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Late Pleistocene expansions from a single climatic refugium and close wild–domesticated relationships in the carob tree

Alex Baumel, Frédéric Médail, Gonzalo Nieto Feliner, Stefano La Malfa, Mario Diguardo, Magda Boudagher Kharrat, Lahcen Ouahmane, Katia Diadema, Hervé Sanguin, Juan Viruel

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Late Pleistocene expansions from a single climatic refugium and close wild–domesticated relationships in the carob tree



Alex Baumel, Médail F, Nieto Feliner G, La Malfa S, Di Guardo M, BouDagher Kharrat M, Ouahmane L, Diadema K, Sanguin H, & Viruel J

XVII OPTIMA Meeting Symposium 1. Mediterranean refugia: importance for plant conservation

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- ❖ **IMBE, Marseille**: A. Baumel, F. Médail, F. Mirleau, M. Juin, N. Le Galliot, D. Pavon, A. Saatkamp, M. Selva, A. Haguenaer, M. Moakhar, V. Frelon, P. Mirleau, L. Miché, C. Rocher
- ❖ **RBG Kew**: J. Viruel, S. Pironon,
- ❖ **RBG Madrid**: G. Nieto-Feliner,
- ❖ **University of Catania**: S. La Malfa, M. Brugaletta, M. Di Guardo, E. Potenza
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- ❖ **CBNMED, Hyères** : K. Diadema,
- ❖ **ISTEP, Paris**: J.P. Suc



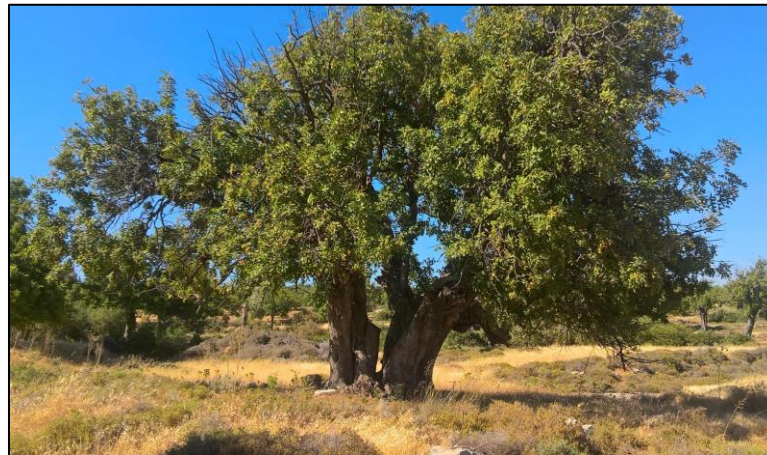
Leader: Hervé Sanguin
<https://dynamic.cirad.fr/>



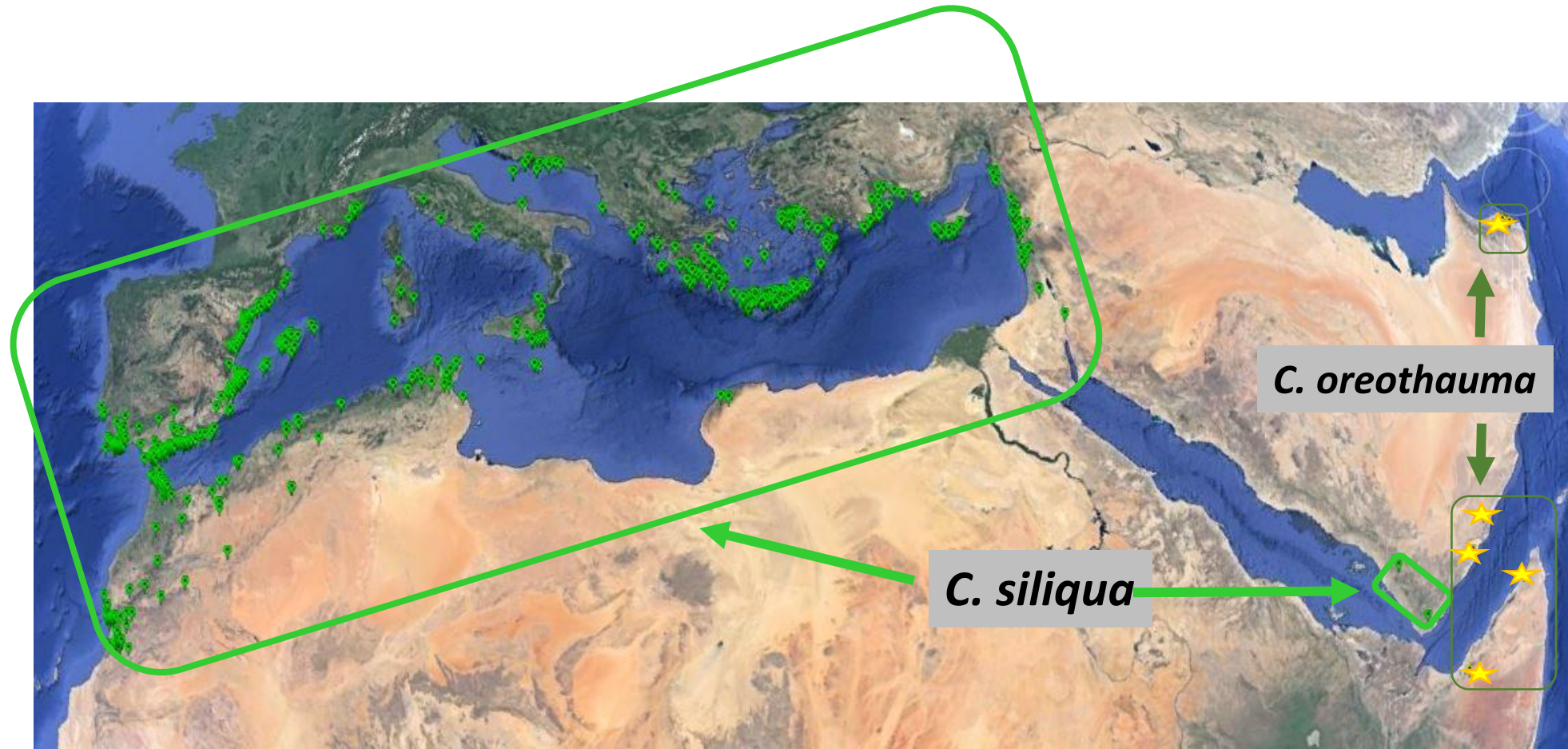
The carob tree, *Ceratonia siliqua* L.



- *Leguminosae, Caesalpinioideae*
- **Composed leaf**
- **Male and Female trees**
- **Wind and insect pollination**
- **Diploid with 24 chromosomes**



Mediterranean and Near-East range



Initial hypothesis

Eastern Refugia Hypothesis and eastern domestication followed by westward dispersals by Greeks, Romans and Arabs

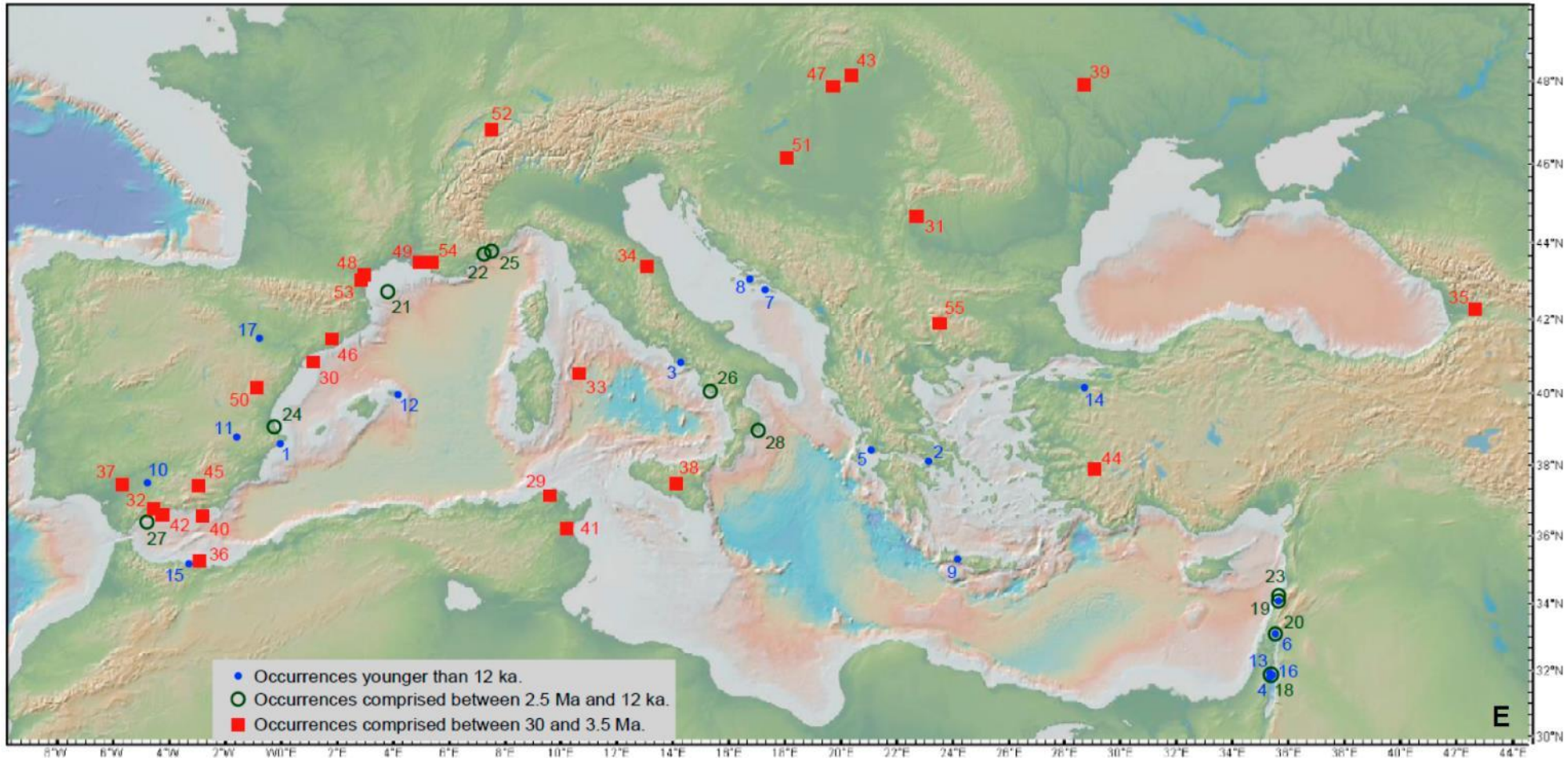
Arguments:

- great abundance of the carob in the East Mediterranean
- Arab or Greek origin of the words to name the carob
- Two species in the Middle East: *C. siliqua* et *C. oreothauma*



