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Impact of Quaternary climatic changes and interspecific competition on the demographic history of a highly mobile generalist carnivore, the coyote

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Recurrent cycles of climatic change during the Quaternary period have dramatically affected the population genetic structure of many species. We reconstruct the recent demographic history of the coyote (*Canis latrans*) through the use of Bayesian techniques to examine the effects of Late Quaternary climatic perturbations on the genetic structure of a highly mobile generalist species. Our analysis reveals a lack of phylogeographic structure throughout the range but past population size changes correlated with climatic changes. We conclude that even generalist carnivorous species are very susceptible to environmental changes associated with climatic perturbations. This effect may be enhanced in coyotes by interspecific competition with larger carnivores.

Keywords: canid; Pleistocene; North America; mtDNA; Bayesian Skyline Plot; *Canis latrans*

1. INTRODUCTION

The Pleistocene was characterized by recurrent climatic perturbations resulting in dramatic environmental changes that affected the distribution and population structure of plants and animals [1]. In temperate species, glacial periods were generally associated with range reductions owing to restriction of habitat, whereas interglacial periods were typically associated with range expansion. Many taxa illustrate the effects such climate changes had on phylogeographic and demographic patterns [2]. In particular, the last glacial–interglacial transition coincided with major extinction events and population declines in numerous species distributed in the Northern Hemisphere [1,3]. In contrast, distribution and phylogeographic patterns

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from other organisms were amplified by the process of colonization of newly available habitat after the last glacial maximum [2,4] and basic patterns in the routes of post-glacial expansions have emerged [5].

The degree of habitat specialization is likely to affect the ability of species to persist during rapid environmental changes, and specialist species had a higher risk of extinction during the Pleistocene [6]. Generalist species, on the other hand, are more likely to survive because a subset of habitats allowing their existence remains throughout climate fluctuations. To examine the role of Late Pleistocene and Holocene climatic changes in shaping the genetic structure of a highly mobile generalist carnivore, we inferred the phylogeographic structure and demographic history of the coyote, *Canis latrans*, in North America based on sequences of the mitochondrial control region.

2. MATERIAL AND METHODS

Our study is based on 837 sequences of a 414 bp fragment (including gaps) of the mitochondrial control region from coyote samples spanning the entire current distribution in the US and Canada (electronic supplementary material, table S1). To visualize the phylogenetic relationships among the coyote haplotypes, we conducted a Bayesian phylogenetic analysis using MRBAYES v. 3.1.2 [7]. Spatial genetic structure of coyotes was analysed by spatial analysis of molecular variance using SAMOVA v. 1.0 [8]. To test for signals of population expansion, we calculated a mismatch distribution and conducted two neutrality tests (Tajima's *D*, Fu's *F_s*). We excluded samples from the most recently (last century) colonized eastern North America because recurrent gene flow between the invading coyotes and resident eastern wolves [9–11] might bias demographic inferences. Past population size trajectories were inferred using a Bayesian coalescent (Bayesian Skyline Plot, BSP [3]) approach as implemented in BEAST v. 1.5.4 [12]. To estimate absolute ages of demographic events, we applied a substitution rate of 4.68 (and additionally 9.36 and 3.64) per cent per million years which is based on an average sequence divergence of 13.1 per cent [13] and the estimated split between coyotes and gray wolves 1.4 (0.7–1.8) Myr [14]. A detailed description of the analytical procedure is given in the electronic supplementary material.

3. RESULTS AND DISCUSSION

Regional phylogeographic structure was neither detected in our Bayesian phylogenetic analysis (figure 1; cf. [15]) nor in our spatial analysis of molecular variance (electronic supplementary material, figure S1) which is consistent with a lack of a strong population structure on a continental scale [11,16]. Given that (i) coyotes are good dispersers (individual dispersal distances over 100 km have been reported [17]), (ii) they are highly adaptable to different resources and (iii) their natural distribution range (the grasslands of the Great Plains) was not fragmented during the Late Pleistocene glacial cycles, then their population genetic structure is expected to be low. However, the lack of a clear phylogeographic structure across the coyote's entire distribution is quite remarkable and rather unusual among North American mammals. Most larger mammals that survived the Last Glacial Maximum (LGM) in North America and now inhabit a large part of the continent show a distinct phylogeographic pattern consistent with survival at reduced population sizes in two or more isolated, ice-free refugia [18–21]. A similar pattern has been reported on a continental scale in the closely related gray wolf [13]. On small geographic scales, habitat-associated population partitions have been observed both in coyotes [22] and gray wolves [9,23,24].

