonstrated with new radiocarbon dating of fossils of other taxa from those regional collections (e.g. Zazula et al., 2014).

Morphological characters, such as body size, antler shape, coat colour and premaxillary shape, divide *A. alces* into two major groups: one in Europe and northwestern Asia to the Yenisei River (~90°E) that we term the 'western lineage', and another in northeastern Asia and North America, the 'eastern lineage' (Flerov, 1960; Groves & Grubb 1987; Geist, 1999; Lister, 2005). Up to nine subspecies are recognized: one in Europe and western Asia, one (extinct) in the Caucasus region, three in eastern Asia and four in North America (Groves & Grubb 1987; Trense, 1989; Vereshchagin, 1955). However, this ninefold division has been questioned on both morphological and genetic grounds (Flerov, 1960; Groves & Grubb 1987; Geist, 1999).

The morphological separation of moose into two major groups is supported, to some degree, by karyotypic data (Groves & Grubb 1987) and by a 75bp insertion/deletion in the control region (CR) of mitochondrial DNA (mtDNA; Hundertmark, Shields, Udina, et al., 2002; Mikko & Andersson 1995; Udina, Danilkin, & Boeskorov, 2002; and see below). Moose from Europe and more western parts of Asia have a karyotype of $2N = 68$, while all North American and some eastern Asian moose have a karyotype of $2N = 70$. The North American and some of the eastern Asian group also lack a 75 bp section of the mtDNA CR. At present, the geographical border between specimens expressing these differences in Asia is poorly defined (Hundertmark & Bowyer, 2004; Nemoikina, Kholodova, Tyutenkov, & Moskvitina, 2016; Niedziałkowska, 2017).

Previous studies have demonstrated the potential for combining ancient DNA and radiocarbon data to reconstruct dispersal and
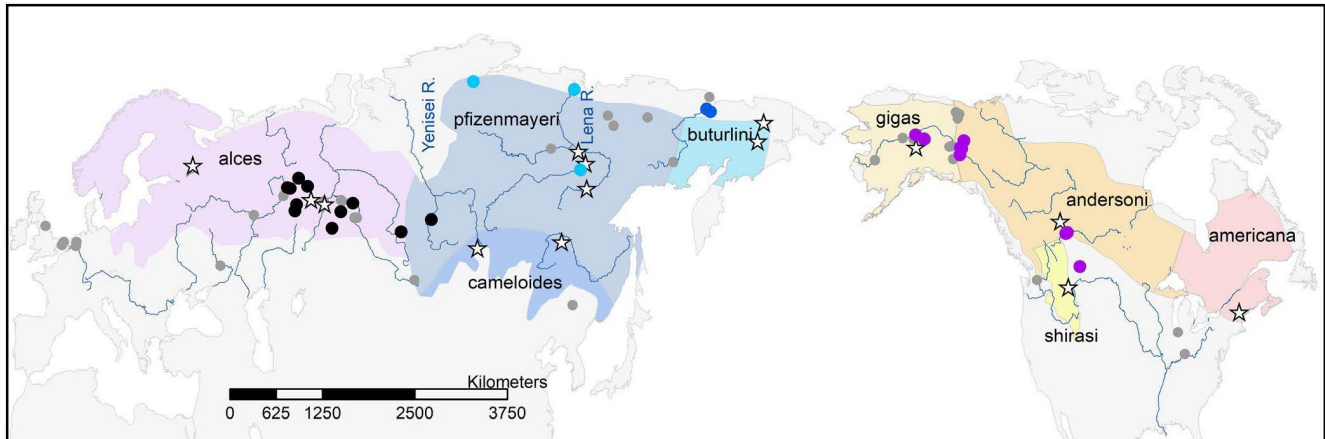
FIGURE 1 The present-day distribution of moose (modified from the IUCN red list map: https://www.iucnredlist.org/species/56003 281/22157381), and its subspecies (after Groves & Grubb 1987; Trense, 1989). Locations of modern and ancient *Alces* samples used in this study: modern samples (white stars) and ancient samples (black—western and central Asia up to the Yenisei river, light blue—east Asia up to Lena river, dark blue—northeast Siberia, purple—North America, grey—samples that did not yield DNA). World Equidistant Cylindrical Projection. For additional data, see Tables S1 and S2

expansion events and understand phylogeographical patterns (e.g. Brace et al., 2012; Meiri et al., 2018). Here, we sample fossil moose across their entire range, extracting and analysing ancient mtDNA in conjunction with radiocarbon dating to investigate the history of *A. alces* during the last glacial.

Genetic studies on present-day moose have found little variation across the range and especially among different populations in North America, suggesting a recent bottleneck or a recent origin of the entire species (Cronin, 1992; Hundertmark, Shields, Bowyer, Shields, Bowyer, & Schwartz, 2002; Niedziałkowska, 2017; Udina et al., 2002). The low genetic variation across North American moose populations suggest a single colonization event across the exposed Bering Isthmus to Alaska, at around 15,000 yr BP (Cronin, 1992; Hundertmark, Shields, Bowyer, et al., 2002).

