

Origins and spread of domestic cats in Europe through the lens of Ancient DNA



Egyptian cat mummies
(photo: British Museum)

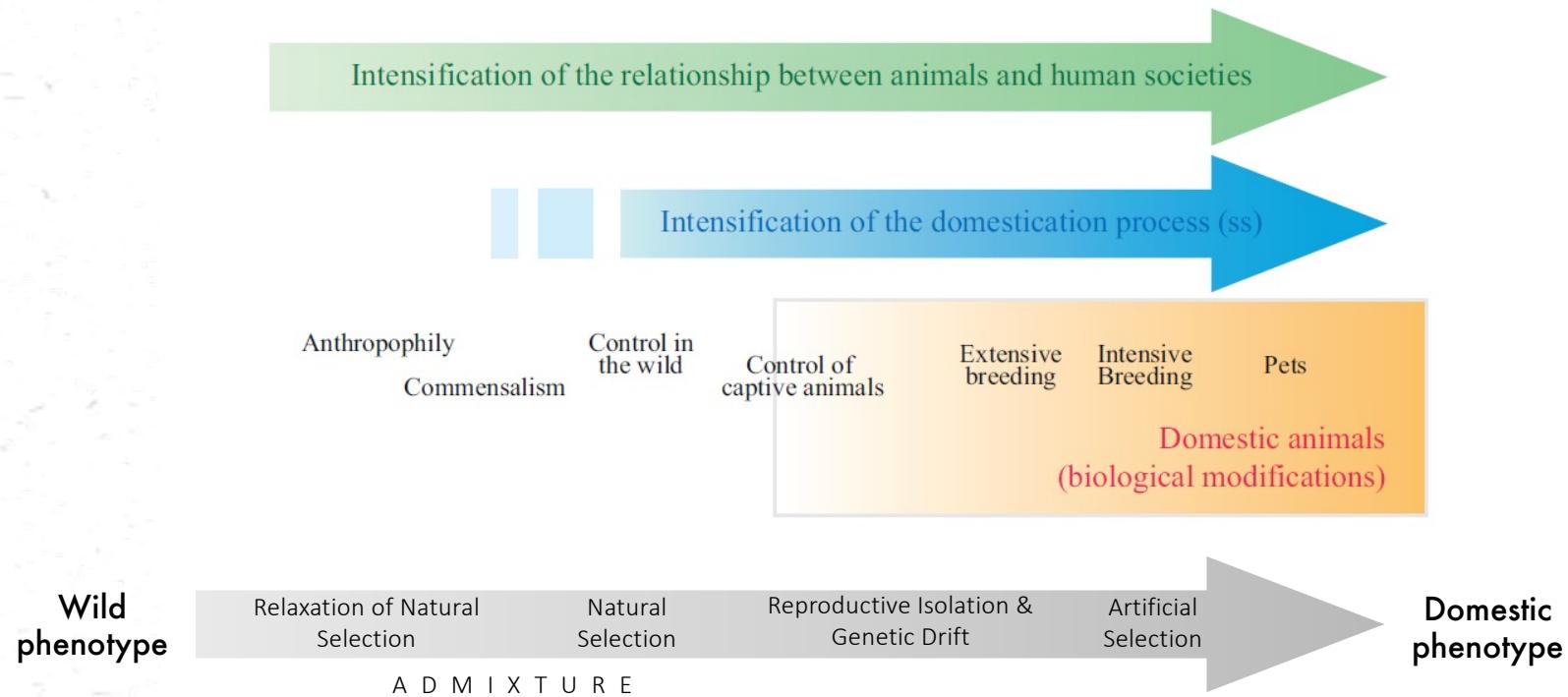
Claudio Ottoni

University of Rome Tor Vergata, Department of Biology

SIBE Summer School, 9 September 2025

Domestication

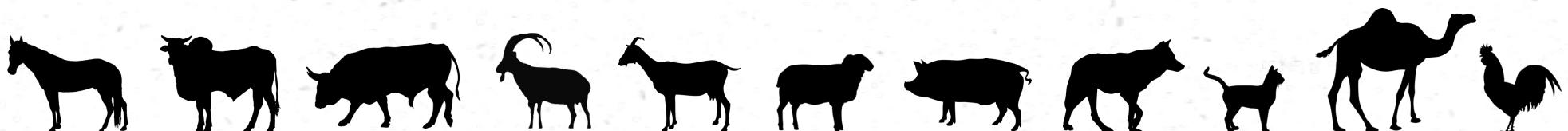
A long-term continuous process



(mod from Vigne 2011, Zeder 2012)

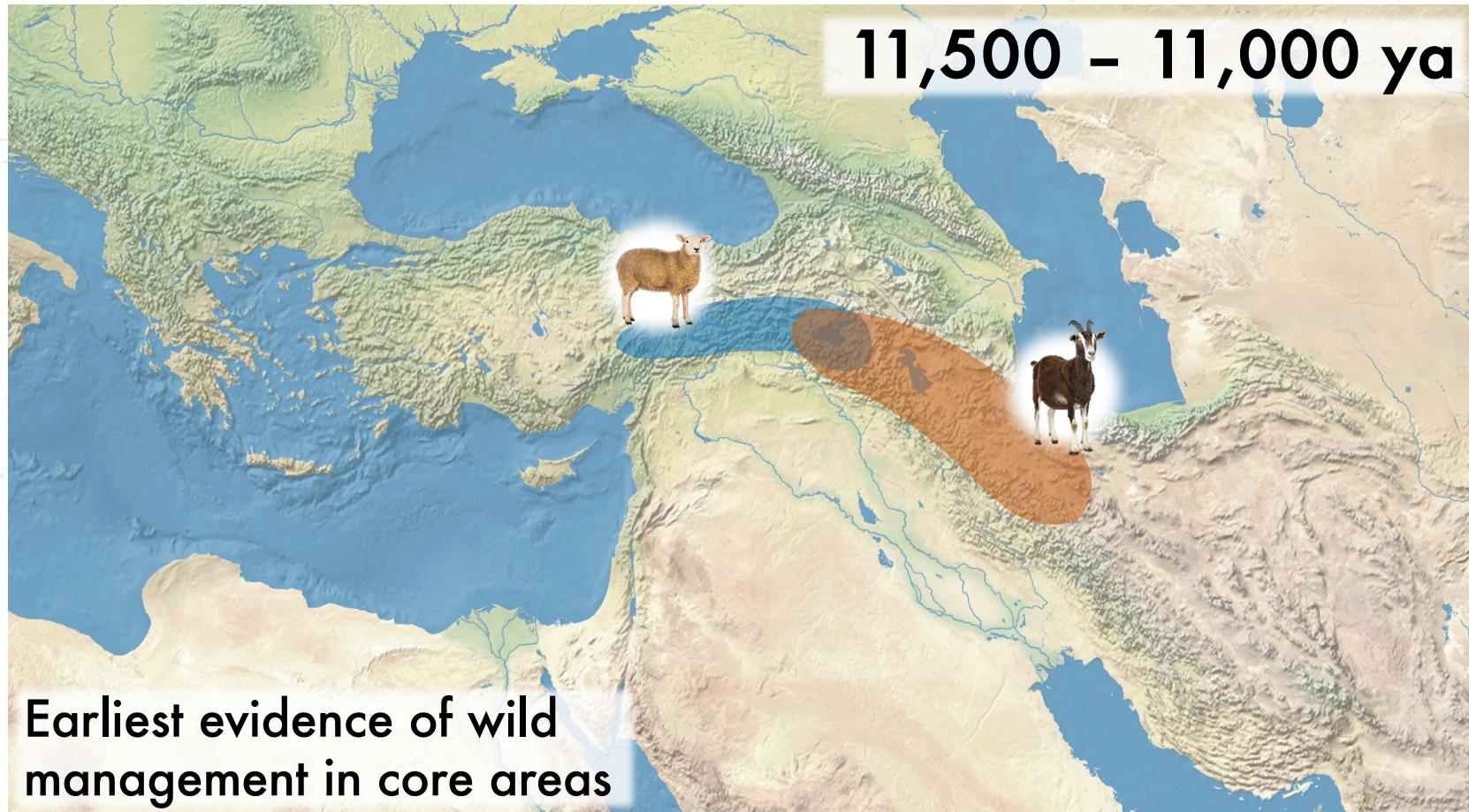
Key questions

When ?
Where ?
How?



Archeozoology

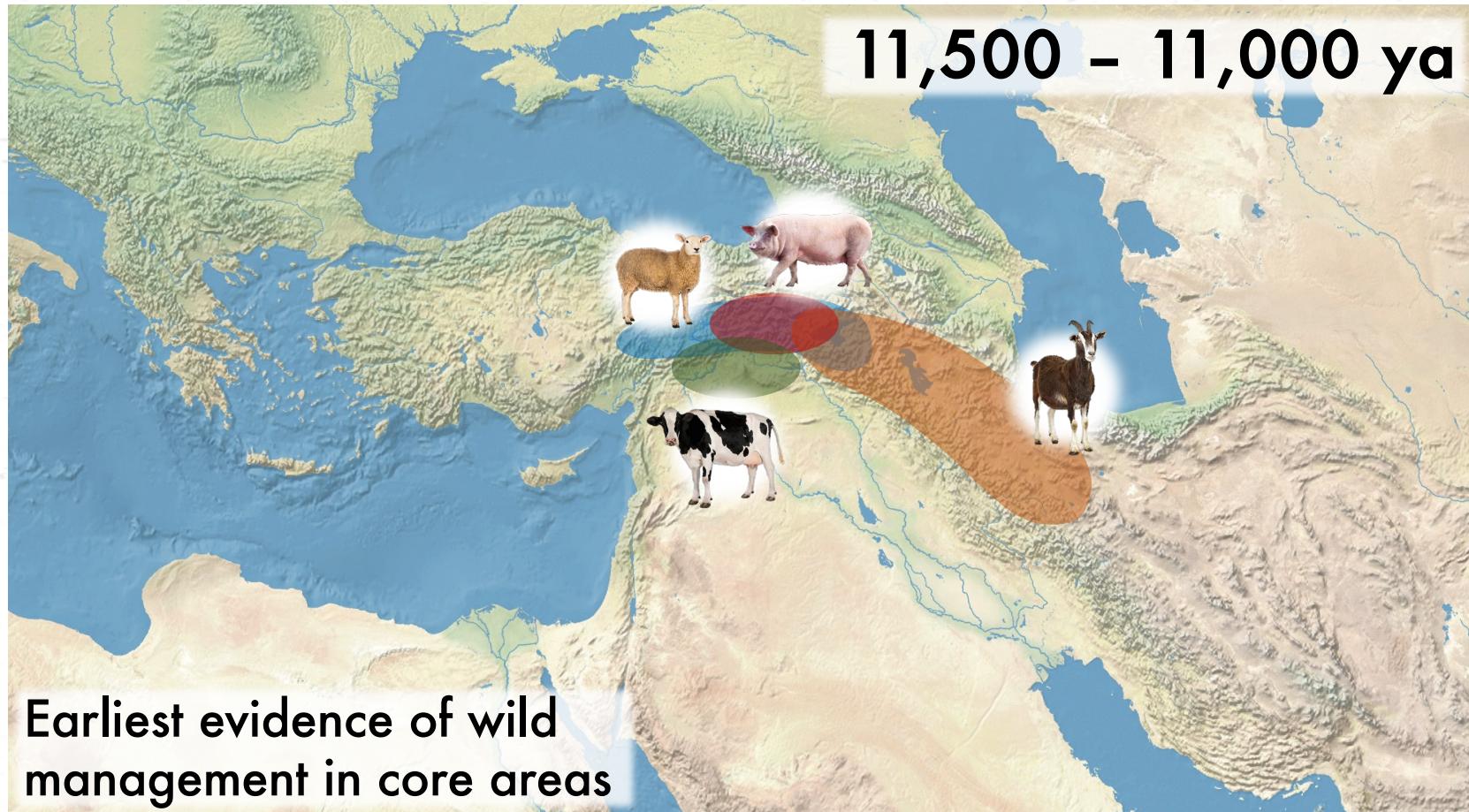
Wild ancestors and early management



Adapted from Zeder 2008 (PNAS)

Archeozoology

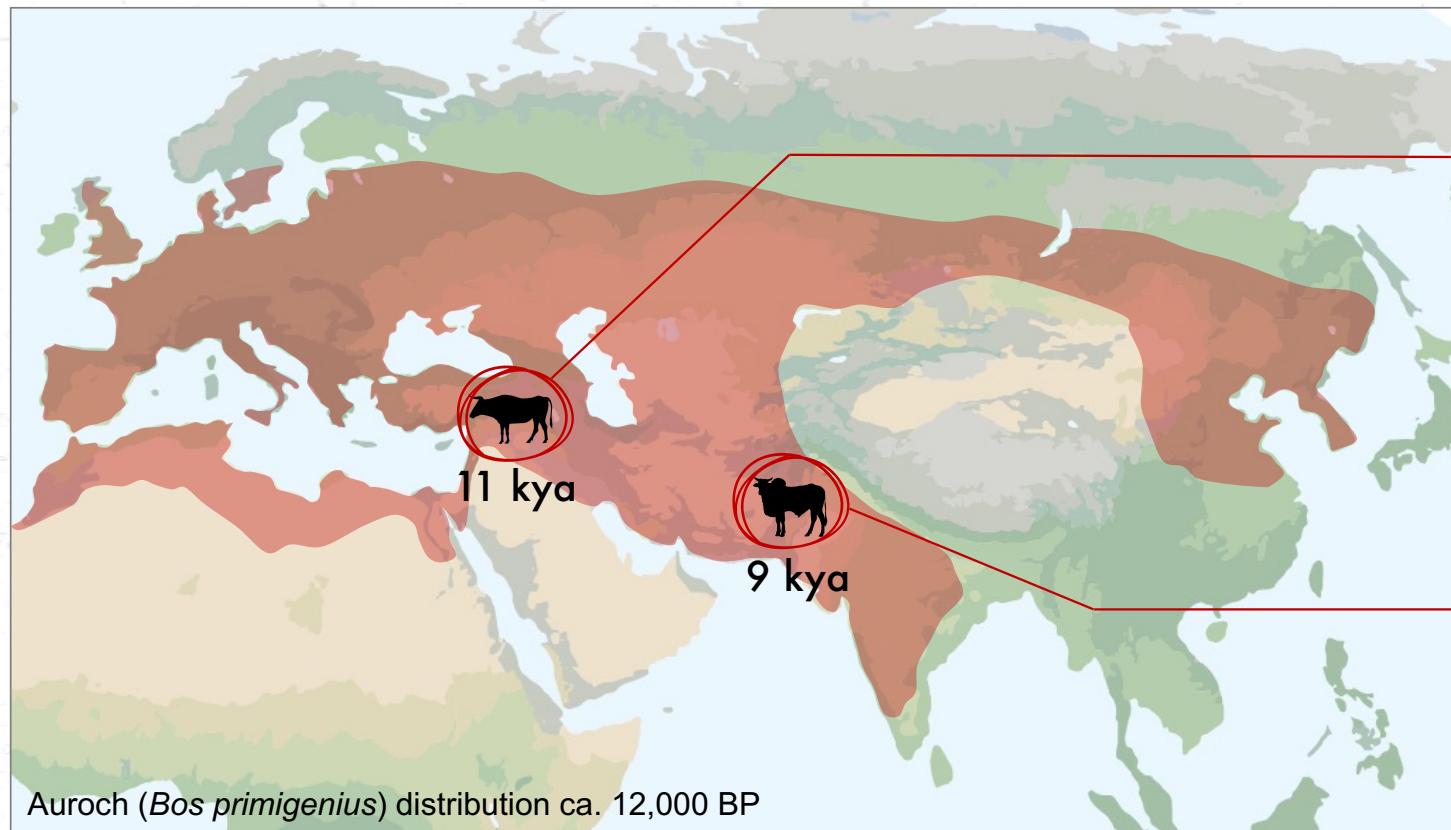
Wild ancestors and early management



Adapted from Zeder 2008 (PNAS)

Cattle

Archaeological and genetic evidence



Taurine cattle
Humpless (*Bos taurus*)

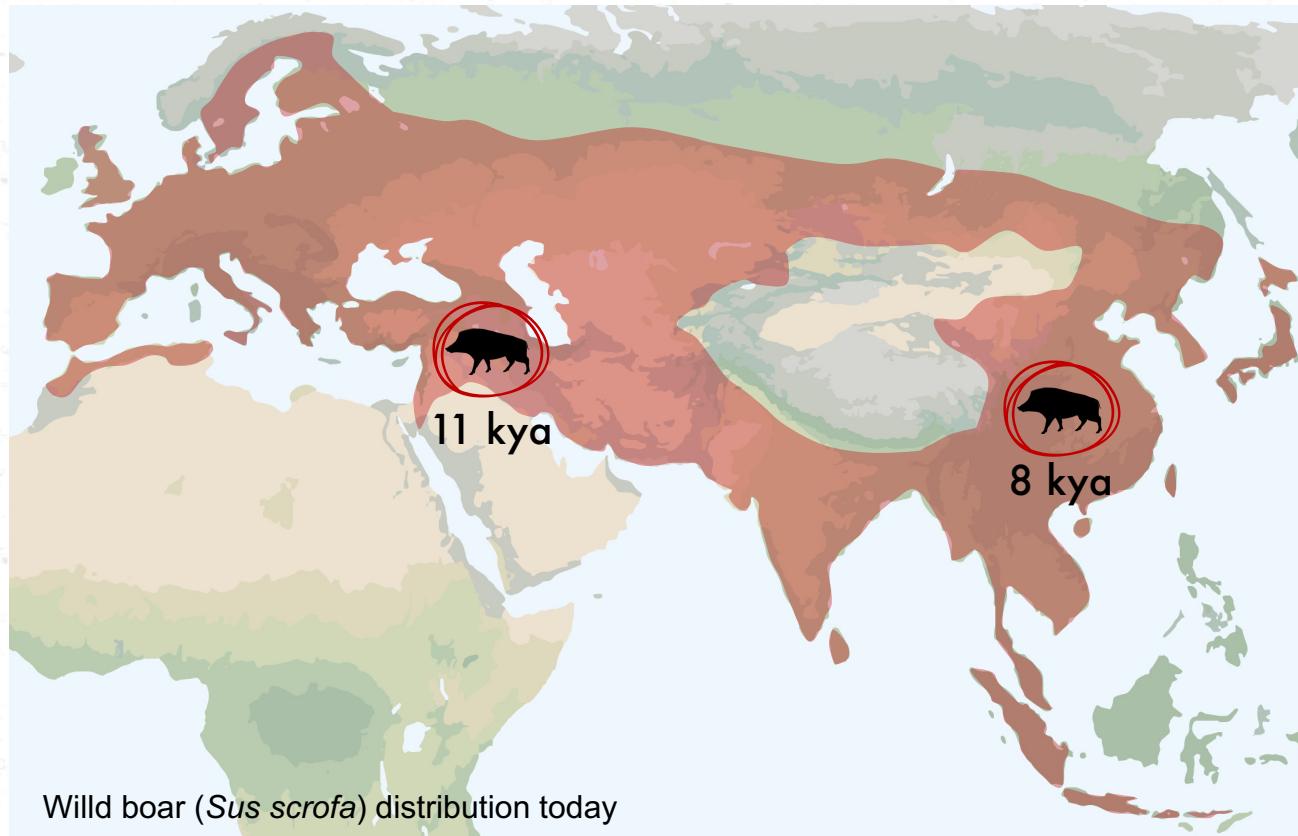


Zebu cattle
Humped (*Bos indicus*)

Two domestication centers

Pig

Archaeological and genetic evidence



Pig
(*Sus scrofa*)

Two domestication
centers

Dog

Archaeological and genetic evidence



Dual ancestry of domestic dogs

Initial domestication in east Eurasia.
Secondary contribution from
Southwest Asian wolves.

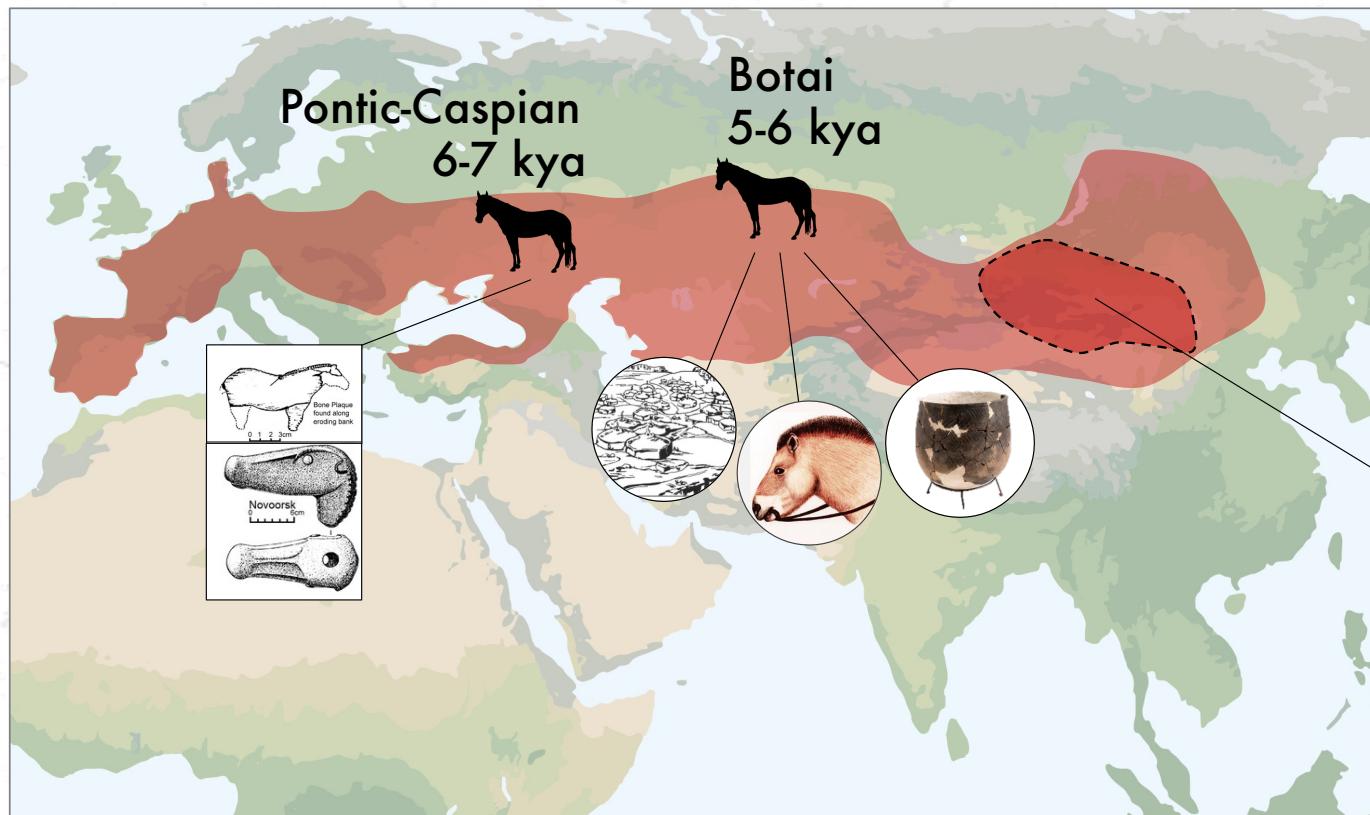
Independent domestication
process or admixture from
local wolves?



Dog
(*Canis familiaris*)

Horse

Cultural evidence and distributions



Horse
(*Equus caballus*)



Przewalski horse
(*Equus ferus ssp. przewalskii*)
considered as the last true remaining wild horses, never domesticated. Extinct and then reintroduced in reserves.

Distribution from Wutke 2016, adapted from Benecke (2002); Sommer et al. (2011); Warmuth et al. (2012).

Cat Domestication

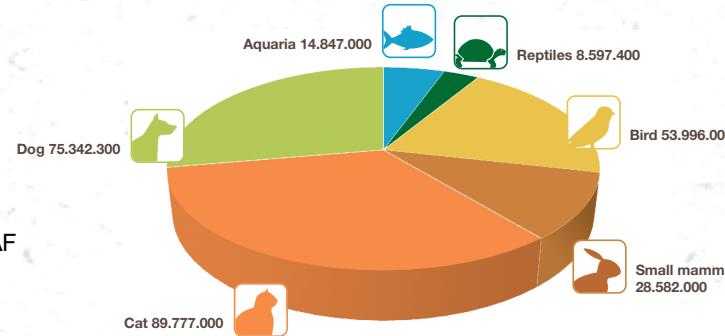


Popularity of Cats

24%

of European households (dog: 21%)

Source: FEDIAF



6,5 billion photos

Source: BBC

2 million videos



Source: CNN



Tardar Sauce (Grumpy Cat)



Lil Bub



Motimaru

The cat domestication conundrum

No evident physical skeletal changes
What is wild? What is domestic?



Felis silvestris lybica
(ancestor of domestic cats)



Felis silvestris catus
(domestic cat)

GMM of mandibles, higher resolutions, more promising

(Vigne et al. 2016)

The cat domestication conundrum

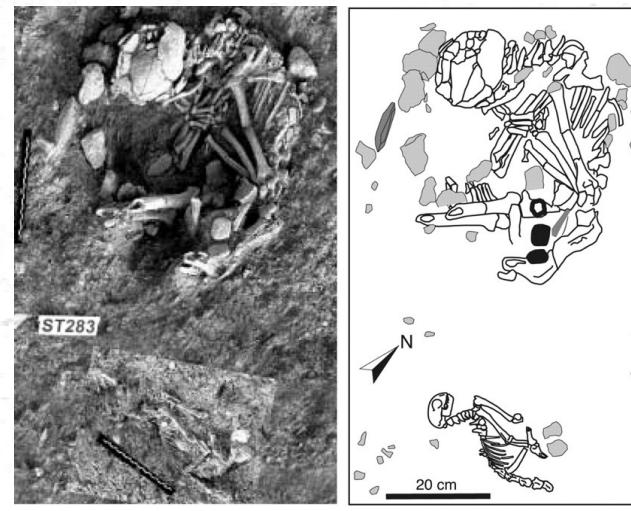
Cats are (relatively) rare
in the archaeological records



Traditional zooarchaeological
approaches are difficult

Archeological evidence

Cyprus



Cats are not native to Cyprus

Their earliest introduction is documented by remains at Klimonas, 11,100-10,600 ya (PPNA)

Shillourokambos – 9,500 ya

(Vigne et al. 2004)

Archeological evidence

Cyprus



Shillourokambos – 9,500 ya

Archeological evidence

Cyprus

Spiritual link between
cats and humans?



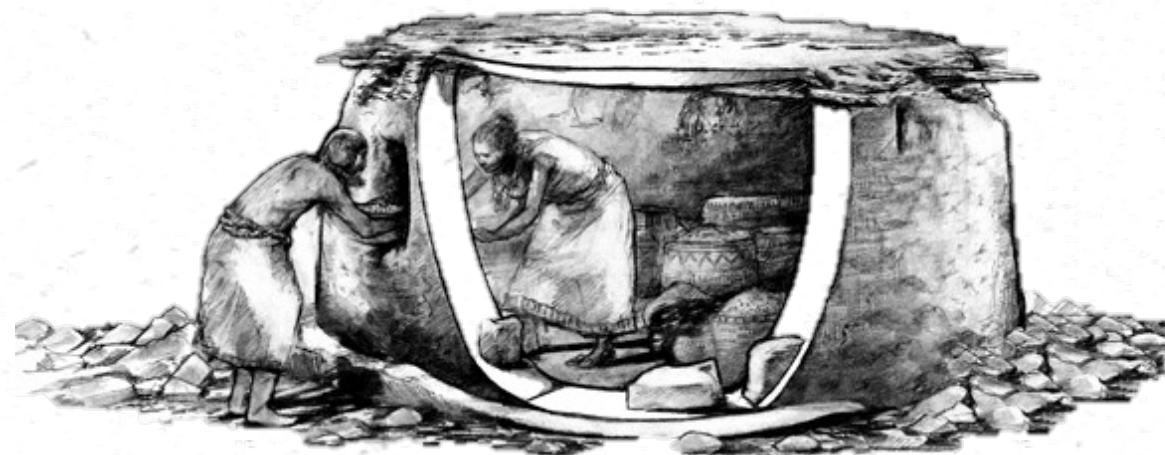
Shillourokambos – 9,700 ya

(Guilaine 2000)

Archeological evidence

Cyprus & the Levant

Neolithic and the onset of farming in the Near East ~11,500 ya.



Reconstruction of a granary in Jordan at Dhra', 11 kya

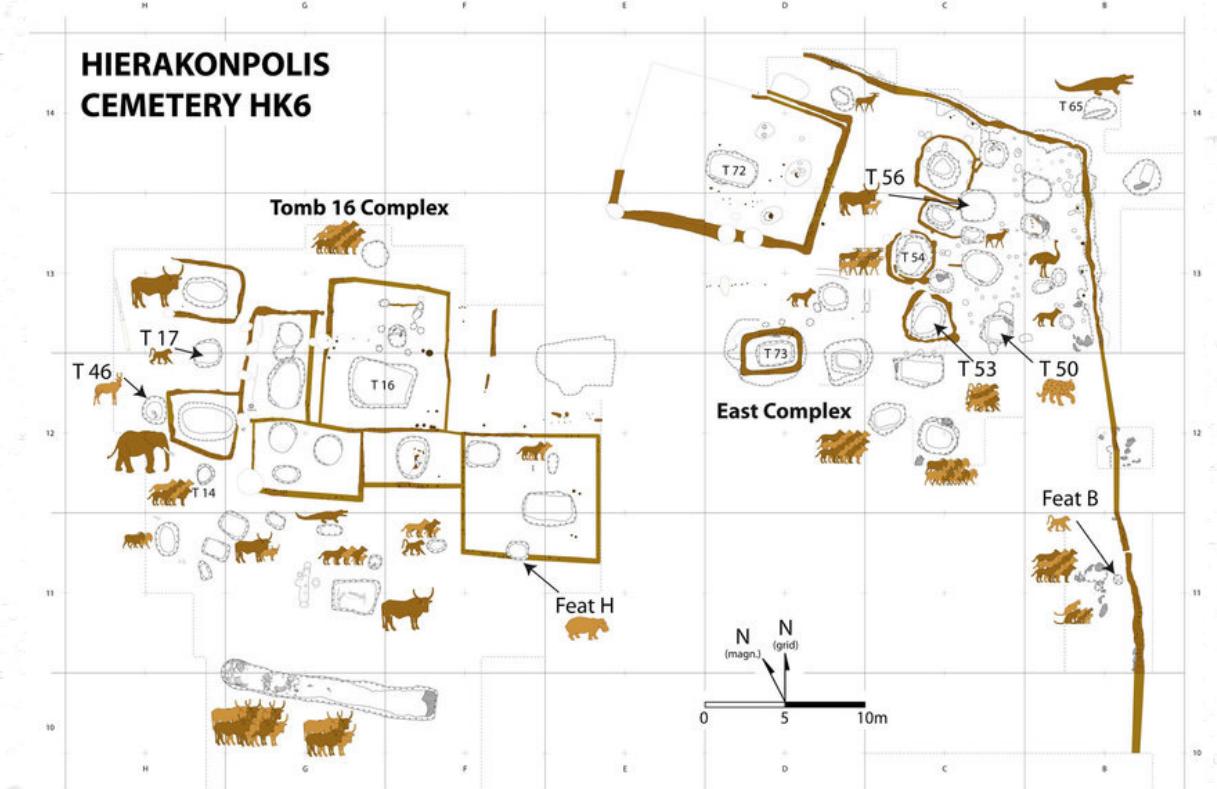
(Kuijt & Finlason 2009, PNAS)

Commensalism

Cats were attracted by pests, vermin and food scraps, keeping them away from food storage areas.