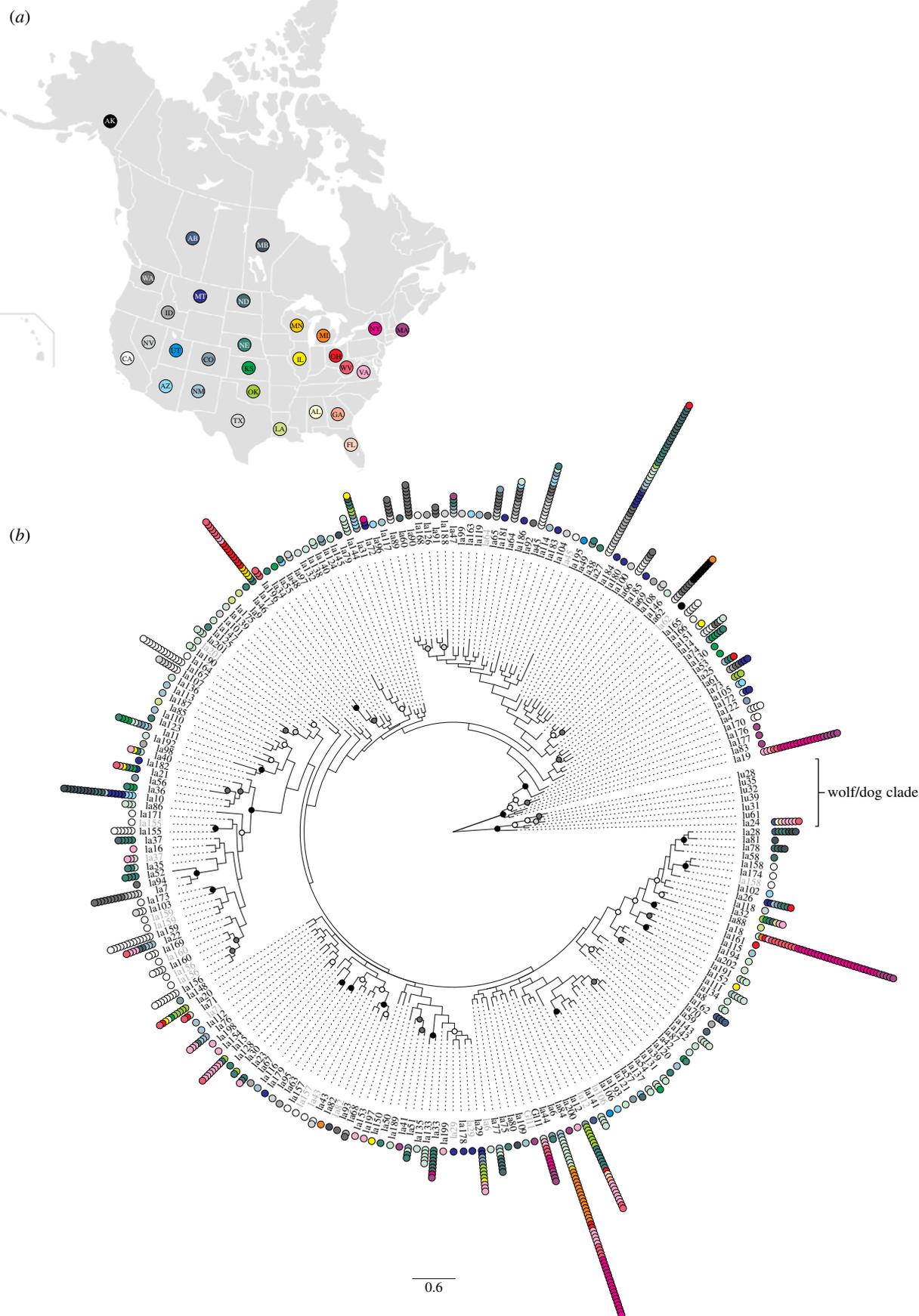


Figure 1. (a) Map of North America showing sample localities. (b) Bayesian phylogenetic tree of coyote haplotypes analysed in this study. The number of coloured circles per haplotype corresponds to the number of individuals sharing a particular haplotype. Colours refer to the state or province of origin (see part a). Nodal support in form of posterior probabilities of ≥ 0.99 , ≥ 0.95 , ≥ 0.90 and ≥ 0.70 is indicated by black, dark grey, light grey and white circles, respectively. Haplotype IDs in grey refer to sequences that were assigned to a particular haplotype but contained some missing data. Some coyote samples from recently colonized regions had a dog haplotype.

