



Genetic analysis of European red foxes reveals multiple distinct peripheral populations and central continental admixture

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ABSTRACT

Temperate terrestrial species in Europe were hypothesized to have been restricted to southern peninsular refugia (Iberia, Italy, Balkans) during the height of the last glacial period. However, recent analyses of fossil evidence indicate that some temperate species existed outside these areas during the last glacial maximum (LGM). Red foxes (*Vulpes vulpes*) in particular, could have been distributed across the southern half of the continent, potentially forming one continuous population. To investigate these hypotheses, we used 21 nuclear microsatellite loci and two fragments (768 bp) of mitochondrial DNA to characterize the population structure among a continent-wide sample of 288 European red foxes. We tested whether European red foxes clustered into discrete populations corresponding to the hypothetical peninsular refugia. Additionally, we sought to determine if distinct northern populations were formed after post-glacial recolonization. Our results indicated that only the foxes of Iberia appeared to have remained distinct over a considerable period of time (32–104 kya). Spanish red foxes formed their own genotypic cluster; all mtDNA haplotypes were endemic and closely related, and together both the mitochondrial and nuclear datasets indicated this population contributed little to postglacial recolonization of Northern Europe. In contrast, red foxes from Italy and the Balkans contributed significantly to, or were part of, a wider, admixed population stretching across mid-latitude Europe. In Northern Europe, we identified a Scandinavian population that had an ancestral relationship with red foxes to the south, and a more recent relationship with those to the east, in Russia. We also resolved two distinct populations on the islands of Ireland and Britain that had been separated from one another, and from those on the continent, since the late Pleistocene/mid Holocene (–4–24 kya).

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1. Introduction

The climatic oscillations of the Pleistocene caused range expansions and contractions, extinctions and the evolution of novel lineages (Hewitt, 2000; Lister, 2004; Stewart et al., 2010; Morales-Barbero et al., 2017). During the last glacial maximum (LGM, 26 thousand years ago, kya [Peltier and Fairbanks, 2006]), ranges of many temperate terrestrial species in Europe were pushed

southward, where they became isolated in (primarily peninsular) refugia (Hewitt, 2004). Geographically distinct lineages have been observed in many European species and are attributed to this vicariant event, as well as the uneven range expansion following climatic warming. Although individual species responded differently to potential barriers depending on their particular physiology and dispersal abilities (Taberlet et al., 1998; Stewart et al., 2010), one of three models has been typically invoked to describe common patterns observed across temperate species: the grasshopper (*Chorthippus parallelus*), where northern populations stem from the Balkans; the hedgehog (*Erinaceus europeus* and *E. concolor*), where populations expanded from Iberia, Italy and the Balkans; and the European brown bear (*Ursus arctos*), where populations expanded

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from Iberia and the Balkans (Hewitt, 1999).

A review of faunal assemblages from archaeological sites has called these models into question (Sommer and Nadachowski, 2006). An examination of fossil records dated to the LGM not only revealed the presence of temperate fauna in putative southern peninsular refugia of Iberia, Italy, and the Balkans, but also in a number of mid-latitude European sites from Southwestern France through Austria, Hungary, Czech Republic, Slovakia, Slovenia, to Moldova, in the east. This pattern suggests that temperate species could have retained a more continuous distribution than typically assumed throughout much of southern Europe, potentially facilitating genetic exchange and therefore countering population differentiation. Nevertheless, subsequent phylogeographic analyses indicate major subdivision attributable to contraction into refugia during the last glaciation, even for large vagile species such as the red deer (*Cervus elaphus*; Skog et al., 2009). Thus, it remains unclear what impact the last glacial cycle had on the generation or maintenance of distinct lineages across Europe.

Red foxes (*Vulpes vulpes*) are currently distributed across Europe, from the south of Spain to the most northerly point of Norway (Macdonald and Reynolds, 2004). During the last glacial period red foxes exhibited a more southerly distribution (Sommer and Benecke, 2005); in particular, sub-fossil remains indicate the presence of red foxes no farther north than England and Poland just prior to the LGM. For a period of >7000 years (23–16 kya), red foxes were apparently pushed further south. Sub-fossil remains from this time indicate that red foxes were present in the southern peninsulas of Iberia, Italy, and Balkans, as well in a number of mid-latitude locations stretching from France in the west, through to Moldova in the east (Sommer and Nadachowski, 2006). Thus, red foxes apparently maintained a large continuous population across the southern half of the European continent at the height of the last glaciation (Sommer and Nadachowski, 2006). By 16 kya, red foxes had expanded as far north as southeastern Germany (Sommer and Benecke, 2005). By the mid Holocene (8.2–4.2 kya; Walker et al., 2012), red foxes had apparently expanded into most of their current range (Sommer and Benecke, 2005). Given the species' history of responding to changing climate, and its ability to cope with a range of environmental conditions (Macdonald and Reynolds, 2004), the extent to which populations were isolated and subdivided during the LGM is unknown. Such demographic changes, however, often leave genetic signatures in modern populations.