The European lineage is composed of two main clades: a west-central European and an eastern European (Niedziałkowska, 2017; Niedziałkowska et al., 2014). It was thought based on morphological criteria that the border between European and east-Asian/American type moose was the Yenisei River (Flerov, 1960). However, haplotypes of the east-Asian/American lineage were found further to the west, up to the Ob River (Moskvitina, Nemoikina, Tyuten'kov, & Kholodova, 2011), while Nemoikina et al. (2016) suggest a third, western Siberian haplogroup. Similarly, with morphology, Lister (2005) found broad agreement with the east-west divide, but a few skulls of intermediate and even 'western' type occur in parts of eastern Siberia. Kolesnikov and Kozlovskii (2014) indicated that antlers from western Siberia are as large as those further east, but they did not examine the taxonomically significant feature of beam branching that separates eastern and western types. Therefore, the location, width and history of the contact zone between the western and eastern lineages of moose in west Siberia is debated (Moskvitina et al., 2011; Nemoikina et al., 2016; Niedziałkowska, 2017). We sampled ancient specimens from the Ural region to test the boundaries

of the contact zone. A recent study showed that the Ural Mountains served as a contact zone between the two main lineages in red deer (*Cervus elaphus*; Meiri et al., 2018). Here, we aim to study whether this situation is similar with the moose.

North American moose comprise only one haplogroup (Hundertmark & Bowyer, 2004) while the east Asian region contains all three or four reported haplogroups of moose worldwide (Hundertmark, Shields, Bowyer, et al., 2002; Hundertmark, Shields, Udina, et al., 2002). However, North American moose share no haplotypes with the geographically closest moose population, on the Asian side of the Bering Strait in northeast Siberia. This contrasts with the significant morphological similarity between moose on either side of the Bering Strait (*buturlini* and *gigas*, cf. Figure 1; Lister, 2005), and appears inconsistent with a simple scenario of moose expanding from Asia to North America through Beringia. Hundertmark, Shields, Udina, et al. (2002) hypothesized that the populations on both sides underwent bottleneck events and re-established their populations only recently, leading to the genetic difference.

In this study, using ancient DNA and radiocarbon dates of *Alces* across the Holarctic, we address the following questions:

1. Is the phylogeographical separation into two major groups (Europe and western Asia vs. eastern Asia and North America) evident in ancient specimens?
2. When did moose arrive in northeast Siberia? Was it just prior to the expansion into Alaska; were they continuously present in the area throughout Marine Isotope Stage 3 (MIS 3; ca. 60,000–27,000 yr BP) as with red deer; or was the species' history more complex—for example, two colonization events with a local extinction during MIS 3 and recolonization after the LGM? To what extent can any inferred extirpation or expansion events be associated with known environmental changes?

3. How can we explain the genetic differences between the north-east Asian moose and the North American ones, despite their similarities in morphology?

4. At present, there is a unique pattern for the demographic and phylogeographical histories of each of the Beringian megafaunal species studied. Do moose have yet another unique history, or do they align more obviously with red deer as the two large herbivores that flourished after the megafaunal extinction?

2 | MATERIALS AND METHODS

2.1 | Sample collection

A total of 114 ancient hard tissue specimens (antlers, teeth and bones) and a single ancient moose skin were sampled from museums and excavation sites across the Holarctic distribution (Figure 1; Table S1). Of these, 82 specimens were morphologically identified as *A. alces*, five as *C. latifrons* and the remainder indeterminate within the tribe Alceini (*Alces* or *Cervalces*).

In addition, 21 modern samples were collected across the Holarctic distribution of moose, including representatives from all eight putative extant subspecies (Figure 1; Table S2).

2.2 | Radiocarbon dating

Out of the 114 specimens used in this study, 20 were already dated and an additional 32 that yielded DNA were submitted to the Oxford Radiocarbon Accelerator Unit (ORAU) for radiocarbon dating (Tables S1 and S3). To review the available fossil record of *Alces* from Eurasia and North America, radiocarbon dates of additional samples were taken from the literature. The radiocarbon dates were calibrated (to 2σ, see Table S3) in OxCal 4.3 (https://c14.arch.ox.ac.uk/oxcal/OxCal.html) using the IntCal13 calibration curve, with only finite dates calibrated (Reimer et al., 2013). The calibrated dates were plotted, and grouped by region (Europe, western and central Asia up to the Yenisei river, eastern Asia up to Lena river, northeast Siberia beyond the Lena River and North America). All dates in the text are median calibrated ages except where stated.

2.3 | DNA extraction, amplification and sequencing

DNA of modern specimens was extracted in one laboratory, and that of ancient specimens in another, dedicated ancient DNA laboratory where no modern moose had been analysed. DNA from soft tissues was extracted using DNeasy Blood & Tissue Handbook (QIAGEN). DNA from bone, tooth and antler was extracted according to a method modified from Yang, Eng, Waye, Dudar, and Saunders (1998) as described in Meiri et al. (2013, 2014). Every eighth or tenth sample served as a negative extraction control with no bone powder (Materials and Methods S1).

A fragment between 273 and 319 bp of the mitochondrial CR was amplified using three to four overlapping fragments (depending on the molecular preservation of the sample) (SI Table 4). This part of the CR was chosen following Hundertmark, Shields, Bowyer, et al. (2002) who found it informative for inferring relationships between populations of modern moose. A 75 bp fragment is absent from all sampled North American and some Asian moose (Mikko & Anderssont, 1995, and see below). If the amplification of the first pair of 248/173 bp (depending on the indel) primers was unsuccessful, the fragment was split into two. PCR amplifications and sequencing were carried out as described in Meiri et al. (2013; Materials and Methods S1). The samples were sequenced in both directions and analysed in an ABI 3730xl DNA Analyzer (Applied Biosystems) by Macrogen Inc, Korea (Materials and Methods S1).