Archeological evidence

Egypt



Hierakonpolis – 5,700 ya

(Van Neer et al. 2014)

Archeological evidence

Egypt



Cats held in captivity

Earliest evidence of cat-human interaction in Egypt based on archaeozoological evidence.

Hierakonpolis – 5,700 ya

(Van Neer et al. 2014)

Archeological evidence

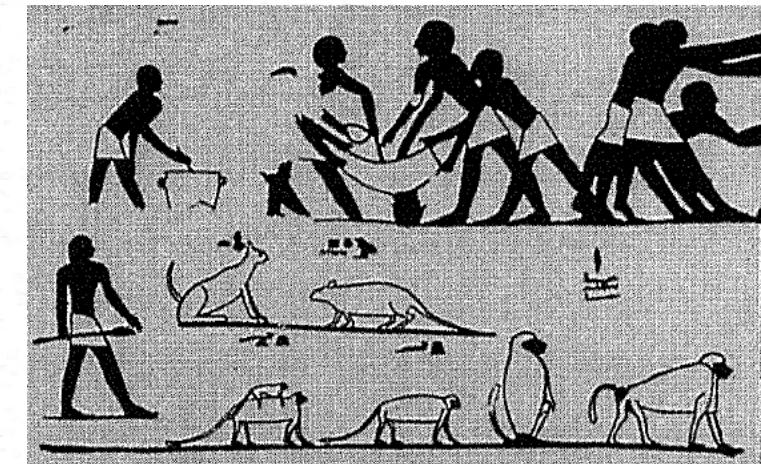
Egypt



Wall relief at El-Lisht (2236-2143 BC)



Saqqara (1950 BC)



Tomb of Beni Hasan (1950 BC)

Funerary contexts – 4,000 ya

(Malek 1997)

Archeological evidence

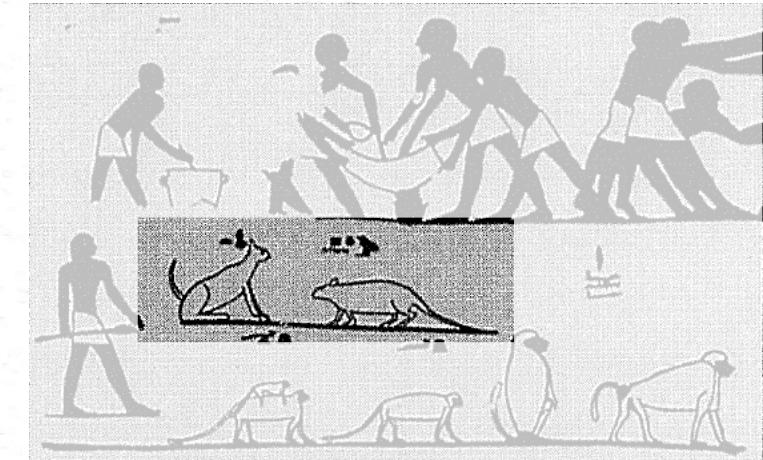
Egypt



Wall relief at El-Lisht (2236-2143 BC)



Saqqara (1950 BC)



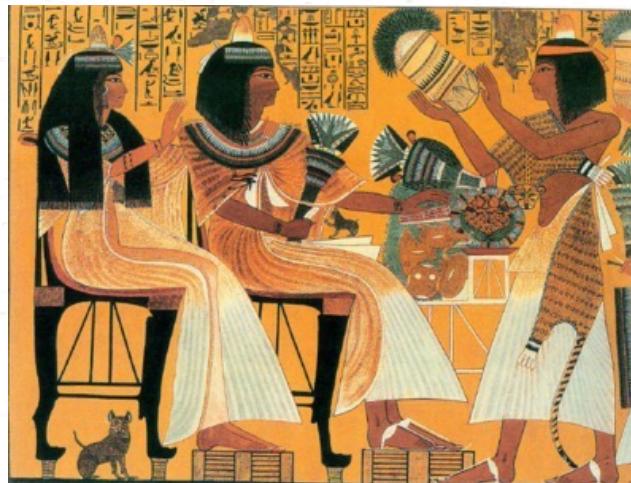
Tomb of Beni Hasan (1950 BC)

Funerary contexts – 4,000 ya

(Malek 1997)

Archeological evidence

Egypt



Tomb of Ipuay (1250 BC)



Tomb of Nebamun and Ipuky (1360 BC)



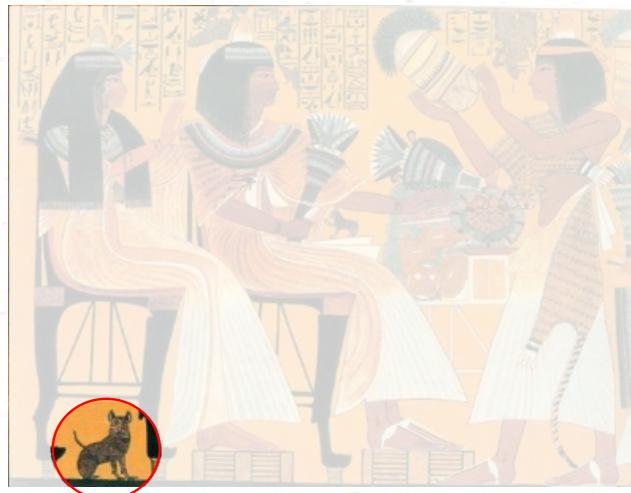
Tomb of May (1450 BC)

Iconography – 3,500 ya

(Malek 1997)

Archeological evidence

Egypt



Tomb of Ipuay (1250 BC)



Tomb of Nebamun and Ipuky (1360 BC)



Tomb of May (1450 BC)

Iconography – 3,500 ya

(Malek 1997)

Archeological evidence

Egypt



Cult of the
goddess
Bastet

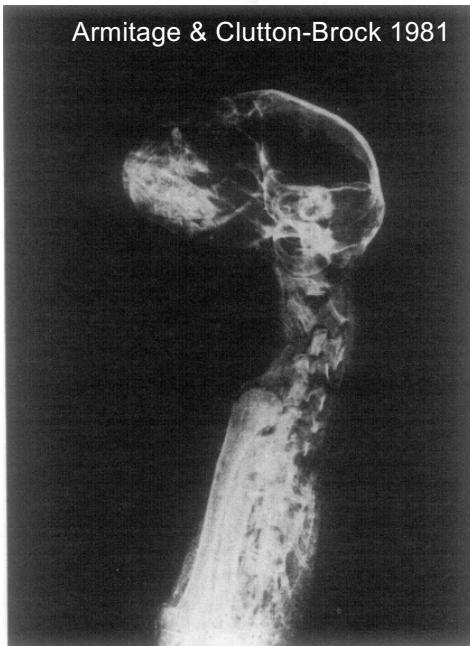
Cat statuette and Bastet statuette
(photos: Metropolitan Art Museum New York)

1st mill BC – 4th cent. AD

Archeological evidence

Egypt

Armitage & Clutton-Brock 1981



Egyptian cat mummy
(credits: NHM)

Votive offerings

Cats were held in households, but also in temple precincts and killed as votive offerings to the goddess Bastet.

1st mill BC – 4th cent. AD

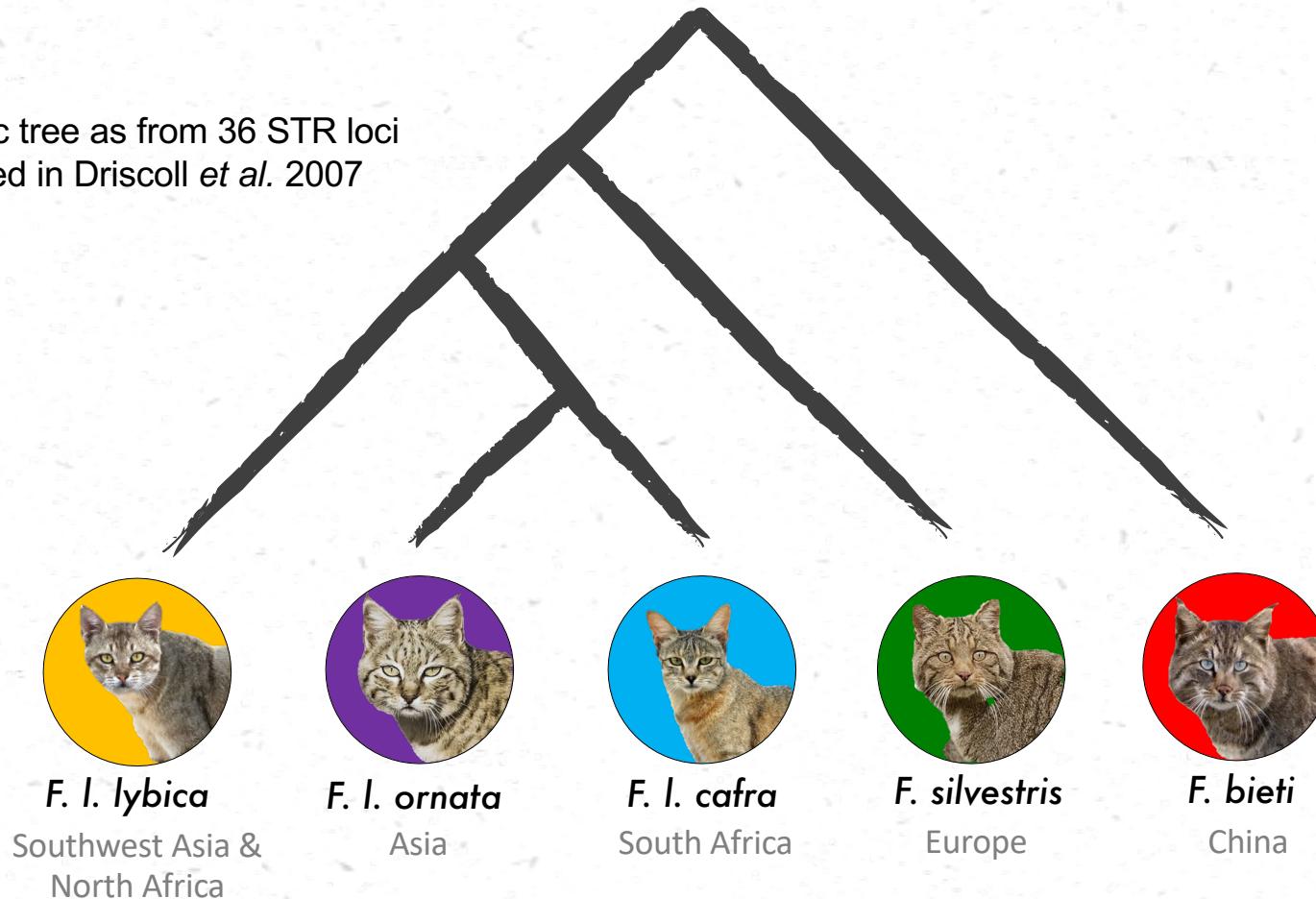
Wildcat distribution



Genetic evidence

Modern DNA

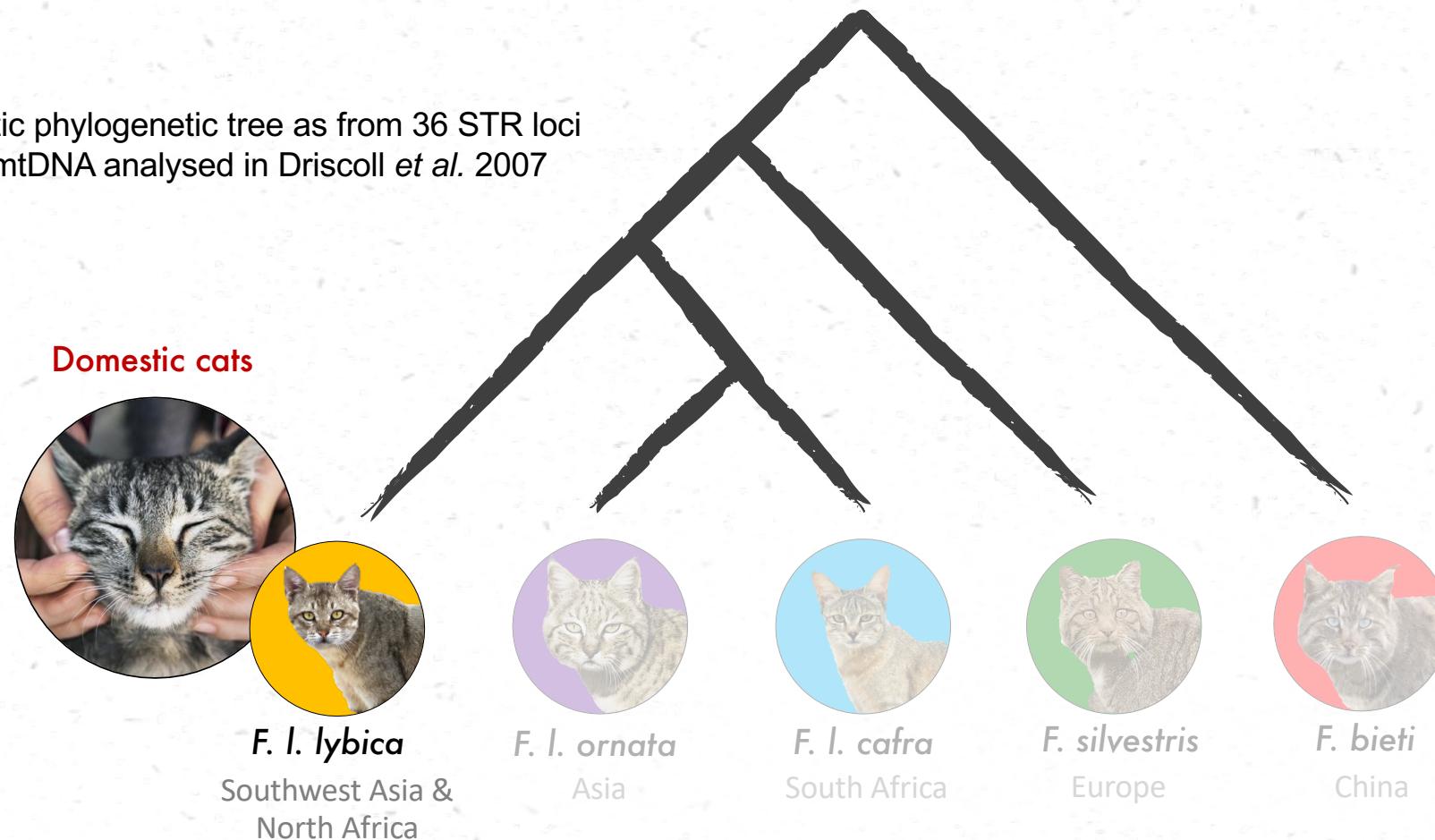
Schematic phylogenetic tree as from 36 STR loci
and the mtDNA analysed in Driscoll et al. 2007



Genetic evidence

Modern DNA

Schematic phylogenetic tree as from 36 STR loci
and the mtDNA analysed in Driscoll et al. 2007



Genetic evidence

Ancient DNA

Over 350 specimens investigated (of which 52 mummies)
209 mtDNAs reconstructed



Sampling cat mummies at the
NHM of London (2012)



Eva-Maria Geigl



INSTITUT
JACQUES
MONOD



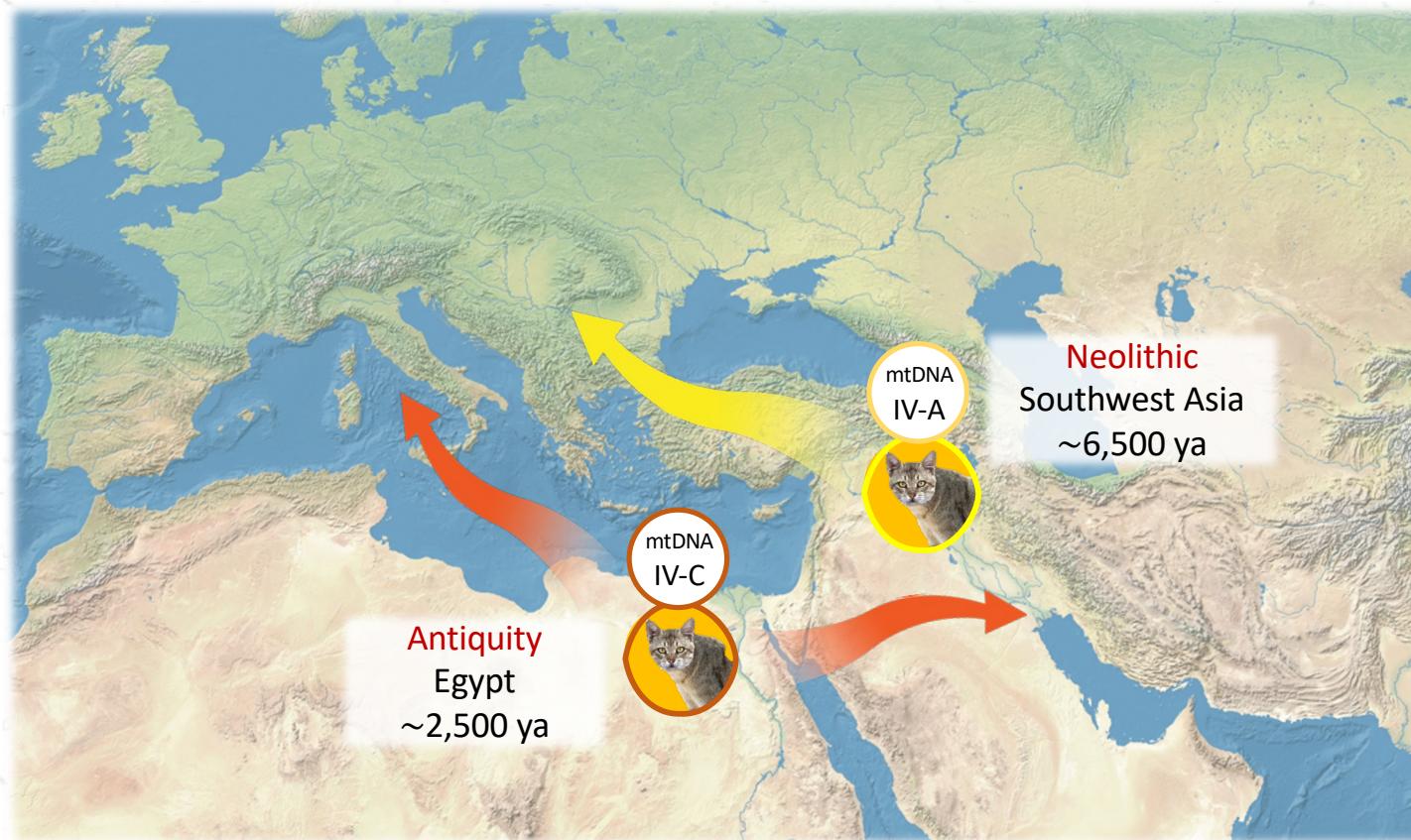
Thierry Grange



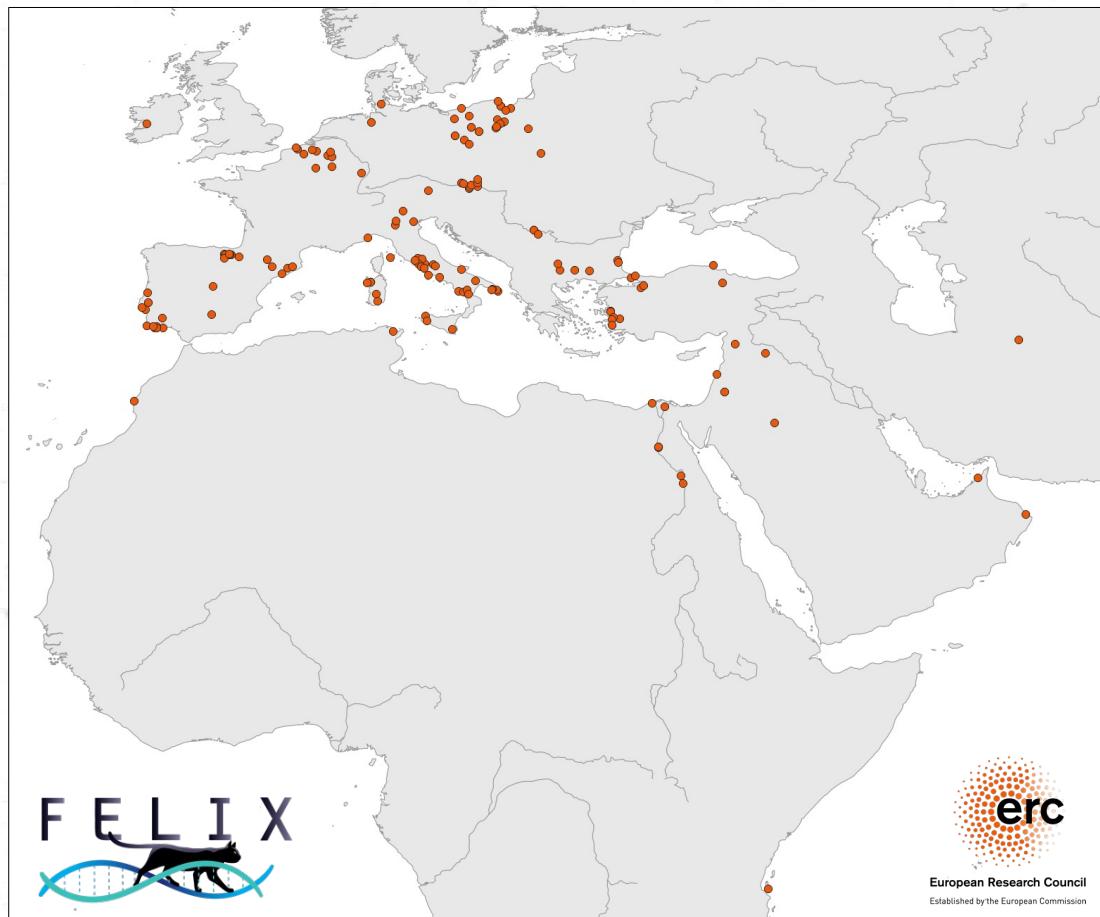
Wim Van Neer
Bea De Cupere
Ronny Decorte

mtDNA from ancient cats

Two main genetic contributions



Ancient cat remains



~1,400 cat remains

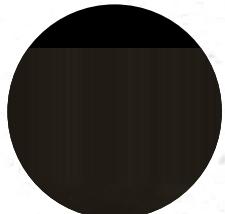
last ~15,000 years



Teeth, mandibles



Petrosal bone



Long bones



Pelvis



Dental calculus



Cat mummy (NHM)

University of Rome Tor Vergata

Department of Biology



Pre-PCR

Ancient DNA laboratory
Villa Mondragone (Frascati)

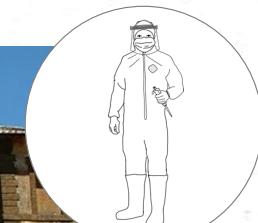


Post-PCR

Department of Biology
Ecologia Sperimentale e Acquacoltura (Roma)

University of Rome Tor Vergata

Department of Biology



Pre-PCR

Ancient DNA laboratory
Villa Mondragone (Frascati)



Post-PCR

Department of Biology
Ecologia Sperimentale e Acquacoltura (Roma)

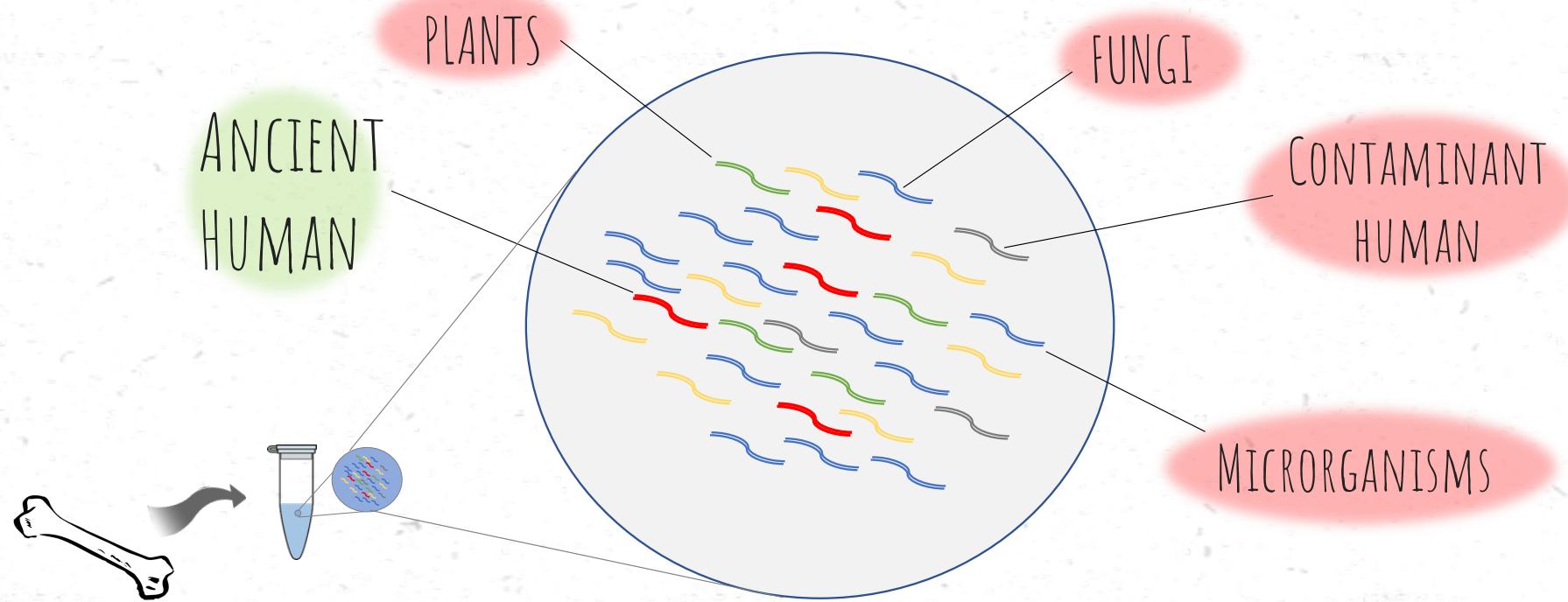
Precautions



Image edited from "Adventures in Archaeological Science" (Warinner C. ed.; Max Planck Institute)

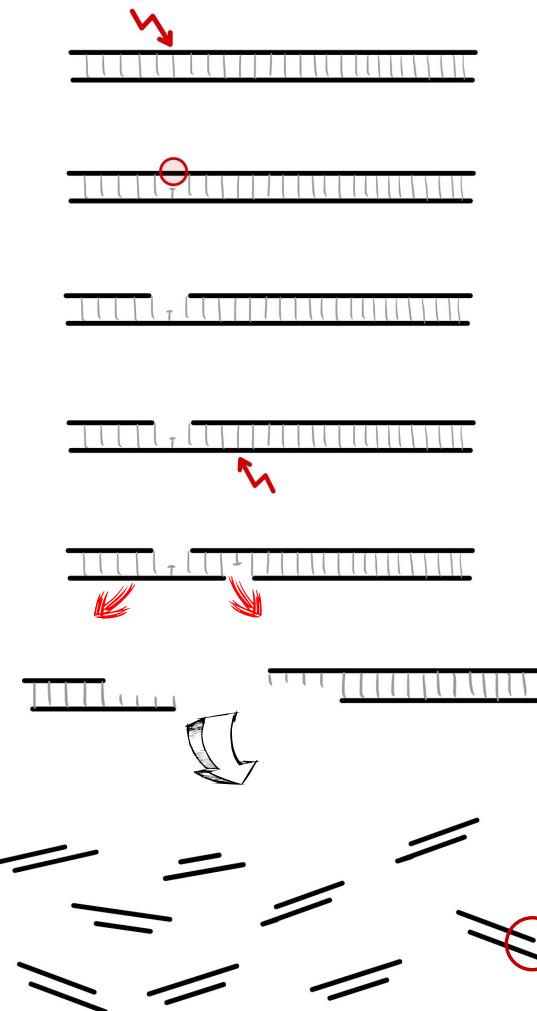
Ancient DNA features

aDNA extracts are metagenomic mixtures



% ENDOGENOUS vs EXOGENOUS DNA

Ancient DNA features



DNA depurination (1)

Abasic site

Beta-elimination and 'nick' formation (1)

DNA depurination (2)

'Nick' formation (2)

Strand break with overhangs

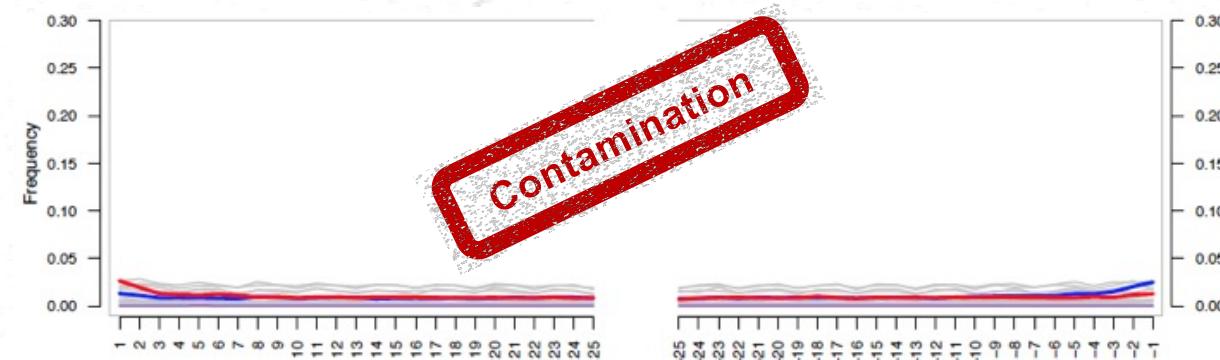
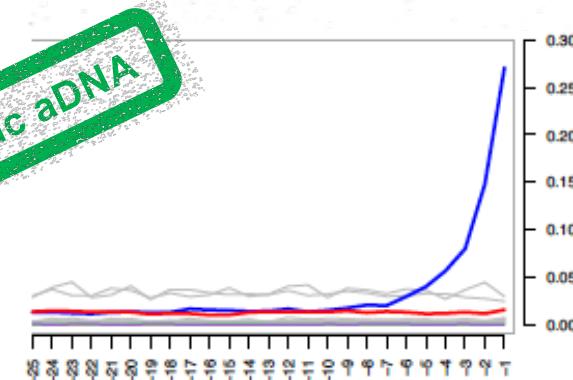
Fragments with single-stranded end (overhangs)