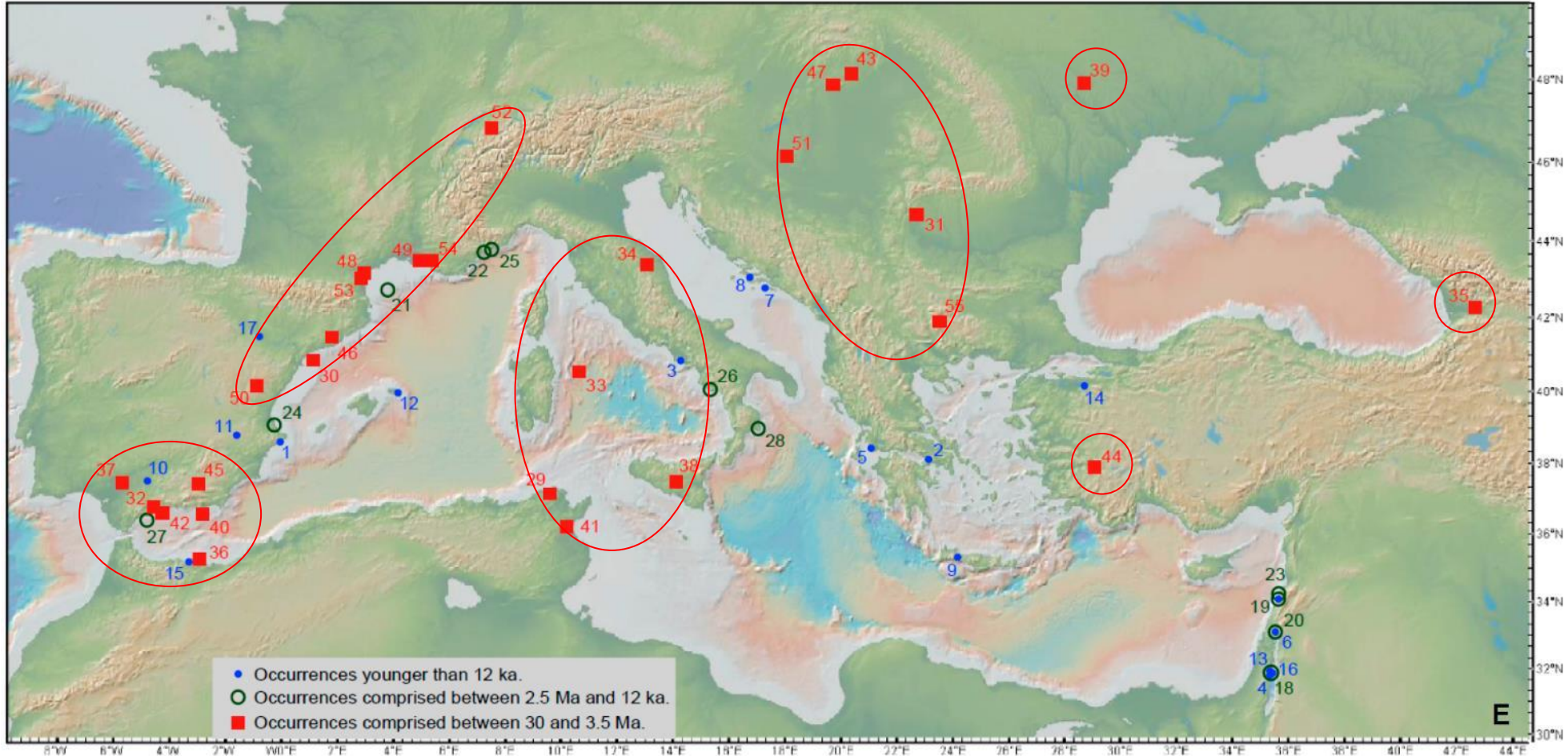
De Candolle 1883; Hillcoat et al 1980; Zohary 2002; Ramon-Laca & Mabberley 2004

Review of past occurrences



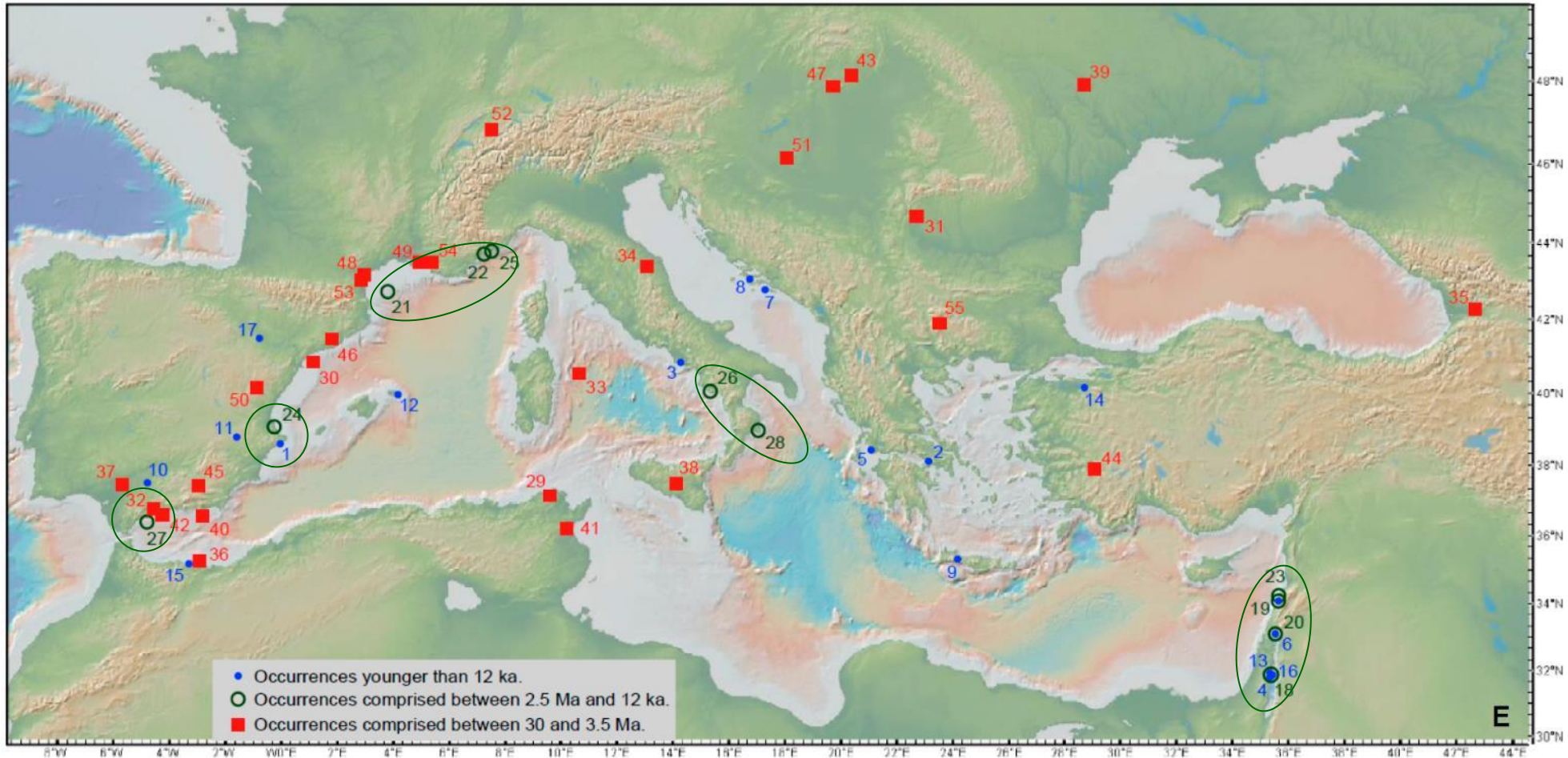
**55 past occurrences (pollens or macro remains)
From Early Oligocene to Middle ages**

Review of past occurrences



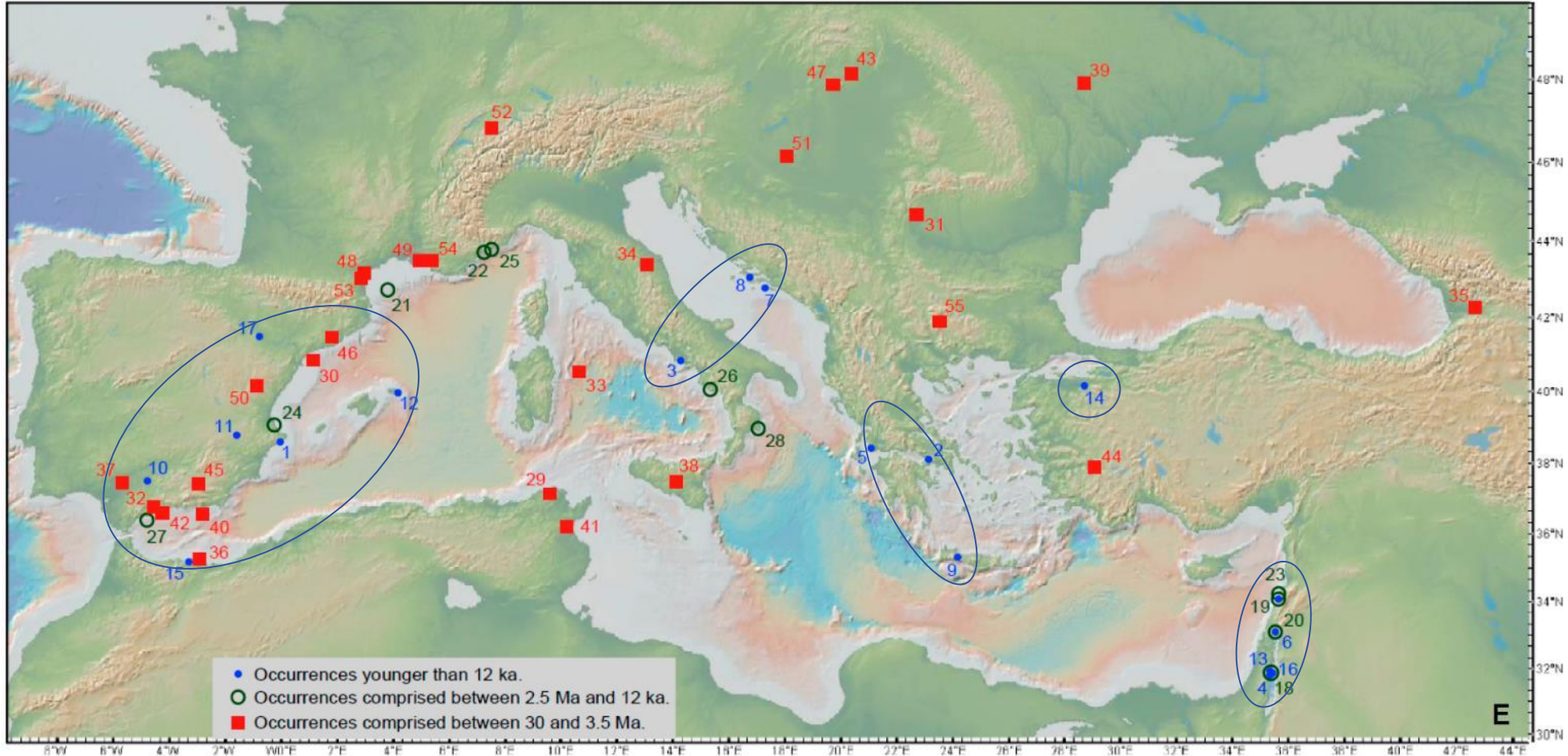
➤ From Oligocene to late Pliocene 30 to 3.5 Ma