To ensure the authenticity of the obtained sequences, negative controls were used during DNA extractions and in all PCR reactions. All reagents used were molecular biology grade, and when possible, were decontaminated using UV irradiation. All working areas and equipment were decontaminated using bleach, and/or UV irradiation. In addition, the amplified overlapping fragments were designed as a measure of replication for each sample, and about 20% of the sequences were replicated. All DNA sequences will be deposited on GenBank.

2.4 | Data analysis

DNA sequences of 137 modern *A. alces* were retrieved from GenBank and added to the analyses (Table S5). Roe deer (*Capreolus capreolus*) and Chinese water deer (*Hydropotes inermis*) were used as outgroups based on phylogenetic reconstructions identifying these species as the closest living relatives of moose, as well as the more distantly related reindeer (*Rangifer tarandus*; Agnarsson & May-Collado, 2008; Gilbert, Ropiquet, & Hassanin, 2006; Heckeberg, 2020).

The best-fit partitioning scheme was identified by PARTITIONFINDER2 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016). Phylogenetic relationships were estimated by Bayesian inference using MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), and Network v.5.0.0.3 (http://www.fluxus-engineering.com/sharenet.htm). We assumed that the 75 bp indel is a recent deletion because of the large amount of variation within the inserted form, and because it is missing in the most recently derived lineage (Hundertmark, Shields, Udina, et al., 2002). We therefore constrained all the samples without this fragment to group together in the analysis. We also ran the analysis without the constraint. The Bayesian tree was reconstructed from 166 modern samples and 31 ancient samples. Markov chain Monte Carlo sampling was performed using 3 million generations with sampling every 100 generations, discarding the first 10% as burn-in. Nodes were considered strongly supported if they received posterior probability support value ≥ 0.95 (Huelsenbeck & Rannala, 2004). A median

joining haplotype network of 30 ancient and 141 modern moose sequences consisting of 244bp (excluding the 75 bp indel) was obtained using Network v.5.0.0.3, using default parameters.

To estimate the time when *A. alces* began to diverge, uncorrelated relaxed-lognormal clock analyses (Drummond, Ho, Phillips, & Rambaut, 2006) were performed using BEAST 1.8.4 (Drummond & Rambaut, 2007; Drummond, Rambaut, Shapiro, & Pybus, 2005). In all, 141 modern DNA sequences of *A. alces*, together with 30 ancient DNA sequences with finite radiocarbon dates, were used. Age was fixed on the median calibrated radiocarbon date, and the nucleotide substitution model assigned by PARTITIONFINDER2. The analyses were performed using two demographic models: one where population size was assumed to be constant through time, and a model where effective population sizes were estimated through time using Bayesian skyline plots (BSP; Drummond et al., 2005). Tip calibration of the mutation rate was carried out using 30 radiocarbon dates. Markov chains were run for 200 million generations and sampled every 1,000 generations with the first 10% discarded as burn-in. The best-fitting model was selected by a Bayes factor (BF, using marginal likelihoods) implemented in BEAST (Suchard, Weiss, & Sinsheimer, 2001). BEAST analyses were carried out in CIPRES Science Gateway (Miller et al., 2010).

3 | RESULTS

The radiocarbon dates of the ancient samples range from modern to >50,200 uncalibrated yr BP (OxA-22248; Table S1). Figure 2 shows the calibrated dates (to 2σ) of alceine fossils divided by region (Table S3). It seems that moose (*A. alces*) was present in Eurasia during MIS 3 (i.e. between 46,740 and 35,210 yr BP). During the interval ca. 30,000–15,000 yr BP, there is only one record of moose, which is from Italy (OxA-24545, 24,840 yr BP), with no recorded presence in other regions (not even in the Urals). Records resume across Eurasia, and in North America, after the LGM (i.e. from ca. 15,000 yr BP).

Mitochondrial CR DNA was successfully amplified and sequenced from 35 specimens out of the 114 extracted (31% success ratio). The 75 bp indel region (above) was missing from all of the North American samples, and from some Asian ones. All European samples west of the Urals had this fragment except one haplotype from Estonia (KJ831599) (another haplotype from Estonia, KJ831609, also lacked the indel but was not included in the analyses; Niedzialkowska et al., 2014). It seems that, in the Urals, both states appear with some temporal overlap; the indel is missing in some samples dated between 30,020 yr BP (MM616) and 3,630 yr BP (MM546), while it is present in both old (46, 740 yr BP; MM599) and modern samples (MM595).