Ancient DNA features

5'-end: C->T



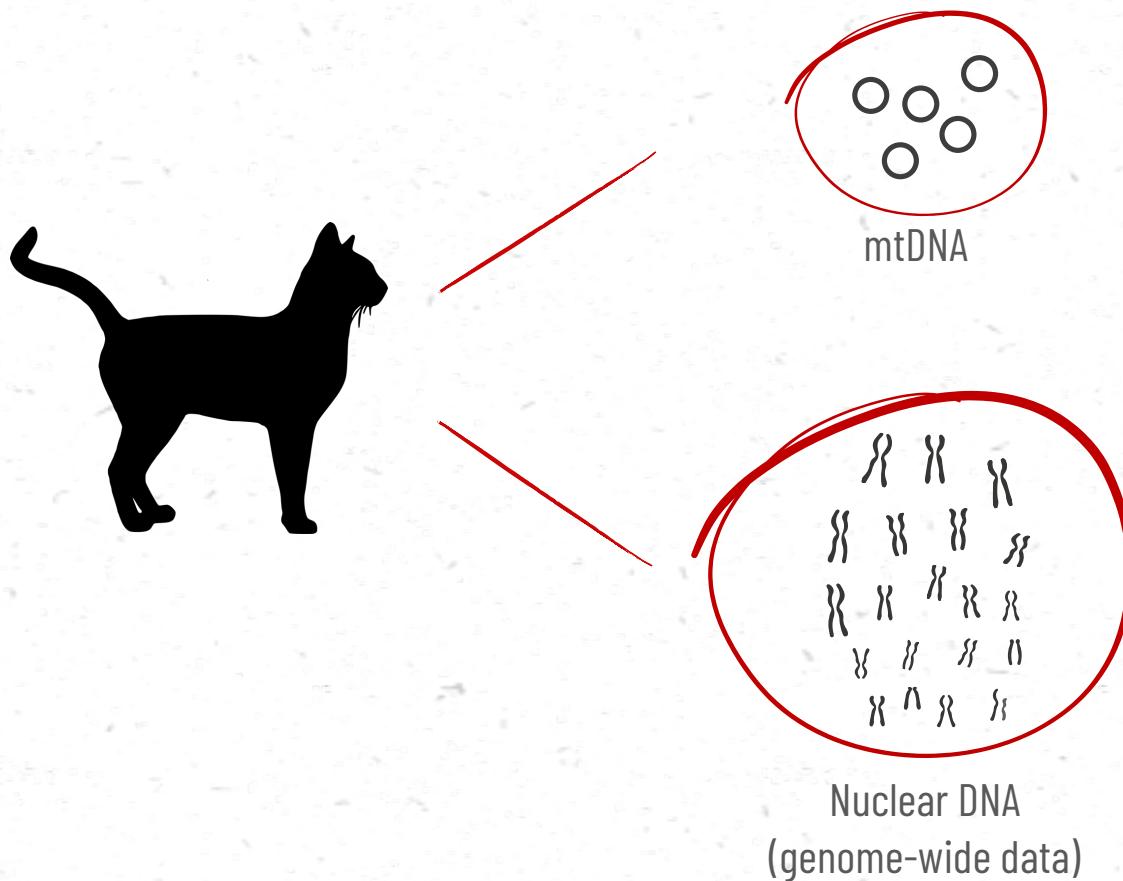
3'-end: G->A



Ancient DNA features

- Ultra-low coverage genomes (e.g. 0.1-fold)
Pseudohaploidization generates genotypes by sampling alleles (randomly or by majority rules) from low coverage sequence data (bam files).
Genotype likelihoods (>0.5-fold) requires higher coverage. Probability of observing a set of sequencing reads D conditional on a true genotype G , $P(D|G)$.
- Artifact mutations due to *post-mortem* damage
 - Remove transitions in the analyses
 - Rescale quality damaged sites
 - Trim ends of the reads
 - Remove uracils upon library preparation (UDG protocols)

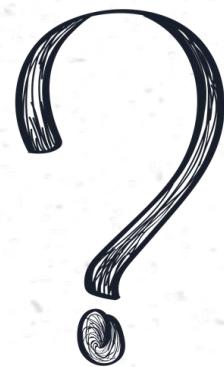
From mtDNA to full genomes



Many copies (good for ancient DNA)
Uniparental (**one story - female**)
Translocation of animals

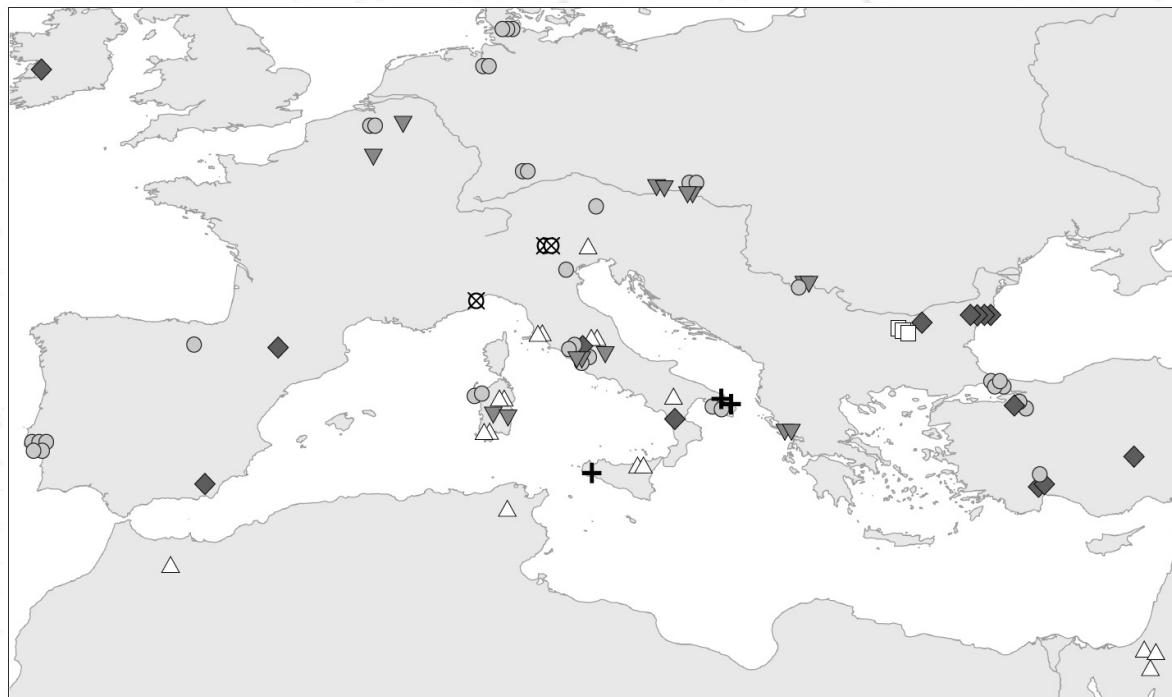
Biparental (**many stories!**)
Admixture
Selections
Original centers of domestication

Times of cat dispersal into Europe



Genome-wide data generated

- ⊗ Paleolithic/Mesolithic
- ◆ Neolithic/Chalcolithic
- ✚ Bronze/Iron Age
- ▼ Antiquity/Roman
- post-Roman
- 20th cent. CE wild
- △ modern



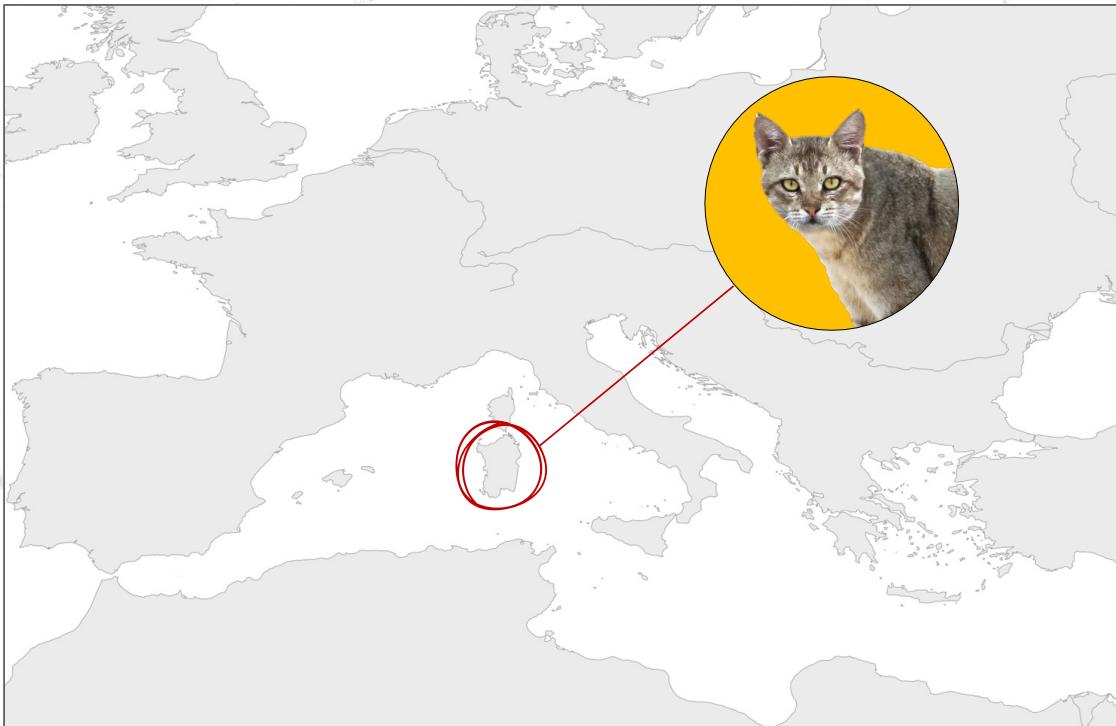
De Martino et al. (bioRxiv, in review)

70 Ancient cats
coverage 0.2–1.4 X
from the last 12,000 years

14 Present-day wildcats
coverage 6–14 X
4 from Sardinia (*F. l. lybica*)
2 from North Africa (*F. l. lybica*)

De Martino et al. (bioRxiv, in review)

Wildcats in Sardinia



F. l. lybica in Sardinia

Introduced in the Neolithic ?

Feral form of domestic cats ?

Reference genome data

44 Modern high-coverage genomes publicly available



13 *F. silvestris* (Germany, Scotland)



3 *F. l. lybica* (Israel)



4 *F. l. ornata* (Kazakhstan, Tajikistan, China)



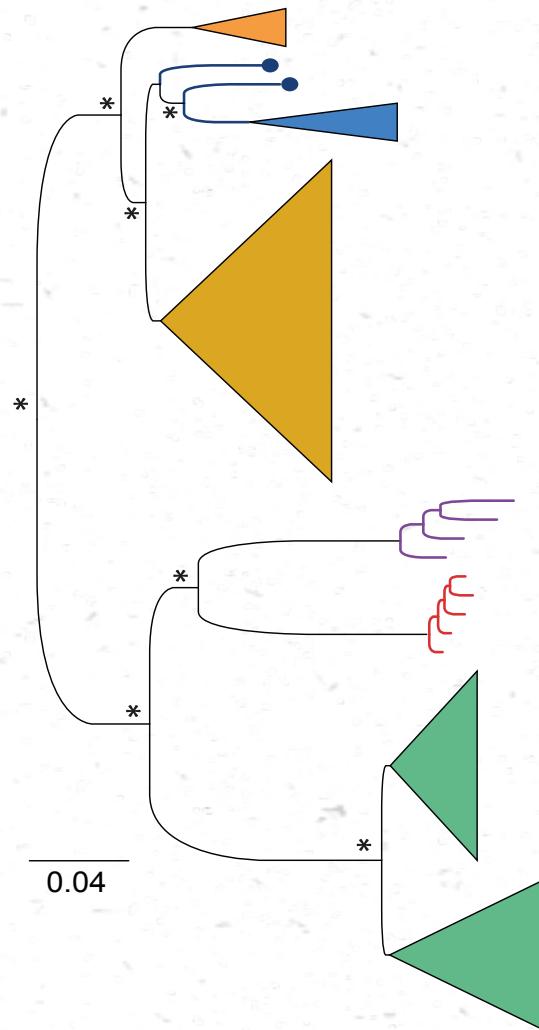
5 *F. bieti* (China)



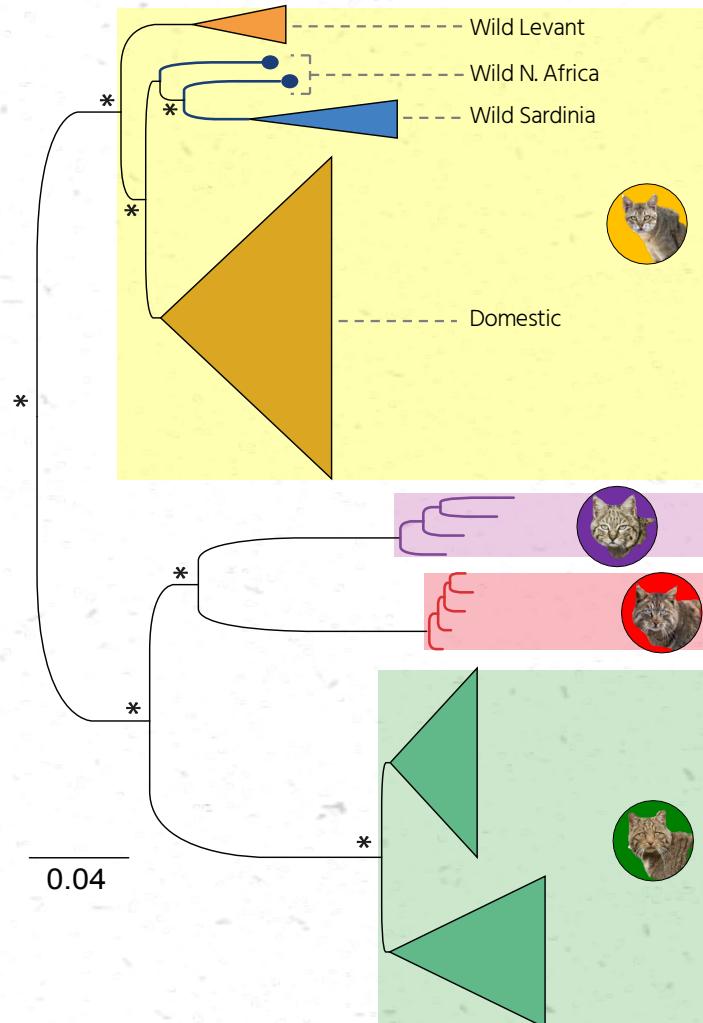
18 Domestic cats (breeds & random-bred)



+1 *Felis chaus*
(outgroup)



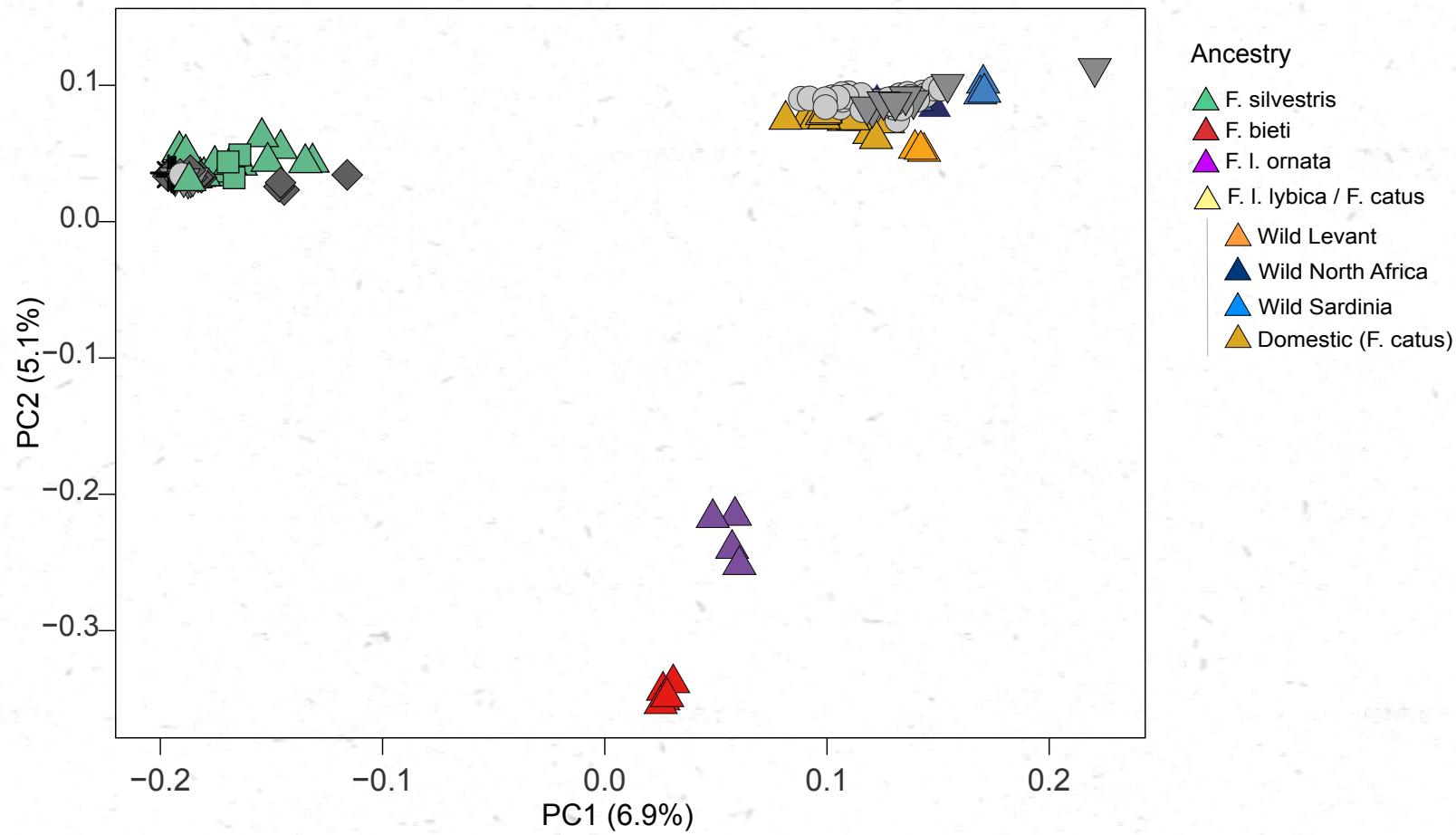
Supermatrix tree of modern genomes



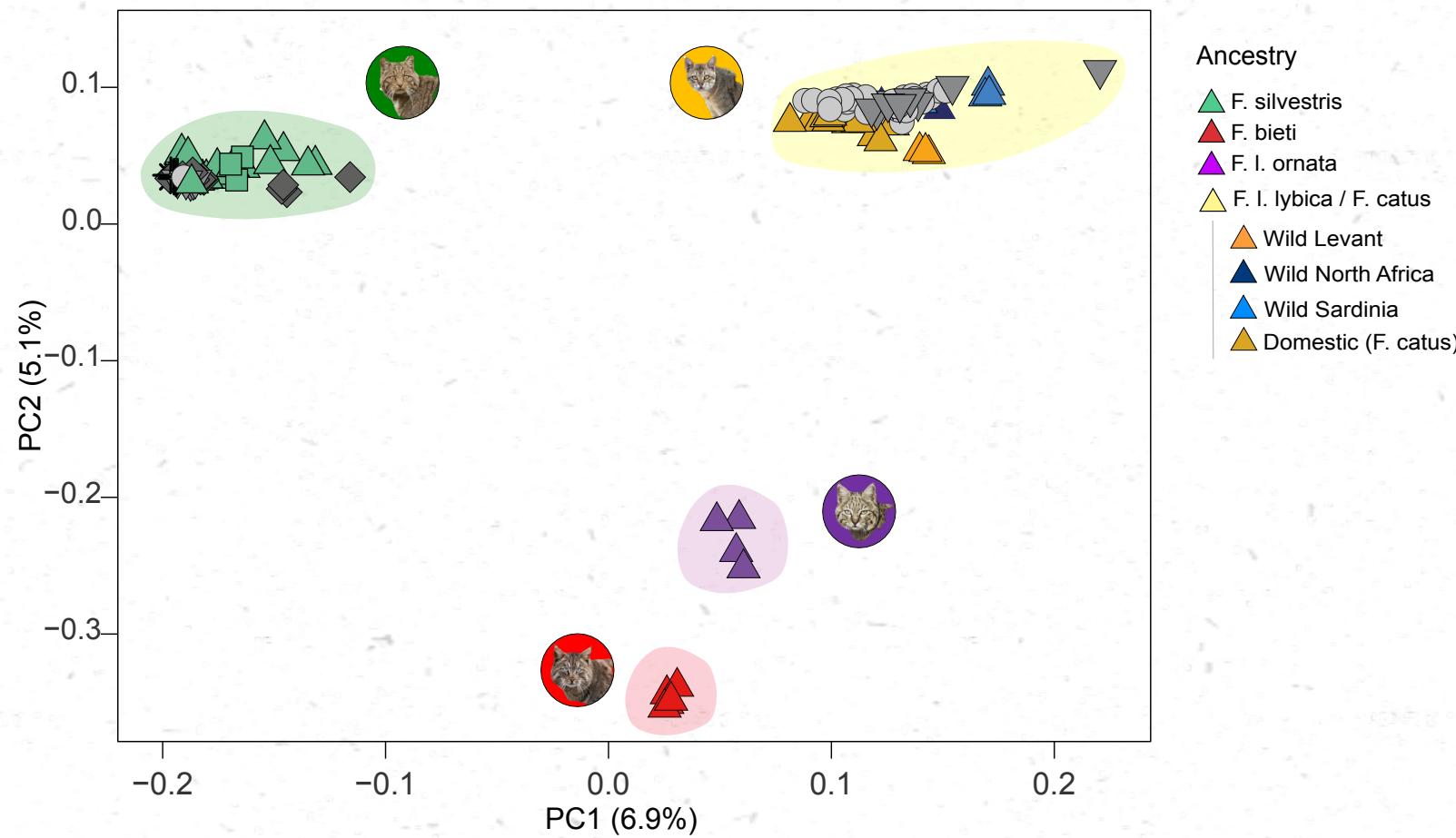
Supermatrix tree of modern genomes

- > **Genetic structure in *F. l. lybica***
Wildcats from the Levant, wildcats from North Africa and domestic cats are distinct.
- > **Sardinian wildcats are not feral**
They originated from North African wildcats.

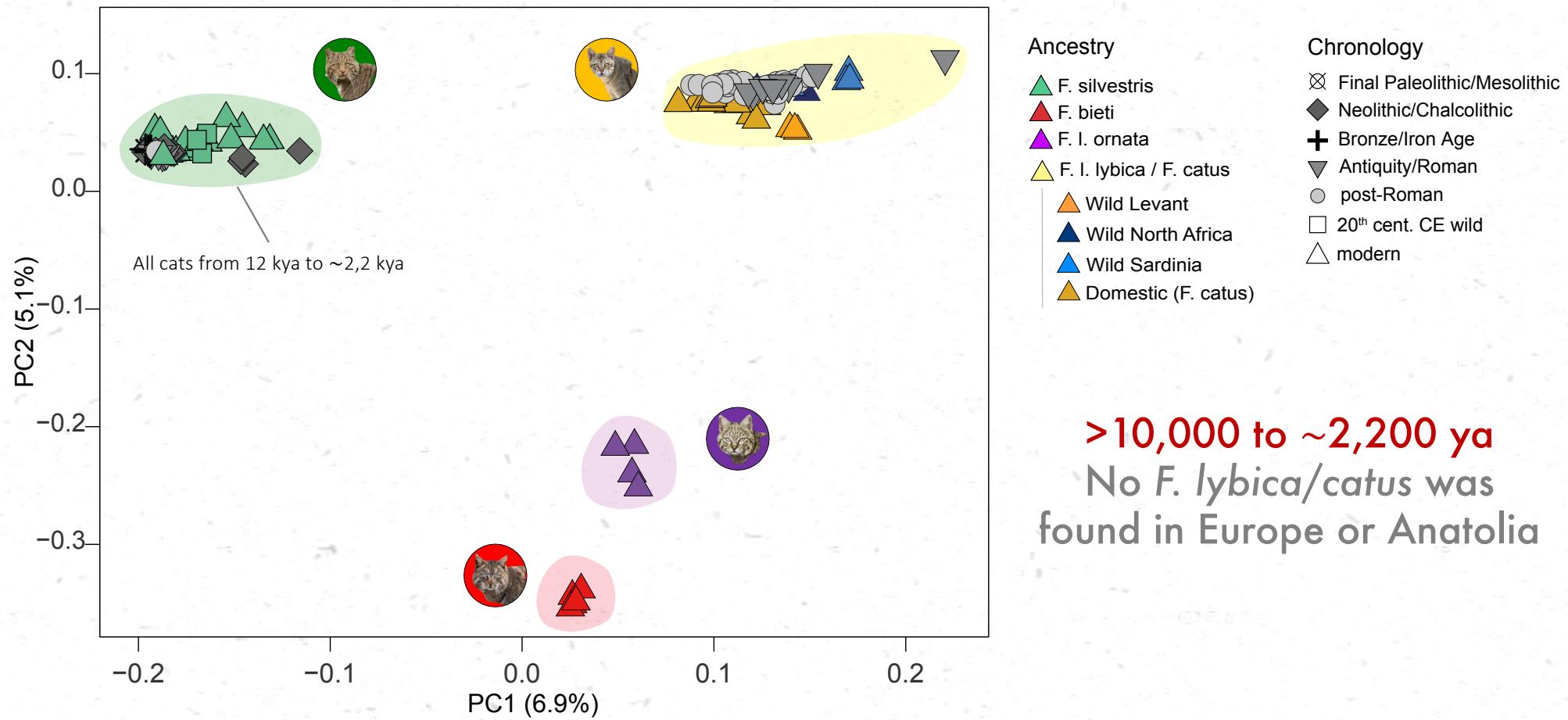
PCA



PCA



PCA

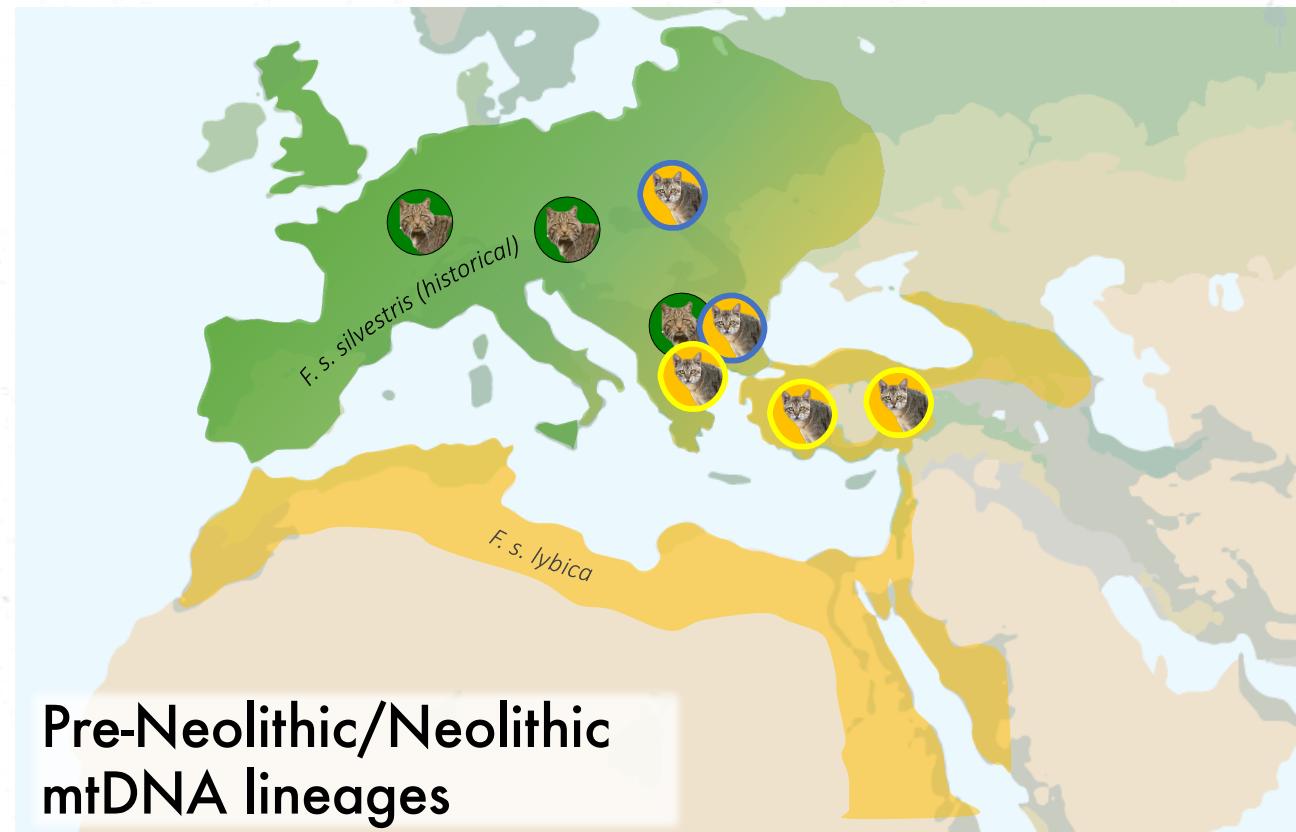


Ancient cat genomes

European and Near Eastern ancestries

mtDNA
(2017)

F. lybica in
Anatolia?



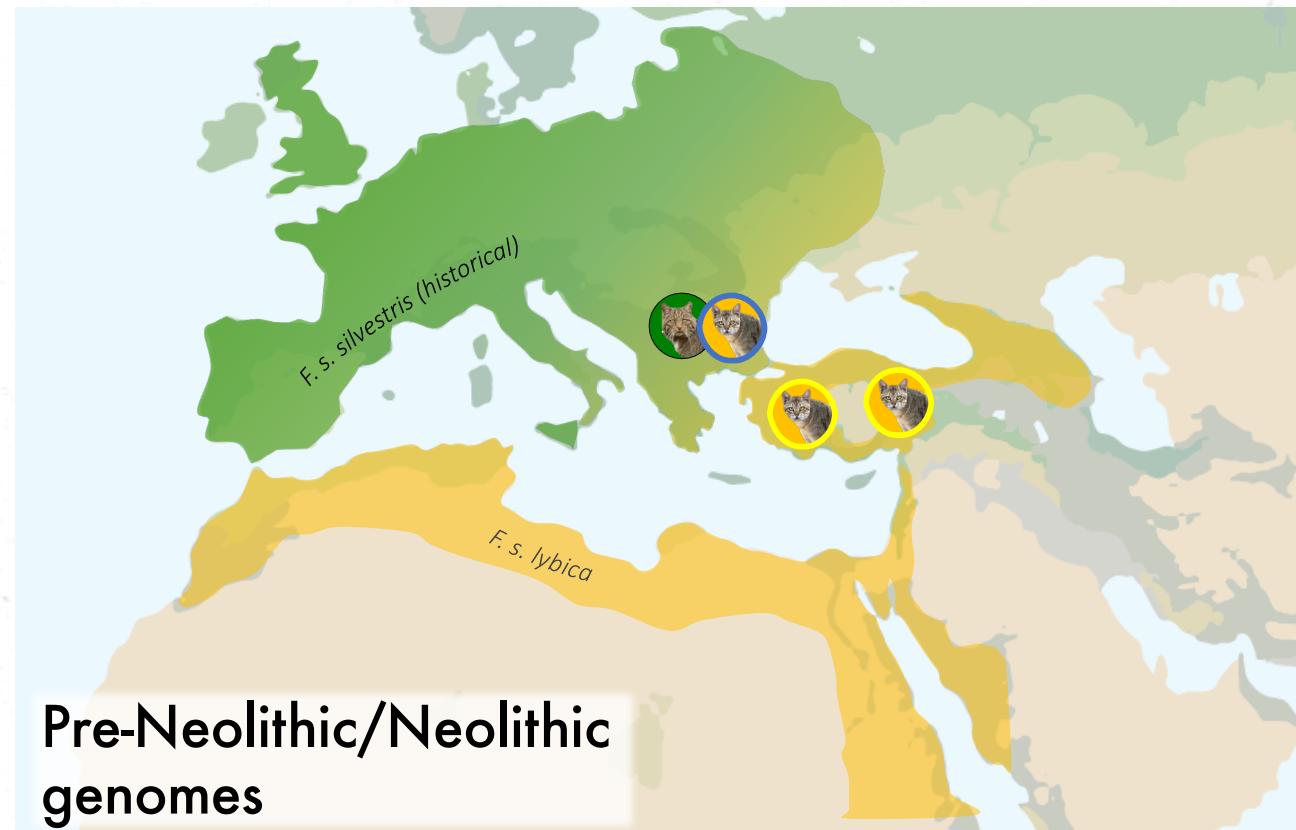
Pre-Neolithic/Neolithic
mtDNA lineages

(Ottoni et al. 2017, Baca et al. 2018)