Review of past occurrences



- From Oligocene to late Pliocene 30 to 3.5 Ma
- Pleistocene 2.5 Ma to 12ka

Review of past occurrences



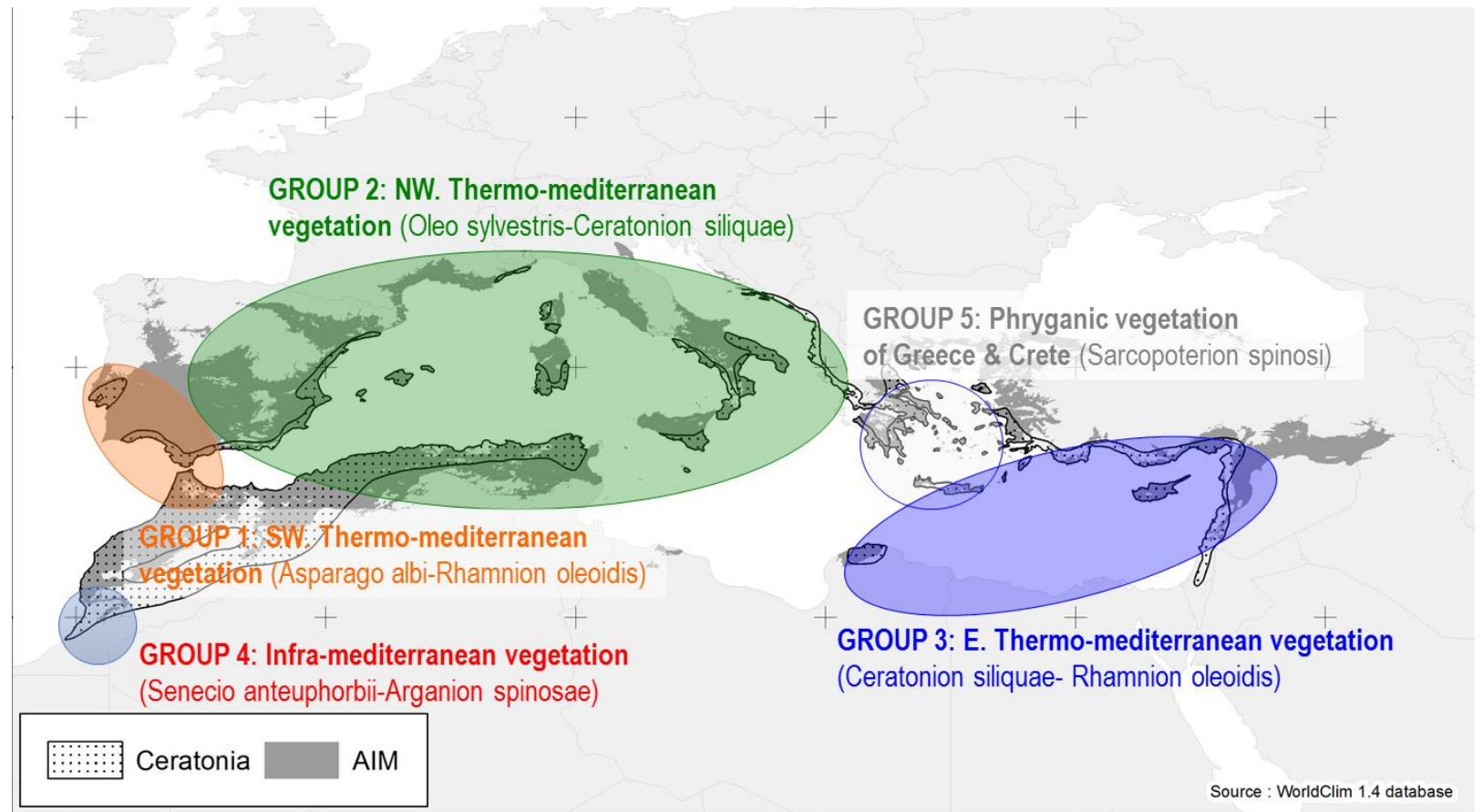
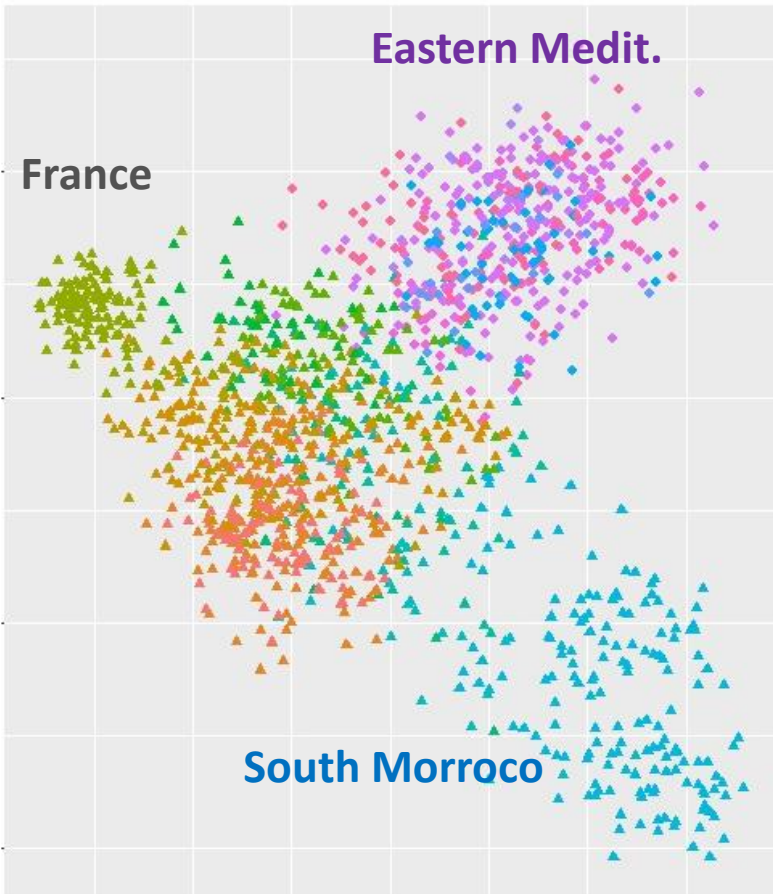
- From Oligocene to late Pliocene
- Pleistocene 30 to 3.5 Ma
- After 12 000 years bp

An aerial photograph of a dry, hilly landscape. The terrain is covered with sparse, low-lying vegetation in shades of brown, tan, and green. A prominent, large, rounded green tree stands in the center of the frame. The background shows rolling hills under a hazy sky.

Phylogeography of the carob tree

How to design the sampling ?

Floristic diversity associated to the carob



Survey of 1542 floristic relevés

→ Higher floristic differentiation in the West

→ Five floristic groups

Mediterranean Carobhabitats



Natural Habitats



Semi-natural habitats



Cultivated habitats



Sampling and molecular markers

- 82 populations sampled : - the 5 floristic groups
- The 3 type of habitats
- Wild and cultivated trees

➔ 1350 DNA extracts

- PCR-Sanger : 4 pDNA markers for 480 trees

pDNA

- Microsat. : 1067 genotypes, 17 loci, sequenced (MiSeq), NA 0.5%

μsat

- RADseq : - 3613 nuclear SNPs, 194 genotypes, NA 9.5 %, 1 SNP/loci
- 10306 bp mtDNA 0% NA
- 13931 bp pDNA 0% NA

RAD

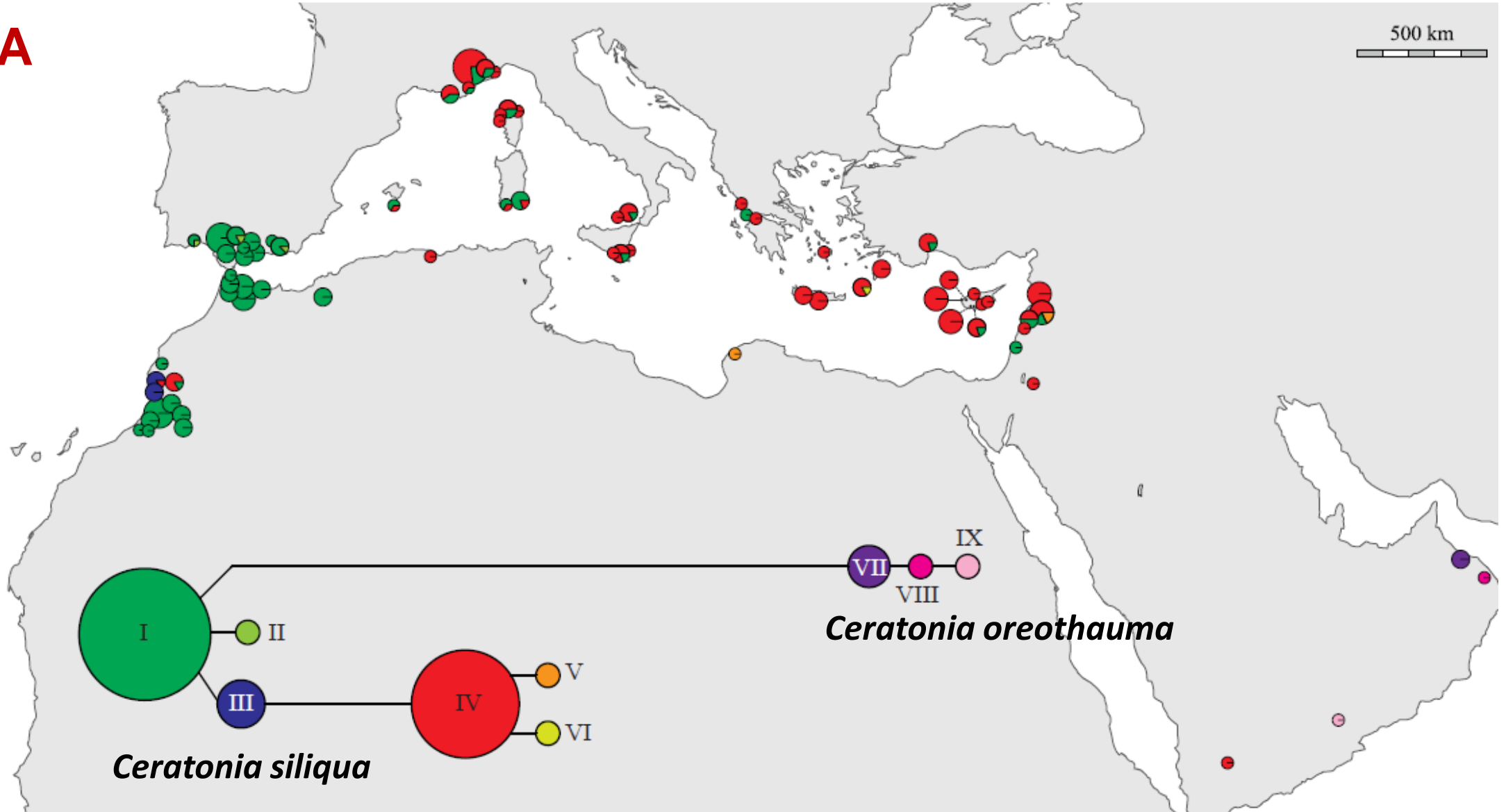
An aerial photograph of a dry, hilly landscape. The terrain is covered with sparse, low-lying vegetation in shades of brown, tan, and green. A large, dense green tree stands prominently in the center of the frame. The background shows rolling hills under a hazy sky.

