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Limited historical admixture between domestic and European wildcats.

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Summary

Domestic cats were derived from the Near Eastern wildcat (*Felis lybica*), after which they dispersed with people into Europe. As they did so, it is possible that they interbred with the indigenous population of European wildcats (*Felis silvestris*). Gene flow between incoming domestic animals and closely related indigenous wild species has been previously demonstrated in other taxa including pigs, sheep, goats, bees, chickens and cattle. In the case of cats, a lack of nuclear, genome-wide data, particularly from Near Eastern wildcats, has made this possibility difficult to either detect or quantify. To address these issues, we generated 75 ancient mitochondrial genomes, 14 ancient nuclear genomes and 31 modern nuclear genomes from European and Near Eastern wildcats. Our results demonstrate that despite cohabitating for at least 2,000 years on the European mainland and in Britain, most modern domestic cats possessed less than 10% of their ancestry from European wildcats, and ancient European wildcats possessed little to no ancestry from domestic cats. The antiquity and strength of this reproductive isolation between introduced domestic cats and local wildcats was likely the result of behavioural and ecological differences. Intriguingly, this long-lasting reproductive isolation is currently being eroded in parts of the species' distribution as a result of anthropogenic activities.

Introduction

Previous analyses of microsatellite markers indicated that modern domestic cats (*Felis catus*) derive most of their ancestry from Near Eastern wildcat (*Felis lybica*)¹. Despite the fact that the remains of domestic cats, their wild progenitor (Near Eastern wildcats) and other wild relatives such as European wildcats (*Felis silvestris*) are difficult to distinguish zooarchaeologically^{2,3}, the archeological record suggests that domestic cats dispersed into Europe and reached France and Britain by ~2800-2200 years before present [BP]³.

Mitochondrial and nuclear genetic approaches have been used to distinguish domestic cats from European, and Near Eastern wildcats^{1,4}. These data have then been interpreted to address both domestic cat migration and the degree of introgression between European and Near Eastern wildcats at the boundary of their overlapping natural distributions in southeastern Europe⁴⁻⁷. In addition, numerous studies have demonstrated that European wildcat populations across Europe have experienced gene flow from domestic cats as a consequence of anthropogenic activities⁸⁻¹¹.

This recent gene flow between introduced domestic cats and European wild cats is perhaps unsurprising for two reasons. Firstly, Near Eastern wildcats and domestic cats are morphologically even less divergent than many other pairs of wild and domestic populations (e.g.^{12,13}) suggesting that there are no physical barriers to hybridisation. Secondly, previous studies have demonstrated that numerous domestic animal taxa including pigs^{14,15}, sheep¹⁶, goats^{17,18}, bees¹⁹, chickens²⁰ and cattle^{21,22}, have all acquired a proportion of their genomic ancestry via gene flow with sympatric, closely related wild populations. The notable exception to this rule is domestic dogs who, despite their sympatry with wolves across the Northern Hemisphere, have received little to no gene flow for at least 11,000 years²³⁻²⁵.

Here, to ascertain the spatial and temporal pattern of hybridization between European wildcats and domestic cats following their arrival into Europe, we extracted DNA from 258 archaeological cat samples (8,500 - 100 years BP) excavated from 85 archaeological sites (Figure 1; Table S1; Supplemental Information). We then generated and analysed 75 mitochondrial genomes (>2x coverage) as well as 14 low- to medium-coverage nuclear genomes (0.1x - 4x) (Figure 1; Table S1). To better understand patterns of hybridization between cat species, we also generated 31 modern (Figure 1; Table S2) full nuclear genomes (>15x coverage) including 16 European and 4 Near Eastern wildcats.