Ancient cat genomes

European and Near Eastern ancestries

genomes

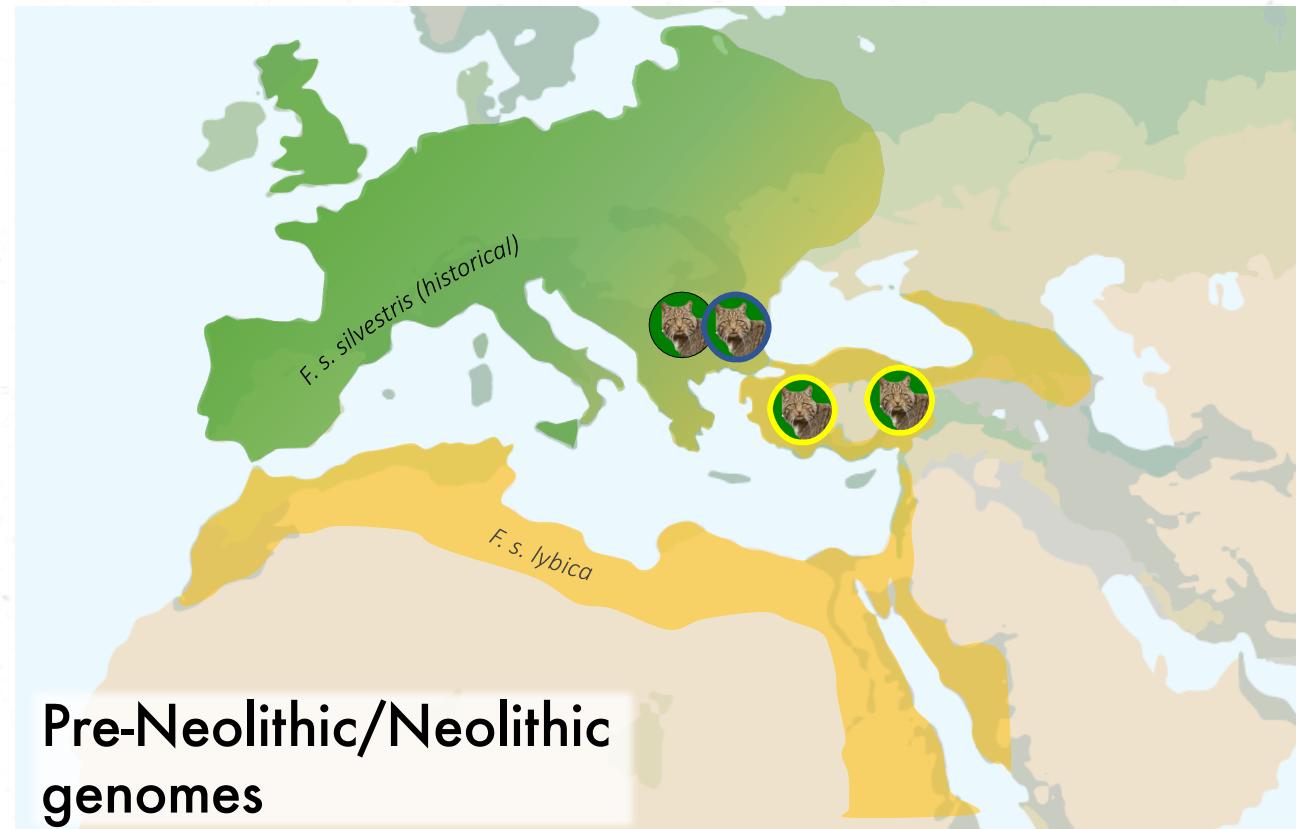


Ancient cat genomes

European and Near Eastern ancestries

genomes

Mitonuclear
discordance

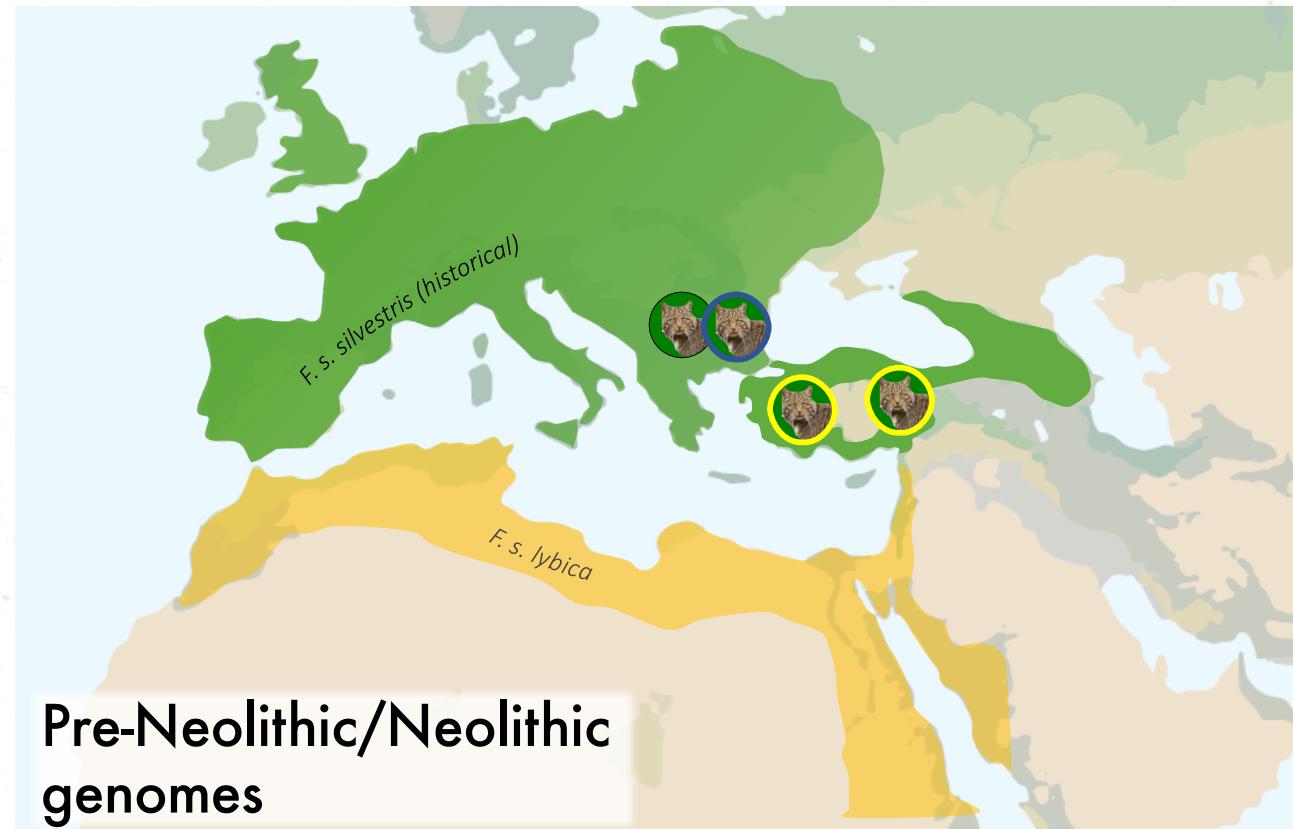


Ancient cat genomes

European and Near Eastern ancestries

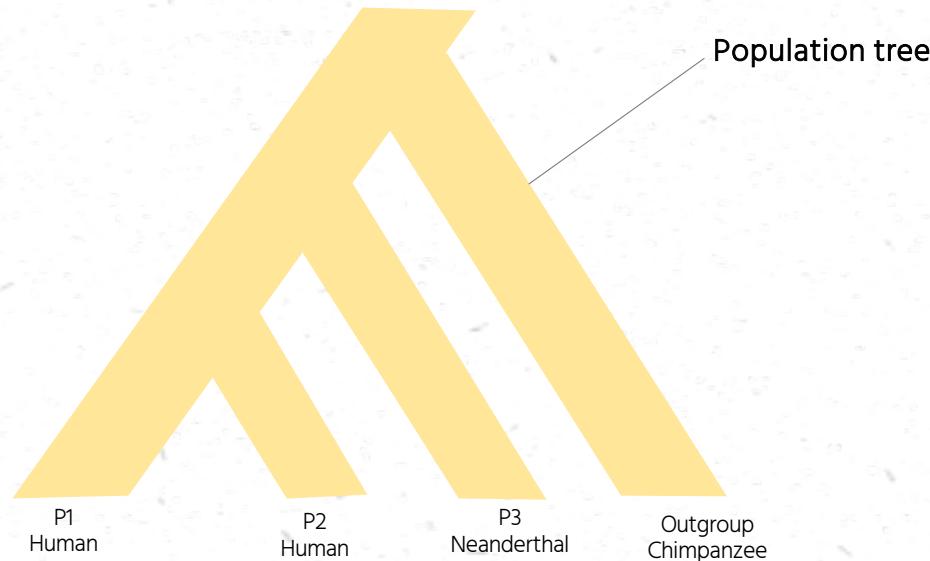
genomes

Mitonuclear
discordance



D-statistics

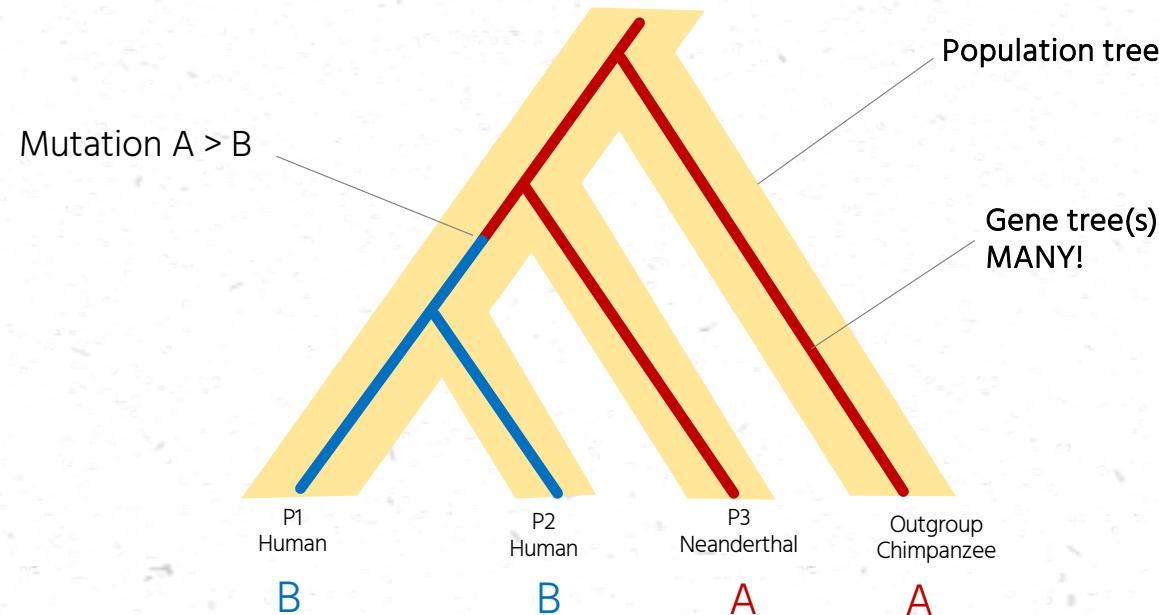
Testing evolutionary models



Green et al. 2010

D-statistics

Testing evolutionary models



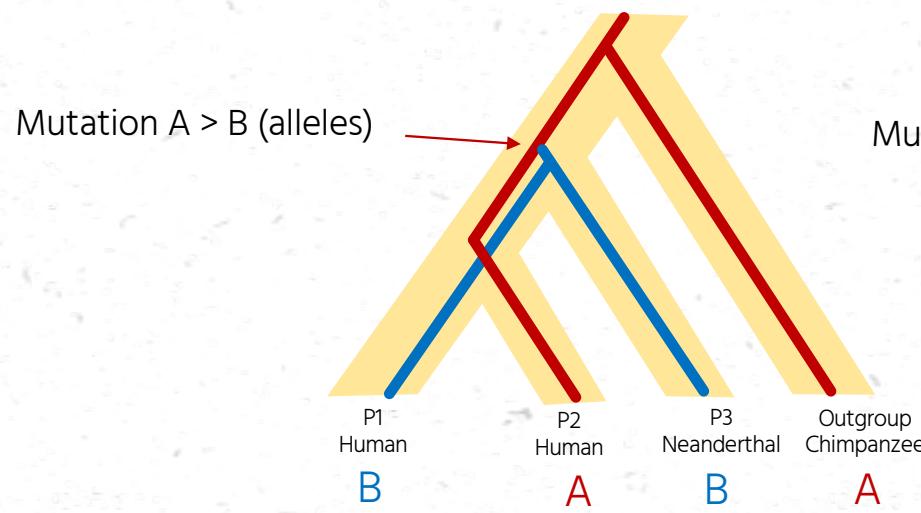
Green et al. 2010

A Ancestral allele
B Derived allele

D-statistics

Testing evolutionary models

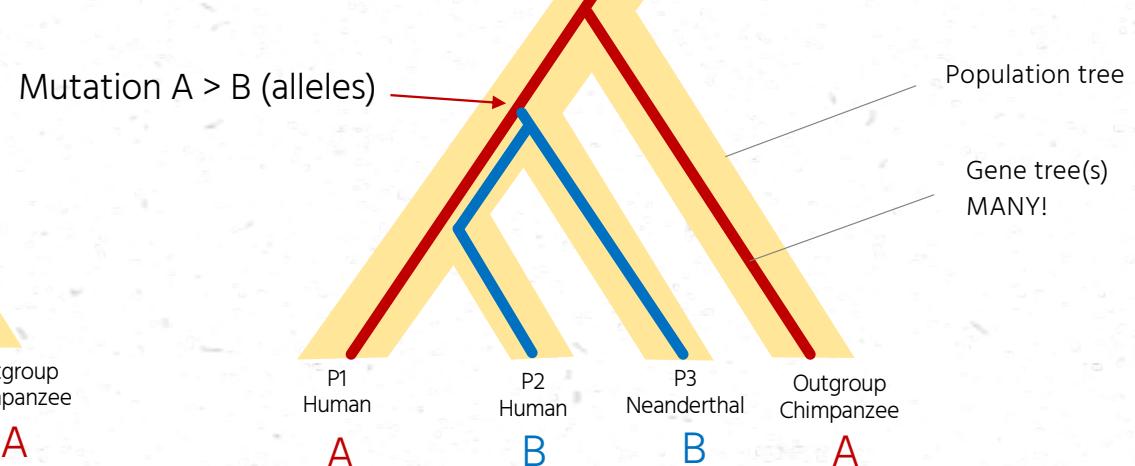
$$D = \frac{N_{BABA} - N_{ABBA}}{N_{ABBA} + N_{BABA}}$$



The **D-value** is a measure of the amount of **shared derived alleles** among four populations. In the presence of an outgroup, it measures the excess of shared derived alleles in one population relative to another (P1 and P2) due to mixing with a third population (P3).



Green et al. 2010



Incomplete lineage sorting is due to the retention of ancestral polymorphisms, which persist across populations splits (or speciation events) and may accidentally lead to the differential sorting of the variants in a following split.

D-statistics

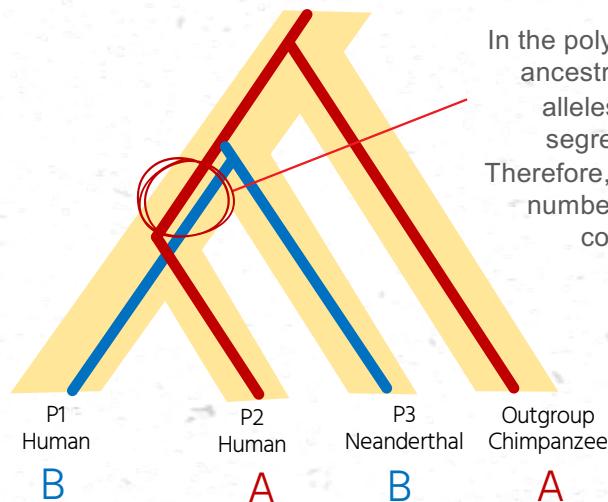
Testing evolutionary models

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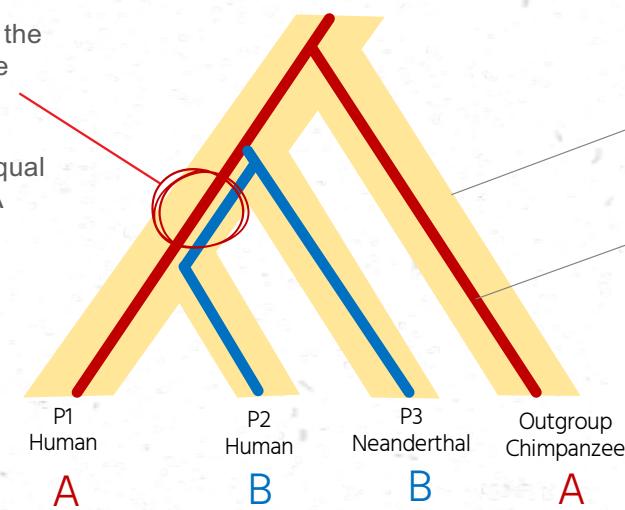
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Green et al. 2010



In the polymorphic sites of the ancestral population, the alleles (red and blue) segregate randomly.
Therefore, we expect an equal number of BABA-ABBA configurations.



Population tree
Gene tree(s)
MANY!

$D = 0 \Rightarrow$ Tree supported!!

Green et al. 2010

D-statistics

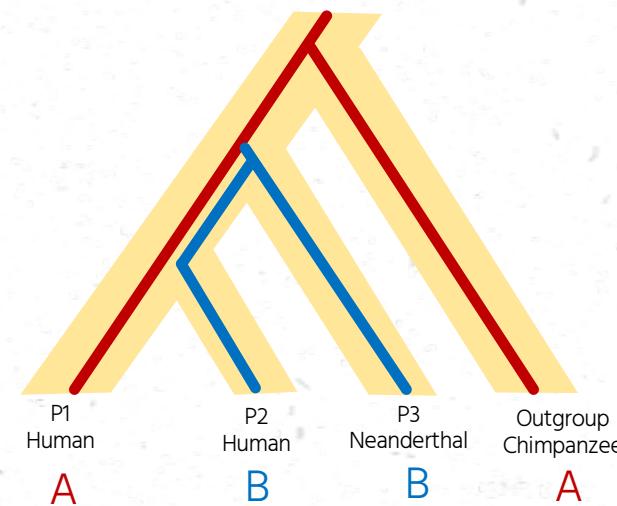
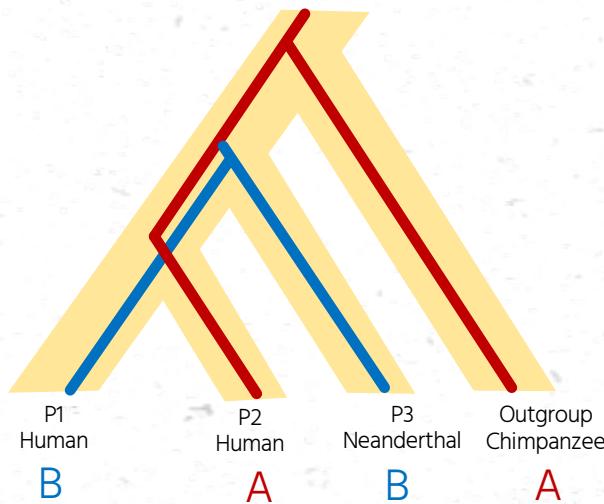
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Green et al. 2010



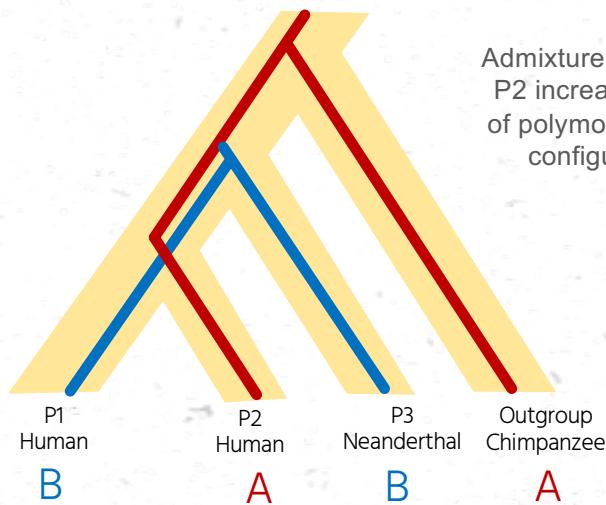
$D \neq 0 \Rightarrow$ TREE NOT SUPPORTED !!

Green et al. 2010

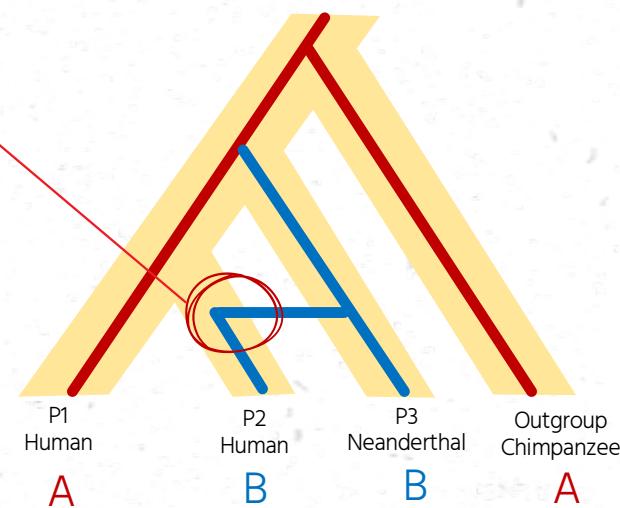
D-statistics

Testing evolutionary models

$$D = \frac{N_{BABA} - N_{ABBA}}{N_{ABBA} + N_{BABA}}$$



Admixture between P3 and P2 increases the number of polymorphic sites in the configuration ABBA



$D < 0 \Rightarrow$ Admixture between P2 and P3



Green et al. 2010

D-statistics

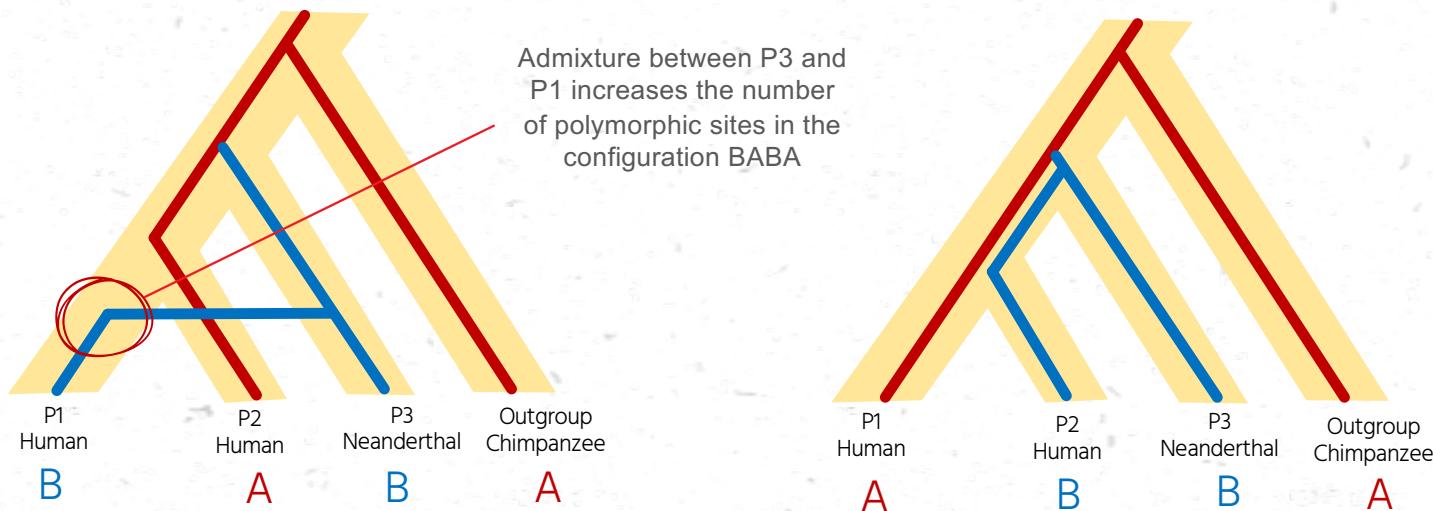
Testing evolutionary models

$$D = \frac{N_{BABA} - N_{ABBA}}{N_{ABBA} + N_{BABA}}$$

The **D-value** is a measure of the amount of **shared derived alleles** among four populations. In the presence of an outgroup, it measures the excess of shared derived alleles in one population relative to another (P1 and P2) due to mixing with a third population (P3).

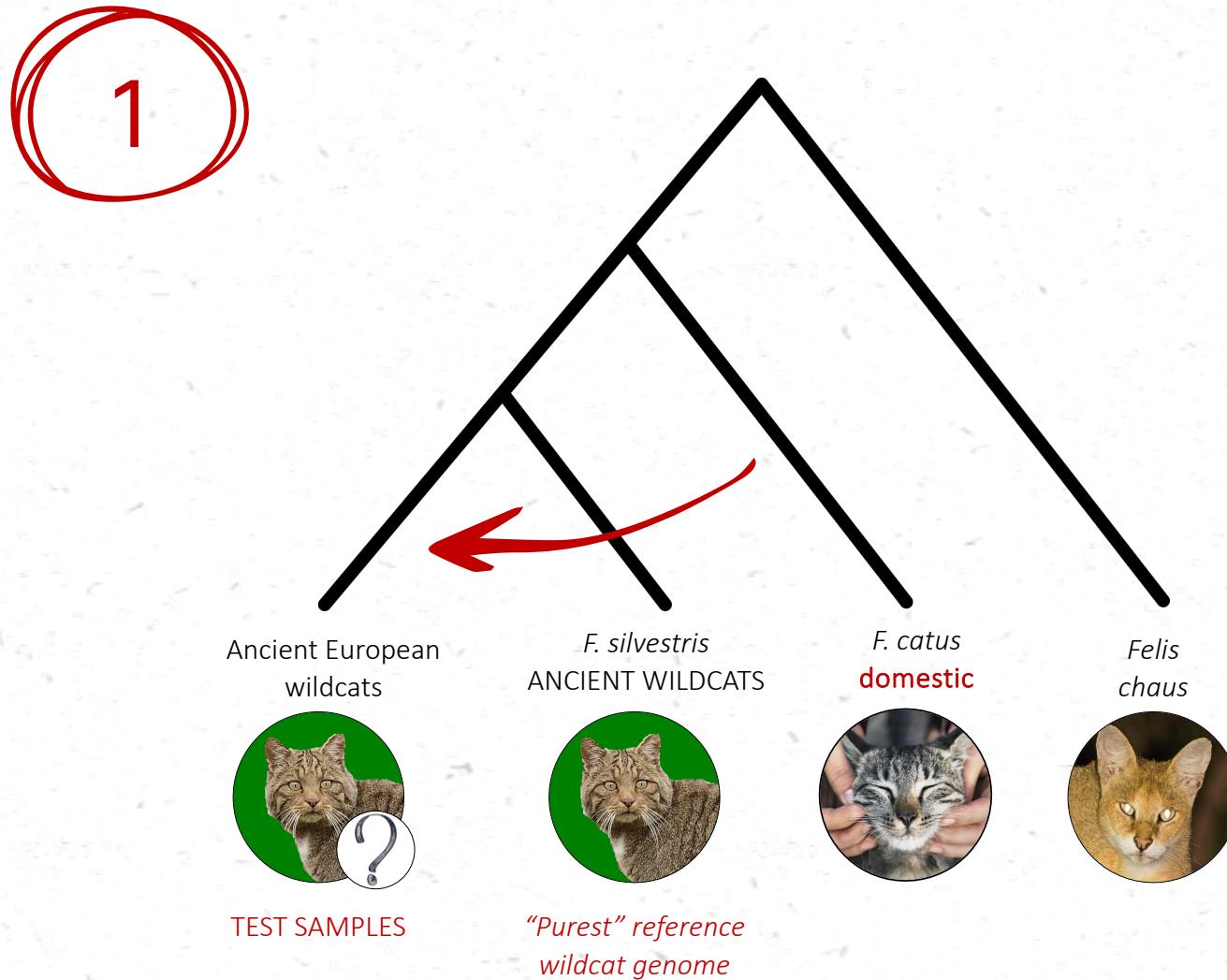


Green et al. 2010



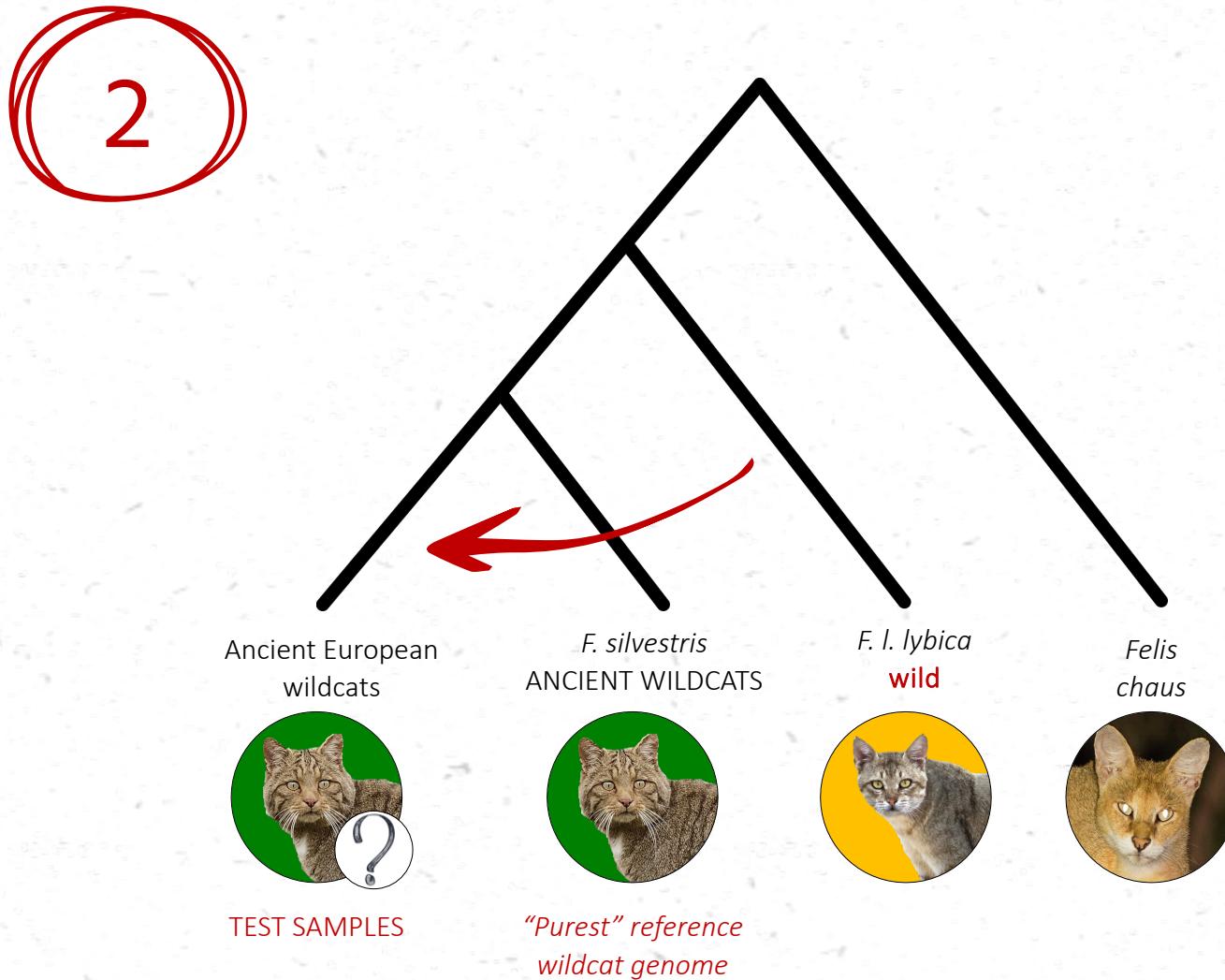
$D > 0 \Rightarrow$ Admixture between P1 and P3

Green et al. 2010



$D > 0$

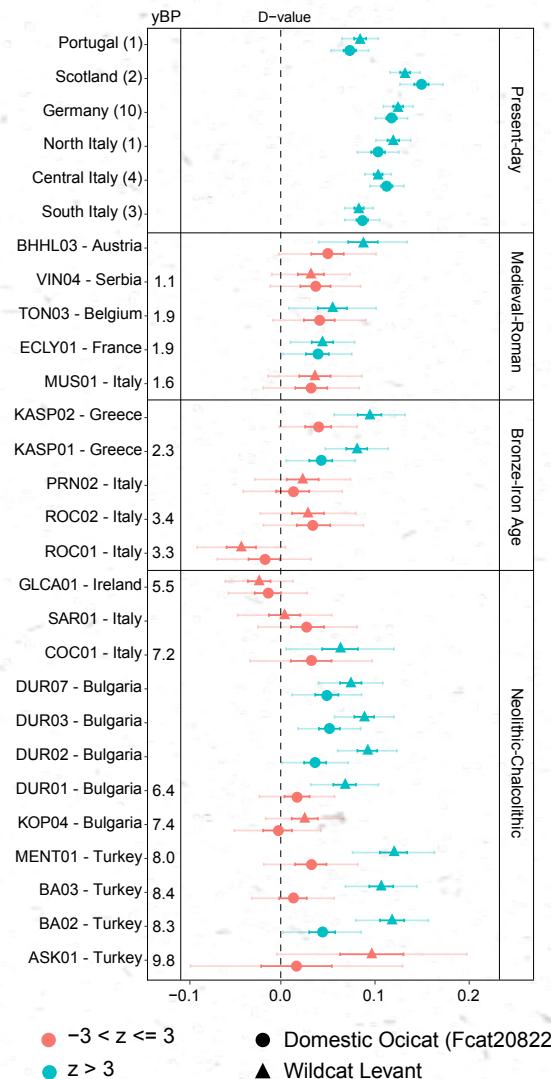
In present-day wildcats
 Recent admixture
 (known also from the literature)



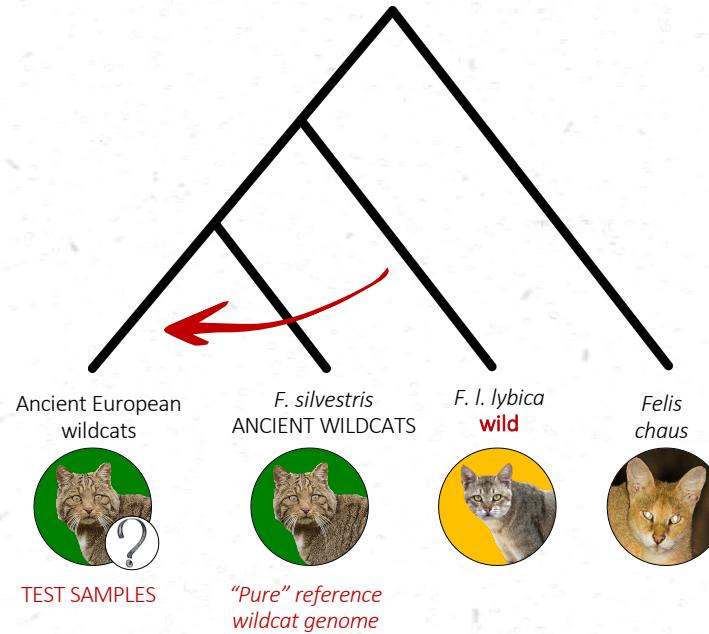
D>0

In ancient European wildcats from Anatolia and Southeast Europe.
Ancient admixture!