Phylogeography of the carob tree

Results

Maternal lineages

pDNA



4 loci ADNp, 6 haplotypes



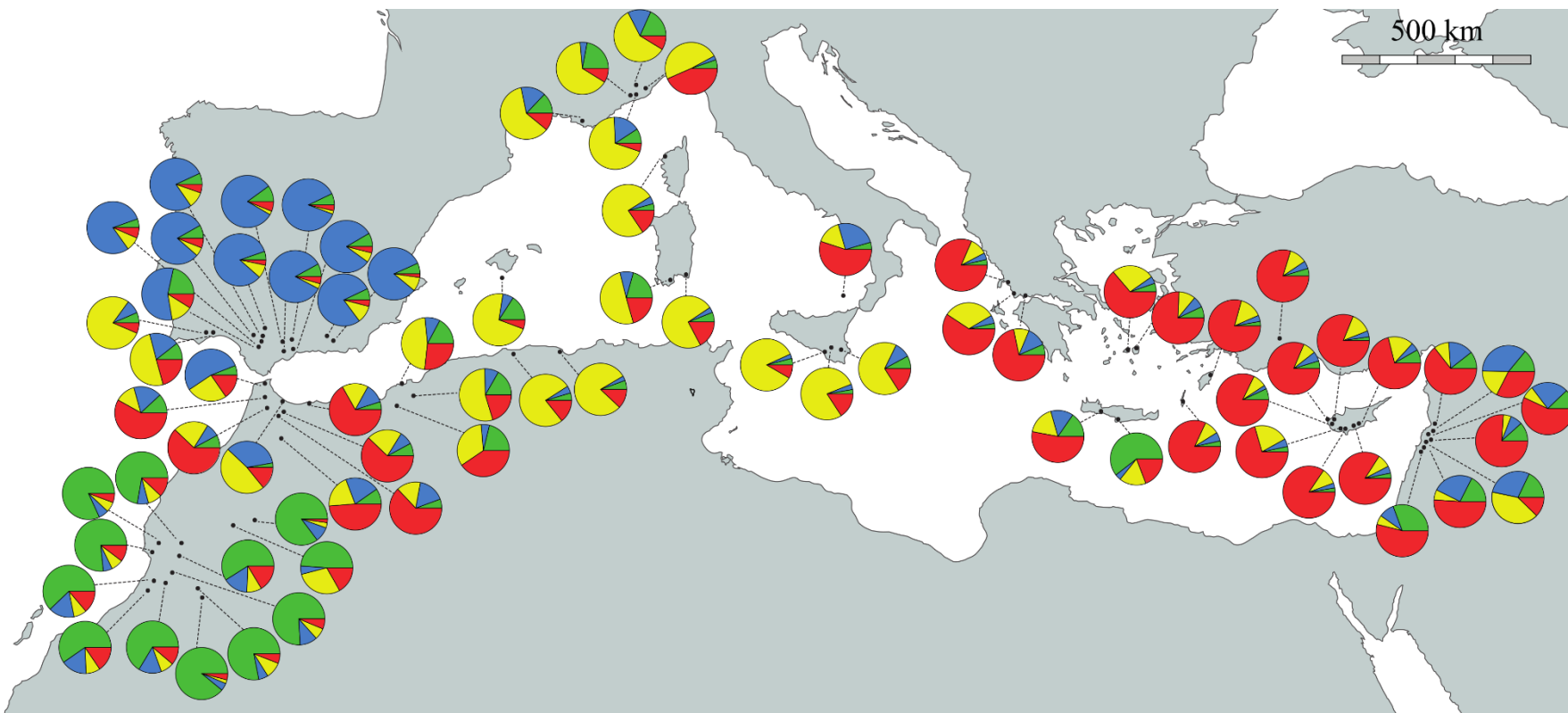
Tajima's D = 3.34***

Viruel et al. 2020 J Biogeo

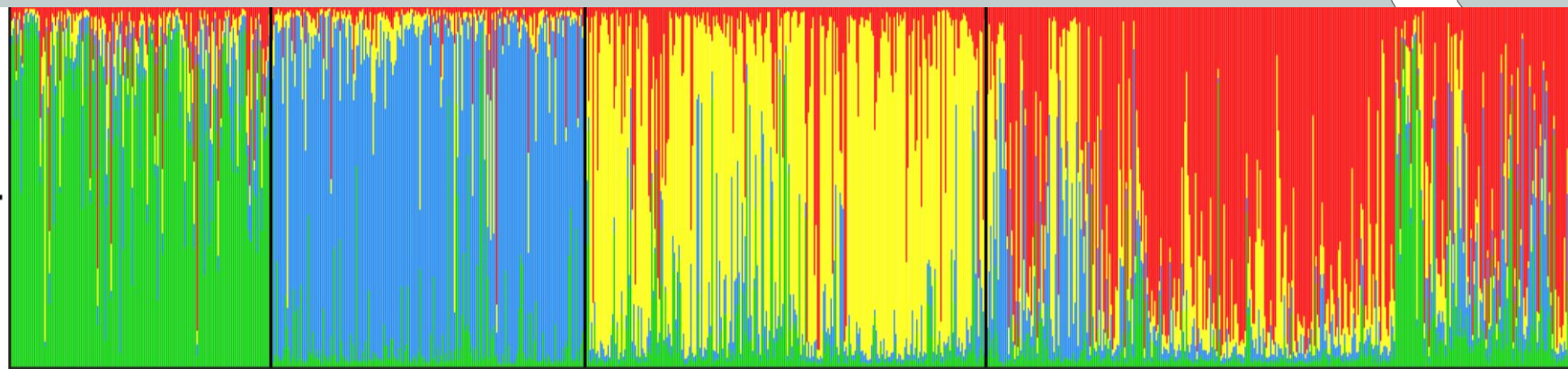
Genetic diversity structure of *C. siliqua*