The best nucleotide substitution model according to PARTITIONFINDER2, both with AIC and BIC, was generalized time-reversible model (GTR; Tavaré, 1986) with gamma correction shape parameter and portion invariable sites (GTR+I+G). Figure 3 shows the phylogenetic tree with corresponding Bayesian

posterior probabilities (BPP). The basal splits of the tree consist entirely of Asian haplotypes (from east to northeast), and represent the oldest haplotypes, but BPPs are low. The two other main groups are mainly European and North American with BPP of 0.99. All the haplotypes missing the 75 bp fragment are included in the North American subgroup with a BPP of 1 (they were constrained to form a monophyletic group in the analyses). Samples from Asian haplotypes (from the west to northeast) fall in the European clade and some in the North American clade. We obtained a similar tree when we omitted the constraint, that is, the major clades (with and without the indel) are maintained, but with lower support. Yet, four samples with the deletion (MM18 from the Altay, MM586, MM588, MM616 all from the Urals) that were clustered together (with no support), are now scattered across the tree (Figure S1). The median joining haplotype network (Figure 4) was based on 171 moose sequences with 244 bp fragment length (with no indel). The division into three main lineages, seen in the tree, emerges in the network as well. The differences between and within the lineages are very small and range from one to six base pairs. The North American and east-Asian haplogroup is structured as a star-like shape with the haplotype in the middle representing modern and ancient samples from across the Holarctic distribution. This main haplotype contains ancient samples from both sides of Beringia (e.g. MM533 Russia, Kolyma River, Duvanny Yar dated to 13,870 yr BP, and MM574 Alaska, Cripple Creek dated to 11,360 yr BP). Similar to the phylogenetic tree, Asian haplotypes (from west to northeast) are scattered across the network, and appear in both main lineages—one of which is primarily European, the other primarily North American.

The estimates of time to the most recent common ancestor (tMRCA) of *Alces* obtained using constant population size, and BSP demographic models, are very similar. With constant population size, tMRCA is estimated as 86,190 yr BP with a 95% higher posterior density (HPD) of 146,780–50,300 yr BP. Using the BSP model, the tMRCA is estimated at 83,715 yr BP (95% HPD of 153, 290–49,810 yr BP). Bayes factor comparison between the two different demographic models showed no evidence that one is superior to the other (BF < 1). The mutation rate obtained from BEAST is 0.17 and 0.19 substitutions/site/Myr using constant population size and BSP, respectively.

4 | DISCUSSION

The combined ancient DNA and radiocarbon data in this study reveal a dynamic history of moose from around 60,000 yr BP until present. It seems that moose were extirpated over much of their northern range during the LGM, although the single record from Italy hints at the existence of one or more southern refugia, from where they recolonized the region towards the end of the last glaciation around 15,000 yr BP. The post-LGM expansion included a movement from northeast Siberia to North America through the Bering Isthmus and Alaska.
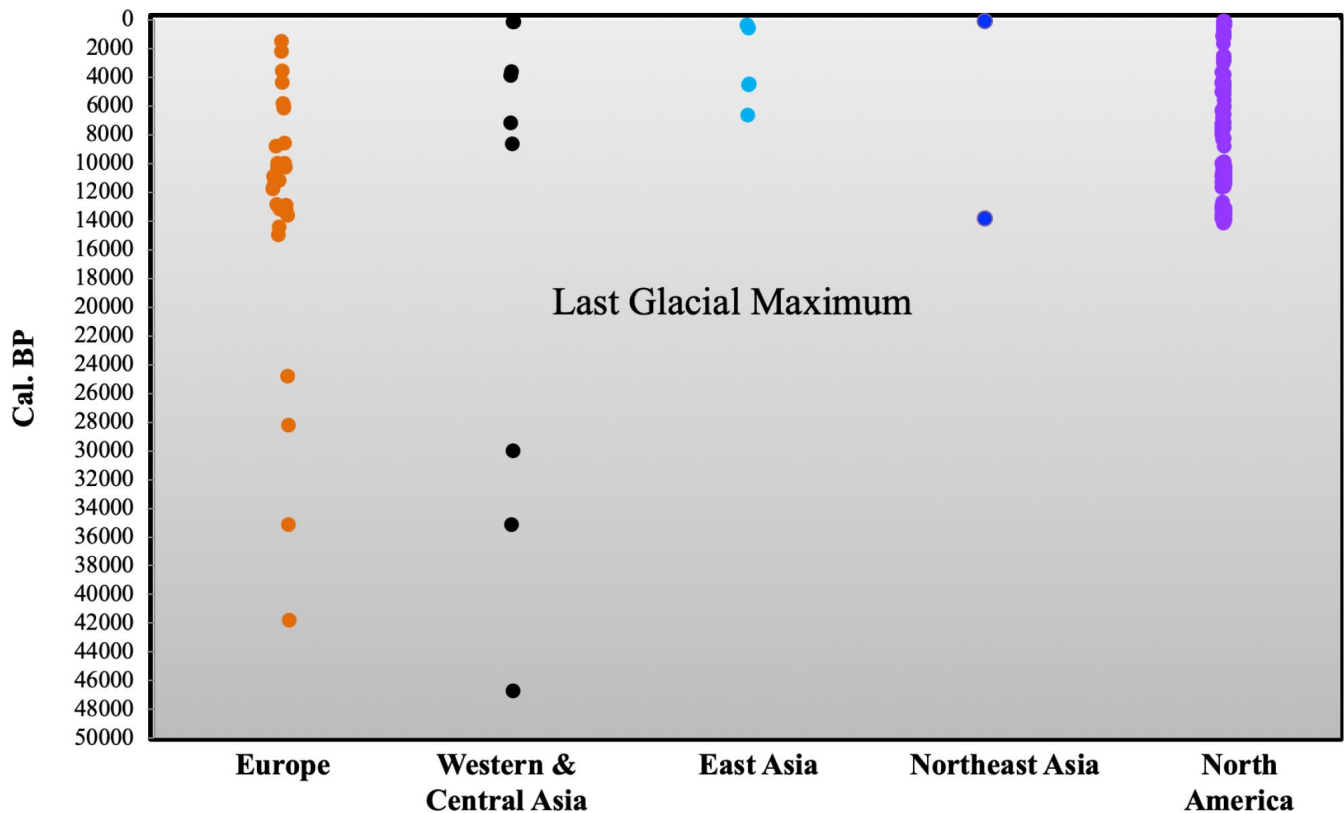
FIGURE 2 Radiocarbon dates (in calendar years BP) of *A. alces* across its distribution. Colours correspond to geographical locations as indicated on the map (Figure 1). Note that a few of the oldest dates from Northeast Asia fall outside the range of calibration curve and are not plotted. Data from Tables S1 and S3