$D(F. chaus, Ocicat/wildcat Levant; F. silvestris-ancient, test)$

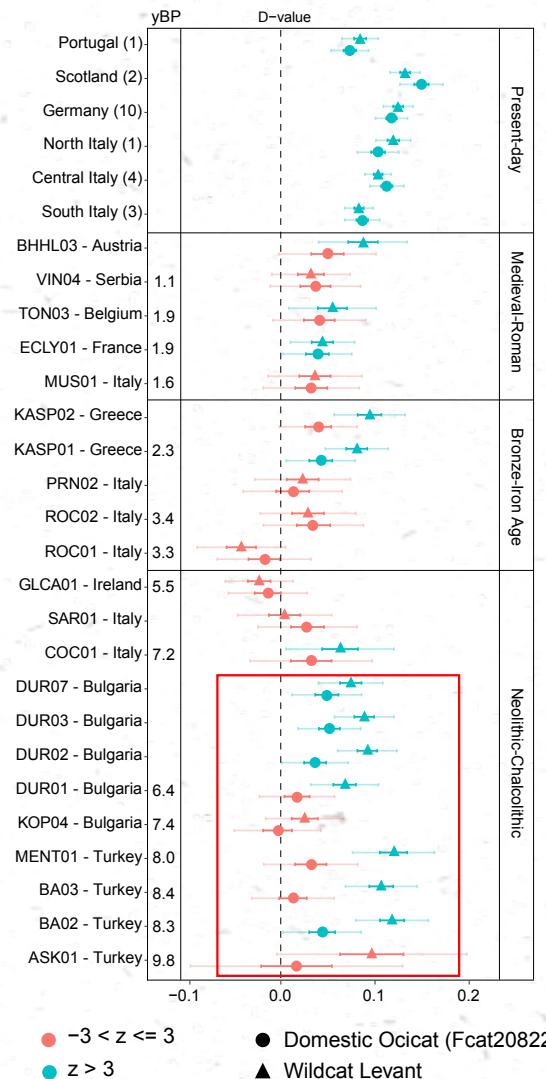


D stats

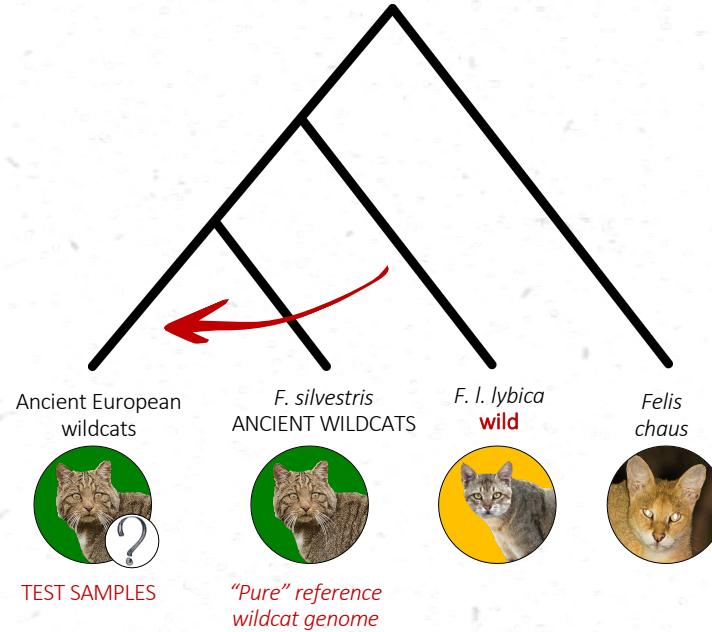


In ancient European
wildcats from Anatolia and
Southeast Europe.
Ancient admixture!

$D(F. chaus, Ocicat/wildcat Levant; F. silvestris-ancient, test)$



D stats

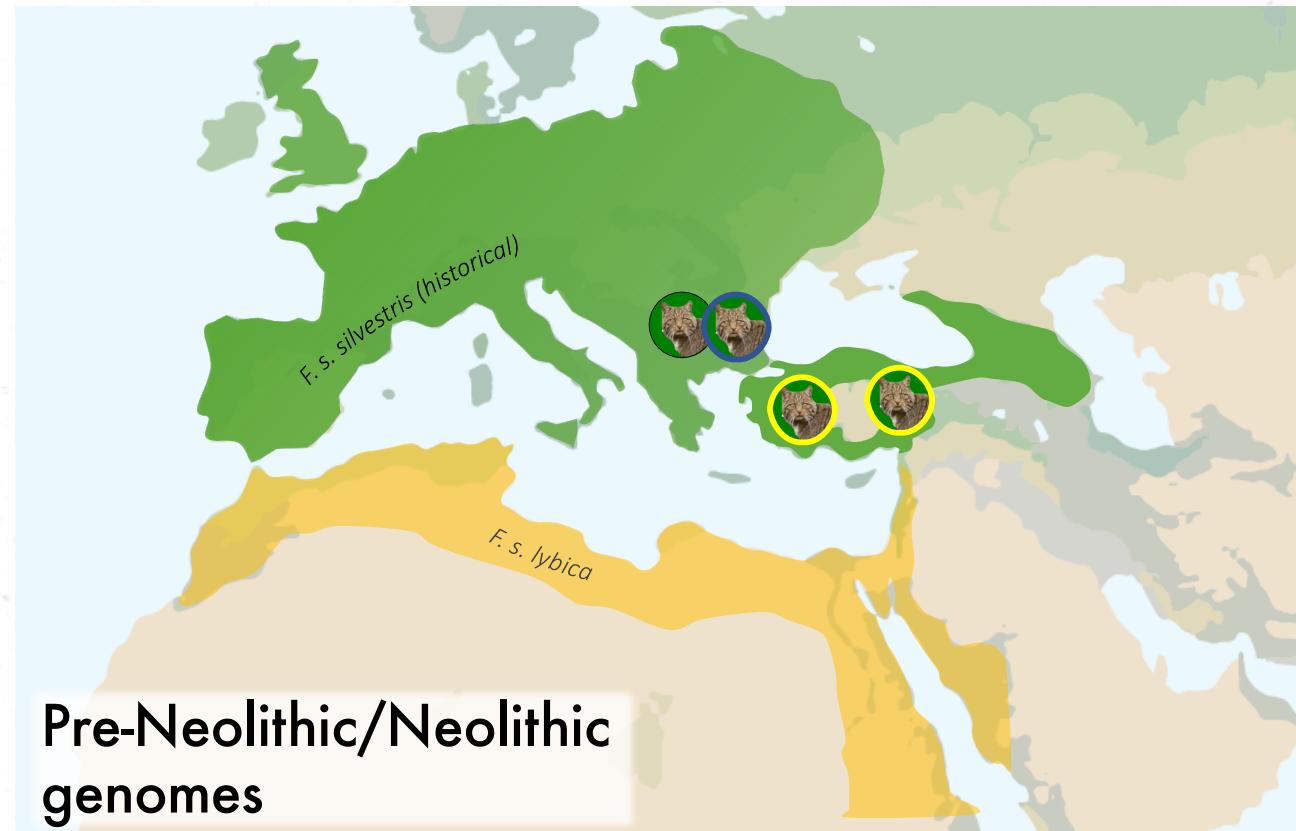


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Ancient cat genomes

European and Near Eastern ancestries

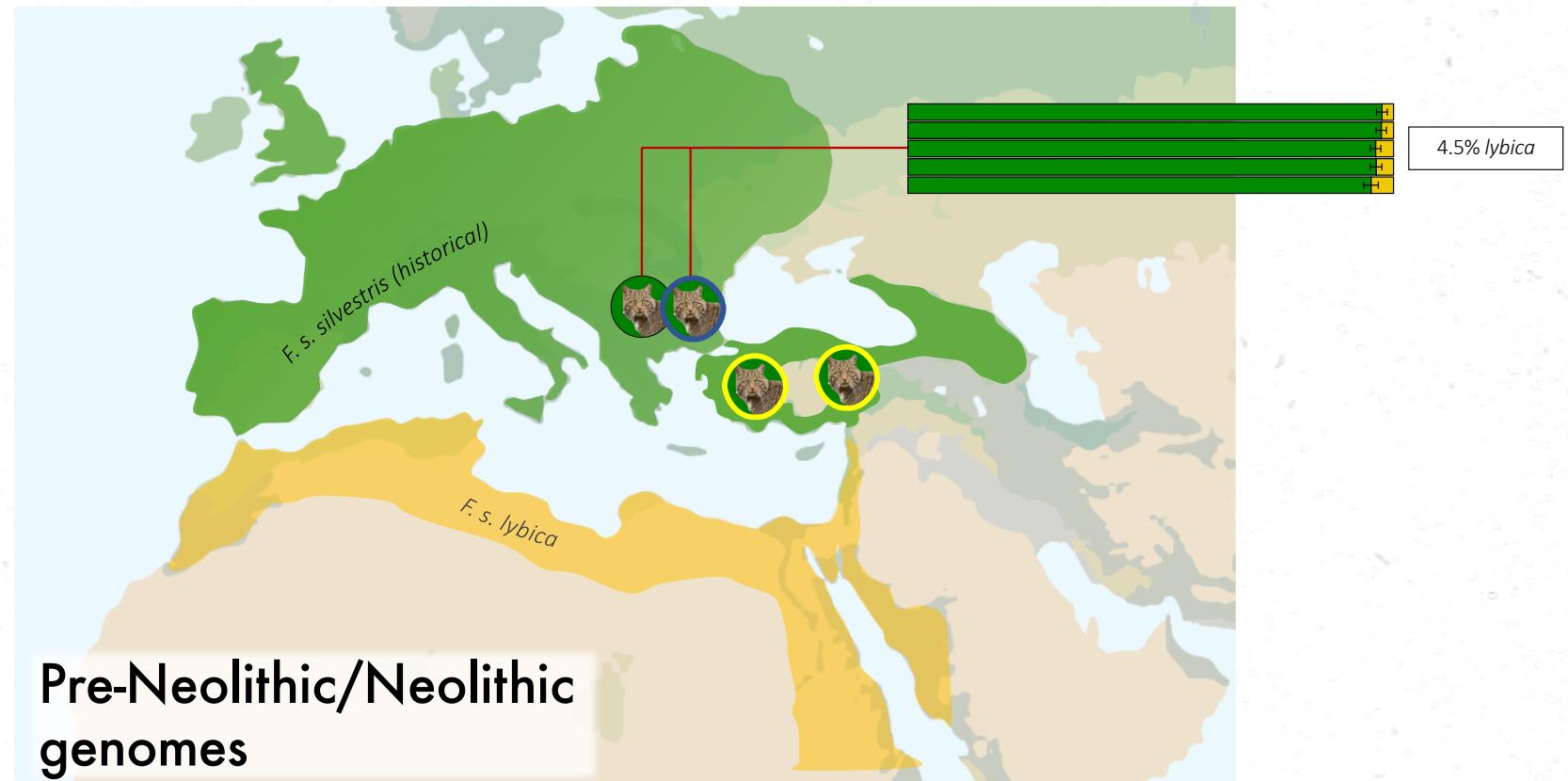
genomes



Ancient cat genomes

European and Near Eastern ancestries

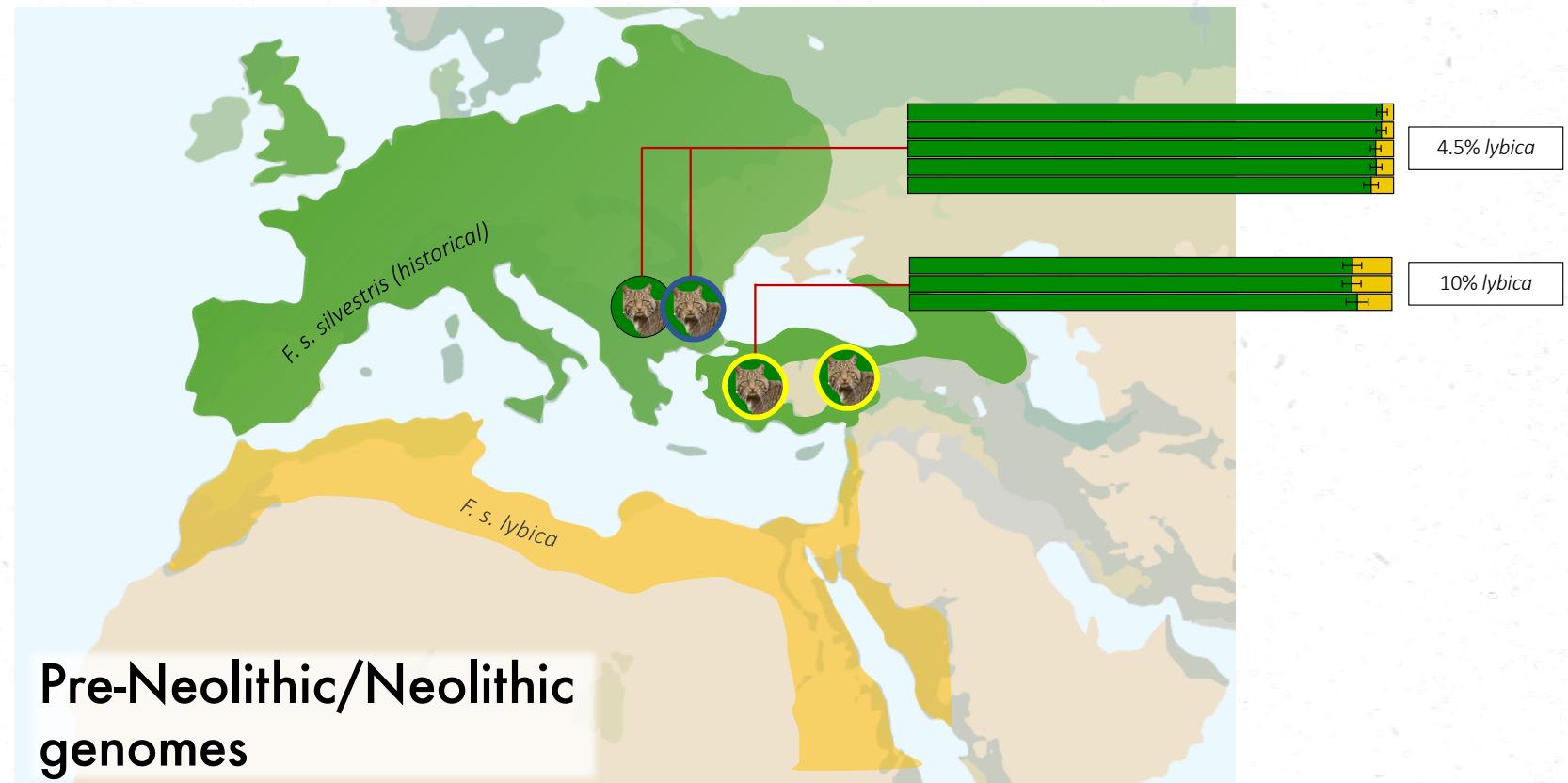
genomes



Ancient cat genomes

European and Near Eastern ancestries

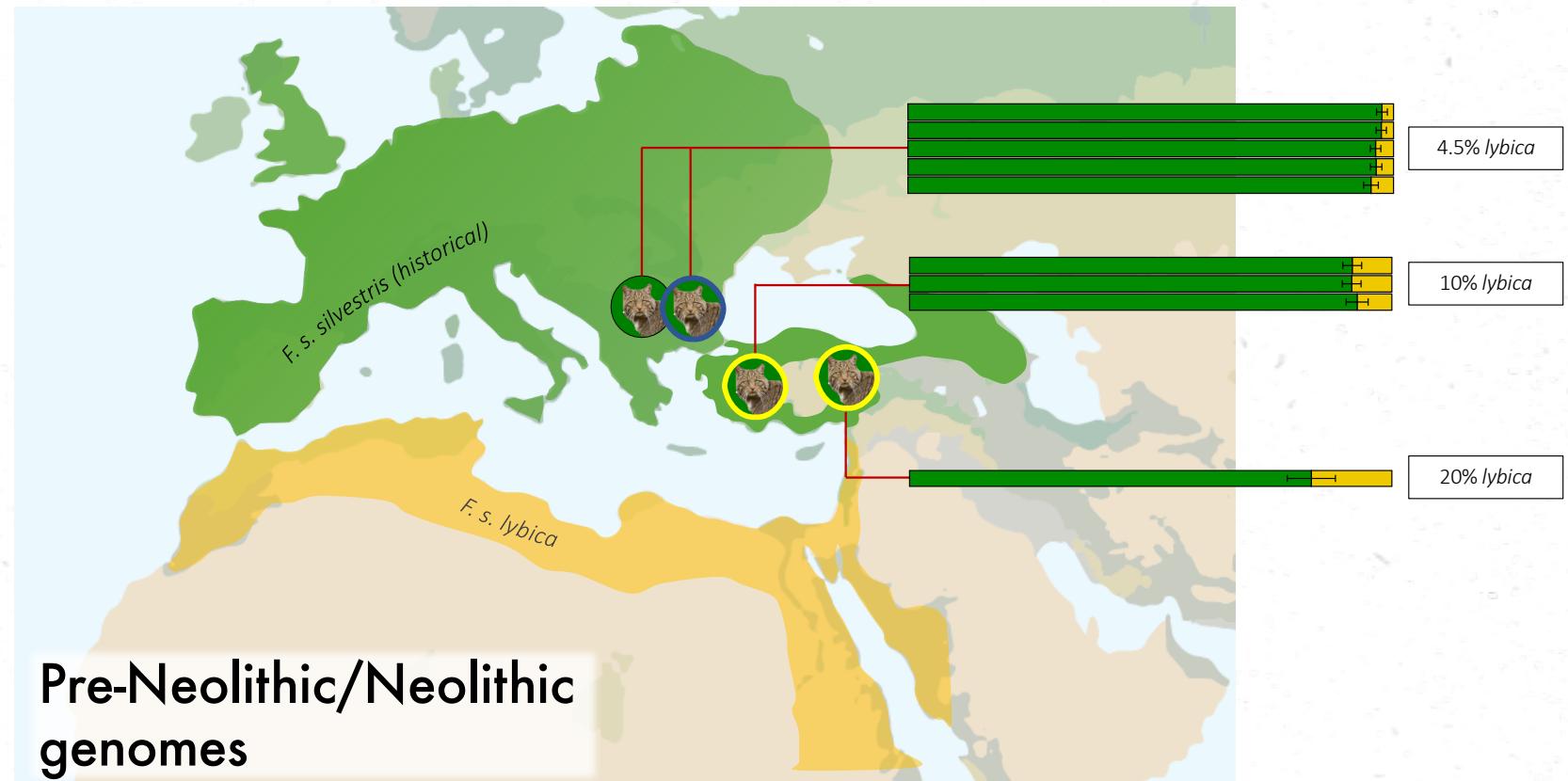
genomes



Ancient cat genomes

European and Near Eastern ancestries

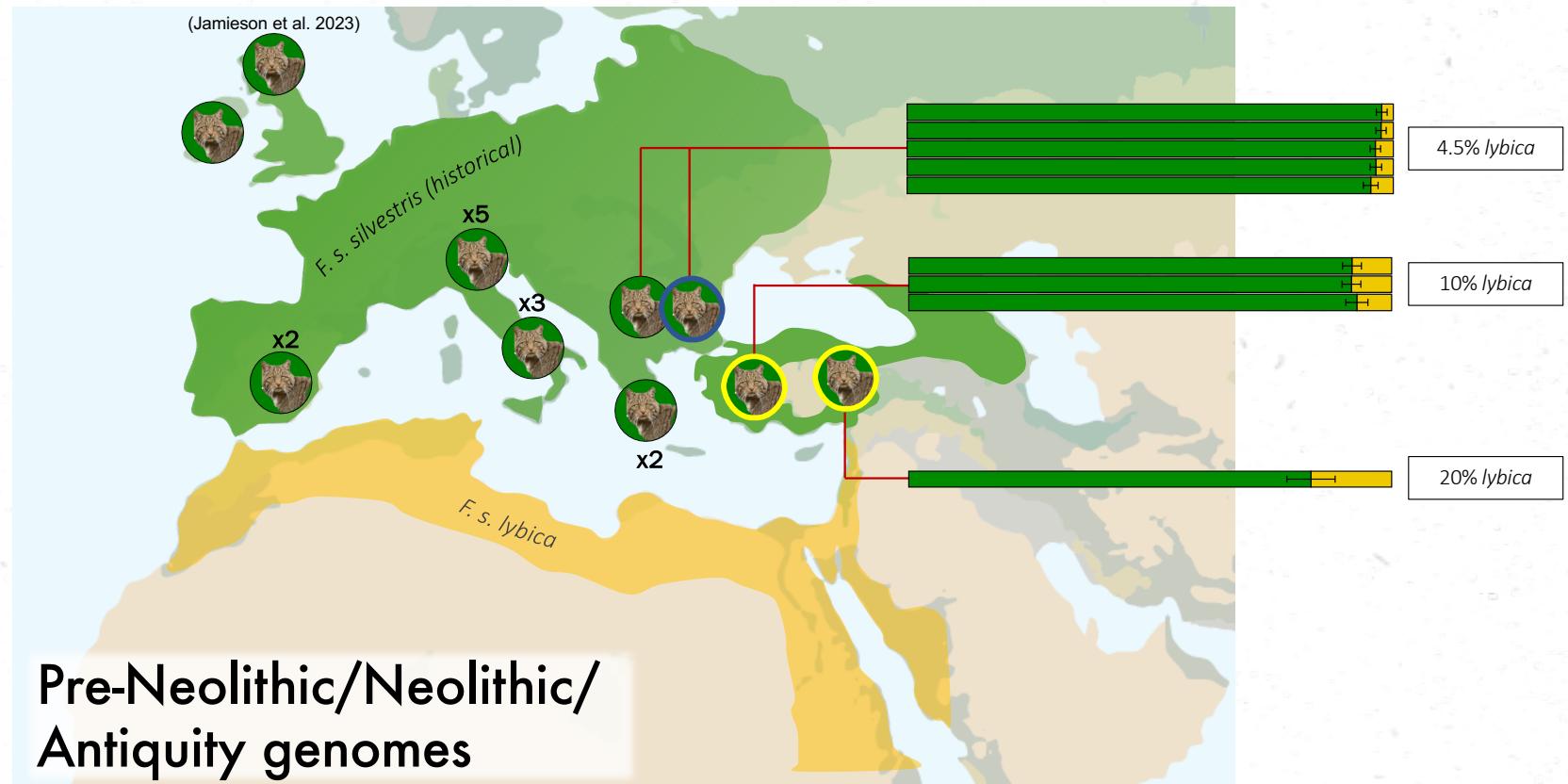
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Ancient cat genomes

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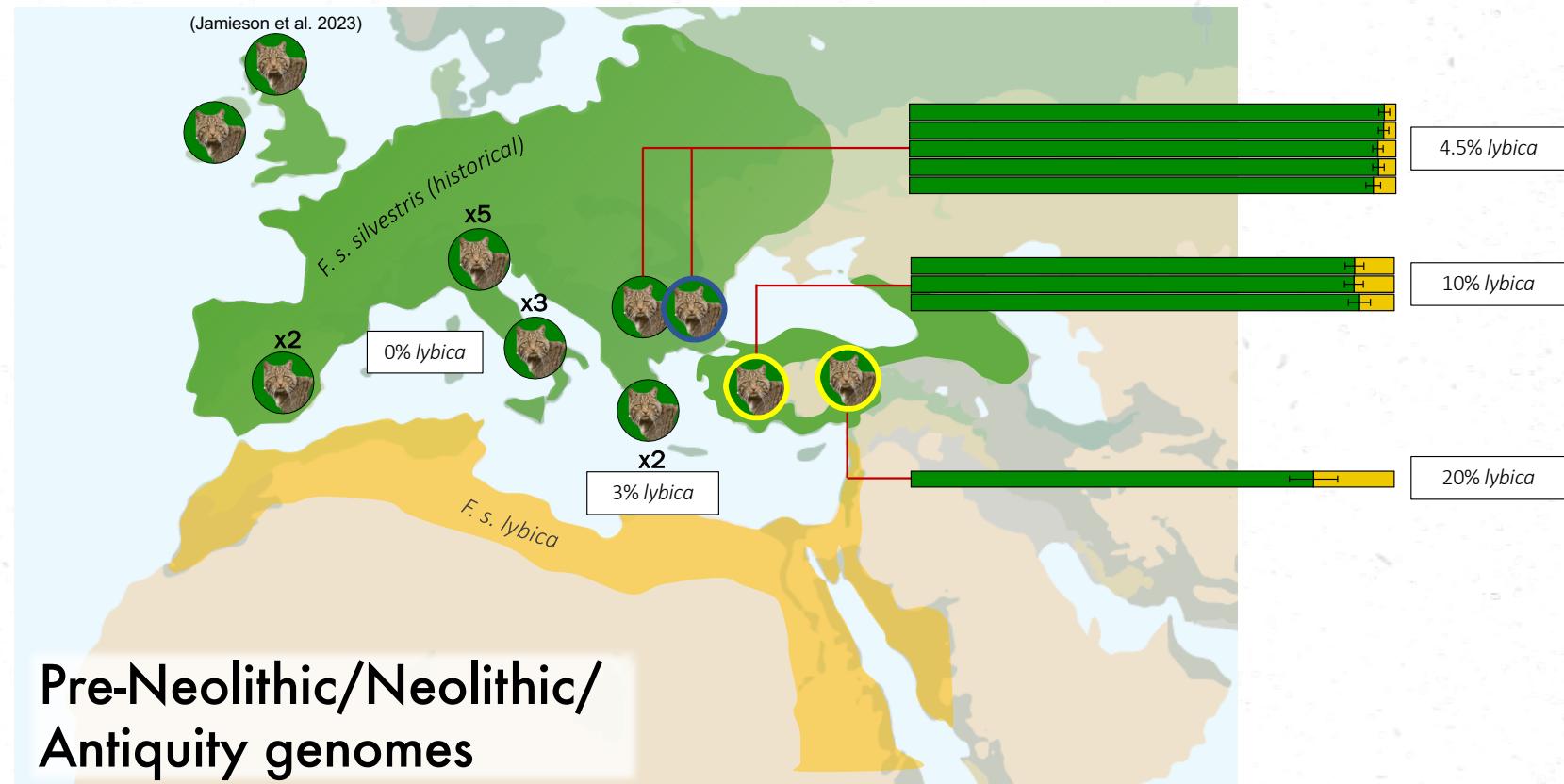
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Ancient cat genomes

European and Near Eastern ancestries

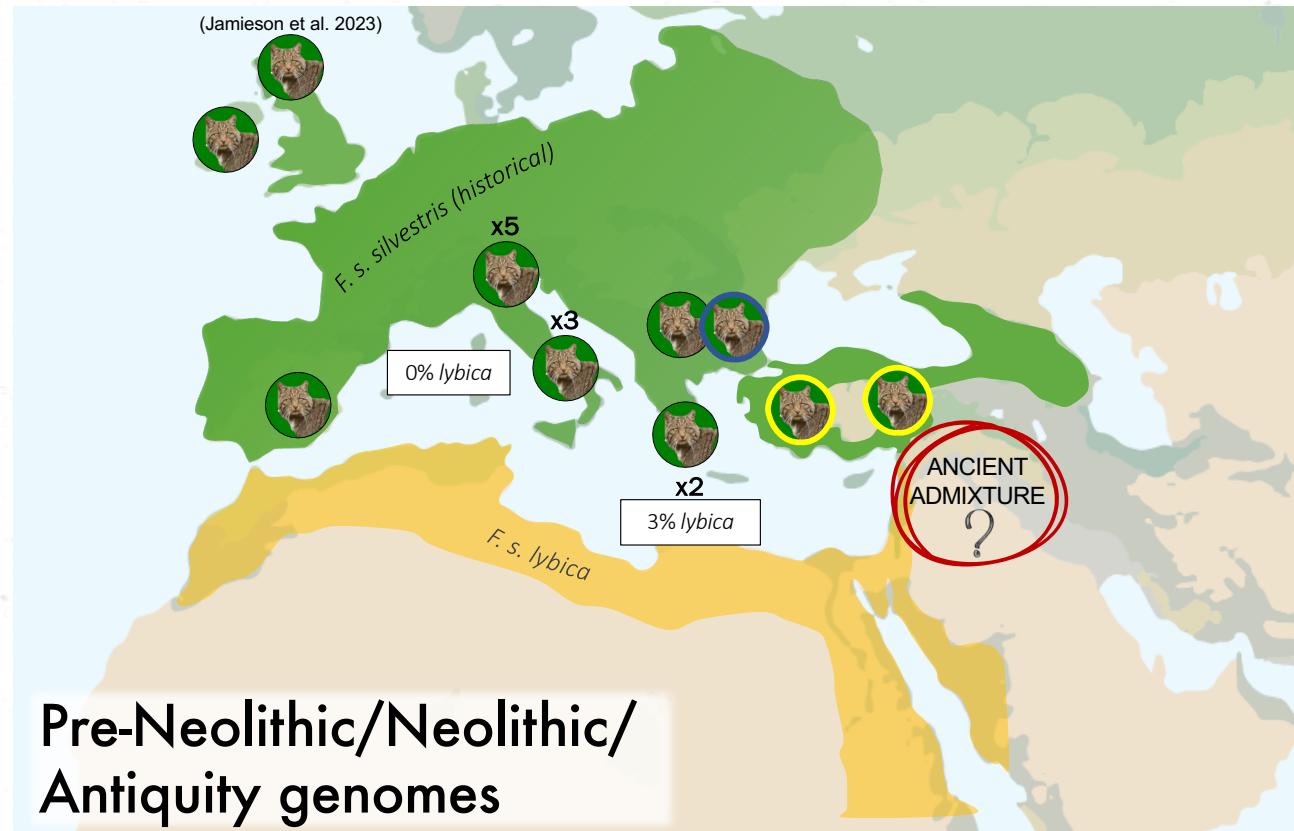
genomes



Ancient cat genomes

European and Near Eastern ancestries

genomes

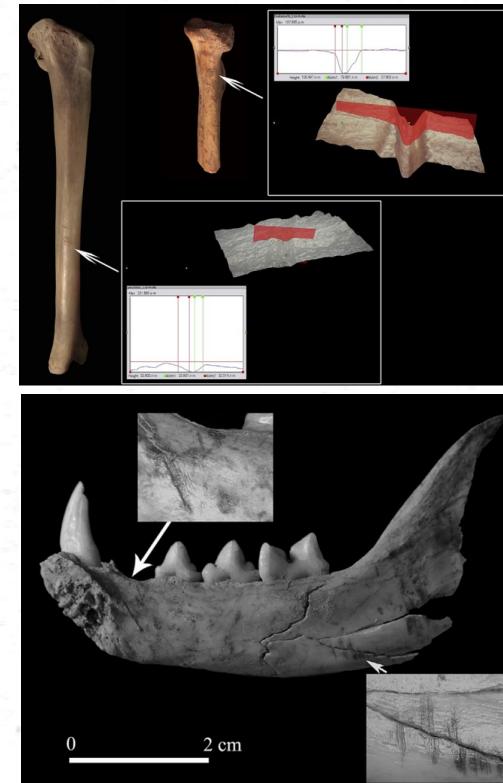


European wildcats & humans

Fur extraction



British Isles, Danish Ertebølle
Mesolithic
Exploitation of fur bearing mammals.



