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The carob tree at the crossroad of domestication center and refugia

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Ceratonia siliqua L. (Fabaceae)

The carob is a dioecious and evergreen termophilous fruit tree widely harvested throughout the Mediterranean for food and forage since antiquity. Currently, the carob is found in cultivation in specialized orchards or in association with other crops, and it has expanded towards industrial, agricultural and soil restoration purposes. It is easily propagated by grafting. Wild populations are found in shrublands, forests as well as rocky outcrops and temporary river banks in both East and West Mediterranean.

As other Mediterranean cultivated plants, the carob tree is supposed to have been native and domesticated in the Middle-East. It is thought to have been spread by humans following East-to-West historical routes. This is the classical hypothesis.

But ... is this the true story?



The project DYNAMIC

DYNAMIC will contribute to fill knowledge gaps in the ecology of carob symbiotic associations. But an issue for this project is that the ecological and biogeographical status of carob tree is not clear.
<https://dynamic.cirad.fr>



SSR sequencing and genotyping

We have isolated and characterized 18 new polymorphic SSR markers for *Ceratonia* and optimized them for NGS. A significant amount of molecular variation that has been detected by the sequencing would have remained unnoticed under standard SSR genotyping procedures.

Genetic cluster	N	Na	Priv	I	Ho	uHe	F
West Med	275	5,12	0,12	0,88	0,43	0,48	0,08
South Spain	206	4,59	0,06	1,03	0,53	0,56	0,06
East Med + Rif	392	5,24	0,18	0,98	0,46	0,53	0,12
South Morocco	167	5,53	0,47	1,08	0,51	0,58	0,11