4.1 | Separation of eastern and western forms

Morphological and karyological studies originally identified two major groups of moose: one in Europe and western Asia to the Yenisei River, and another in eastern Asia and North America (Flerov, 1960; Groves & Grubb 1987; Geist, 1999)—although there are intermediate or mosaic morphologies in the Yenisei/Altai region, suggesting a hybrid zone (Lister, 2005).

Our data support a separation between Europe and North America, but indicate a combination of types across Asia. Ancient haplotypes from the Urals fall both in North American and European groups (Figures 3 and 4). There is no clear time separation to indicate waves of expansion of different forms (e.g. specimens dated to 35,770 and 3,630 yr BP from the Altai and Urals region both lack the 75 bp segment, while specimens dated 46,790 yr BP and a modern one, both from the Urals, have it) though we cannot rule it out. It seems that the contact zone was wider than previously proposed, with dispersal of individuals since at least the Late Pleistocene.

4.2 | History of *Alces* in Eurasia

Moose have been previously shown to exhibit limited mitochondrial genetic diversity (e.g. Hundertmark, Shields, Bowyer, et al., 2002;

Niedziałkowska, 2017; Niedziałkowska et al., 2014). Differences in mtDNA CR sequences between the main clusters consist of only a few base pairs (e.g. four mutations separate the North American group from the group that consists of only Asian haplotypes, Figure 4). The basal splits separate a few east and northeast Asian haplotypes (including the *buturlini* subspecies) from all other moose lineages. The remaining moose from Europe, North America and much of Asia comprise two groups; one containing all European specimens, the other containing all North American specimens, with Asian haplotypes falling in both (Figures 3 and 4). Nemoikina et al. (2016) identified a third haplogroup in west Siberia, but we found no support for that (Figure 3, samples starting with KR). Moose diversity peaks in east Asia where haplotypes from all groups are found, supporting earlier proposals that this is the region of origin of all extant moose. Our data place the most recent common ancestor of all living moose between 150,000 and 50,000 yr BP, with the mean value around 85,000 yr BP. Although the range of estimates is wide, it suggests a relatively recent divergence. This agrees with fossil data indicating that moose originated around 100,000 yr BP, with some suggestions of intermediate fossils (between *A. latifrons* and *A. alces*) ca. 200,000–100,000 yr BP (Lister, 1993, 2004; Sher, 1987).