μ sat

Fst = 6%



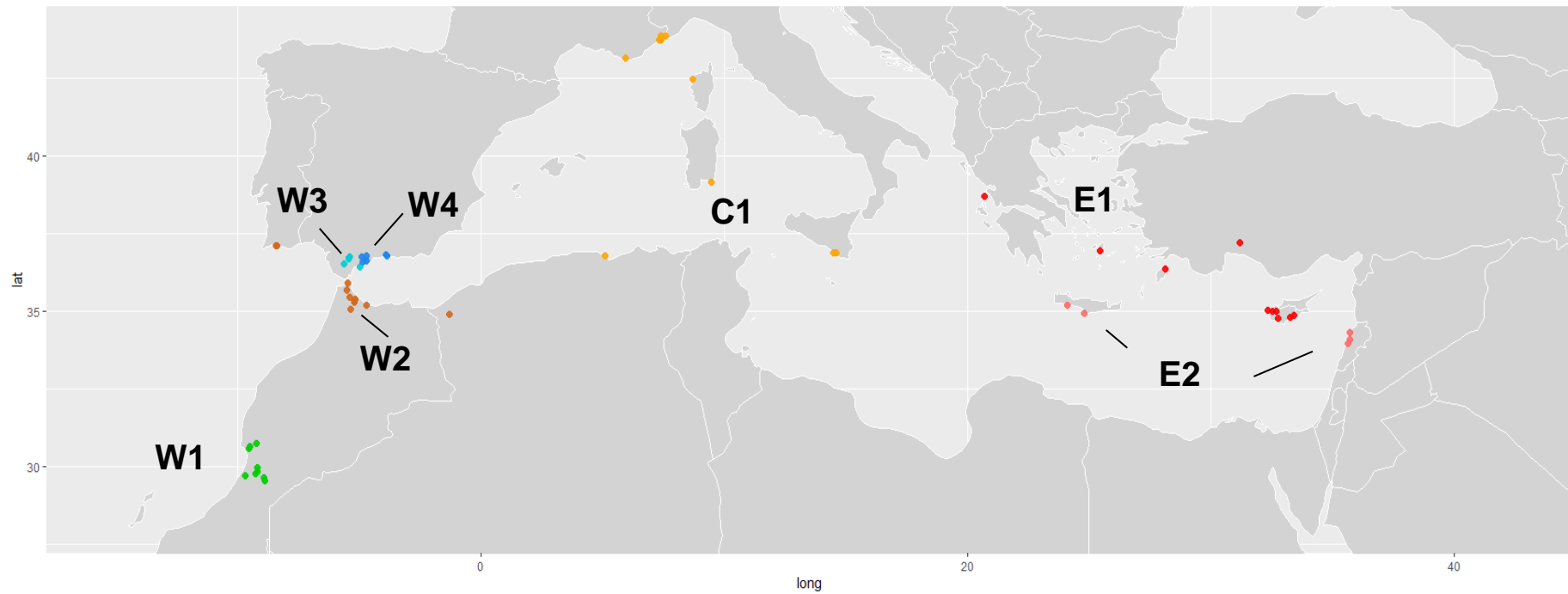
K=4



Viruel et al. 2020
J. Biogeo

Carob Phylogeography

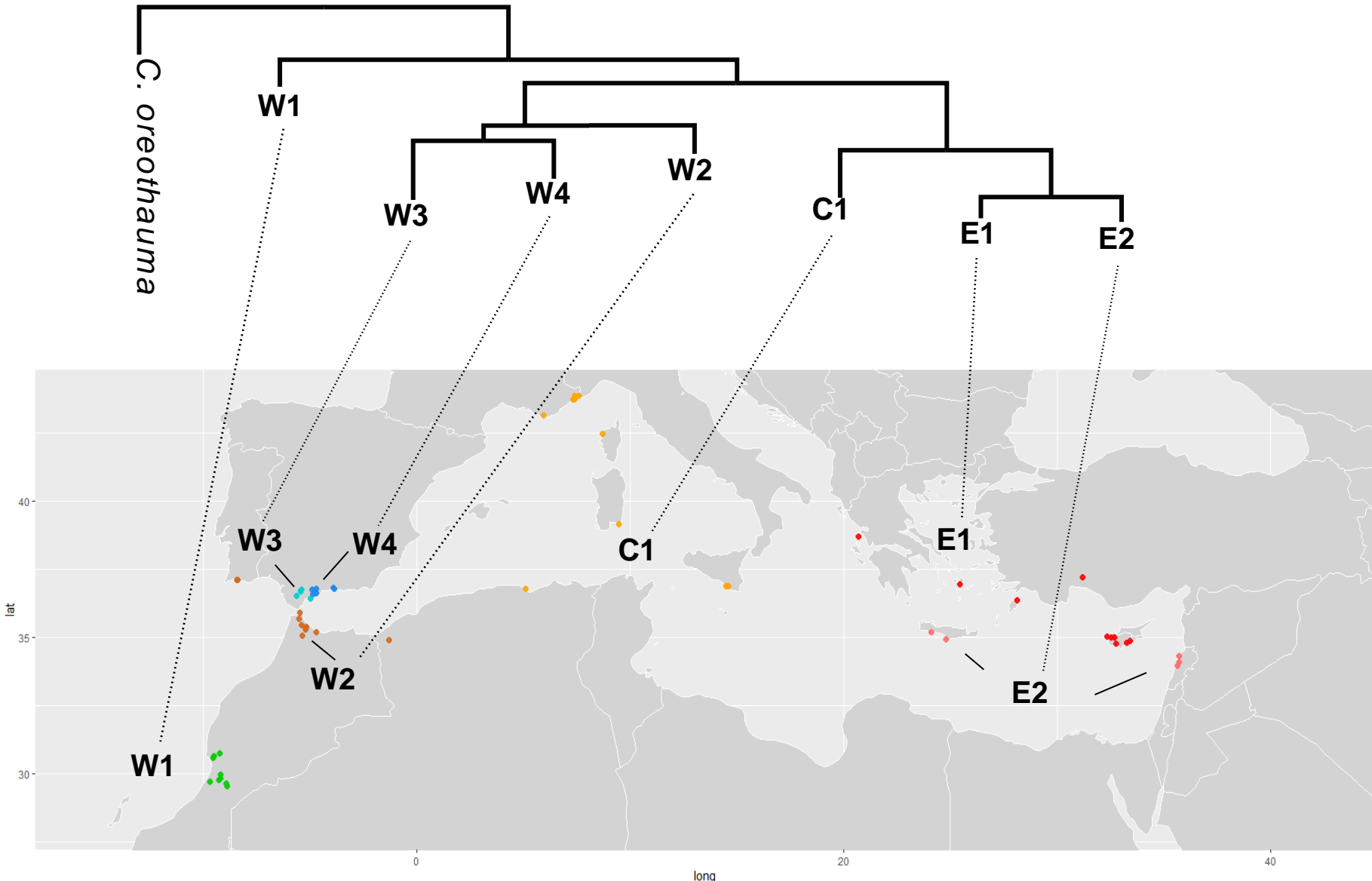
μ sat



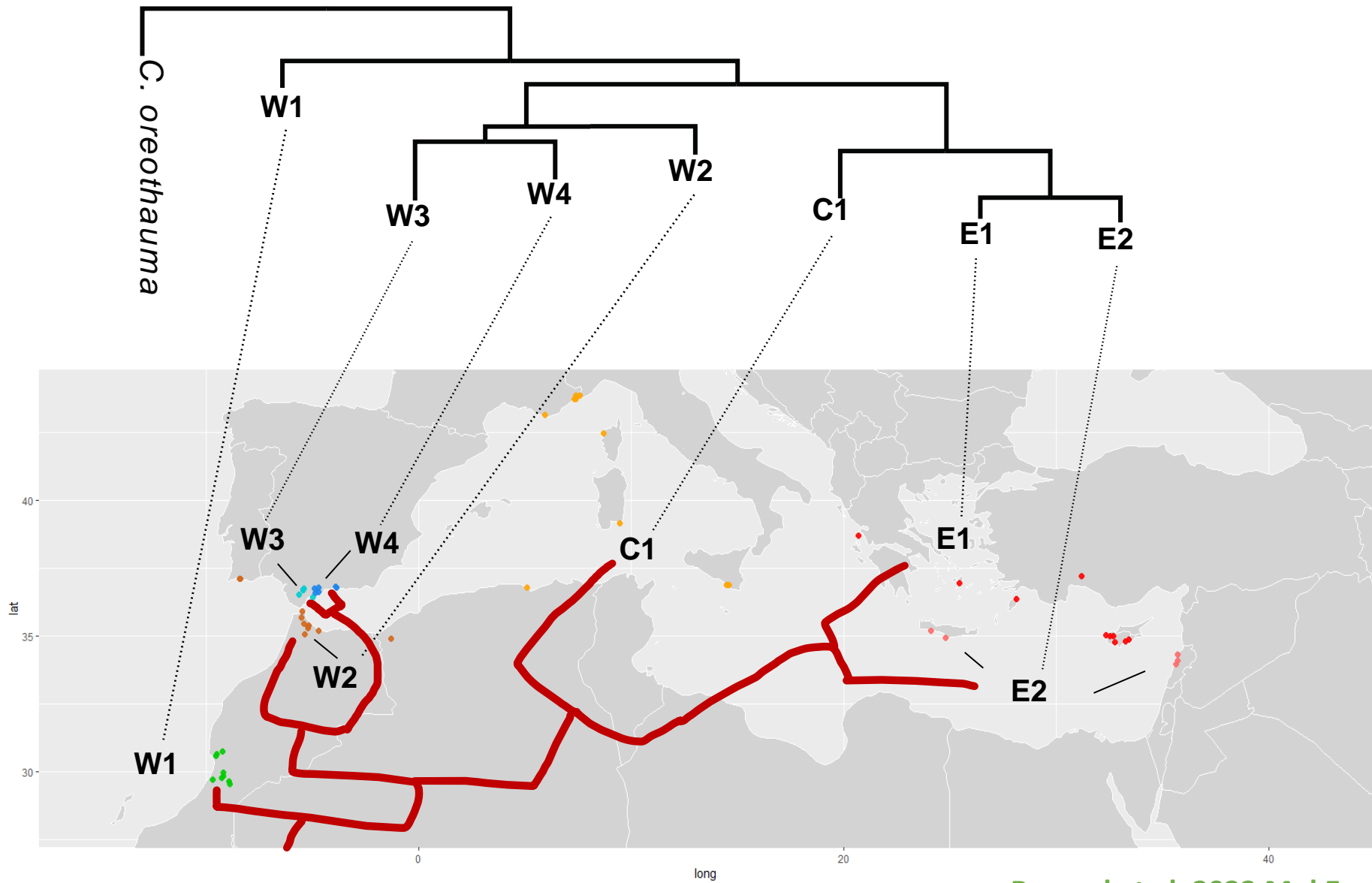
Carob Phylogeography

RAD

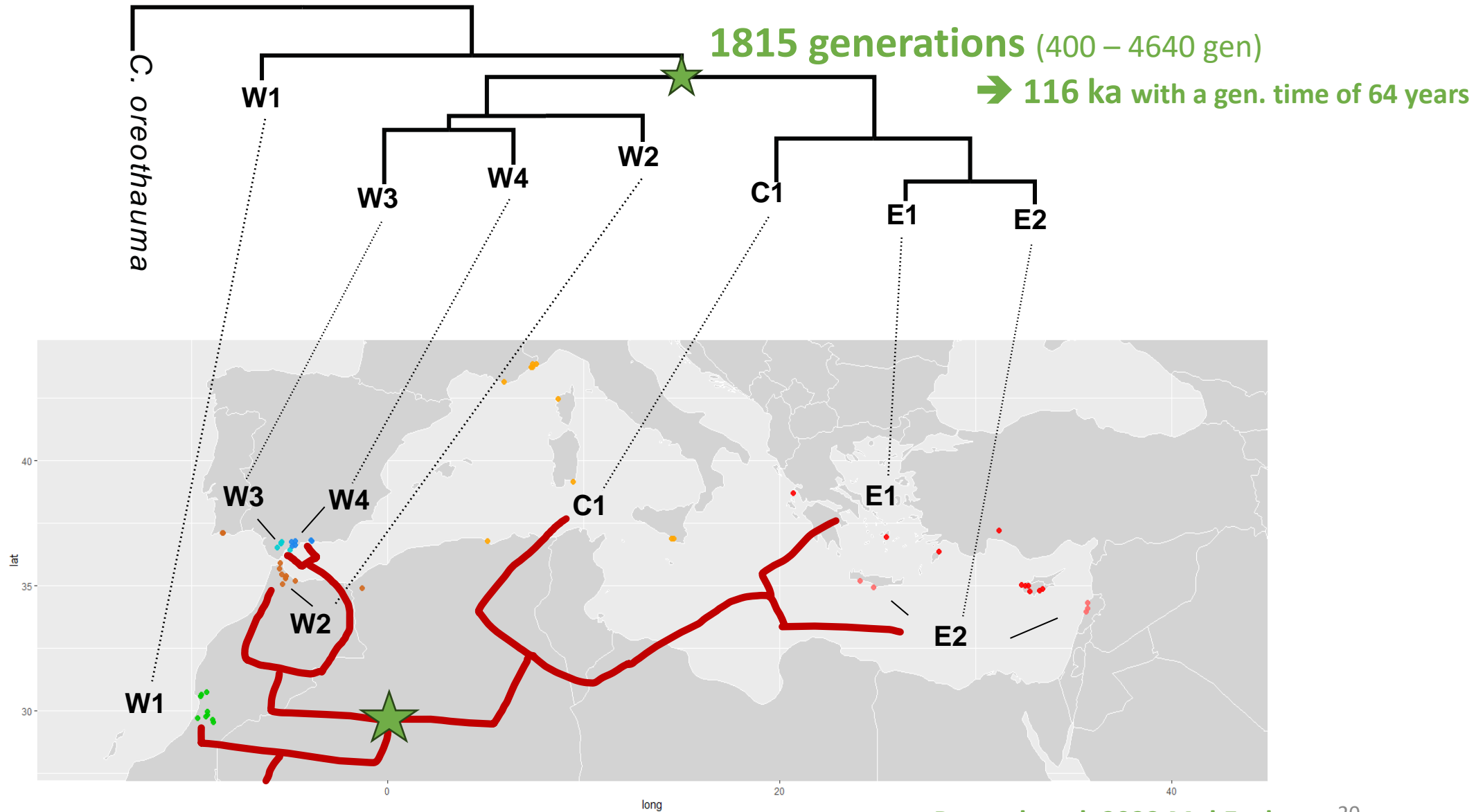
μ sat



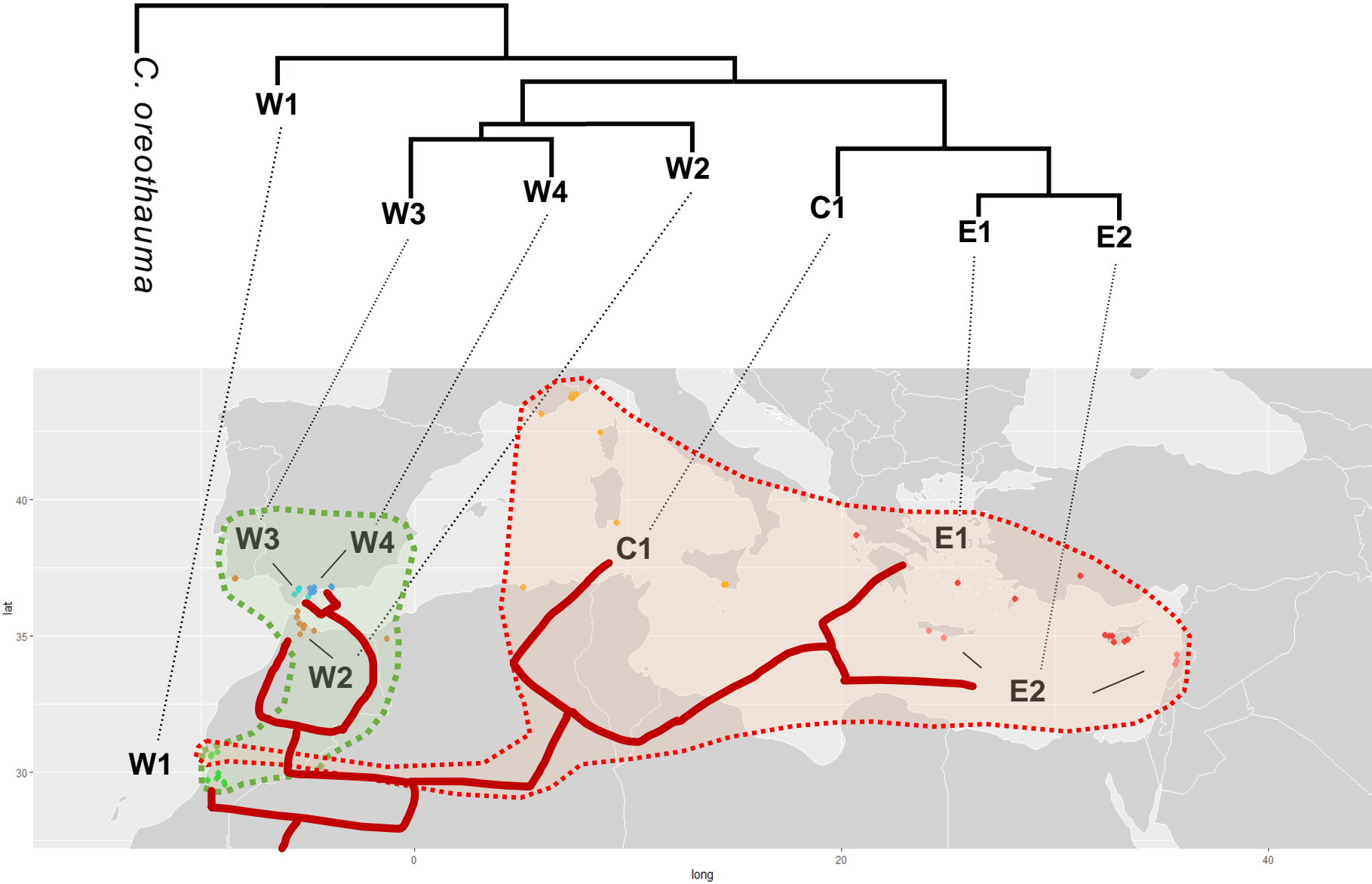
Carob Phylogeography



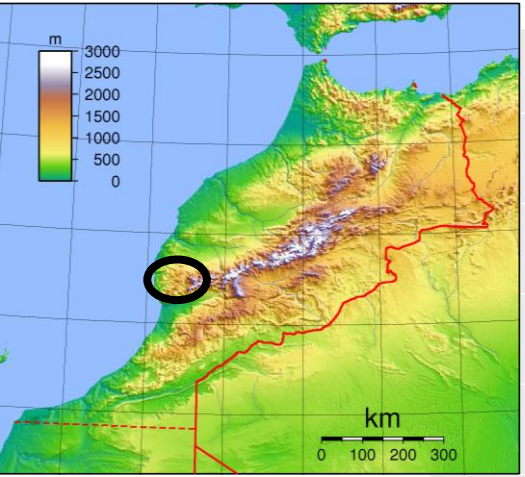
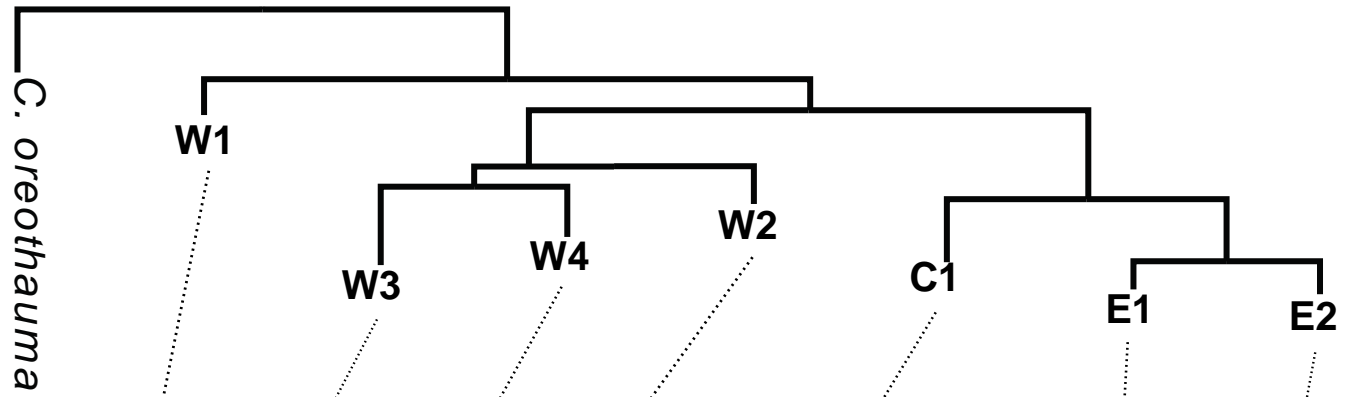
Carob Phylogeography