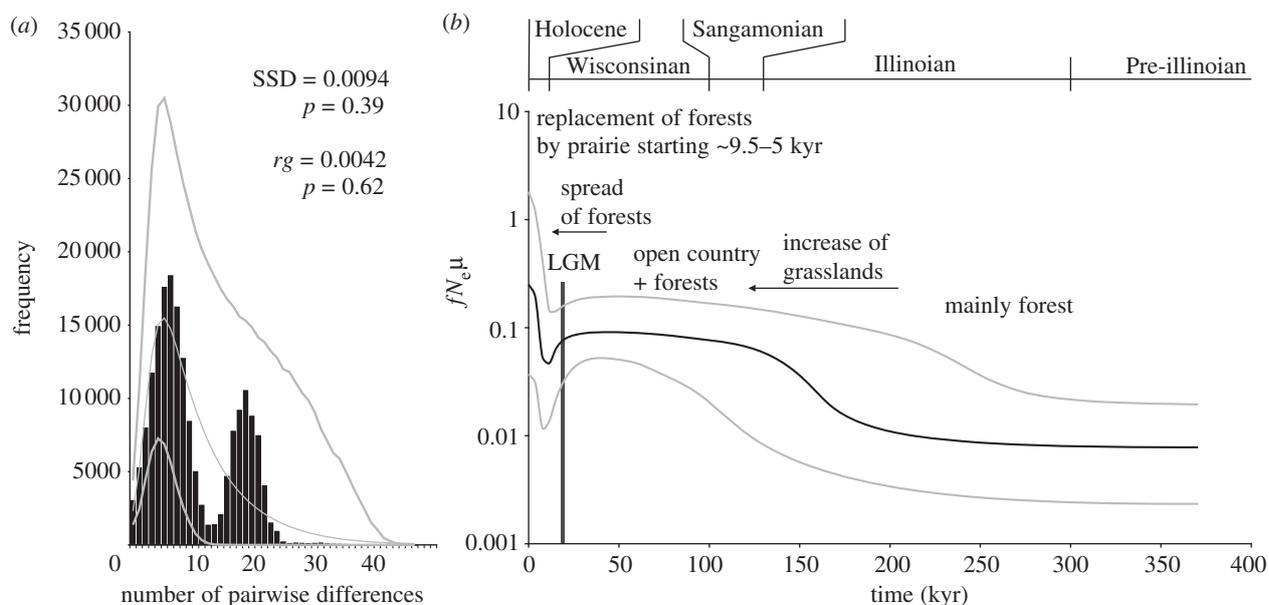


Figure 2. Demographic history of the coyote. (a) Mismatch distribution. Black columns represent the observed frequency of pairwise differences. Gray lines refer to the expected distributions based on parameter estimates and their 95% confidence limits simulated under a model of population growth. Sum of squared differences (SSD) and raggedness index (rg) and their respective p -values are given. (b) Bayesian Skyline Plot (BSP) reconstruction of past population size trajectories. The BSP shows the product of female effective population size (fN_e) and mutation rate (μ) through time, assuming a substitution rate of $4.68\% \text{ My}^{-1}$, according to the best estimate for the coyote/wolf split from [14] and an average interspecific sequence divergence of 13.1% [13]. BSPs with time-scales based on lower and upper 95% confidence intervals for the coyote/wolf split from [14] are shown in electronic supplementary material, figure S1. Glacial and interglacial periods are indicated, as well as major vegetation characteristics/trends for central North America (following [25]). LGM, Last Glacial Maximum (approx. 18–20 kyr).

Mismatch distribution (figure 2a) and neutrality tests ($D = -1.4423$, $p = 0.036$; $F_s = -23.8241$, $p = 0.006$) reject a constant population size through time. The pattern of past population size trajectories, as inferred by BSP, corresponds with environmental and climatic fluctuations in the Late Pleistocene (figure 2b). Population declines might be difficult to infer based solely on contemporary samples, and BSP patterns might be indistinguishable from constant population size through time. However, this should not be true for periods of rapid population growth. It is probable that the inferred population expansions followed periods of reduced population sizes, something impossible to infer with just contemporaneous data, in particular when it concerns events far in the past. Our analysis inferred a population expansion at the penultimate (Illinoian–Sangamonian) glacial–interglacial transition, which was likely facilitated by an associated change of the environment from forested habitats in the Illinoian to more open country in the Sangamonian [25]. Cooling climate and associated vegetation changes during the Late Wisconsinian glacial, in particular the spread of forests in the northern plains region [25], coincides with a population decline with a minimum after the last glacial maximum (approx. 20 kyr), regardless of the substitution rate used (figure 2b, electronic supplementary material, figure S2). Thereafter, the spread of grasslands in the Holocene approximately 9.5–5 kyr (depending upon location) [25] is associated with a drastic population expansion of coyotes. This expansion peaked in the recent rapid colonization of nearly the entire North American continent. However, this recent colonization may have been facilitated by the near

extermination of an interference competitor, the gray wolf, in large parts of North America [26] and changes in the landscape owing to the spread of agriculture. Moreover, as coyotes generally avoid dense woodland habitats, their colonization of such habitats in the North American northeast might have been facilitated by hybridization with ‘eastern’ wolves [12,13]. Today, coyotes are found throughout North America in a variety of habitats, except the High Arctic.

Recent evidence suggests a potentially time-dependent rate of molecular evolution, which could affect the dating of recent evolutionary/demographic events, in particular, if one applies a molecular rate obtained from an ancient split to more recent events [27]. However, even if our estimates were affected by this phenomenon they would be biased towards older ages. This implies that the population decline observed in the BSP by all means post-dates the LGM.

In conclusion, high dispersal distances and adaptability to different resources are likely to have contributed to the lack of large-scale phylogeographic structuring found in this study. However, although coyotes are a generalist species that can exist in a wide range of habitat types and feed on various kinds of prey, the coyote experienced demographic changes that correlate with the Late Quaternary expansion and contraction of dry grasslands. Only recently, with the local extermination of wolves, habitat changes and local hybridization with ‘eastern’ wolves, have coyotes been able to colonize a greater diversity of habitats. The combined effects of interspecific competition and climate change have likely driven demographic changes in coyotes throughout their evolutionary history.

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