Although Late Pleistocene moose fossils in Asia are spatially and temporally scattered (Sher, 1987), our results indicate that moose had already spread across northern Asia during MIS 3 (ca.
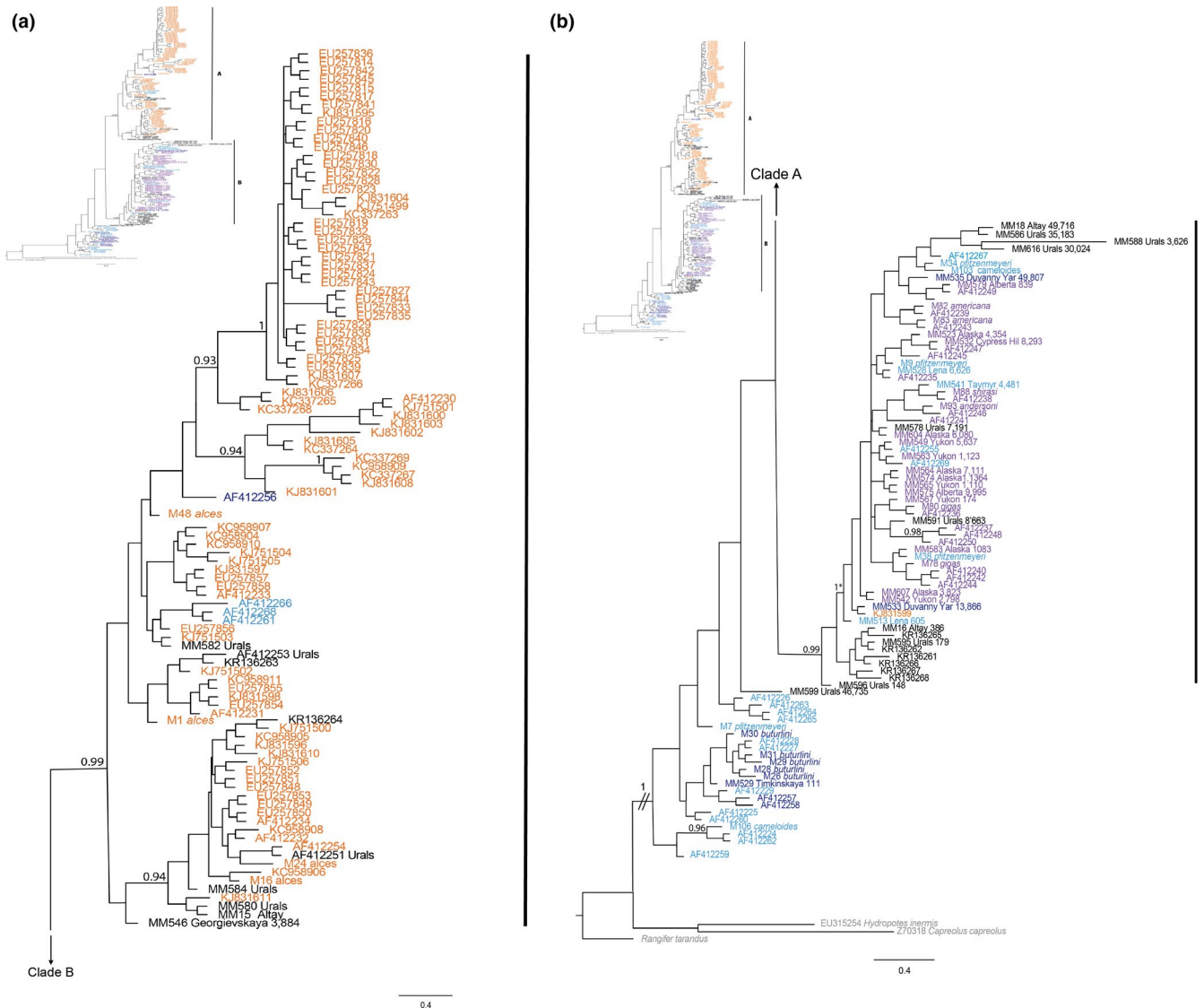
FIGURE 3 Bayesian Phylogenetic tree using 319 bp of mtDNA control region with 194 *Alces* specimens. *Capreolus capreolus*, *Hydropotes inermis* and *Rangifer tarandus* serve as outgroups. Bayesian posterior probabilities ≥ 0.93 are shown above the branches. Clades A and B represent western and eastern lineages, respectively. Modern samples from GenBank are represented by the accession number, modern samples from this study are represented by prefix M and the subspecies name where marked, and ancient samples in this study are represented by prefix MM and median radiocarbon date. For more details, see Tables S1, S2 and S5. Colours correspond to geographical locations: purple—North America, dark blue—northeast Asia, light blue—east Asia, black—western and central Asia, orange—Europe. *The asterisk represents the monophyletic clade with the 75 bp deletion

60,000–30,000 yr ʙᴘ; e.g. MM535 from Duvanny Yar (Kolyma region), dated to 48,100 ± 3,100 uncalibrated yr ʙᴘ; Table S1, samples are outside the range of calibration curve). The range is similar to the species' modern distribution (Figure 1), although few northeast Siberian specimens are dated to this period. The vegetation in east and northeast Asia fluctuated with stadial and interstadial conditions (Sher, Kuzmina, Kuznetsova, & Sulerzhitsky, 2005), but mainly consisted of shrub tundra and tundra steppe, although it also included patches of larch forest including birch and alder, suitable for an obligate browser (Sher, 1987; Frenzel, Pecsi, & Velichko, 1992; Brigham-Grette et al., 2004). During the LGM, there are no dated moose records, presumably due to the reduction in suitable browse in the sampled areas during this period (e.g. Tarasov et al., 2000).