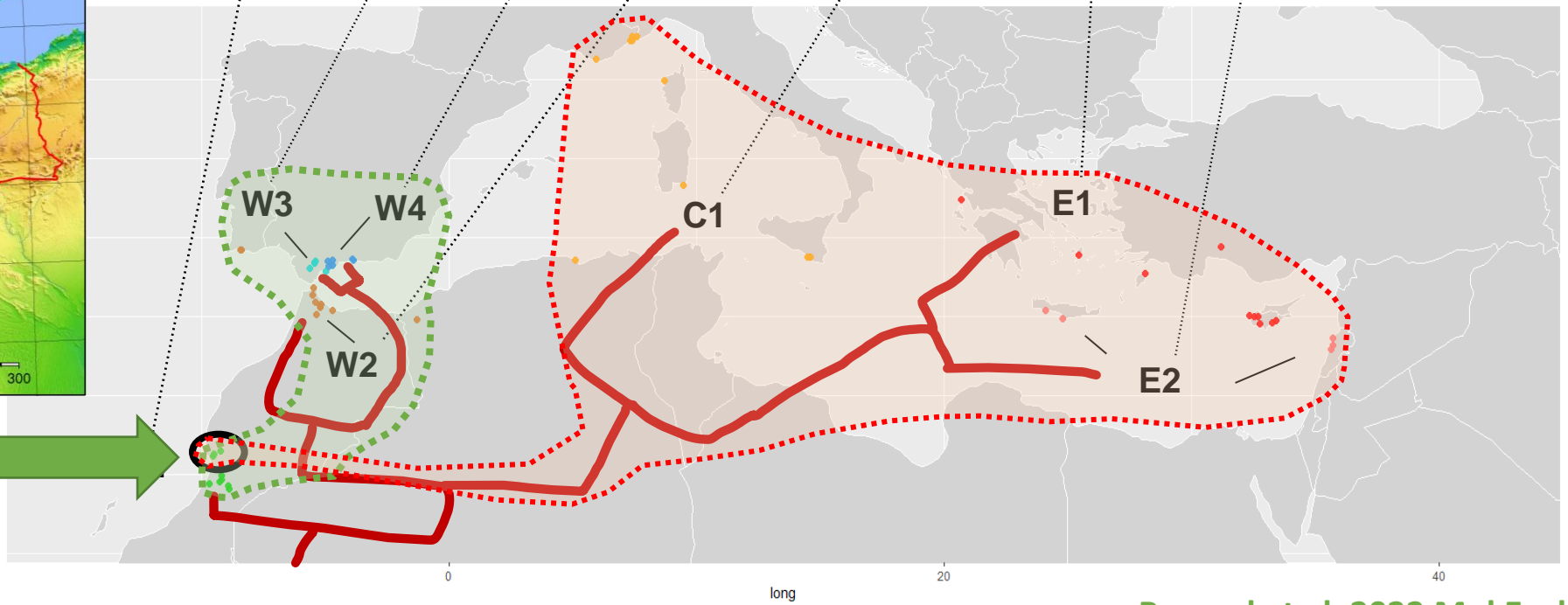
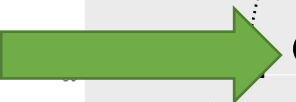
Carob Phylogeography



Carob Phylogeography



Imouzzer
(=waterfall)