Dos de la Forca (Northeast Italy)
Mesolithic, 8500-7500 cal BC
Cut marks features and localisation suggest use of *F. silvestris* as food.

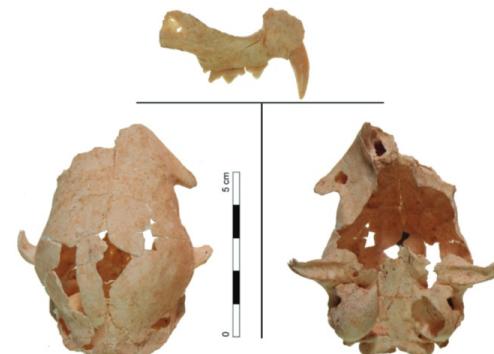
(Crezzini et al. 2014)

Food

European wildcats & humans



(Miccichè et al. 1997)

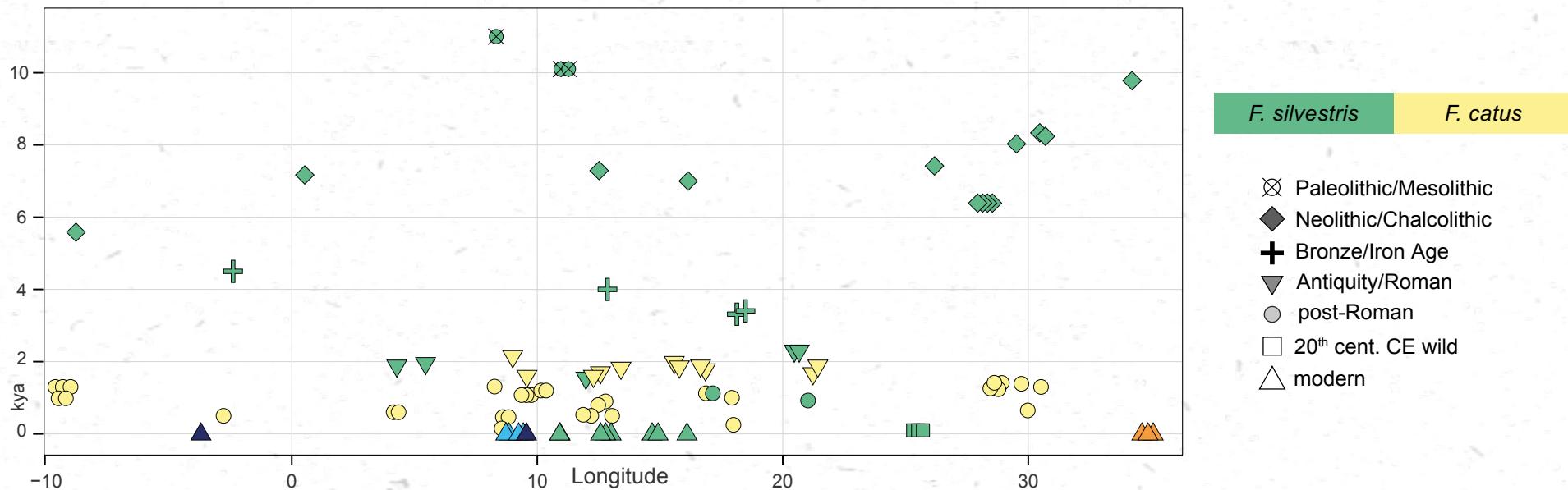


Cult ?

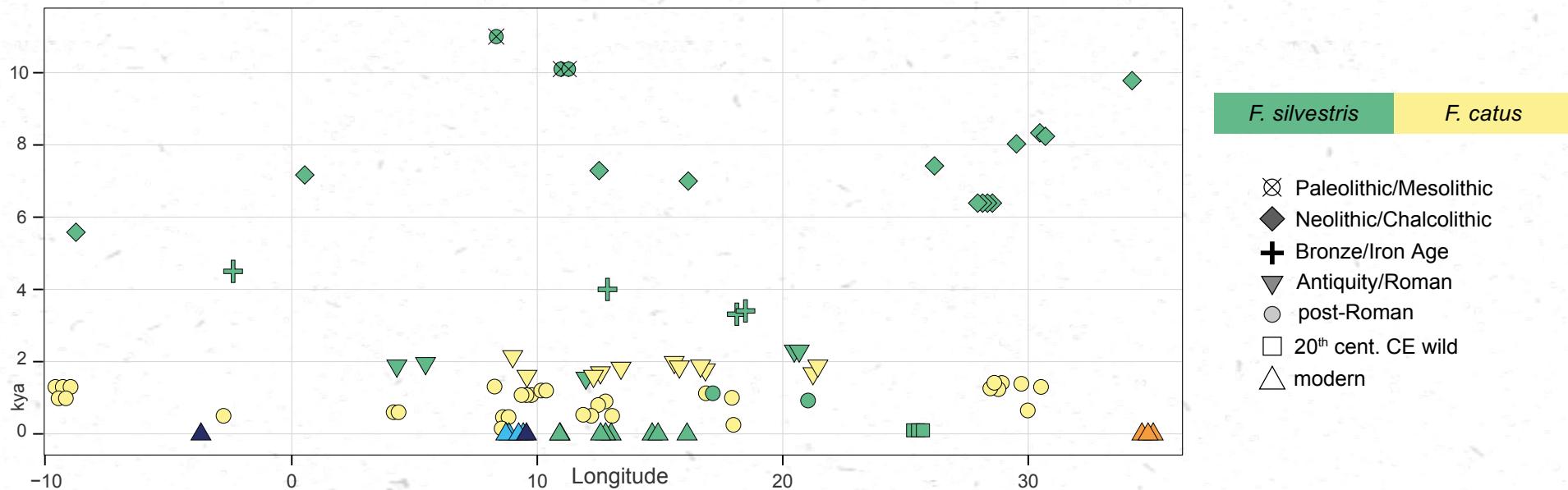
**Stretto Partanna, Sicily (Italy)
Early Bronze Age**

Archaeologists interpreted the context as an expression of religious activities related to a **cult of water**. Inside the large bell-shaped vase, a cat skull was found with other faunal remains

Cats were not introduced to Europe by farmers during the Neolithic

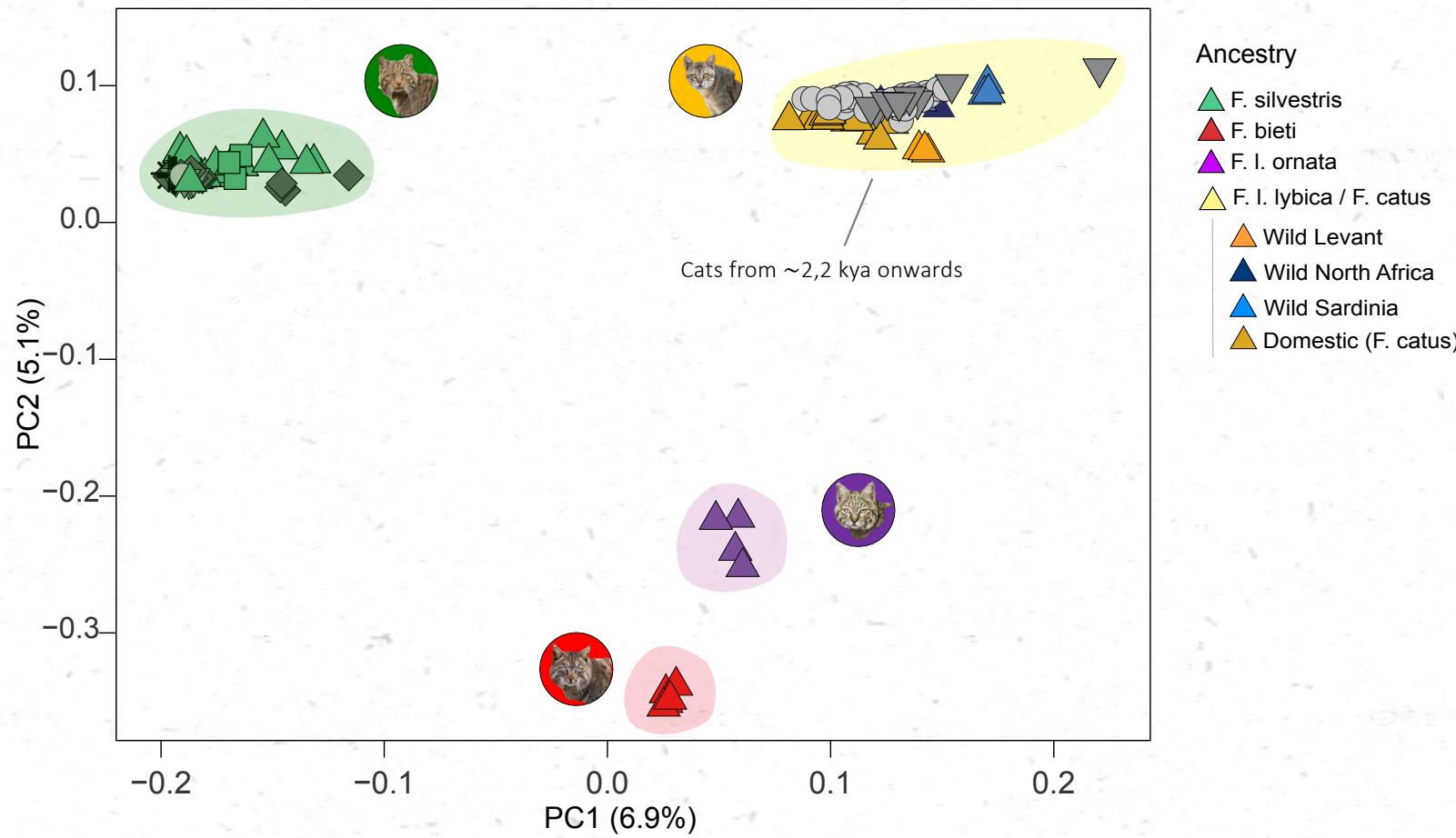


Cats were not introduced to Europe by farmers during the Neolithic



No genetic trace of *F. lybica/catus* in Europe until the 2nd cent. BCE

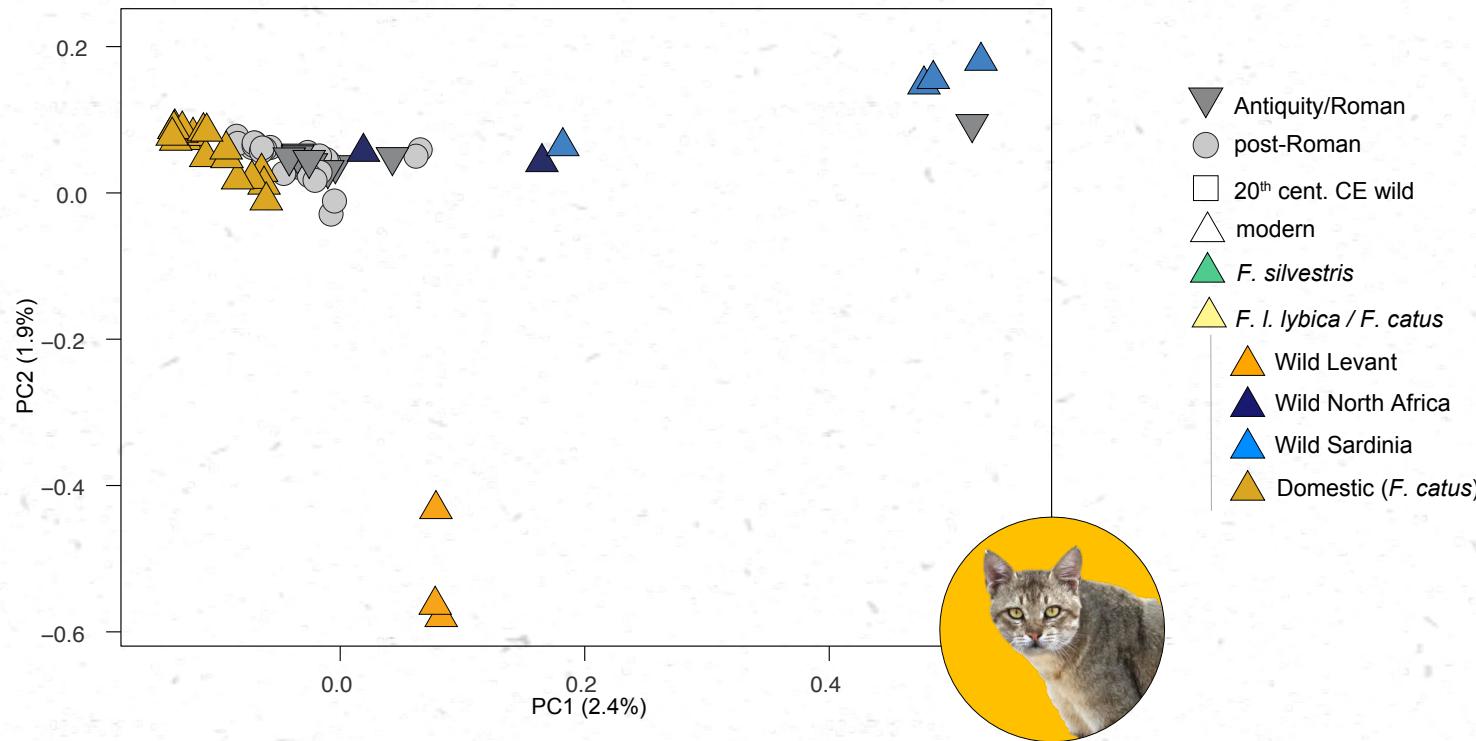
PCA



Places and circumstances of cat dispersal



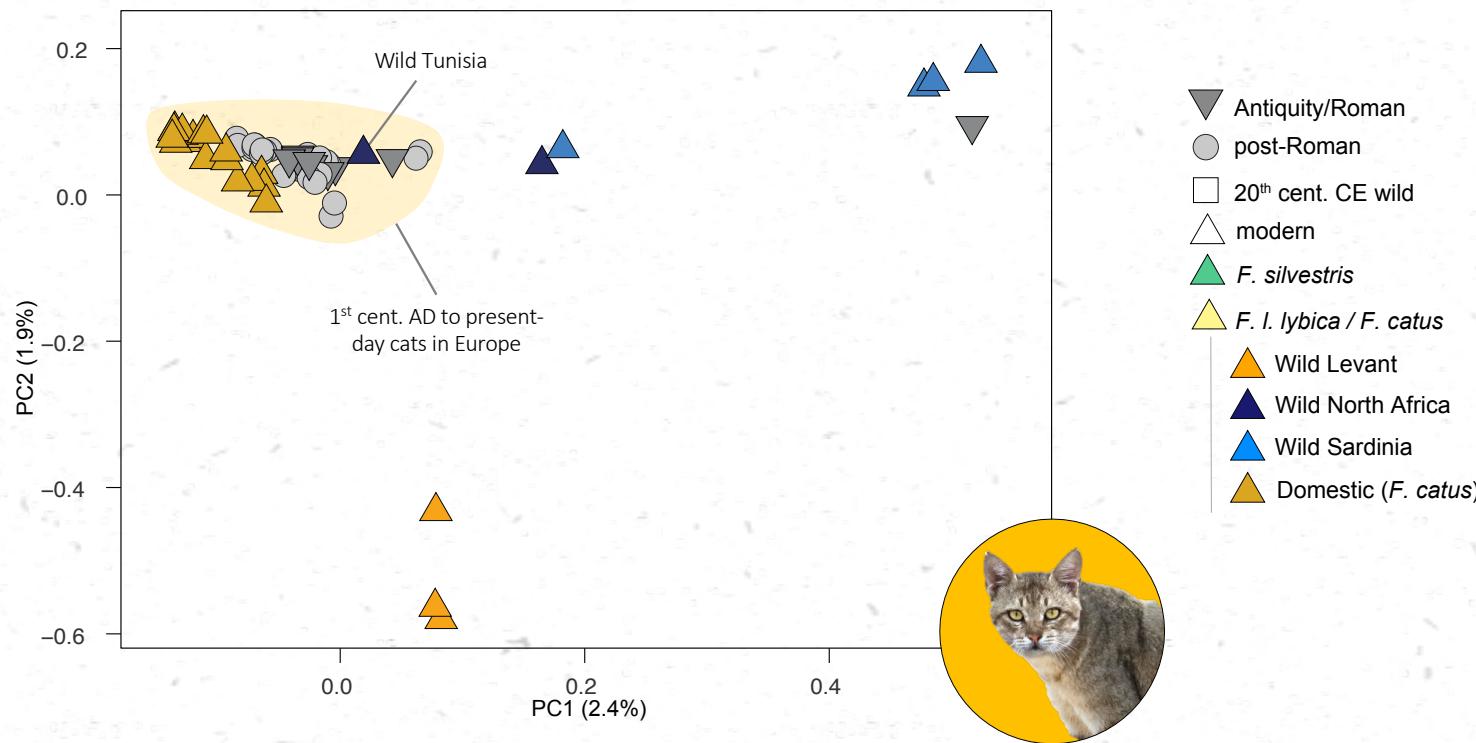
PCA of *Felis lybica*



(based on transversions, ancient samples projected on modern variation)

De Martino et al. (bioRxiv, in review)

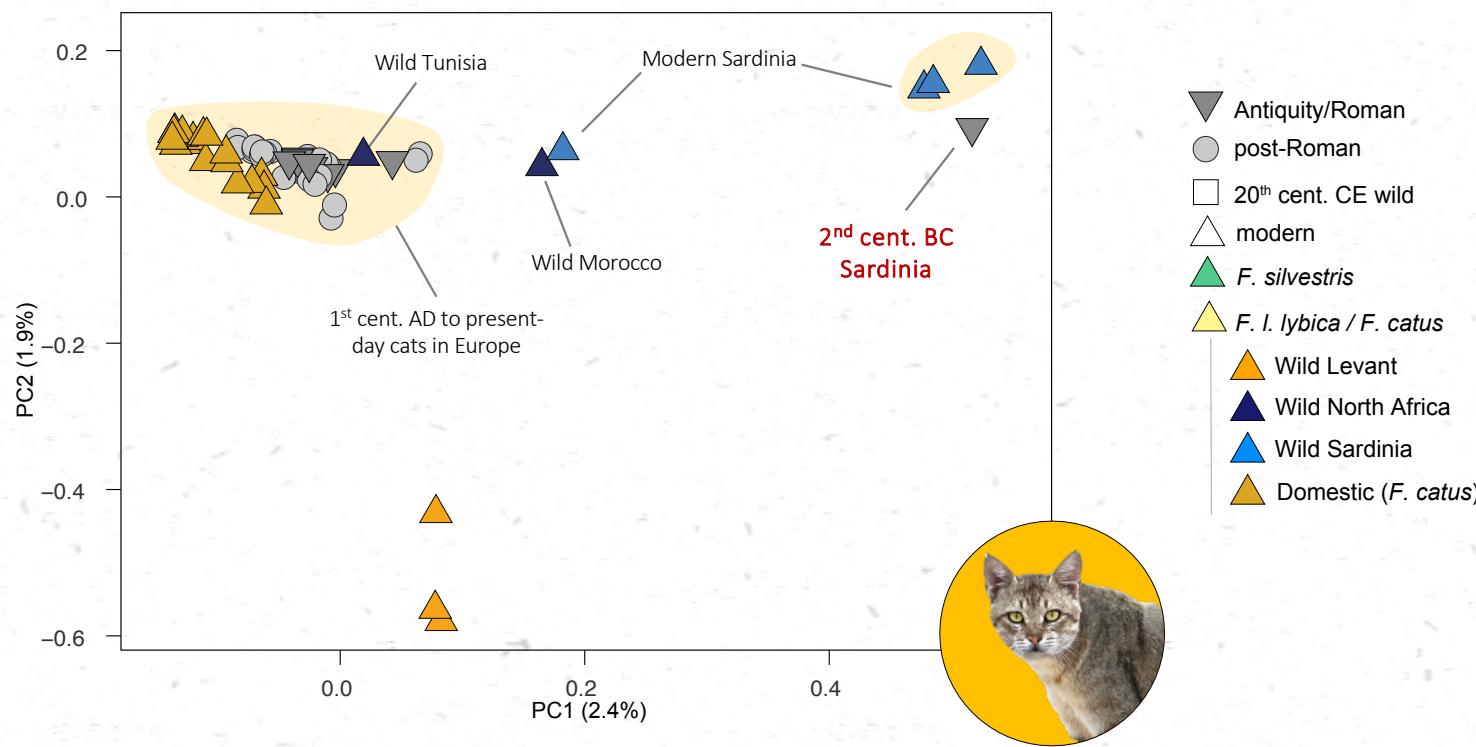
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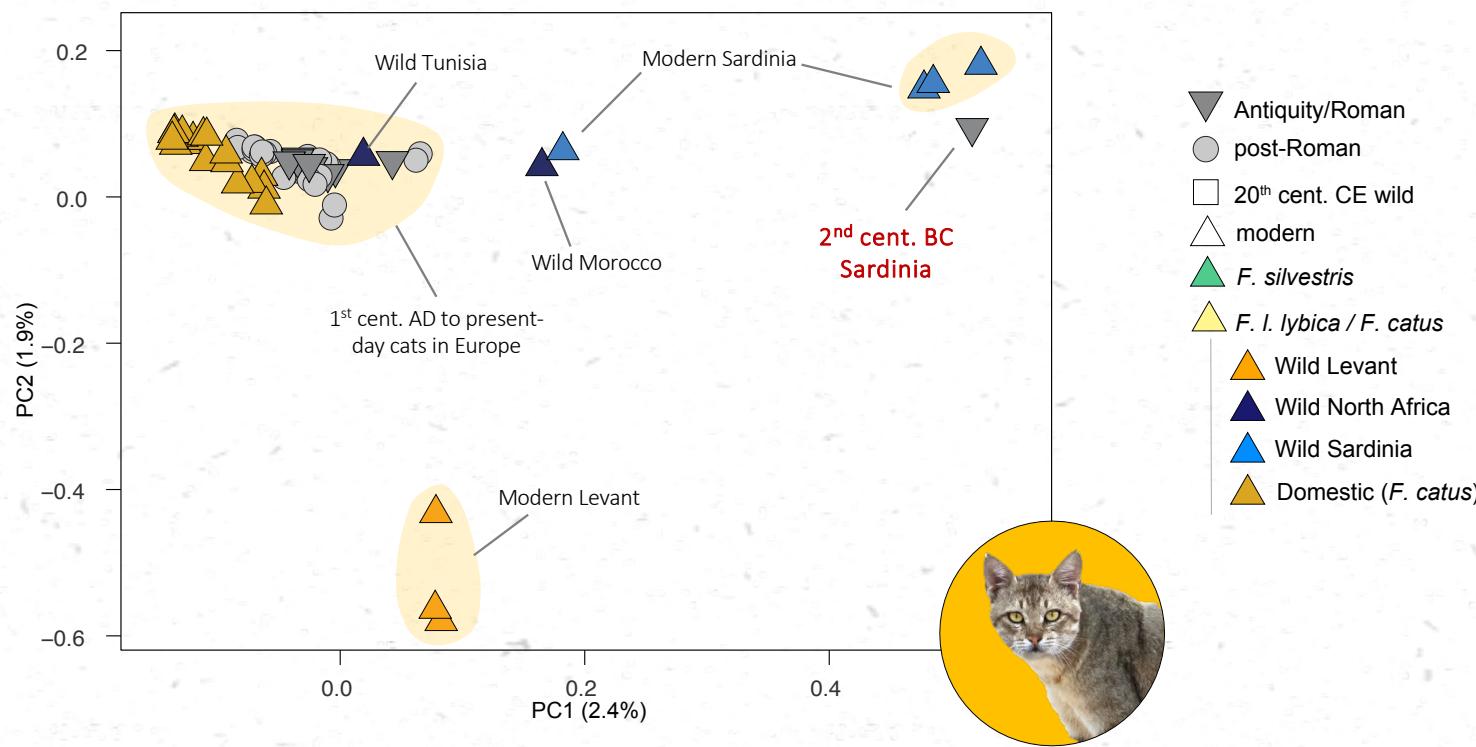
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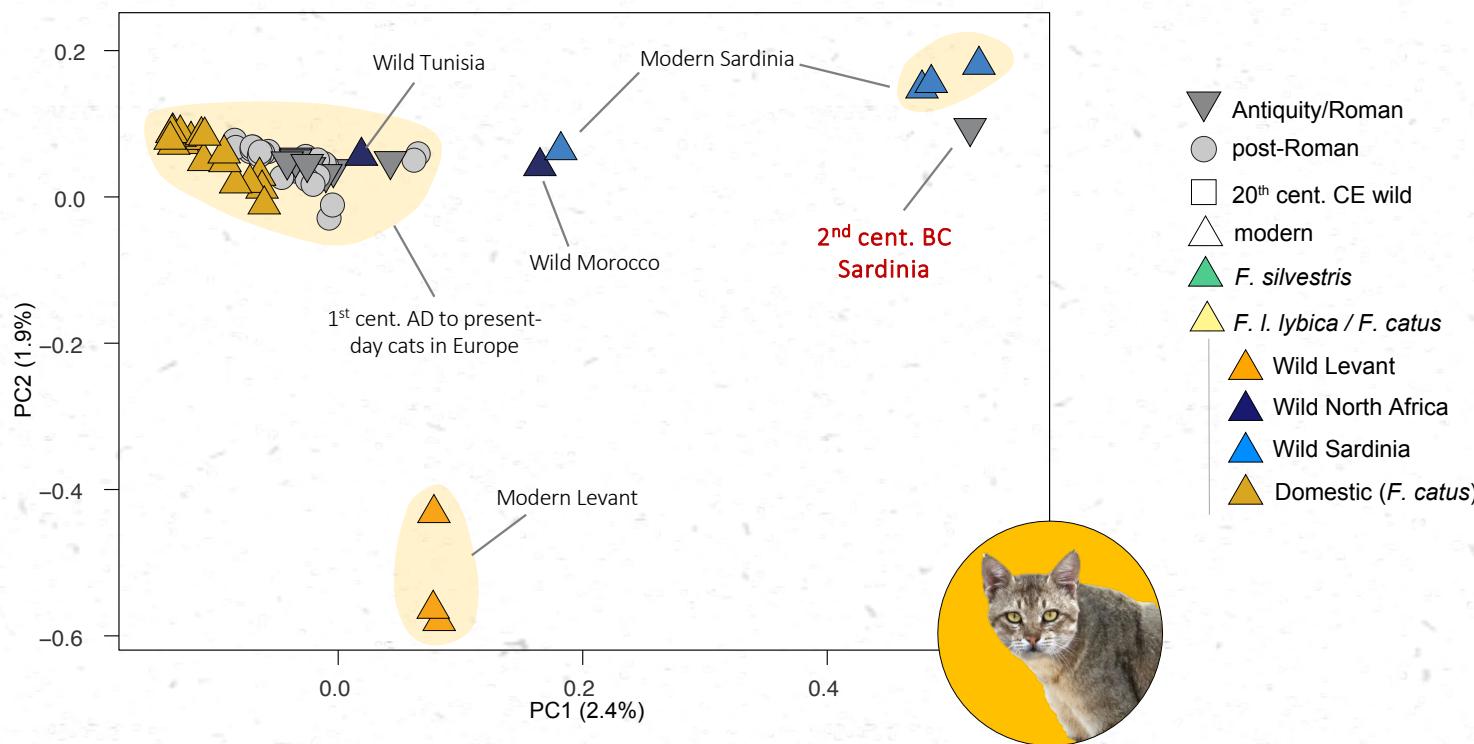
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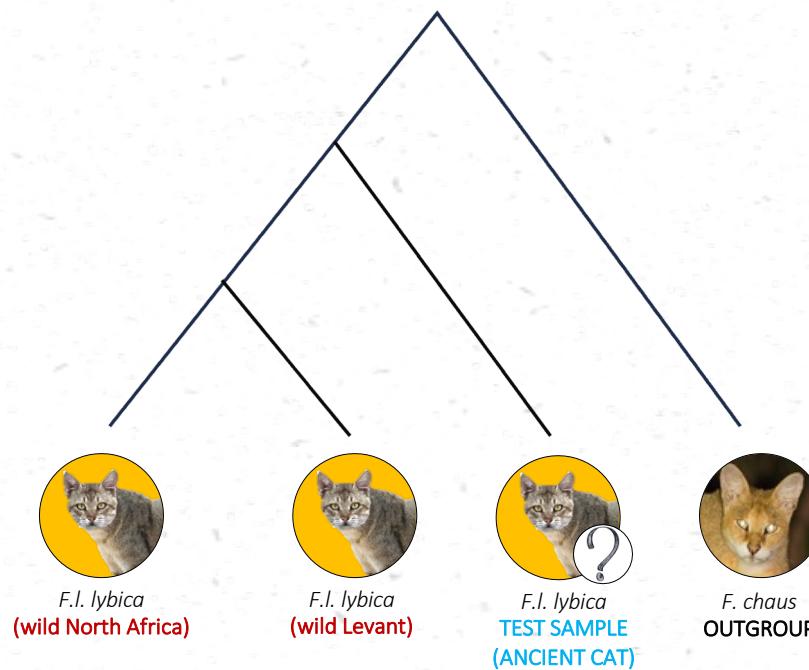
(based on transversions, ancient samples projected on modern variation)

Apparent genetic proximity of ancient and modern domestic cats with **African** samples...
Let's test it with **D-stats!**

De Martino et al. (bioRxiv, in review)

F4-statistics

Testing evolutionary models

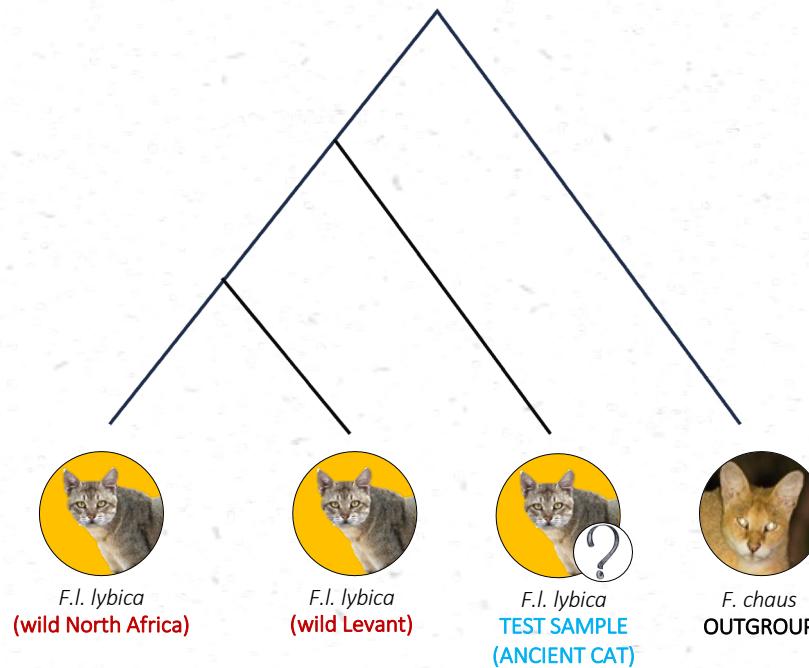


Is a **test sample** genetically closer to **wildcats from the Levant** or **wildcats from North Africa**?