The whereabouts of moose during the LGM are still a mystery, except for Italy where there is one direct radiocarbon date but there are no other dated records for moose anywhere, and the genetic results shed little light on this issue. The subsequent higher genetic diversity in east Asia could indicate that this region was the place where moose remained in the LGM 'gap'. However, this is a vast region, and where the species survived in this region is yet to be discovered. Moose, as a boreal species, might be expected to be confined to southern refugia during the LGM, and to move northwards during interstadials and interglacials. Hundertmark and Bowyer (2004) suggested a single refugium around southern Yakutia (ca. 60°N). It is possible that moose refugia extended even further to the south, likely in southeast Siberia and northern China,
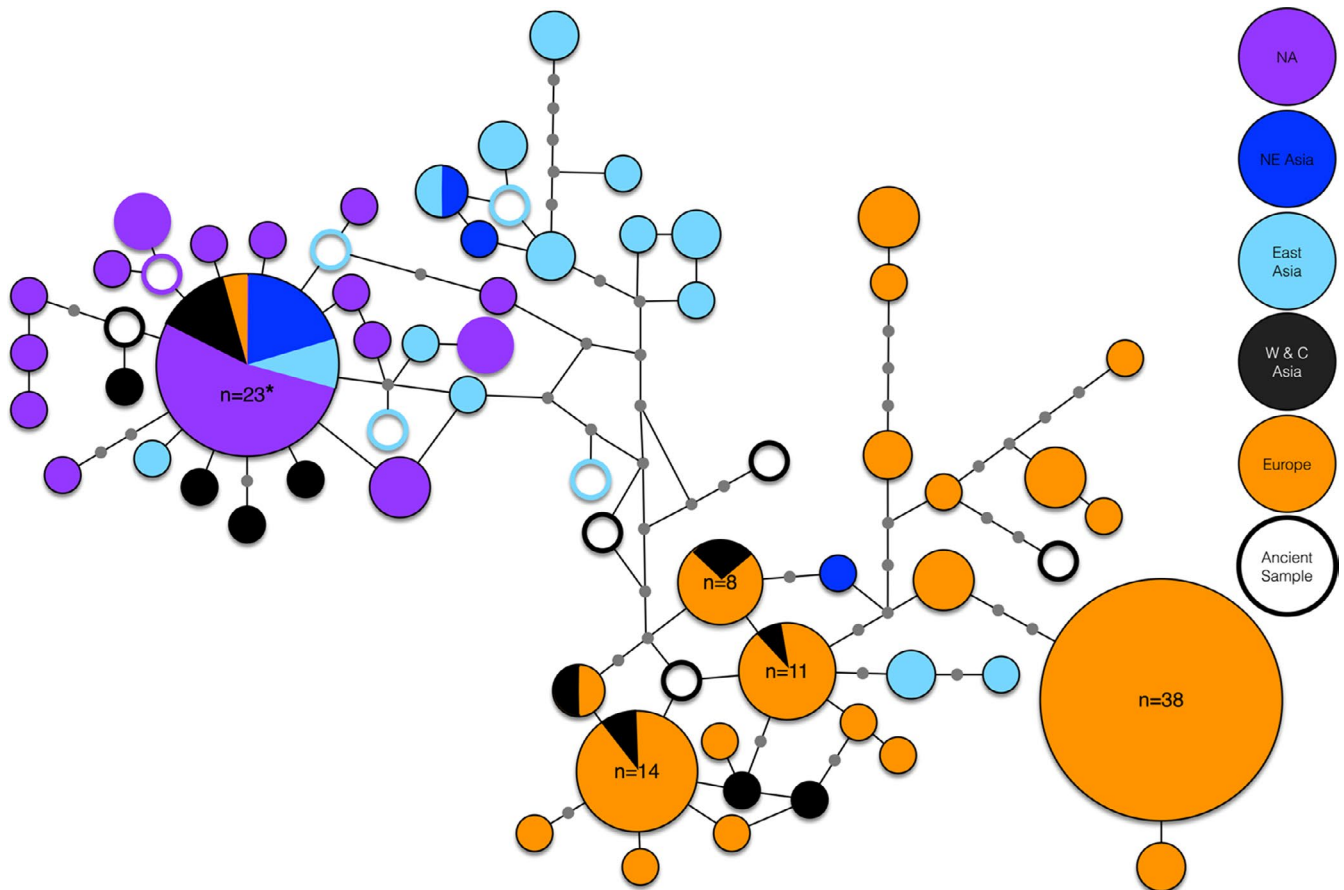
FIGURE 4 Median joining haplotype network of 30 ancient and 141 modern moose sequences consisting of 244 bp. Lines represent a single mutation step. The grey circles represent missing haplotypes. The colours correspond to geographical locations as shown in Figure 3. The haplotype with the asterisk represents modern and ancient samples from North America, northeast Asia (only ancient), east Siberia, and western and central Asia and Europe (only modern)

where *A. a. cameloides* is found today. Whatever the source population(s), our data demonstrate that moose began to recolonize the more northern latitudes around 15,000 years ago, and remained in the region until the present. This reappearance is correlated with a shift to a more forested vegetation type, which includes tree willows and alders (Edwards, Brubaker, Lozhkin, & Anderson, 2005; Guthrie, 2006).

Intriguingly, the genetic data reveal no differences between pre- and post-LGM Pleistocene moose. Two specimens from the Kolyma region (northeast Siberia), for example, dated to 49,810 yr BP (uncalibrated, the sample is outside the range of the calibration curve) and 13,870 yr BP (specimens MM535 and MM533) differ from one another by only two base pairs (Figure 4). Assuming that the temporal gap in moose presence across Asia is real, habitat tracking is a likely explanation for the lack of genetic change through time. This would entail the range of moose shifting south during the LGM, and then expanding back northwards after the ice receded.

Unfortunately, none of the ancient European samples yielded DNA, but according to the available radiocarbon dates, moose was absent from large parts of Europe during the LGM except

for the record from Italy. There might also have been refugia in the Carpathians or Caucasus (Niedziałkowska, 2017), although direct fossil evidence is lacking. Post-glacial colonization resulted in two main mitochondrial clades in European moose: an eastern one, and a western and central one (Niedziałkowska, 2017; Figure 3). A deeper history for moose in Europe seems likely from their genetic distance from Asian and North American populations, and the rarity of European haplotypes, ancient or modern, in those regions. This suggests that the modern suture zone in central Asia may have arisen since the late-glacial, by expansion from east and west, and the fossil data from the Urals suggest this may have been a repeating pattern through Late Pleistocene climate cycles.

4.3 | Expansion and colonization of North America

The pattern of absence up to 15,000 yr BP (including the large majority of MIS 2), followed by colonization, is also seen in North America. Over one hundred radiocarbon dates demonstrate that moose started to appear in American Beringia

towards the end of MIS 2, around 15,000 yr BP (Guthrie, 2006; Figure 2). The only pre-LGM finitely radiocarbon-dated alceine fossil is attributed to *C. latifrons*. Other MIS 3 dates on alceine fossils exist, but these are older than the range that can be calibrated (Guthrie, 2006; Table S1) and are not identifiable to genus (Churcher & Pinsof, 1987).