Results and Discussion

Ancient reticulation in the genus Felis

To establish the genetic ancestry of modern and ancient domestic cat genomes, we first reconstructed the evolutionary relationships of *Felis* lineages using complete nuclear genomes with the jungle cat (*Felis chaus*) as an outgroup (Table S2; Figure 2a; Figure S2). Phylogenetic analyses showed the Near Eastern wildcat represents an outgroup to all other wildcats including the European, Asian (*Felis lybica ornata*), and the Chinese mountain cat (*Felis bieti*; Figure 2a). This indicates that Asian and Near Eastern wildcats do not form a monophyletic group, suggesting the current IUCN taxonomy²⁶, which implies that *Felis lybica ornata* and *Felis lybica* are sister taxa, requires reconsideration. In addition, D-statistics analyses support at least two past admixture events: one involving Near Eastern and European wildcats, and another involving Near Eastern and Asian wildcats (Figure 2b).

Though these admixture signatures could result from modern instances of gene flow from domestic cats into wildcat individuals, we found the same, significant D-statistics signal ($Z > |3|$) using the genome of a Mesolithic Scottish wildcat (8,459-8,272 cal. BP; AnCorran_1; Table S1; Supplemental Information), that predates both the emergence of domestic cats and their arrival to Scotland. This result indicates that at least a portion of the admixture signal is due to ancient reticulation between wild lineages. Our phylogenomic analyses also further confirmed that domestic cats and Near Eastern wildcats are sister clade, corroborating previous studies using microsatellites and mtDNA data¹.

Resolving the origins of the Near Eastern ancestry present in European wild cats

Though ADMIXTURE analyses (both K=4 and K=6; Supplemental Information) suggested that none of the European wildcats in this study possess Near Eastern wildcat/Domestic cat ancestry (Figure S3). Although our analysis did not include samples from known domestic cat wildcat Scottish hybrids, these results contradict previous analyses that show that modern Scottish wild cats possess some degree of domestic cat ancestry due to recent gene flow²⁸. Recent work on human data has shown that ADMIXTURE may not be able to detect admixture events if all admixed individuals analysed possess similar ancestry proportions²⁷. This would mean that ADMIXTURE may not be able to detect admixture if most European wildcats possessed similar levels of domestic cat ancestry. To address this issue, we analysed the genome from the Scottish Mesolithic wildcat (8,459-8,272 cal. BP; AnCorran_1; Table S1; Supplemental Information). We computed D-statistics of the form D (outgroup, Near Eastern, European wildcat, AnCorran_1), in order to take advantage of the fact that the AnCorran_1 cat could not possess any domestic cat ancestry. We found that other than two individuals: Kilton_2, a 16th century cat from Kilton Castle in Northeast England, and FSX360, a modern Portuguese wildcat, all D-statistics involve the other nine European wildcats analysed here yielded significantly negative Z values ($Z < -3$), indicating that these individual possess a degree of Near Eastern/Domestic ancestry (Figure S4; Supplemental Information).

The Near Eastern wildcat ancestry fraction in European wildcats was computed using f4 ratios (Supplemental Information; Figure S6). We used AnCorran_1, Kilton_2, and FSX360 as representatives of non-admixed European wildcats. The Near Eastern ancestry fraction in European wildcats ranged from ~3.5% in an Eastern German wildcat, to ~21% in Scottish wildcats (Figure S8). Although, the high level of ancestry in Scottish wildcats is likely due to recent hybridization with domestic cats²⁸, it remains unclear whether the same is true for German wildcats, which possess low levels of Near Eastern wildcat ancestry. It remains possible that European wildcat populations that live closer to the edge of their distribution in Southeast Europe naturally possess some degree of Near Eastern wildcat ancestry due to admixture, and that the ancestors of these populations may not have experienced any hybridization with introduced domestic cats. In fact, mitochondrial analyses have shown that haplogroup IV, which is typically associated with Near Eastern wildcats, have been found at high frequency in southern Europe in both ancient wildcats that pre-date cat domestication (n = 18, 58%, from the Mesolithic to the 8th c. BC) and modern wildcats (n = 10, 62%)¹¹, suggesting the existence of an admixture zone.