Increasingly extensive sampling and more highly resolving genetic analyses have provided a shifting understanding of European red fox phylogeography and of how current populations are structured. Such studies have either had widespread sampling but were based primarily on mitochondrial DNA (mtDNA), or used multiple nuclear loci but with a more geographically restricted sampling. An early study using mitochondrial cytochrome *b* sequence data and allozymes indicated low contemporary gene flow between populations across the Mediterranean Basin (Fratini et al., 1998). A subsequent analysis used short segments of cytochrome *b* and D-loop from both modern and ancient DNA samples and found a lack of spatial structure and change in population size over the last 40,000 years (Teacher et al., 2011). Edwards et al. (2012) followed with a geographically and numerically larger sampling, with particular emphasis on representation from Britain and Ireland. Analyzing portions of cytochrome *b* and D-loop, these authors identified clear differentiation between continental red foxes and those from the islands of Britain and Ireland along with their closest continental neighbor, the Netherlands. Recently a small number of studies have used nuclear microsatellites to investigate regional population substructure within Europe, in Poland (Mullins et al., 2014), Britain (Atterby et al., 2015), and Scandinavia (Norén et al., 2015). However, no study has used high-

resolution nuclear markers to investigate the continent-scale population genetics of a large number of European red foxes.

We used a panel of 21 nuclear microsatellites and mitochondrial DNA sequences to assess the population substructure, phylogeography, and the timing of vicariant events within a continent-wide sample of European red foxes. The use of multiple loci allowed an independent assessment of the population structure relative to that identified with maternally-inherited mtDNA. Specifically, we sought to determine whether (a) red foxes across southern Europe constituted a single continuous population, or if (b) multiple discrete populations were evident. Given that much of northern Europe was uninhabitable by the red fox during the period around the LGM and that current populations in those areas stem from postglacial colonization, we also tested the predictions of (c) little or no differentiation among northern populations and their southern sources, versus (d) geographically discrete populations consistent with colonization from different sources populations or subsequent isolation. Our analyses also allowed us to assess the validity of current subspecies designations within the red fox.

2. Methods

2.1. Samples

All samples used in this analysis were collected and DNA extracted as described in previous studies (Edwards et al., 2012; O'Mahony et al., 2012; Statham et al., 2014). In total, 288 DNA samples were collected from across Europe: Ireland, Britain, Spain, Italy, Serbia, France, Netherlands, Germany, Denmark, Poland, Estonia, Norway, Sweden, and Russia (Fig. 1; Appendix). These samples comprised tissue ($n = 232$) and faeces ($n = 56$). The faecal samples were from Ireland ($n = 52$) and the Kola Peninsula, Russia ($n = 4$), and were previously genetically identified to species (O'Mahony et al., 2012; Statham et al., 2014).

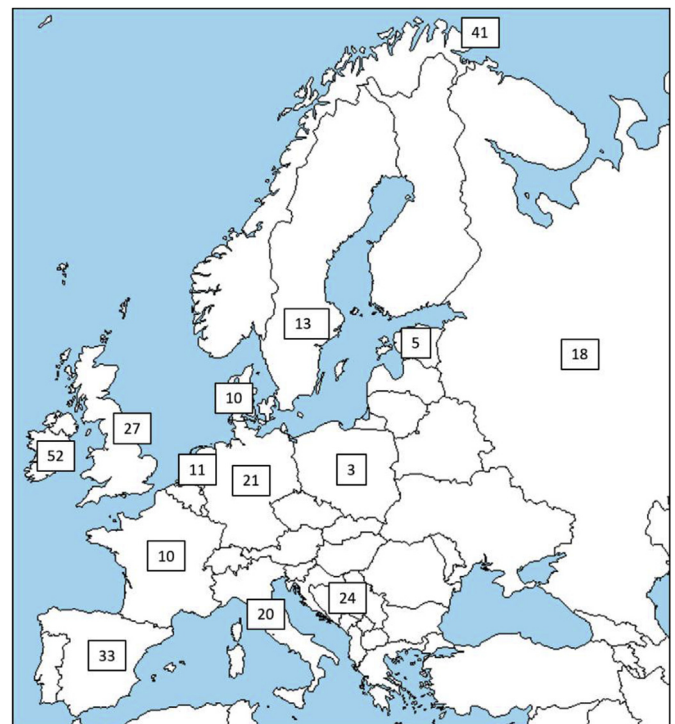


Fig. 1. Map of red fox samples. The number indicates the total number of samples from that country. More specific sampling information is provided in the Appendix.

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