All sampled North American individuals, ancient and modern, lack the 75 bp fragment in the mtDNA CR. Genetically, they are all very close to one another and to Asian specimens, with only one to three base-pair differences (Figure 4). The most common haplotype spans an area ranging from the Urals to North America (Figure 4). The low genetic diversity between North American and East Asian haplotypes signals a rapid and recent expansion and agrees with the radiocarbon dates in suggesting that moose arrived in Alaska around 15,000 yr BP. These results also agree with other studies that demonstrate a recent expansion of *A. alces* to North America by crossing the Bering Isthmus around ca. 15,000 yr BP (Geist, 1999; Guthrie, 1995, 2006; Hundertmark, Shields, Udina, et al., 2002; Lister, 2005; Udina et al., 2002). If earlier migrations occurred, they have not yet been detected in either the fossil record or the genetic composition of modern North American populations.

The genetic differences observed by Hundertmark, Shields, Udina, et al. (2002) between present-day moose on each side of the Bering Strait are not seen in ancient DNA. Two specimens from northeast Siberia (Kolyma region, where the *buturlini* subspecies is found today), which are dated to 49,810 and 13,870 yr BP (specimens MM535 and MM533), group with the North American group (Figure 3). An effectively modern sample dated to 111 yr BP (MM529) from the same region falls together with *buturlini* subspecies. These results imply that the haplotype that crossed the Bering Isthmus went extinct from the northeast Siberian region to be replaced, from an unknown geographical source, by the *buturlini* population sometime after 15,000 yr BP. This further implies that the phenotypic similarities between NE Siberian *buturlini* and the Alaskan subspecies *gigas* (Geist, 1999) might be parallel acquisitions, perhaps in response to similar environmental conditions.

The expansion of moose in North America correlates with the transition from arid steppe environment based on grasses, sedges and sages of the Late Pleistocene to mesic shrub tundra with woody plants (Guthrie, 1995, 2006). The dependence of moose on browse forage would have enabled them to expand only when the tree line expanded northward with late-glacial climatic amelioration. Moose expansion in North America also coincides with the spread of early humans (Goebel, Waters, & O'Rourke, 2008; Kitchen, Miyamoto, & Mulligan, 2008; Mulligan, Kitchen, & Miyamoto, 2008), and red deer (Meiri et al., 2013) into the continent.

Compared to other megafauna which colonized Beringia in the Late Pleistocene, moose seem to follow a unique history. Red deer were long-term residents of Asian Beringia, even though they also colonized North America only at the end of last glaciation (Meiri et al., 2013). North American brown bear populations experienced

a local extinction around 35,000–30,000 yr BP, with a subsequent recolonization across the Bering Isthmus from Asian Beringia around 20,000 yr BP (Barnes et al., 2002). Moose, however, seem to have been absent from most, perhaps all, of its present-day range during these times, and its colonization occurred much later, by populations that are genetically indistinguishable from the preceding ones. A major obstacle to reconstructing the Late Pleistocene phylogeography of moose is the lack of fossil material, especially the lack of radiocarbon dated fossils, or those from reliable stratigraphic contexts, that yield DNA. Such specimens, together with advanced sequencing methods, a moose reference genome and population-level sampling across the genome, will be essential for further clarifying the details of moose LGM biogeography, and for identifying how many glacial refugia it occupied and their positions. Our results suggest that moose is a young species that has limited genetic diversity, but a diversity that, in turn, seems to have remained stable during the last 50,000 years despite a major range contraction during the LGM. While moose colonized North America together with other large mammals after the LGM, their population history does not closely resemble that of other megafaunal species. Thus, the responses of species to changing environmental conditions are individualistic and are the result of complex interactions between their autecology, physiology and the changing climate.

5 | CONCLUSIONS

Moose are obligate browsers, and they are therefore sensitive to environmental change. The combined radiocarbon and ancient DNA evidence indicates substantial range contraction during MIS 3 and MIS 2, with subsequent recolonization across northern Europe and Asia, as well as entry into North America, coincident with amelioration of climate and consequent vegetation changes. By analogy, the species may also have undergone contraction into refugia during the late MIS 6 (191–123 kyr) glaciation, with re-expansion in the generally milder, more forested environments of the MIS 5 (123–71 kyr) interglacial. The tMRCA for all our living and fossil *Alces* indicates that their diversity originated within the last 150 kyr (95% limit). This encompasses the coldest part of MIS 6, the MIS 5 interglacial complex, and the MIS 4 glacial (71–57 kyr); by MIS 3 our ancient DNA data indicate that present-day diversity was in place. This study shows the power of ancient DNA together with radiocarbon dates in revealing the population histories of species.

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BIOSKETCH

The team is interested in processes of species-level evolution of large mammals such as red deer (*Cervus elaphus*/*Cervus canadensis*) and moose (*Alces alces*) to study evolutionary divergence, migration and expansion since the Late Pleistocene—around 60,000 years ago. See more at: http://www.nhm.ac.uk/our-science/departments-and-staff/staff-directory/adrian-lister.html#sthash.W1R1xTFT.dpuf. And: http://www.nhm.ac.uk/our-science/departments-and-staff/staff-directory/ian-barnes.html.

Authors' contributions: M.M., A.L. and I.B. conceived the study; M.M., P.K., G.D.Z., A.L. and I.B. collected the data; M.M., A.L. and I.B. analysed the data; M.M., A.L. and I.B. wrote the paper. All authors read, commented on and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.