Low levels of European wildcat ancestry in modern and ancient domestic cats

Principal component analysis (PCA) of nuclear genomes, including 14 ancient and 52 modern genomes, further demonstrated the affinity of both AnCorran_1 and Kilton_2 with modern European wildcats, particularly FSX360 (Figure 3a). This analysis also indicated that all 12 archaeological cats (excluding ancient wildcats) analysed here, most of which (10/12; Figure 1) originated in Europe, likely derived the majority of their ancestry from Near Eastern wildcats/domestic cats, rather than European wildcats. The earliest evidence of nuclear Near Eastern wildcat ancestry north of the Alps was found in a Roman domestic cat from the site of Fishbourne dated to 1,926-1,827 cal. BP (Fishbourne_2), demonstrating that domestic cats with primarily Near Eastern wildcat nuclear ancestry were present north of the Alps by at least the Roman period.

Our PCA further indicated that some ancient cats, including a Roman cat from the Isle of Man (Perwick_1) and a 17th century cat from Ireland (Eyre_3), were slightly shifted toward European wildcats on the PCA. This positioning suggests a possible history of gene flow with European wildcats. To test this, we first used ADMIXTURE. At K=4, ADMIXTURE detected European wildcat ancestry in all but one of the ancient domestic cats (from the site of Dhzankent, Kazakhstan, 1,175–1,010 cal BP) 30, and in most (8/9) modern European and Middle Eastern samples (Figure S3). At K=6, ADMIXTURE only found detectable levels of

European wildcat ancestry in two ancient samples, an 18th century cat from Ireland (Eyre_3), and a Roman cat from the Isle of Man (Perwick_1; Figure S3).

We then computed D-statistics of the form D (outgroup, FSX360/AnCorran_1/Kilton_2, Near Eastern wildcat, Domestic cat). All tests involving modern and ancient domestic cats from Europe, Turkey and North America, including Denmark, England, Ireland, Italy, Portugal, Scotland and the USA yielded significant Z values ($Z > 3$). This result shows that all European (ancient and modern), Turkish (ancient), and North American (modern) domestic cats analysed in this study possessed a degree of European wildcat ancestry (Figure S5).

The same D-statistics computed using modern cat data from the Middle East, including Iraq, Jordan, and Oman, as well as when using the genome of a Madagascan cat, were either non-significant, or borderline significant (Figure S5). This result suggests that these non-European cats possessed either fleetingly small or no European wildcat ancestry. In addition, a Central Asian ancient domestic cat from Kazakhstan and modern cats from China, South Korea and Thailand all yielded negative ($|Z| > 3$), significant, D-statistics values (Figure S5). This result suggests that these cats may possess either or both Chinese and Asian wildcat ancestry (neither of which were represented in this test), corroborating a previous genomic study of wild and domestic Chinese cats²⁹. This was confirmed through D-statistics analyses of the form D (outgroup, Chinese mountain cat, Near Eastern wildcat, Domestic cat) which showed that these individuals share significantly more alleles with Chinese mountain cat than expected under a model with no gene flow (Figure DBIEITI).

To improve our power to estimate the contribution of European wildcat ancestry in domestic cats, we computed ancestry proportions using f4 ratios (Figure S6; Supplemental Information). We used an explicit model (Figure S6), in which each domestic cat received its ancestry from European wildcats represented by AnCorran_1, Kilton_2, and FSX360 (all un-admixed wild individuals; Figure S4), and Near Eastern wildcats represented by two modern Israeli samples (FSI48 and FSI51) and a modern wildcat from the United Arab Emirates (FSI7). This analysis detected significant levels of European wildcat ancestry in eight ancient cats (Kongens_3, Perwick_1, Lyminge_20, Lincoln_1, Hungate_2, Timberyard_1, Eyre_3, Snusgar_7; Figure 3b), including the two detected by ADMIXTURE at K=6 (Figure S3). The proportion of European wildcat ancestry in cats from Ireland and Britain, identified by both f4 ratio and ADMIXTURE at K=6 (Eyre_3, Perwick_1) was 11-14%, while those only identified by f4 ratio had values less than 10%. Similar results were obtained using qpAdm (Figure S7)³¹ and struct-f4 analyses (Figure S9; Supplemental Information)³²

Overall, the proportion of European wildcat ancestry in ancient domestic cats ranged from 0 - 14% (+-2%) (Figure 3b). Slightly lower levels of European wildcat ancestry were also identified across modern domestic cats (between 0-11%; +-1%) (Figure 3b). This is consistent with the results of recent analyses that estimated the proportion of Chinese mountain cat ancestry in Chinese domestic cat genomes²⁹, though the restricted distribution of the Chinese mountain cat significantly lowers opportunities for introgression into domestic cats. Overall, the relatively low proportion of wild ancestry found in domestic cats is much more similar to dogs, and substantially less than the reported percentages in pigs^{14,15}, sheep¹⁶, goats^{17,18}, bees¹⁹, chickens²⁰ and cattle^{21,22}.