Here we are testing individuals of the same species!

F4-statistics

Testing evolutionary models



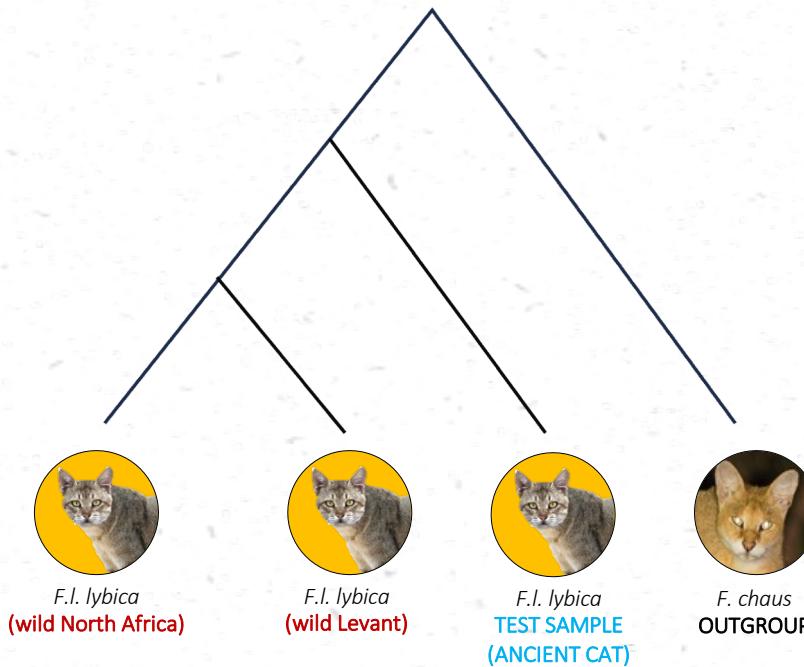
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$F4 > 0 \Rightarrow$ TREE NOT SUPPORTED!

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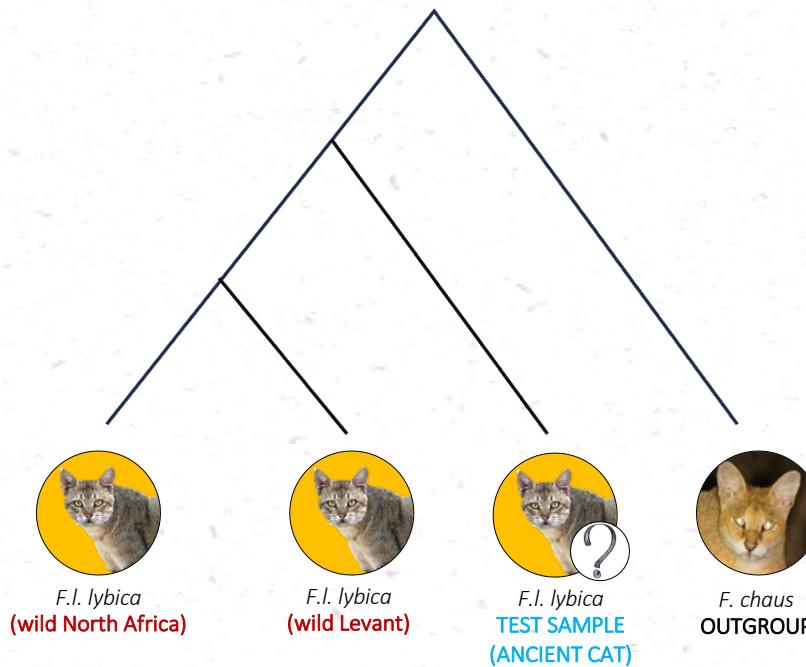
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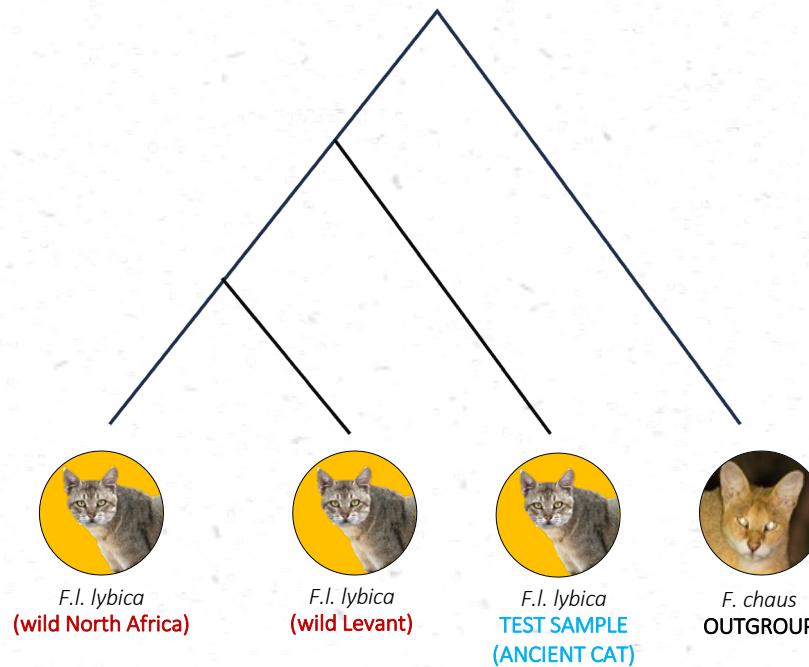


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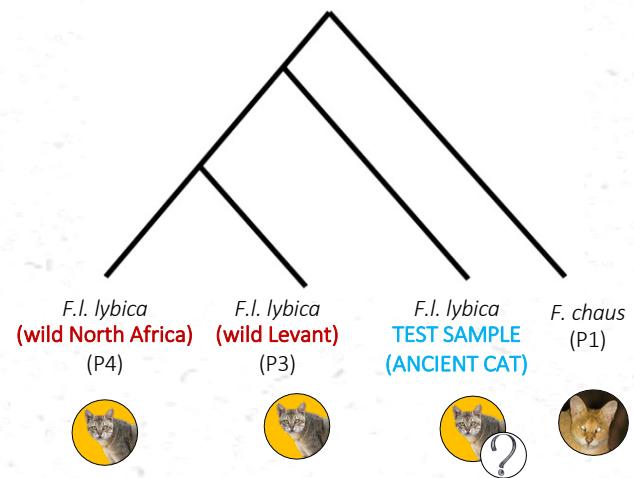


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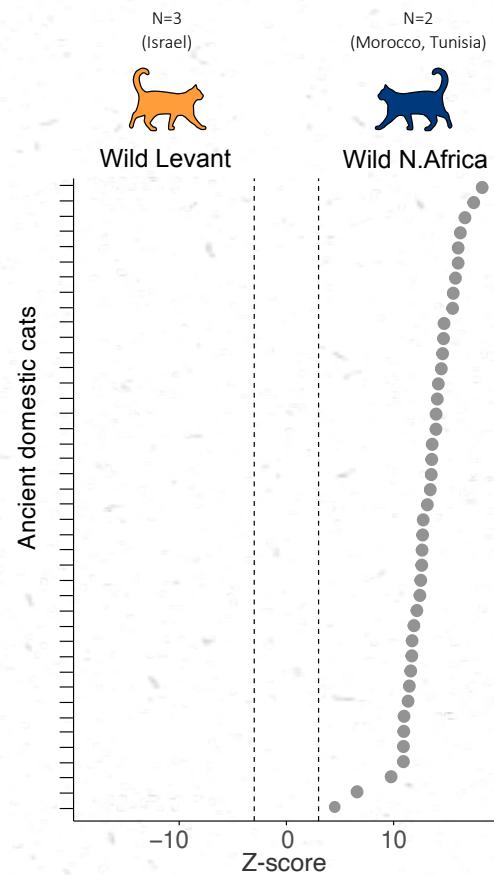
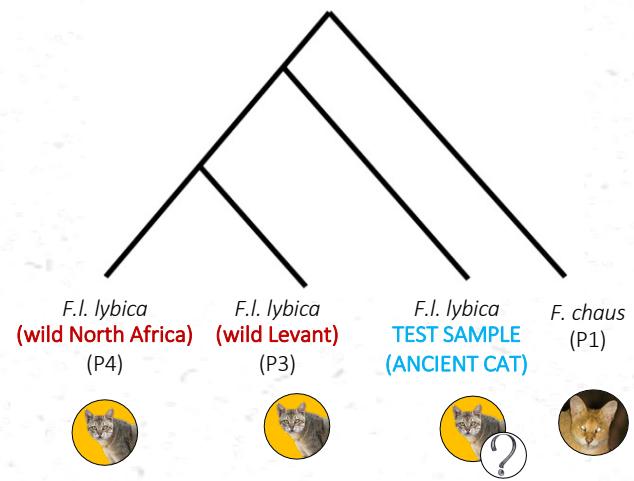
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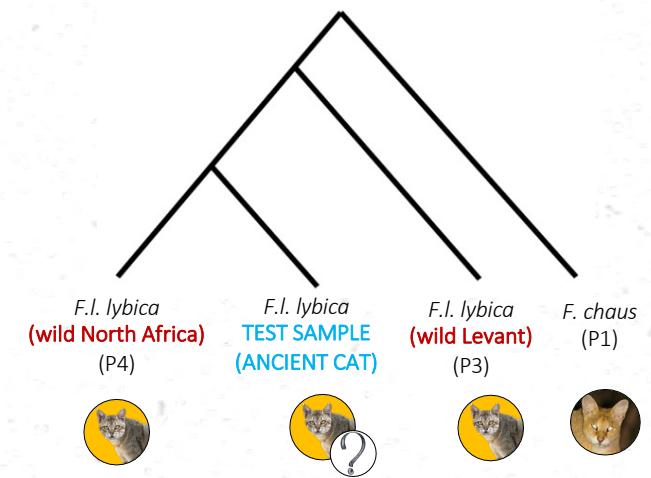
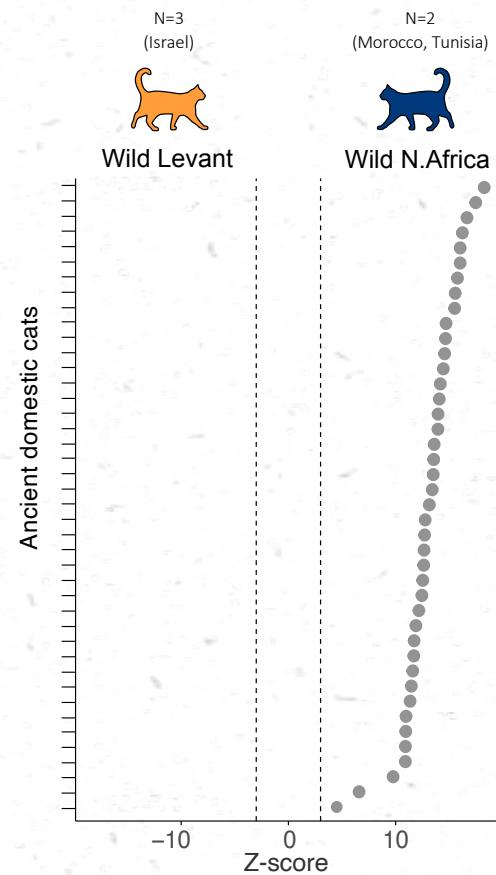
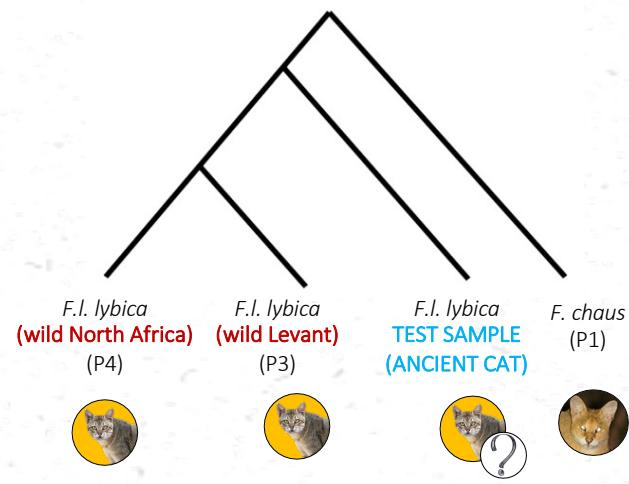
F4-statistics



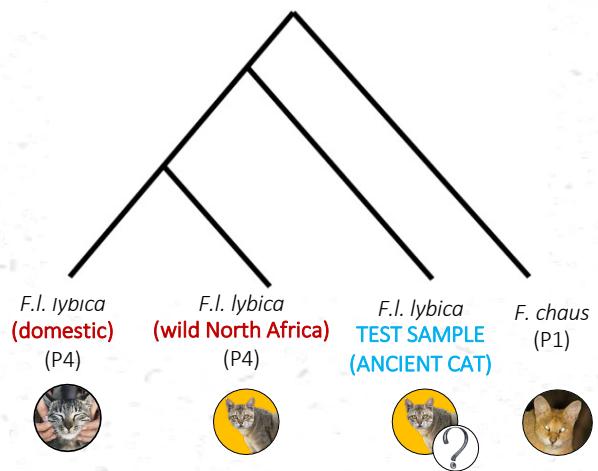
F4-statistics



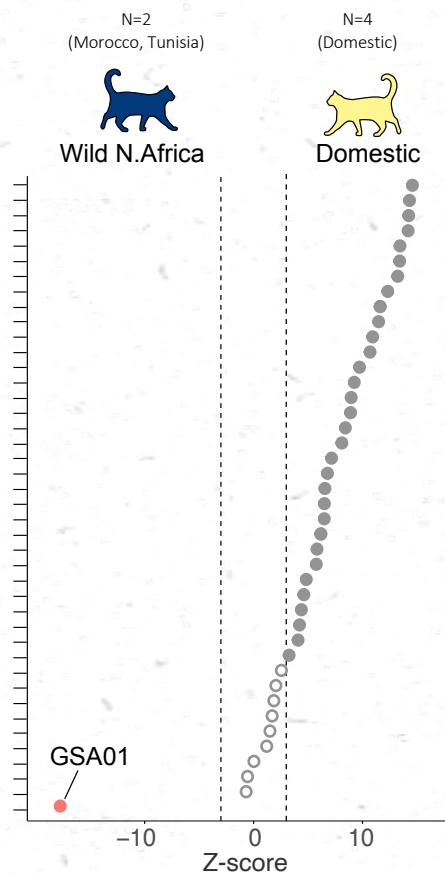
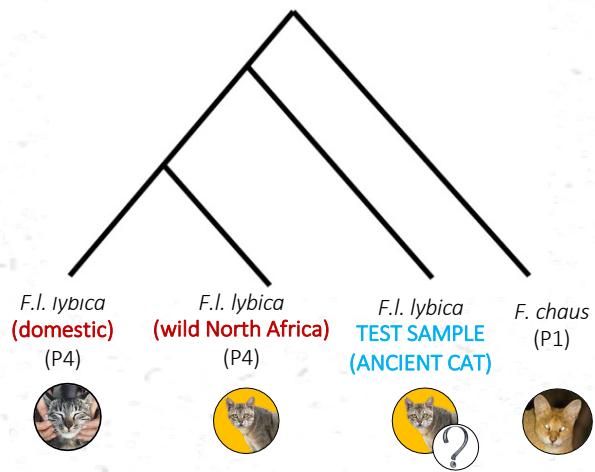
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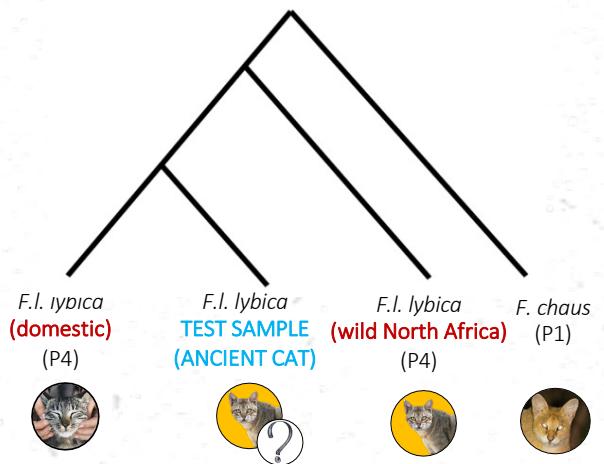
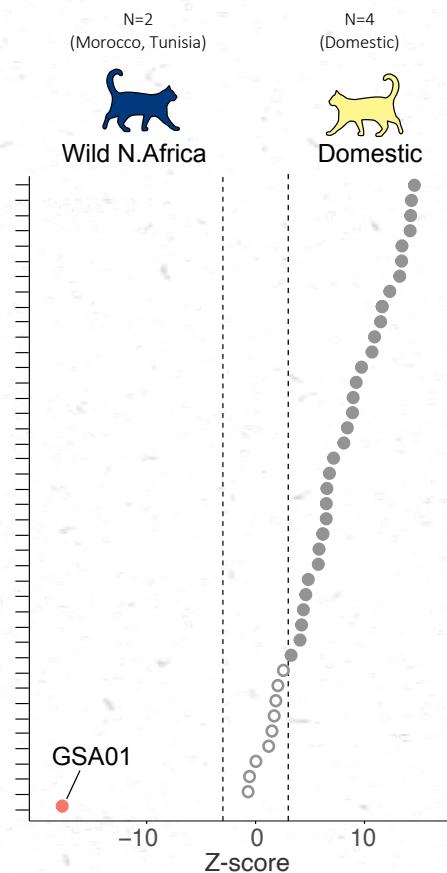
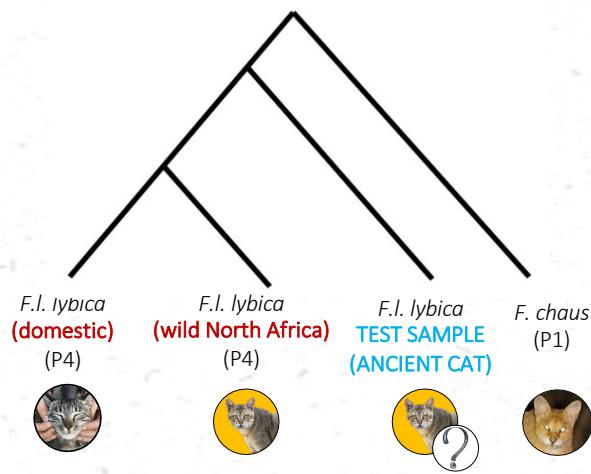
F4-statistics



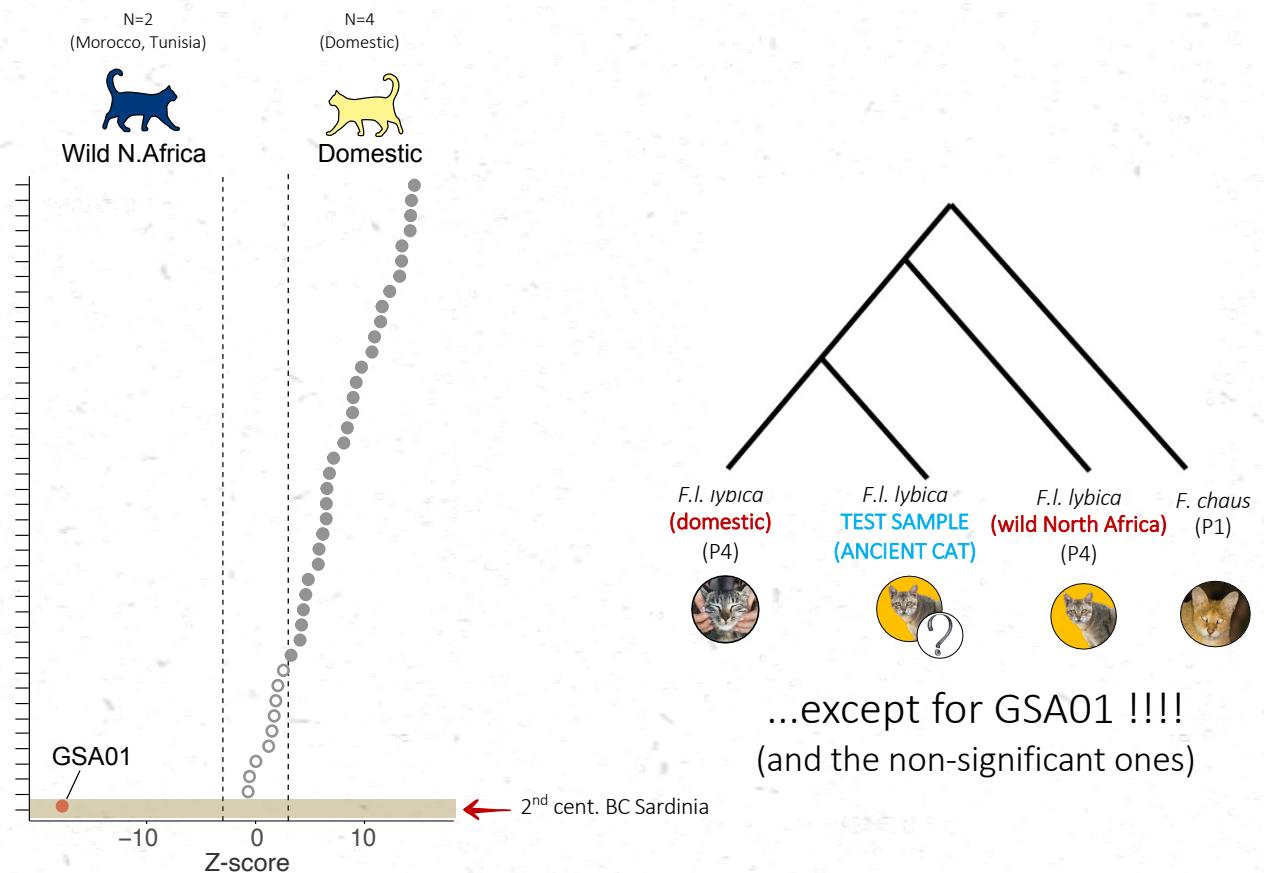
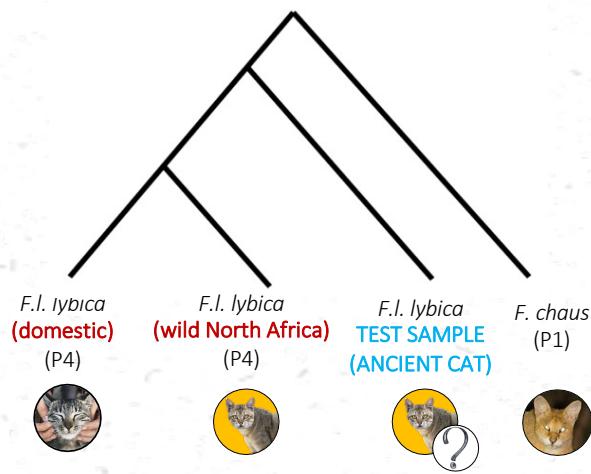
F4-statistics



F4-statistics



F4-statistics





Genoni Santu Antine, Sardinia

Monumental buildings (Nuraghi) typical of the Bronze and Early Iron Age in Sardinia (Nuragic Age, 1900-238 BC). Fortification reused in the Punic era (from 6th cent BC) and Roman era (from 238 BC).



Genoni Santu Antine, Sardinia

Monumental buildings (Nuraghi) typical of the Bronze and Early Iron Age in Sardinia (Nuragic Age, 1900-238 BC). Fortification reused in the Punic era (from 6th cent BC) and Roman era (from 238 BC).

Introduction of (wild)cats from Northwest Africa in Genoni with the Punic people or Romans.

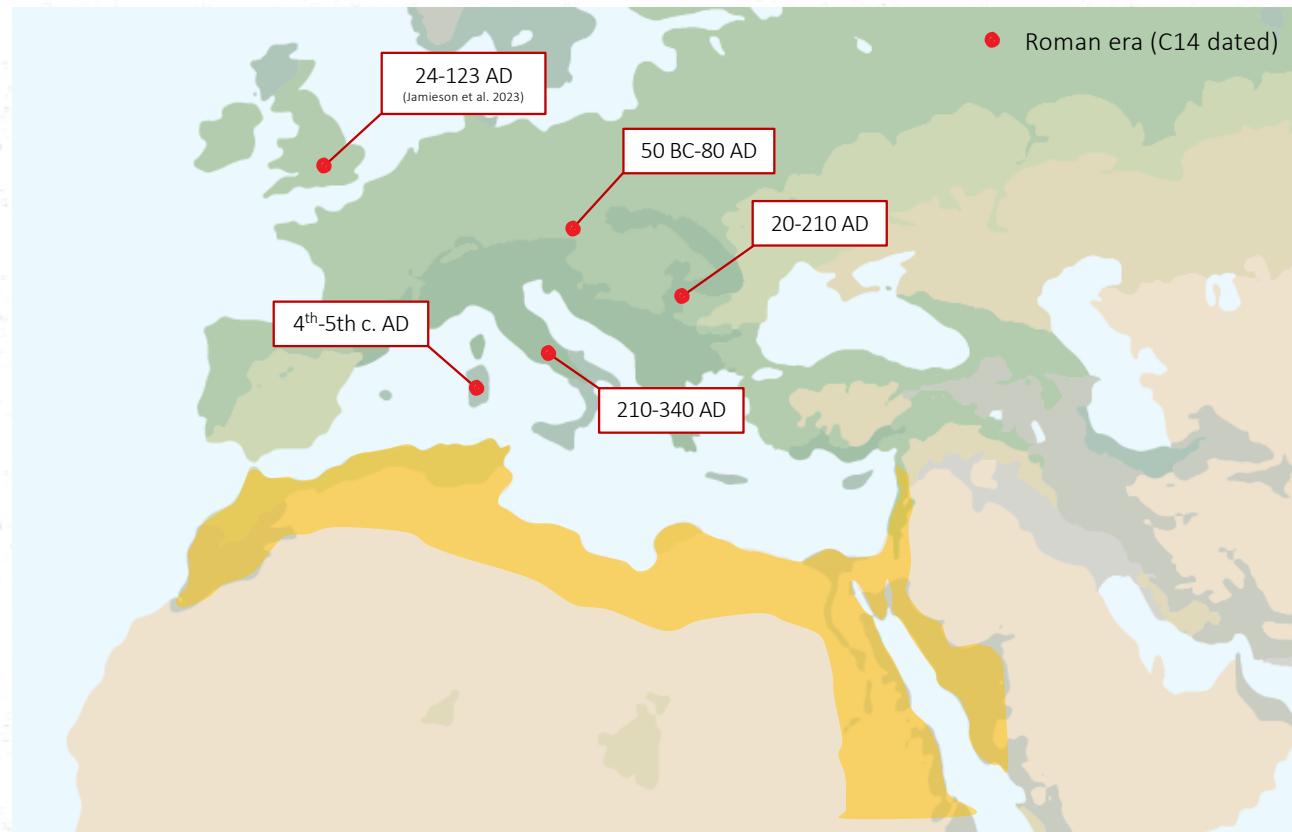
Dual introduction of cats in Sardinia (and Iberia?)

- 1st introduction from Northwest Africa that originated the Sardinian wildcat population.
- 2nd introduction of domestic cats (following the dispersal Europe-wide).