Consequences on evolutionary legacy

μ sat

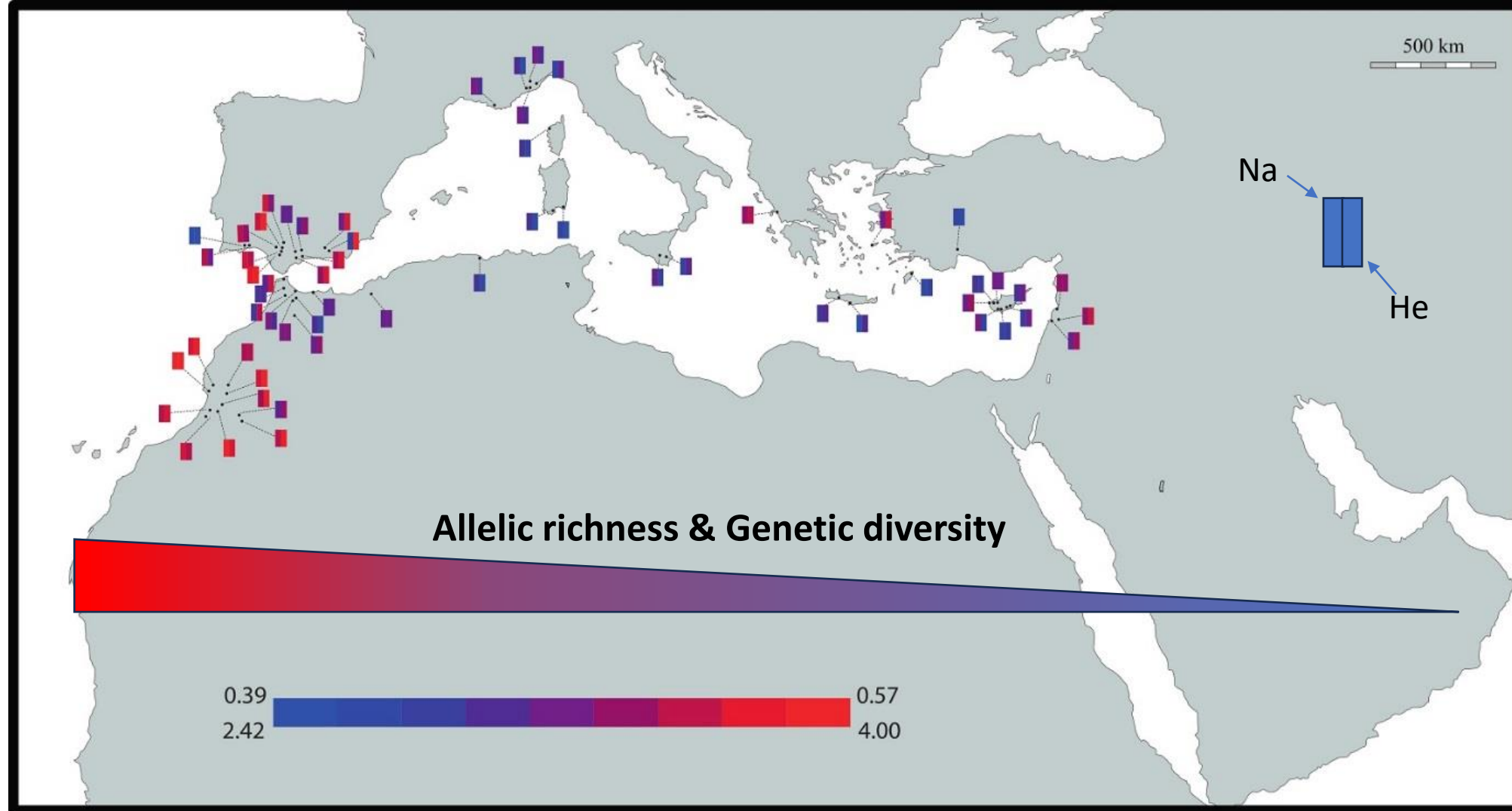
Allelic richness

Na = 6.2

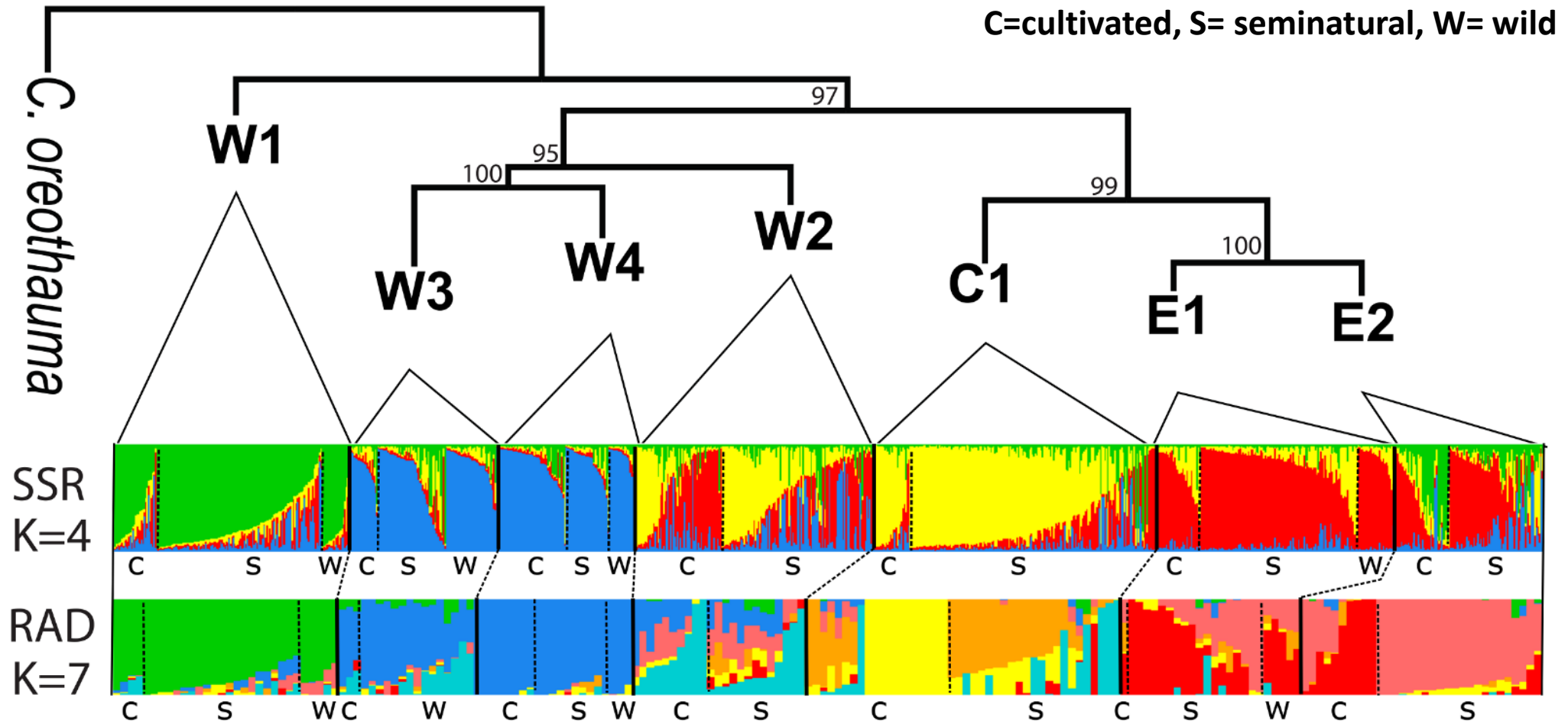
Na(>5%) = 3.2

Genetic diversity

He = 0.56



Wild-domesticated relationships



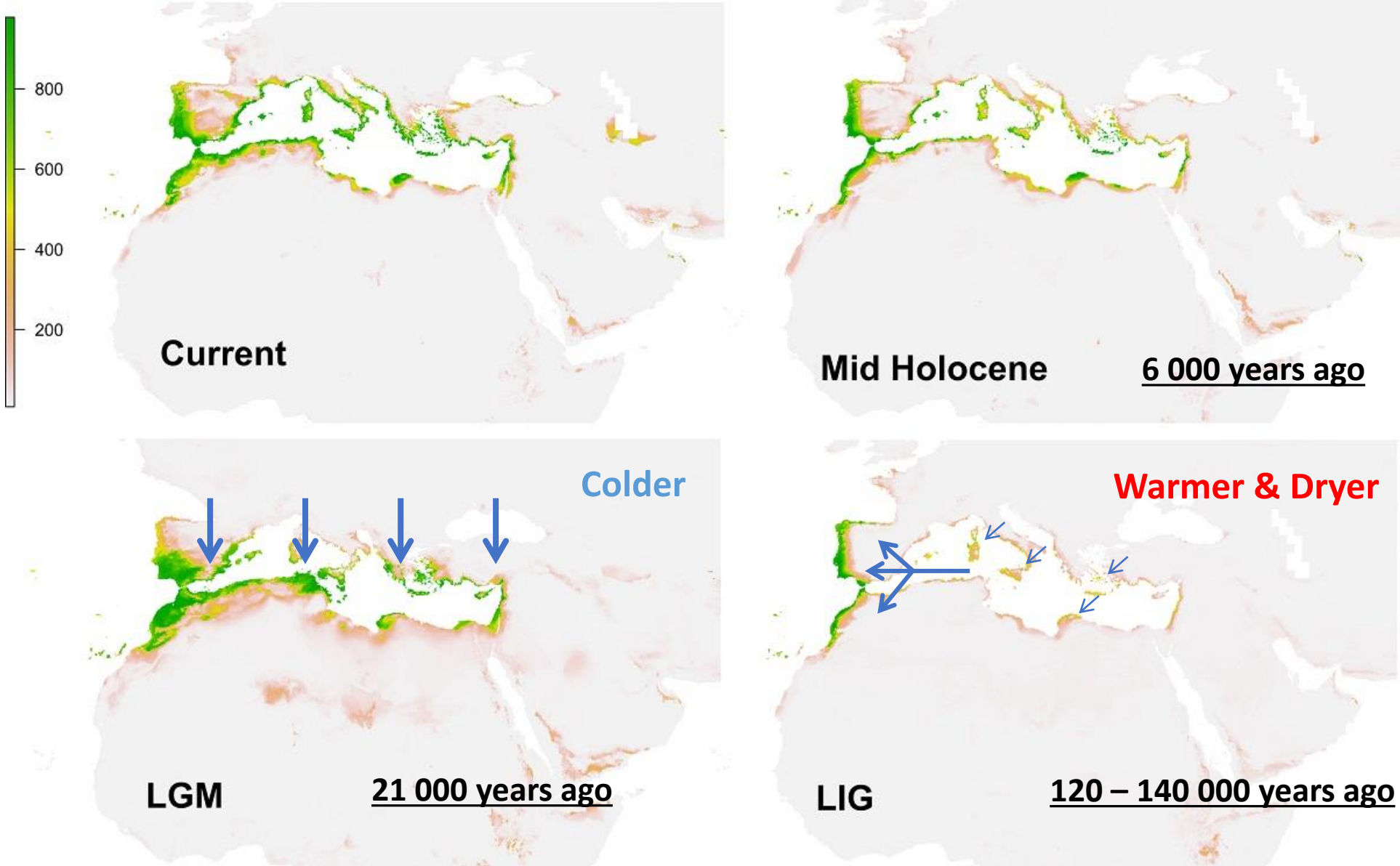
Genetic structure and admixture support that domestication was mainly based on local resources

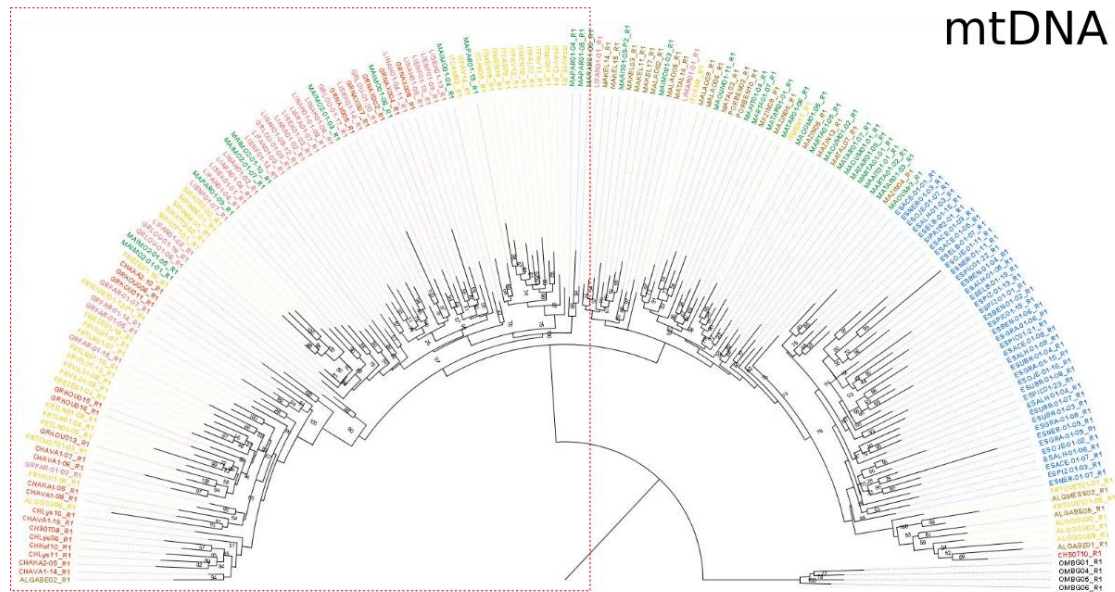
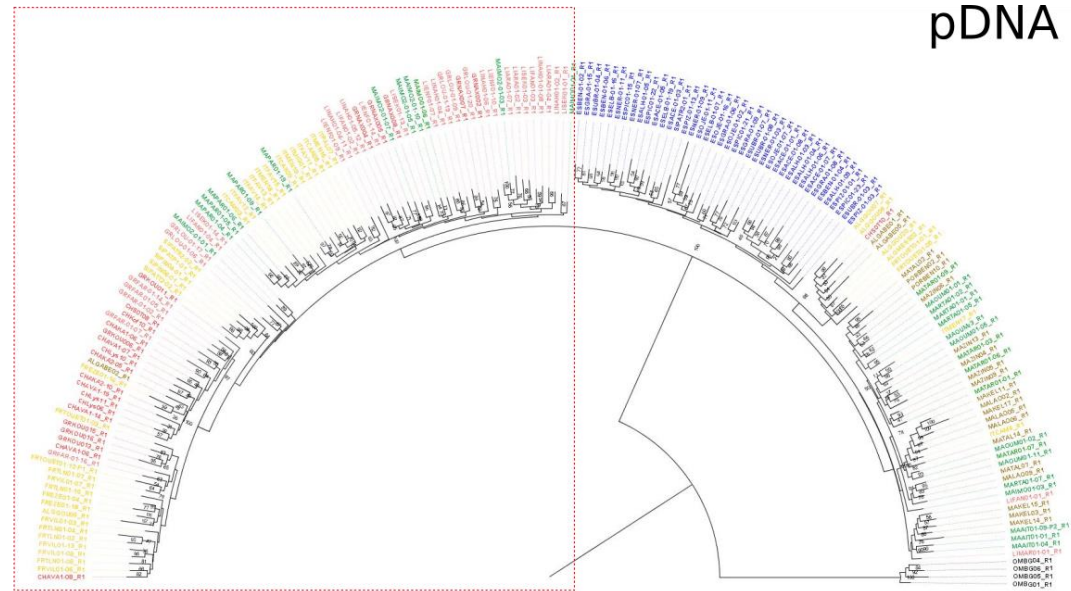
- **The eastern refugia hypothesis is rejected**
- **A single west refugium hypothesis is proposed**
- **Domestication has mainly used local genetic resources**
- **Importance of refugia for conservation**
 - **True, crucial for genetic diversity**
 - **Past refugia = future refugia ? → Phylogeography helps modelling and forecasting**