Near Eastern mitochondrial haplogroups present in European wildcats

These low levels of hybridization between wildcats and domestic cats raises the possibility that the Near Eastern wildcat ancestry identified in the European wildcats was not mediated by admixture with domestics. If true, this would undermine the use of mitochondrial data as a definitive proxy to determine the domestic status of ancient cats. Domestic cats, and Near Eastern and European wildcats belong to two mitochondrial haplogroups: I and IV¹. Haplogroup I is found exclusively in European wildcats, while haplogroup IV is

found in all domestic and Near Eastern wildcats, as well as in multiple European wildcats. The presence of haplogroup IV in European wildcats has traditionally been interpreted as the result of hybridization with domestic cats¹, though it is possible that these signatures were introduced into European wildcats through hybridization with Near Eastern wildcats living in the admixture zone at the edge of their distribution¹¹.

We found that all four Near Eastern wildcats (labelled *Felis lybica* in [Figure S13](#); [Figure S14](#)) and all 22 modern domestic cats analysed here belonged to haplogroup IV ([Figure S13](#); [Figure S14](#)). However, haplogroup I was found in 10 out of the 16 modern European wildcats, while the other six possessed haplogroup IV (IV-A; see individual highlighted in Figure S13-14). Intriguingly, haplogroup IV was also found in the three Eastern German wildcats, two of which had low levels of Near Eastern wildcat ancestry (3-4%; *Felis silvestris_ex9*, *Felis silvestris_ex19*; [Figure S8](#)), and one possessed >10% Near Eastern wildcat ancestry (*Felis silvestris_ex38*). This suggests that they did not acquire their mitochondrial genome through very recent admixture with domestic cats (i.e. ~3-5 generations ago). All modern European wildcats with haplogroup IV, however, aside from a single individual from Scotland, possessed sub-haplogroup IV-A, which was also most frequently identified in previous studies of domestic cats¹. This sub-haplogroup was also the most common in both our total dataset (~74% of all domestic cats), and in specific geographical populations, including ancient cats from Britain and Ireland (28 of 43 cats dated between 339 BCE - 1,799 CE). This suggests that sub-haplogroup IV-A in wild cats could have been acquired through gene flow with domestic cats.

Altogether, while the presence of haplogroup IV-A in European wildcats is, at least to some degree, due to admixture with domestic cats, the low-level Near Eastern wildcat ancestry in the Eastern German cats raises the possibility that ancient, natural hybridization, in the admixture zone of southeastern Europe and Anatolia resulted in the spread of haplogroup IV into European wildcats. This suggests that mitochondrial data alone may not provide an adequate proxy to determine the domestic status of ancient cats, or to assess the timeframe of their dispersal into Europe.

Conclusions

Our analyses indicate that domestic cats with Near Eastern nuclear ancestry were present in Britain by at least ~2,000 years ago (1,926 - 1,827 cal. BP; *Fishbourne_2*), and that European wildcats and domestic cats have been coexisting in Northern Europe ever since. Despite this long-term co-existence, 30 of the 35 domestic cats analysed in this study possessed less than 10% of their ancestry from European wildcats, and 17 out of 35 possessed less than 5%. This proportion of wildcat ancestry in both ancient and modern domestic cats is substantially less than many other introduced domestic taxa, and more similar to dogs³³. In addition, mitochondrial analyses of four cats from the English Medieval site of Kilton Castle ([Table S1](#)) revealed individuals with both sub-haplogroup IV-A (2/4), the most globally common haplogroup in modern domestic cats, and haplogroup I (2/4), which is only found in European wildcats, co-existed at the site. Nuclear analyses of one of the wildcats from Kilton Castle that possessed haplogroup I (*Kilton_2*) revealed a lack of any domestic cat ancestry (Supplemental Information; [Figure S4](#)), indicating that introgression from domestic cats into European wildcats was limited in the past.