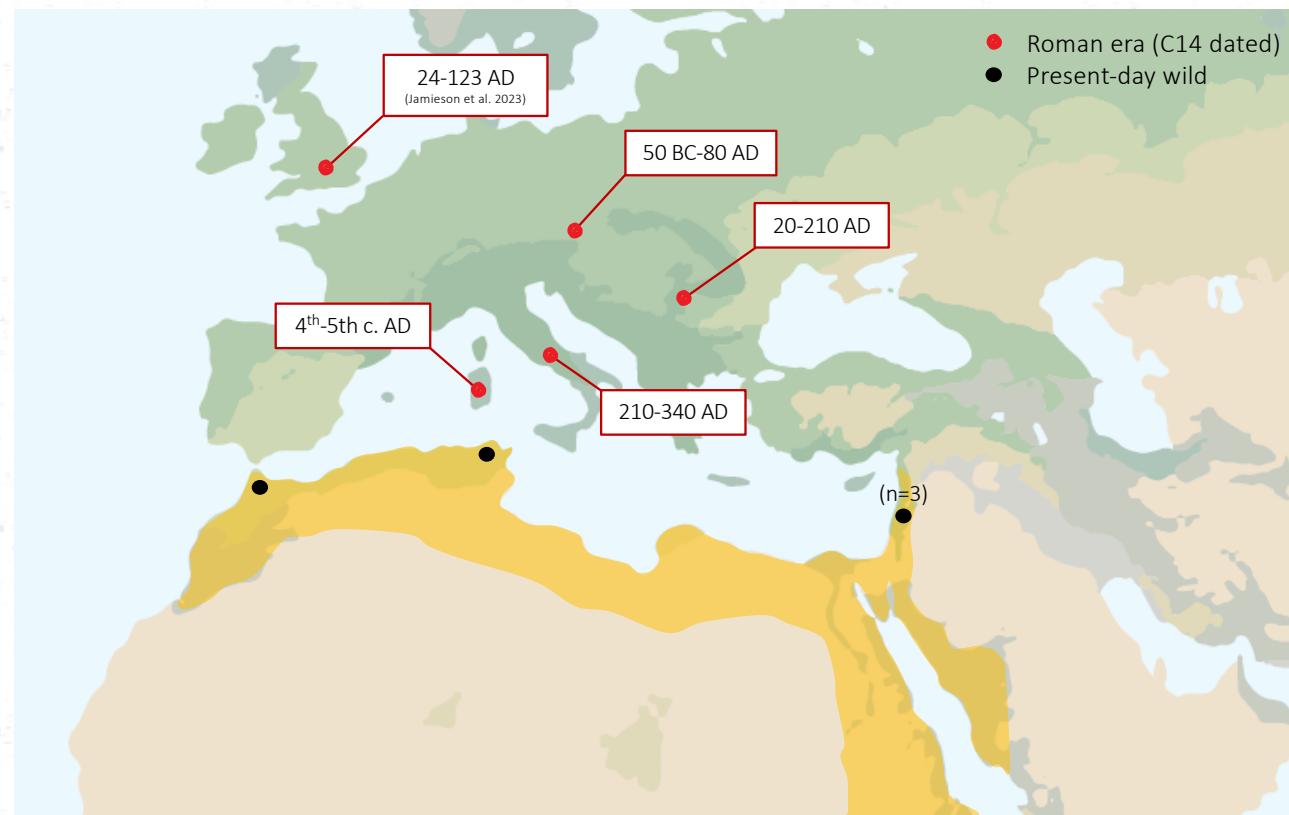
Ancient cat genomes

The dispersal of cats with humans



Ancient cat genomes

The dispersal of cats with humans

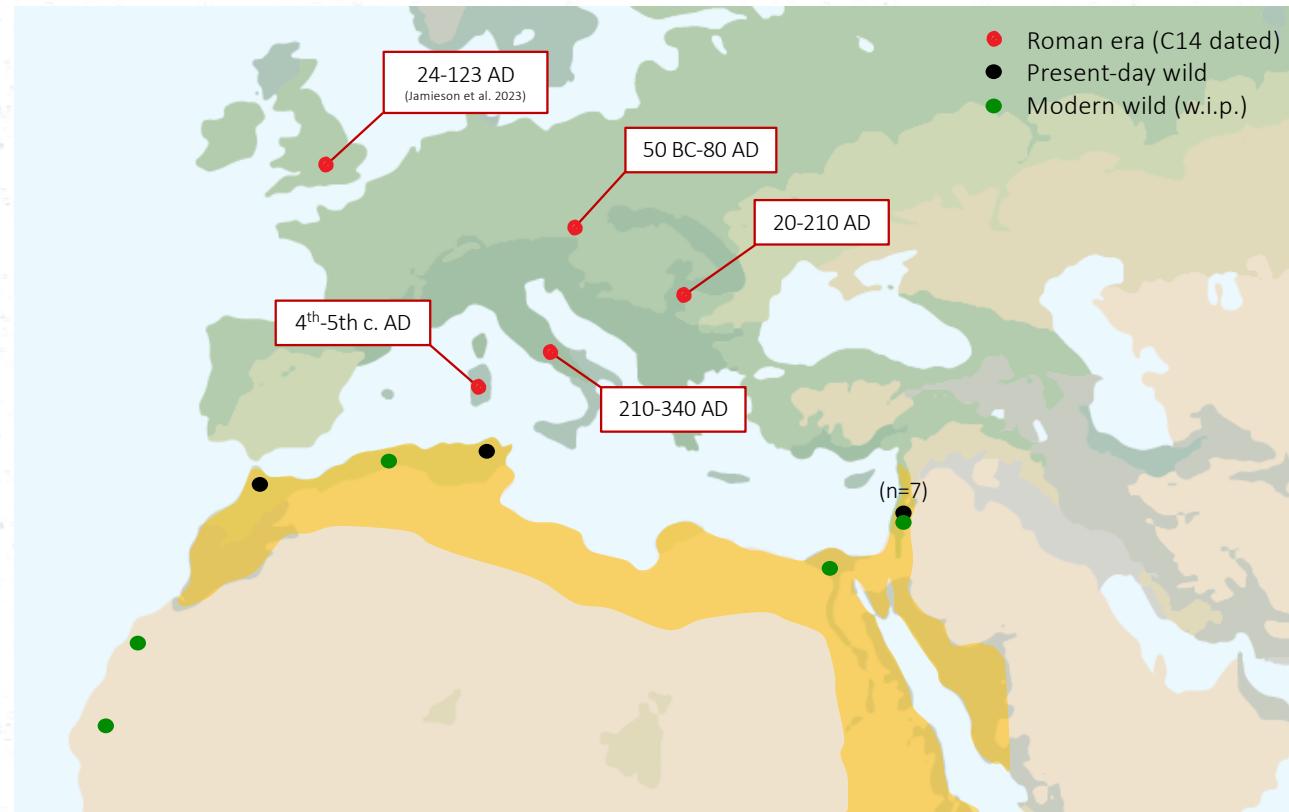


Original source population?

The Tunisian wildcat is our best proxy so far, yet more ancient and modern (wild) African genomes are needed!

Ancient cat genomes

The dispersal of cats with humans



Original source population?

The Tunisian wildcat is our best proxy so far, yet more ancient and modern (wild) African genomes are needed!

New modern genomes (including museum) of *F. lybica* wildcats from Western Sahara, Mauritania, Algeria, Egypt and Israle.

Domestic cats in Europe

Religious and economic motivation



Doherty et al. (bioRxiv, in review)



Bastet statuette
(photo: Metropolitan Art Museum New York)



Egyptian cat mummy (photo: NHM London)

Religious motivation?

Cult of the goddess Bastet in Egypt and other other and association with deities in other Mediterranean civilizations

Domestic cats in Europe

Religious and economic motivation



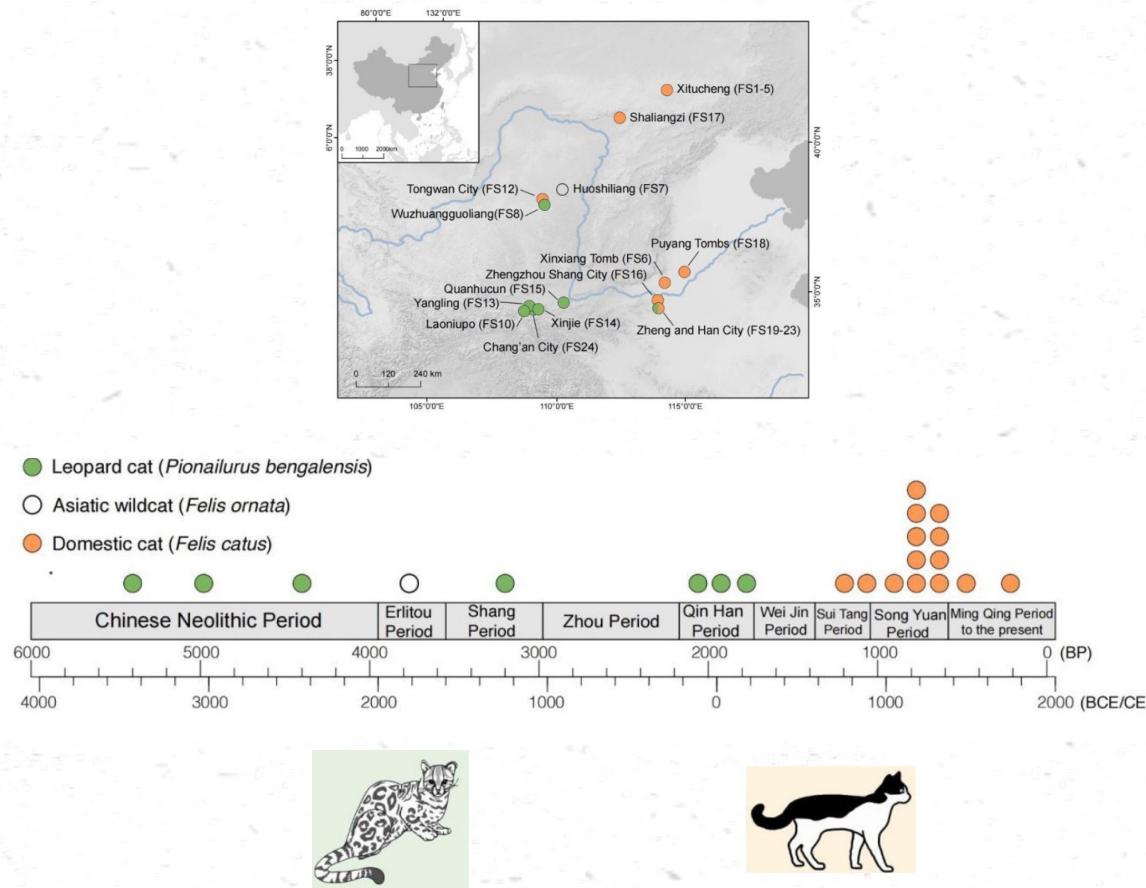
Farina and Correia 2006

Economic motivation?

Egypt as “the granary” of the Roman Empire and cats used as pest control agents in ships across trade routes of the Mediterranean.

Cat dispersal in east Asia

Cats in China



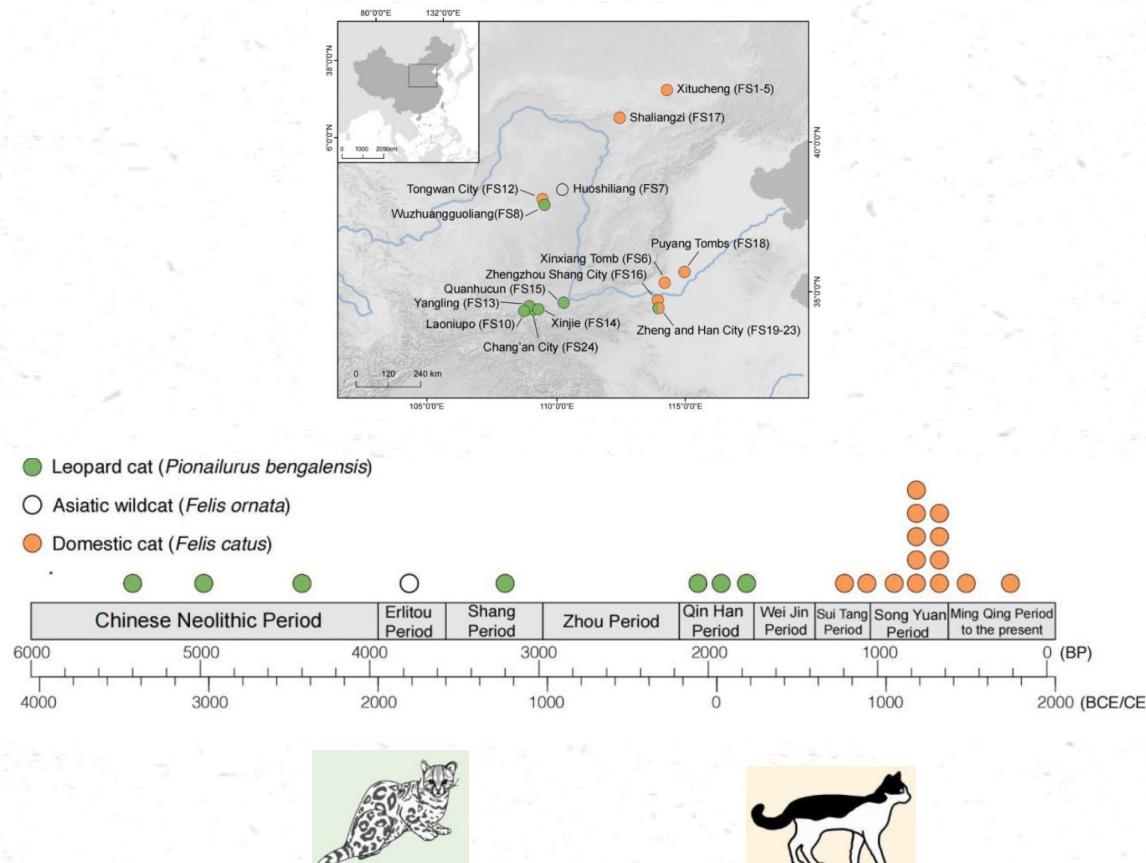
Earliest domestic cat in China

730 CE, Tongwan City, Shaanxi

Paleogenomic analysis of 22 feline bones revealed a turnover from leopard cat to domestic cats in the anthropogenic niche.

Cat dispersal in east Asia

Cats in China



Han et al. (bioRxiv)

Earliest domestic cat in China

730 CE, Tongwan City, Shaanxi

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Ancient cats from North Africa and Southwest Asia.
Patterns of domestic cat dispersal in West and East Eurasia.
(work in progress)



Valentina Rovelli



Patrizia Serventi

Domestic cats in Europe

Earlier introduction to Europe?

Mosaic in Pompeii (1st cent BC)
Naples National Archaeological Museum



Stele depicting a fight between a dog and a cat in 510 BC, Greece
City Of Athens Museum, History Museum



Cat depictions
1st millennium BCE
Often found in Etruscan and Greek art

Domestic cats in Europe

Earlier introduction to Europe?



Neck Amphora (490 BCE)
Getty Villa, Gallery 110, The Etruscans



Ancient Greek vase (ca. 5th c. BCE)
Nicholson Museum at the University of Sydney

Cat depictions
1st millennium BCE

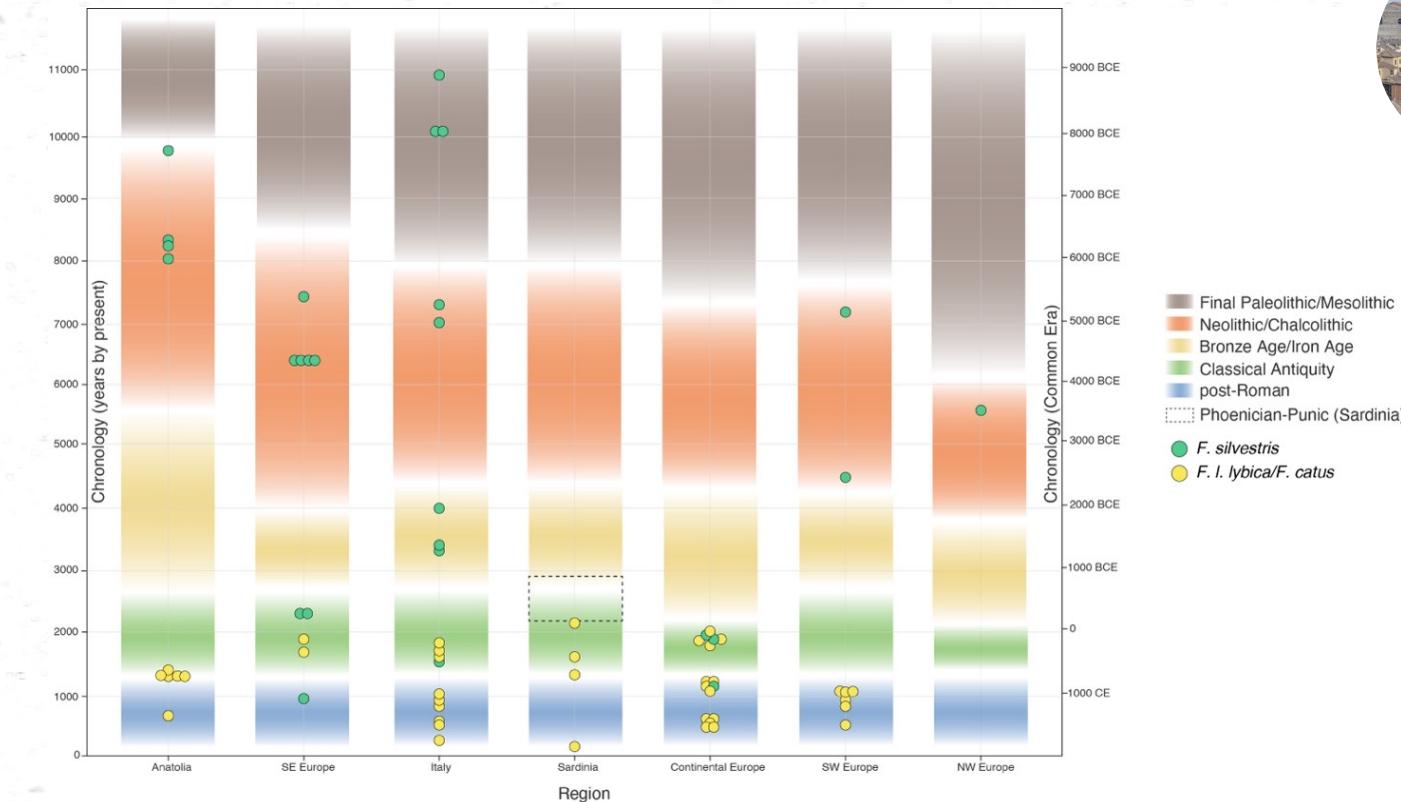
Often found in Etruscan and Greek art

Domestic cats in Europe

Earlier introduction?



Betty Mouraud



Pre-Roman introduction to Europe?
Only three specimens analyzed in the 1st millennium BC.

Domestic cats in Europe

Testing earlier introduction



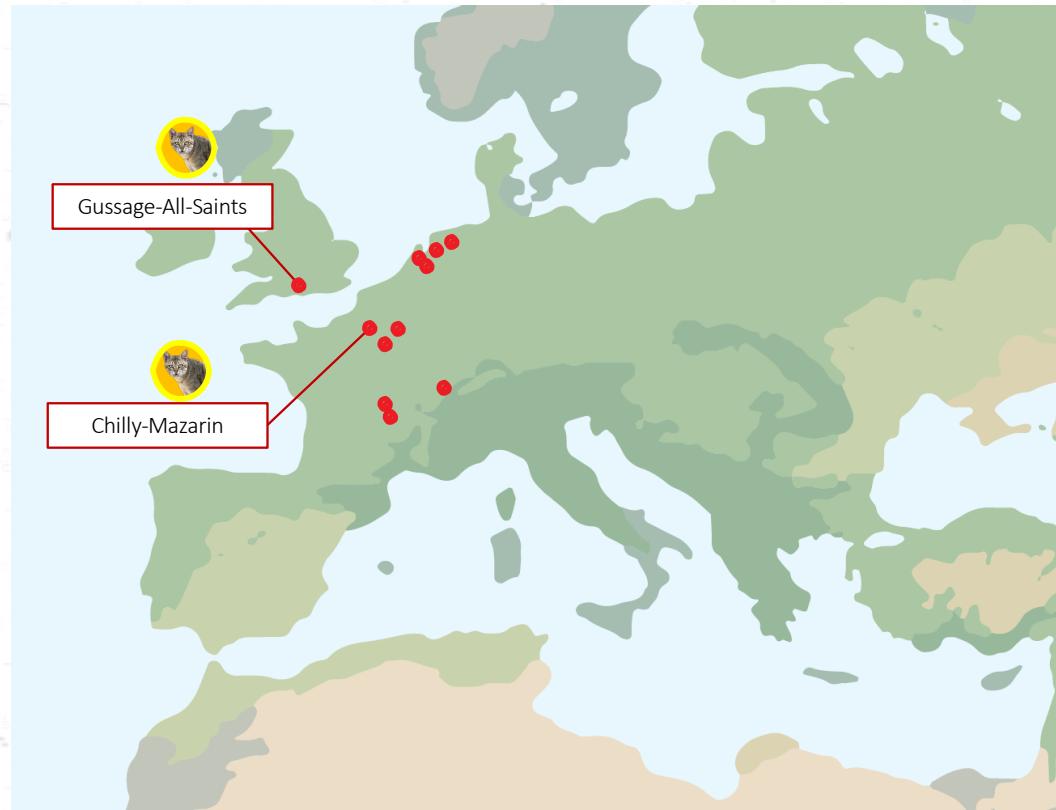
Bronze & Iron Age sites



Betty Mouraud

Domestic cats in Europe

Testing earlier introduction



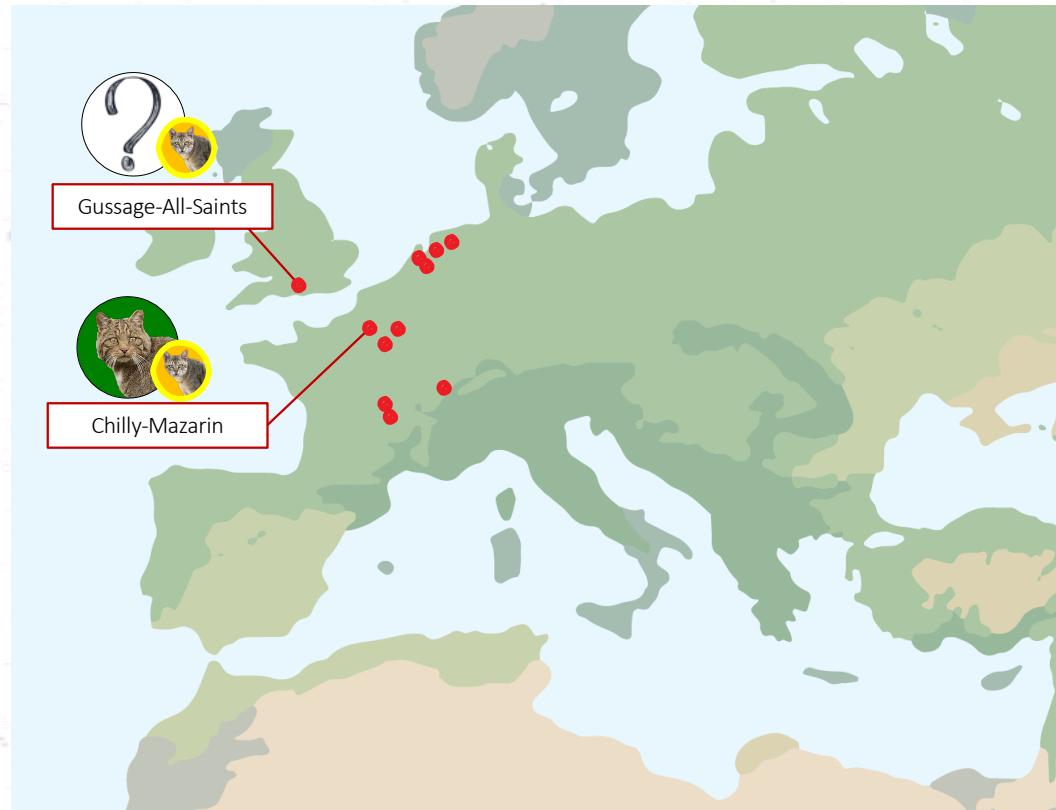
Bronze & Iron Age sites



Betty Mouraud

Domestic cats in Europe

Testing earlier introduction



Bronze & Iron Age sites



Betty Mouraud

Viking cats

Ancient genomes & stable isotopes

Viking cats

103 cats (mandibles) from the sites of Haithabu, Schleswig and Elisenhof (Germany), covering the Viking era (800-1250 AD).



Sampling cats from Schleswig/Haithabu (Germany)
Photo: Bea De Cupere



Haithabu, reconstruction of the port in the 10th century (Harbourscapes, Müller 2020)



Patrizia Serventi



Betty Mouraud

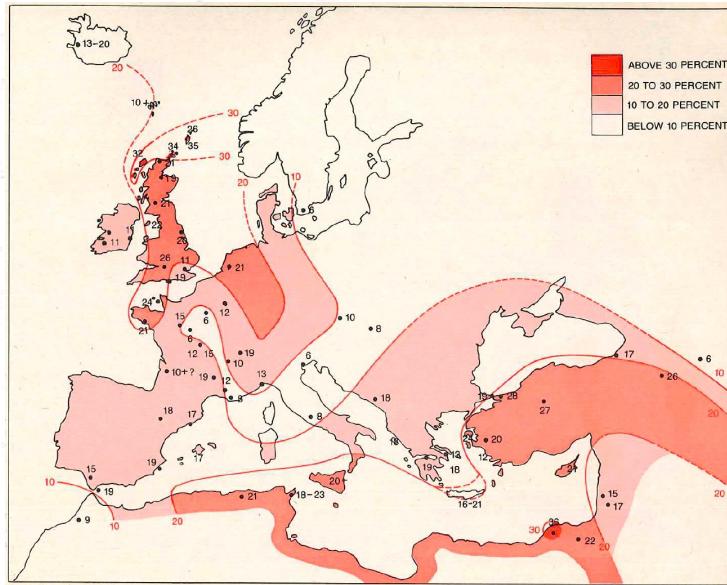
Ulrich Schmölcke
Zentrum für Baltische und
Skandinavische Archäologie
Schloss Gottorf



Landesmuseen
Schleswig-Holstein
Kultur des Nordens.

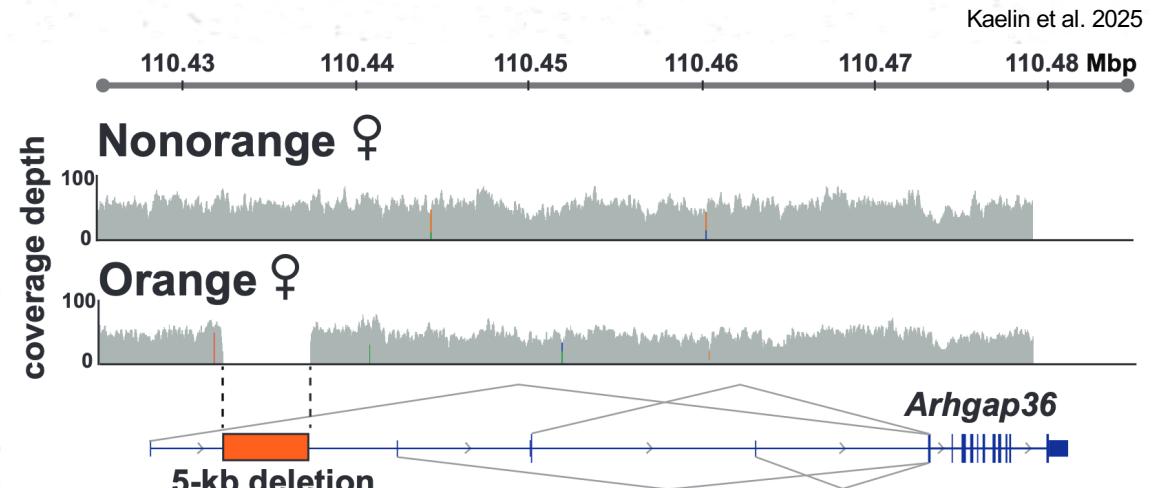
Viking cats

Ancient genomes & stable isotopes



Todd et al. 1977

Did Vikings fancy orange cats?



Orange



Calico



Tortoiseshell

Conclusions

- Two sources of admixture are present in European wildcats, an ancient one (from the wild) and a recent one (from domestic cats)
- Cats were not introduced to Europe by farmers during the Neolithic
- Domestic cats were spread in the last 2,000 years, most likely from North Africa
- In Sardinia, an earlier introduction of *F. lybica* originated the wildcat population still present today

Acknowledgements

Francesca Alhaique (Museo delle Civiltà Luigi Pigorini)

Jacopo De Grossi Mazzorin (Università del Salento)

Claudia Minniti (Università del Salento)

Paolo Boscato (University of Siena)

Francesco Boschin (University of Siena)

Barbara Wilkens (Università degli Studi di Sassari)

Marco Romboni (University of Pisa)

Joris Peters (Ludwig-Maximilians-Universität München)

Cleia Detry (University of Lisbon)

Daniel Makowiecki (Nicolaus Copernicus University)

Didier Berthet (Musée des Confluences Lyon)

Frank Zachos (Naturhistorisches Museum Wien)

Günther Karl Kunst (University of Vienna)

Hervé Monchot (Université Paris-Sorbonne – Paris IV)

Idoia Grau (University of Sheffield)

Jordi Nadal (University of Barcelona)

Kristina Killgrove (University of North Carolina)

Kamila Braulińska (University of Warsaw)

Konstantina Saliari (Naturhistorisches Museum Wien)

Hans Christian Küchelmann (National Maritime Museum Bremen)

Lionel Gourichon (CNRS – Université Côte d’Azur)

Lluís Lloveras (University of Barcelona)

Maria João Valente (University of Algarve)

Marjan Mashkour (CNRS – National Museum Natural History Paris)

Marta Moreno (Spanish National Research Council)

Nicolai Spassov (National Museum of Natural History of Sofia)

Quentin Goffette (Royal Belgian Institute of Natural Sciences)

Sonja Vuković Bogdanović (University of Belgrade)

Ula Iwaszczuk (Polish Academy of Sciences)

Ulrich Schmölcke (Centre for Baltic and Scandinavian Archaeology, Germany)

Vedat Onar (University of Istanbul)

Vera Pereira (Universidade de Coimbra)

Anna Gręzak (University of Warsaw)



(2012-2017 study)

Ursula Wierer (Soprintendenza Archeologia della Toscana)

Nikolai Spassov (National Museum of Natural History at the Bulgarian Academy of Sciences)

Mary E. Prendergast (Harvard University)

Nicole Boivin (Max Planck Institute Jena)

Arturo Morales (Universidad Autónoma de Madrid)

Adrian Bălăşescu (National History Museum of Romania)

Cornelia Becker (Free University Berlin)

Norbert Benecke (German Archaeological Institute)

Adina Boronenant (Vasile Pârvan’ Institute of Archaeology of the Romanian Academy)

Hilke Buitenhuis (University of Groningen)

Jwana Chahoud (Université Lumière Lyon II)

Alison Crowther (The University of Queensland)

Laura Llorente (Universidad Autónoma de Madrid)

Nina Manaseryan (National Academy of Sciences of Armenia)

Hervé Monchot (Université Paris IV la Sorbonne)

Marta Osypińska (Polish Academy of Sciences)

Olivier Putelat (Archéologie Alsace)

Jacqueline Studer (Natural History Museum of Geneva)

Acknowledgements

Felix team

TOR VERGATA
UNIVERSITY OF ROME

**Marco
De Martino**
(PhD student, aDNA)



**Valentina
Rovelli**
(post-doc, aDNA)



**Partizia
Serventi**
(post-doc aDNA)



**Betty
Mouraud**
(PhD aDNA)



**Gene
Shev**
(post-doc isotopes)



**Tullia
Di Corcia**
(post-doc aDNA, project
manager)



Bea De Cupere
(archaeozoology, RBINS)



Wim Van Neer
(archaeozoology, RBINS)



Steven Bouillon
(geochemistry,
KU-Leuven)



**Marica
Baldoni**
(post-doc, aDNA
metagenomics,
Until Dec 2024)



**Anastasia
Brozou**
(post-doc isotopes,
until Feb 2023)

Support team & partners

Joris Peters (LMU Munich)
Ben Fuller (University of Tolouse)
Marcello Mannino (University of Aarhus)
Emanuela Cristiani (Sapienza University)
Federica Mattucci (ISPRA)
Romolo Caniglia (ISPRA)



This project has received funding from the European Union's Horizon 2020 research and innovation programme under Grant agreement n°101002811

THANKS FOR YOUR ATTENTION