<https://amu.hal.science/hal-02460403>



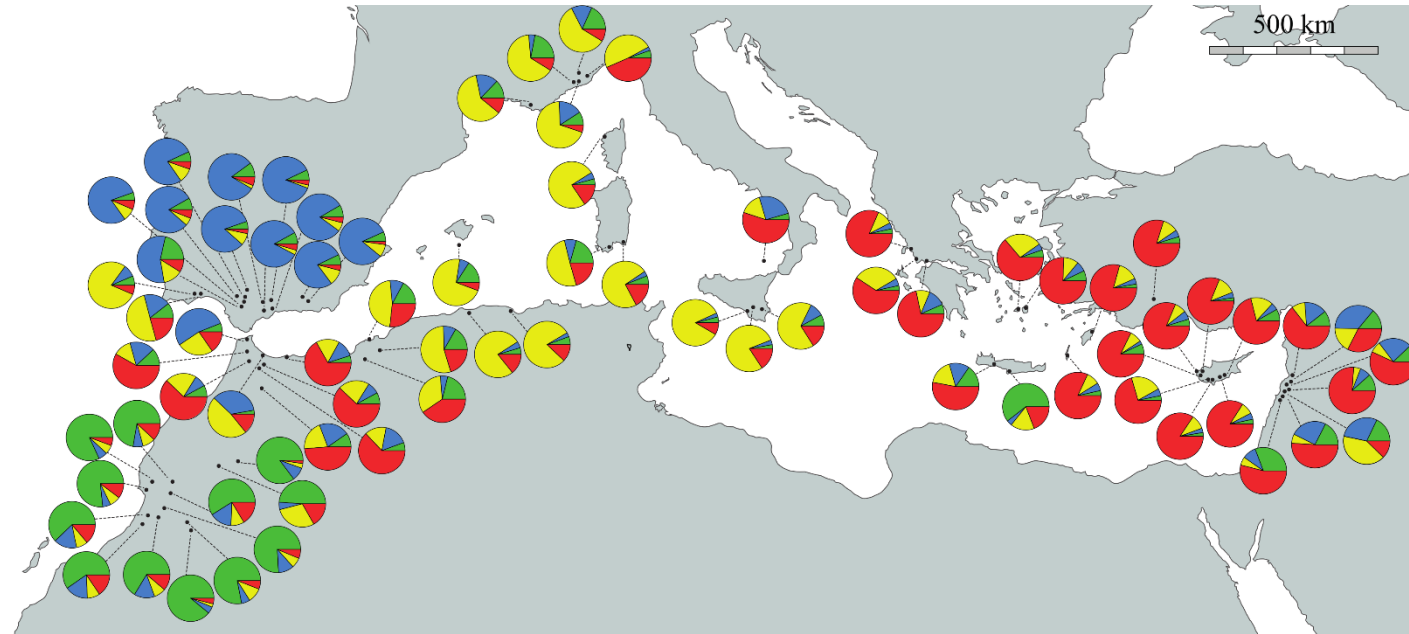
Species Distribution Modelling



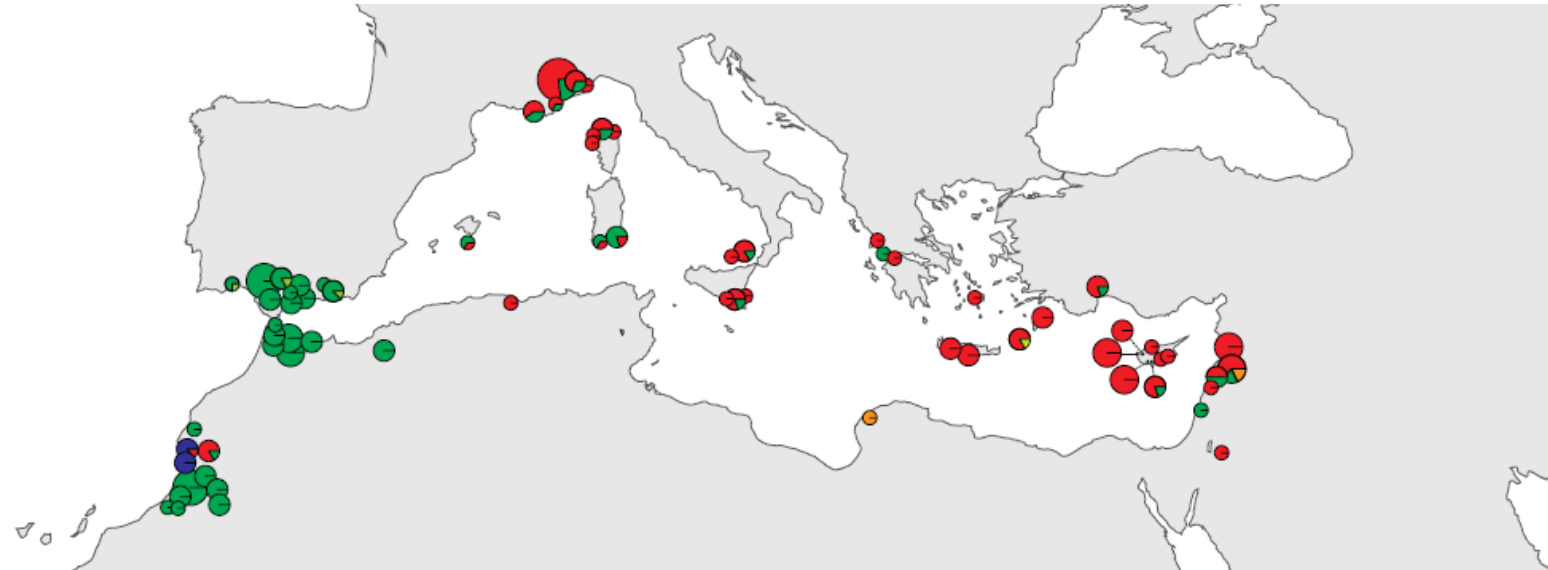


Carob genetic admixture

μ sat



pDNA



No	ka	Fossil type	Locality
1	0.7	m	Rock of Ifach, Calp, SE. Spain
2	1.9	p	Psatha, Corinth Gulf, Greece
3	2	m	Herculaneum, S. Italy
4	3	p	Ein Feshkha, Jericho, West Bank
5	3	p	Katochi, W. Greece
6	3	p	Lake Hula, N. Israel
7	3.1	p	Mljet, S. Dalmatian Islands
8	3.3	p	Dalmatian Islands
9	3.5	p	Kournas, Crete
10	4	p	Laguna de Zoñar, S. Spain
11	4	m	Bastida de Totana, SE. Spain
12	6	p	Addaia lagoon, Minorca, E. Spain
13	7.5	m	Cave V/49, Jebel Quruntul, N. Israel
14	7.5	m	Aktopraklık, NW. Turkey
15	11	p	Ifri Oudadane, N. Morocco
16	11	m	Tell es-Sultan, West Bank
17	11.3	p	Salada Mediana, Ebro Valley, NE. Spain
18	12	m	Jericho, West Bank
19	35 to 7, and ca. 2	p	Nahr Ibrahim Cave, Lebanon
20	65	p	Nahal Mahanayem Outlet, N. Israel
21	350 to 40	p	Core PRGL1-4, NW. Mediterranean
22	112 to 62	p	Lazaret Cave, SE. France
23	ca. 125	p	Batroum, Lebanon
24	600 to 120	p	Bolomar Cave, SE. Spain

No	ka	Fossil type	Locality
25	1	p	Vallonnet Cave, SE. France
26	1.4	p	Camerota, S. Italy
27	2.3	p	WellAndalucia G1, SW. Mediterranean
28	2.5 to 1.8	p	Crotone, S. Italy
29	3.5	m	Ichkeul Lake, N. Tunisia
30	3.8	p	Well Tarragona E2, NW. Mediterranean
31	4.95	p	Husnicioara, Turnu Severin, SW. Romania
32	5.3	p	Malaga, S. Spain
33	5.3	p	Site 654, W. Tyrrhenian Sea
34	5.37	p	Maccarone, Apiro, E. Italy
35	6	m	Kodor River, Kutaisi, Georgia
36	6	p	Ifounassene, N. Morocco
37	6.2	p	Carmona, SW. Spain
38	8 - 6	p	Capodarso, Enna, Sicily, S. Italy
39	10 - 9	m	Bursuc, Moldavia
40	11	p	Well Andalucia A1, SW. Mediterranean
41	12 - 11	p	Saouaf Basin, Tunisia
42	12 - 11	p	Well Alborán A1, SW. Mediterranean
43	12.6	m	Dédestapolcsány, NE. Hungary
44	13	m	Soma, W. Turkey
45	14	p	Gor, SE. Spain
46	15	p	La Rierussa, Gelida, NE. Spain
47	16	m	Szurdokpüspöki, N. Hungary
48	16	p	V. Hugo College, Narbonne, S. France
49	17	p	Estagel, Istres, S. France
50	17.5	p	Rubielos de Mora, E. Spain
51	18	m	Abaliget, S. Hungary
52	19	p	Häutligen, Bern, Switzerland
53	23	p	Portel, S. France
54	23	m	Aix en Provence, SE. France
55	30	m	Eleshnitsa, SW. Bulgaria

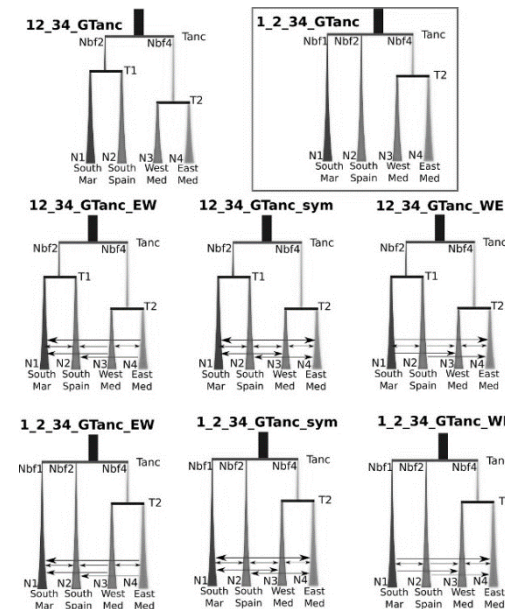
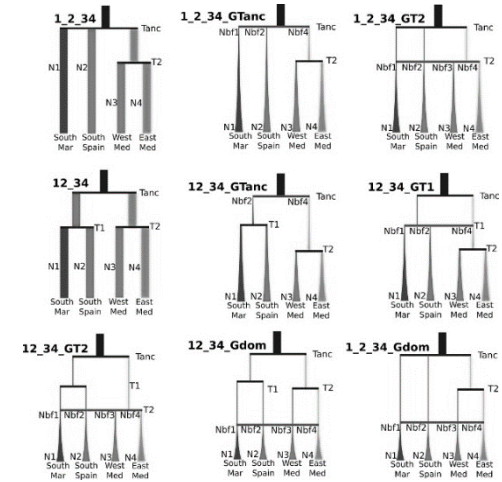
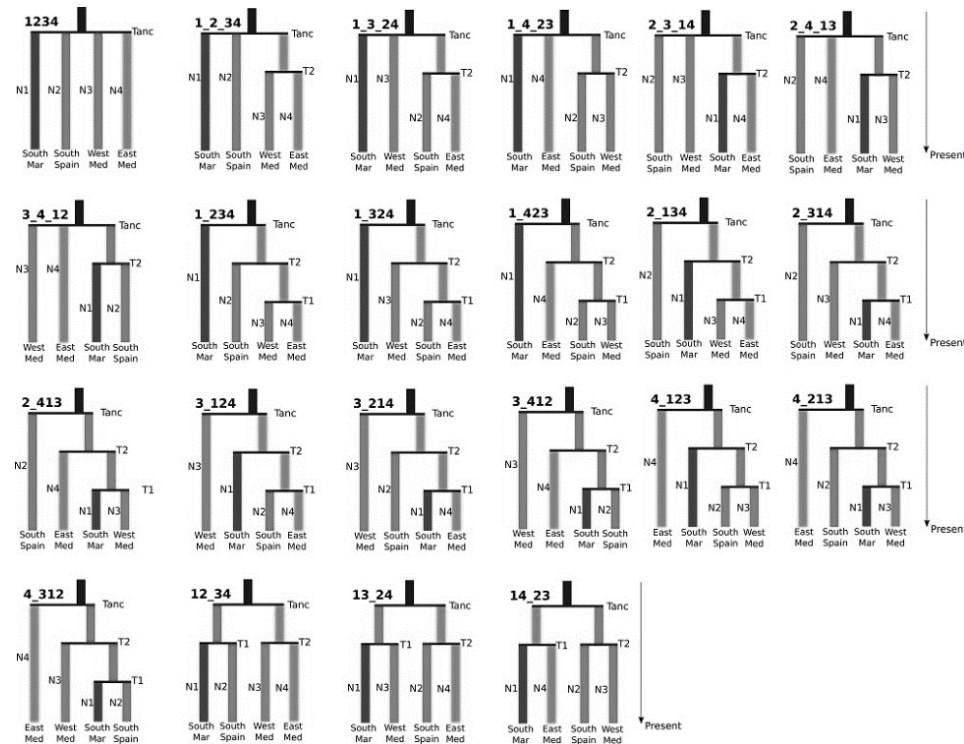
Phylogeographic hypotheses testing

Only μ sat stats

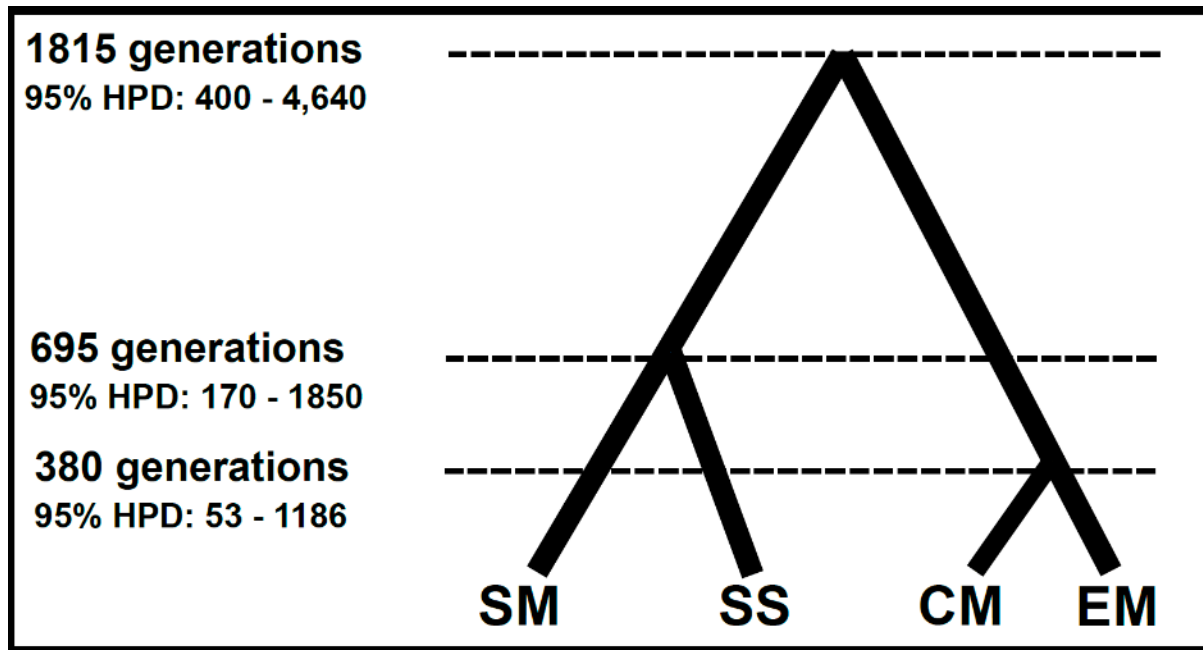
Coalescent simulation with Fastsimcoal 2,

ABC with arlsumstats, abc R, abcrf

39 hypotheses tested in 3 rounds



Best hypothesis



← c. 116 000
years BP
(for a
generation
time = 64)