These results indicate that although domestic cats were not subjected to strong, conscious selection by people until the last century, they acquired biological adaptations, as the result of their association with people, that led to at least partial reproductive isolation from European wildcats. While domestic cats possess the ability to tolerate living in anthropogenic environments with much higher population density (Biró et al. 2004), they are also likely to be competitively excluded by larger, more aggressive, wildcats in other habitats with less abundant food. Combined with differences in male reproductive behaviour (i.e. male wildcats are only reproductively active in winter and spring while domestic cats are active all year), this ecological separation likely reduced both the opportunity for hybridisation, and the ability of hybrids to survive (Germain et al. 2008).

Despite this resistance to introgression, several studies have presented evidence for recent gene flow from domestic cats into indigenous European wildcat populations, including in France¹¹ and Scotland²⁸. In Britain, this was likely triggered by a drastic reduction of the range of wildcats, which began prior to the 19th century^{34,35} which intensified in the second half of the 20th century³⁶. This indicates that habitat degradation and the encroaching human presence has led to the erosion of the reproductive isolation that had maintained the genomic integrity of domestic and European wildcats for at least two thousand years.

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Data Availability:

The raw FASTQ files for the DNA Sequencing data have been deposited on the European Nucleotide Archive (<https://www.ebi.ac.uk/ena/browser/home>) under project ID PRJEB57412.

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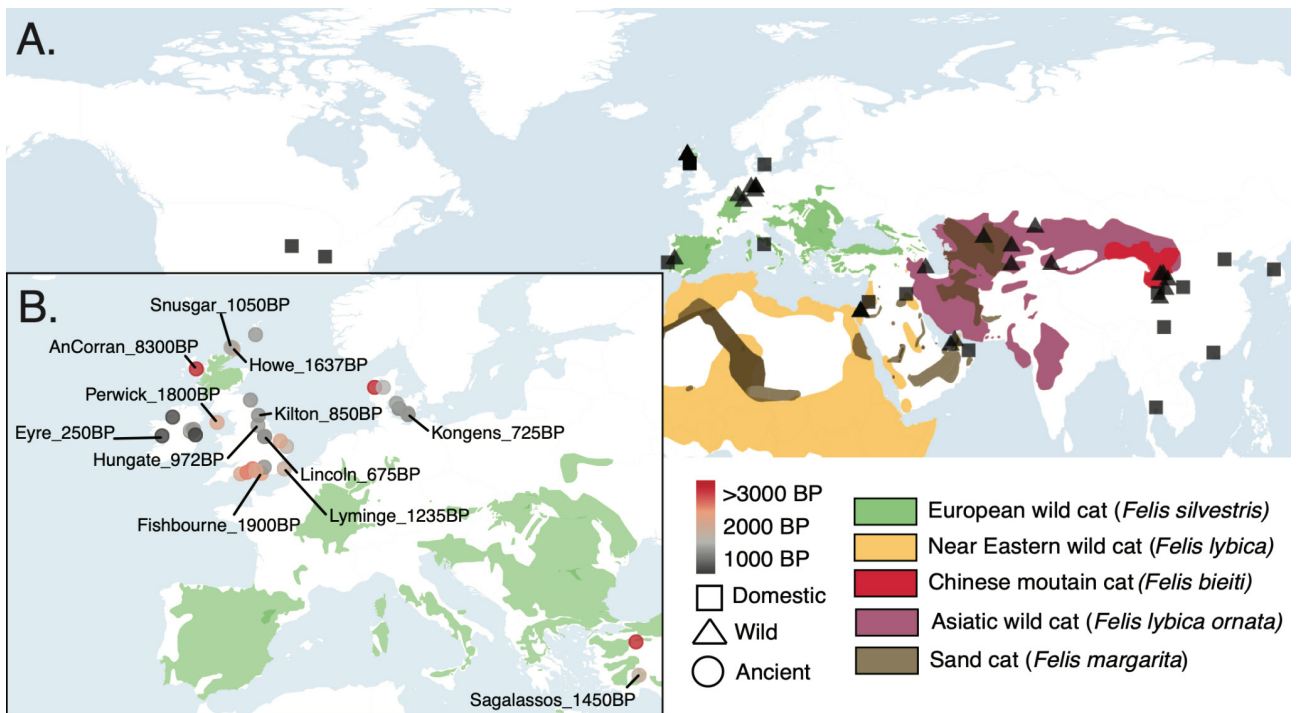


Figure 1. Location of cat samples sequenced in this study. Maps representing the geographical range of the *Felis* species investigated in this study (except for *Felis chaus*, which was used as an outgroup). The data (shape files) for this plot were obtained from the IUCN Red List database³⁷. **A.** Location of modern genomes analysed in this study **B.** Location and age of ancient cat samples for which DNA information (either mtDNA, nuclear or both) was obtained. The archeological sites from which samples possessing enough DNA to generate nuclear data are highlighted (time Before Present [BP]).

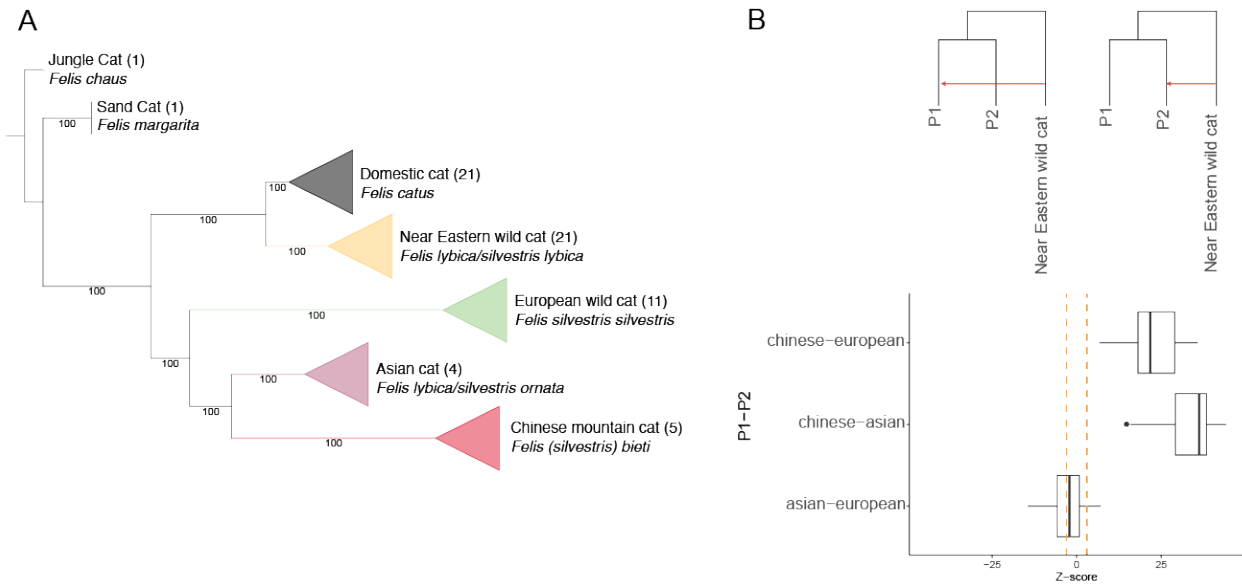


Figure 2. Nuclear phylogeny and admixture between wildcat species. **A.** Maximum likelihood tree built using genome-wide SNP data (Supplemental Information). Support values based on 100 bootstrap replicates are indicated near the nodes; values in brackets represent the number of samples in each collapsed clade. Species name reflects the two most used taxonomic nomenclatures by Driscoll et al.¹ and Kitchener et al.²⁶ **B.** Z-score obtained from D-statistics of the form $D(\text{outgroup [Jungle cat]}; \text{Near Eastern wildcat}; P1, P2)$.

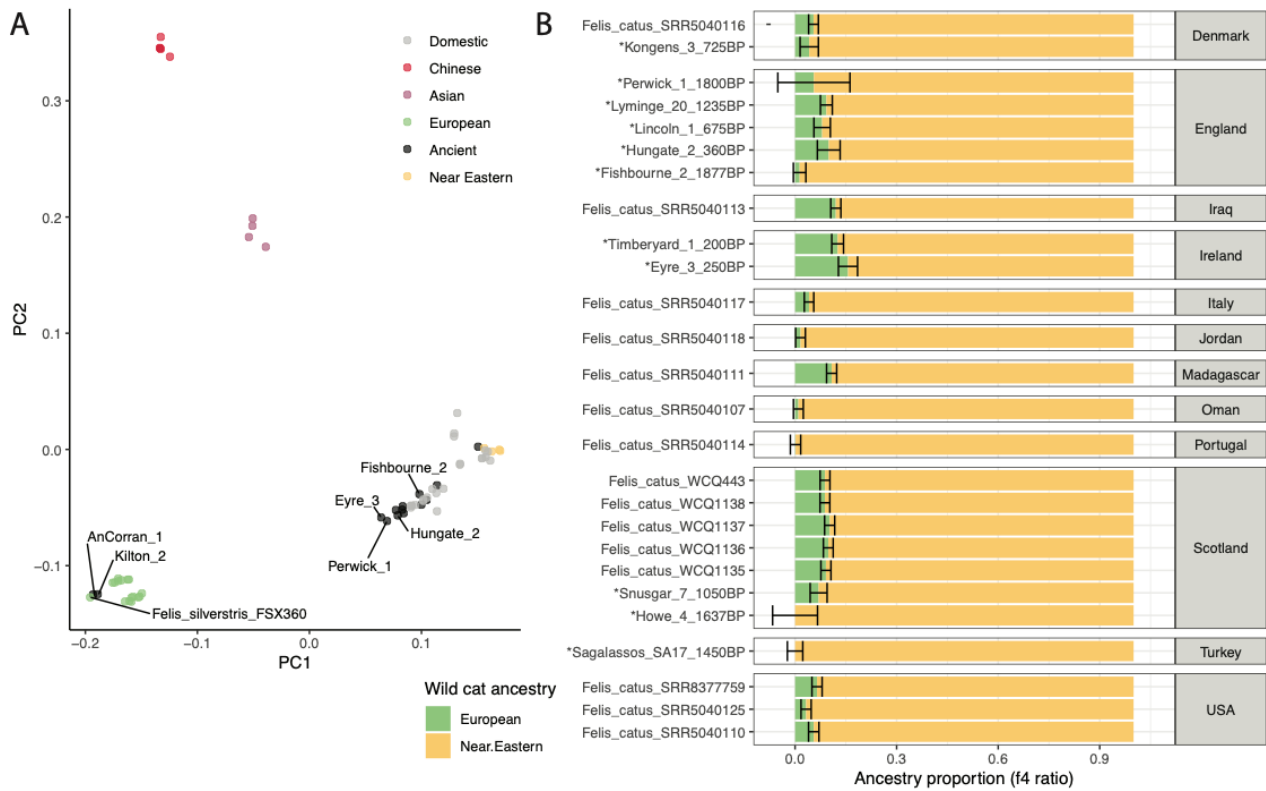


Figure 3 Principal component and f4 ratio. **A.** Principal component analysis (PCA) built using 67 genomes, including 14 ancient cat genomes (projected). **B.** Proportion of European wildcat ancestry in modern and ancient (denoted by an *) domestic cat genome computed using an f4 ratio as described in Figure S6. Error bars represent standard errors computed across multiple f4 ratio using different European (AnnCorran_1, Kilton_2 and Felis_silverstris_FSX360) and Near Eastern (Felis_lybica_lybica_FSI47, Felis_lybica_lybica_FSI48, Felis_lybica_lybica_FSI51, Felis_lybica_lybica_FSI7) wildcats as sources.