- Mean Fst = 6%

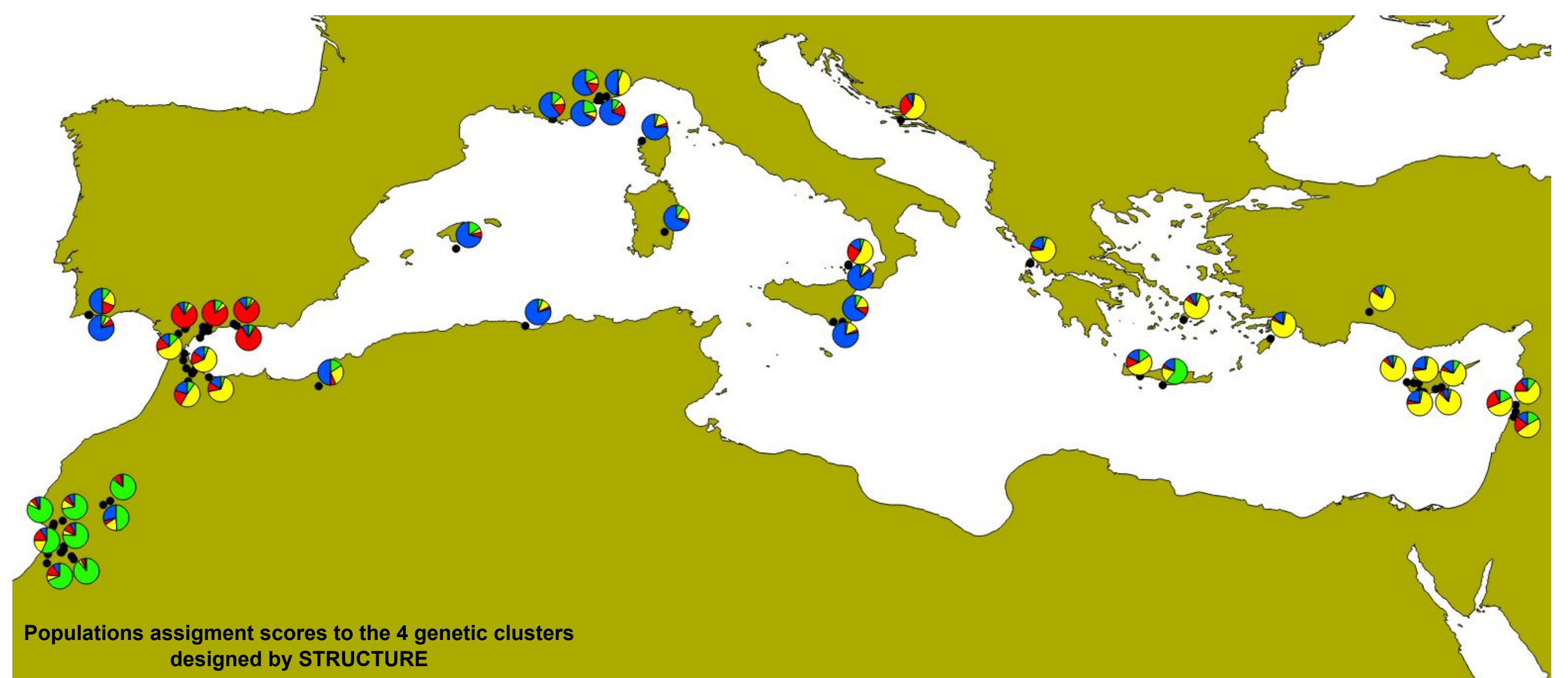
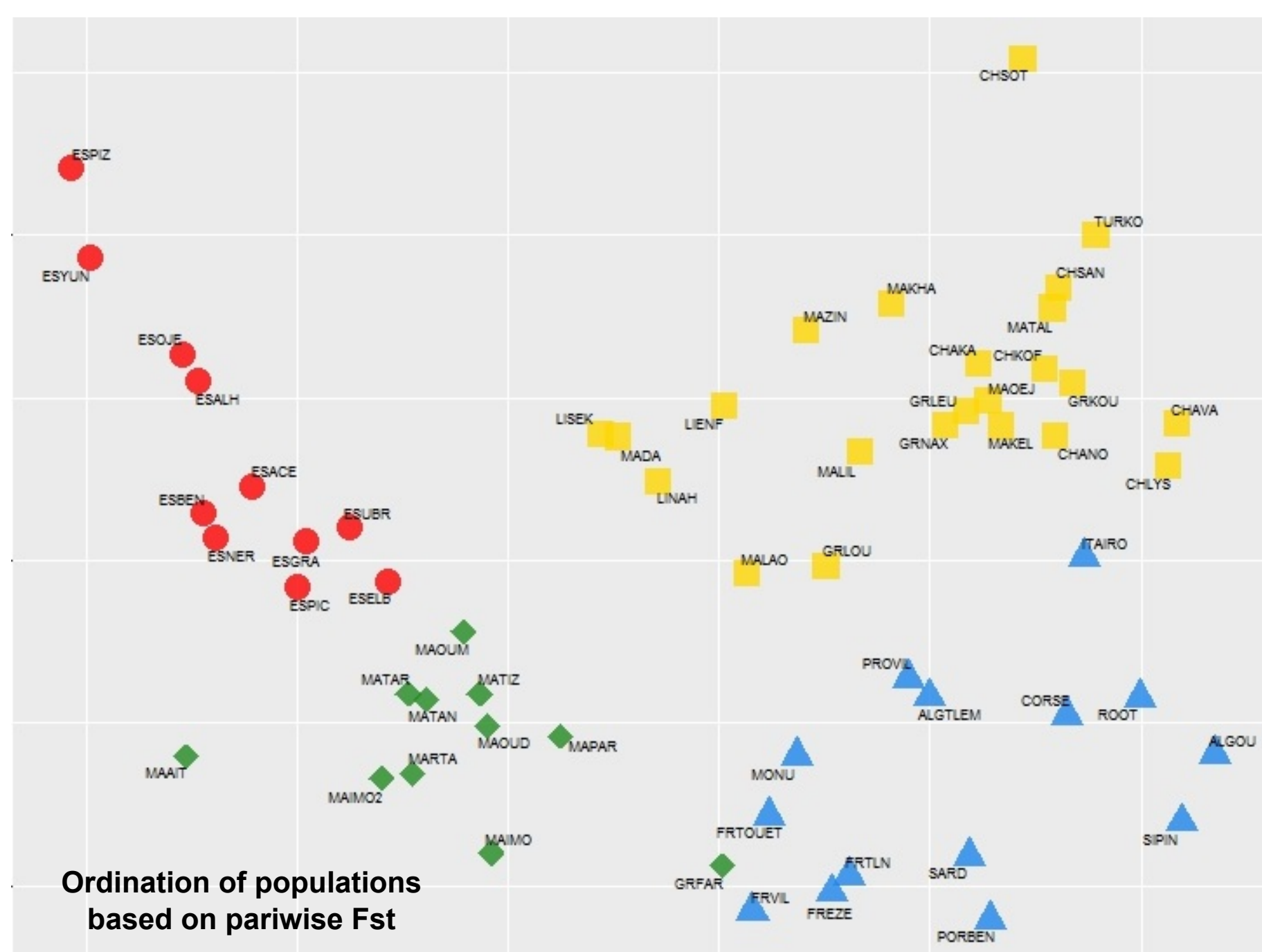
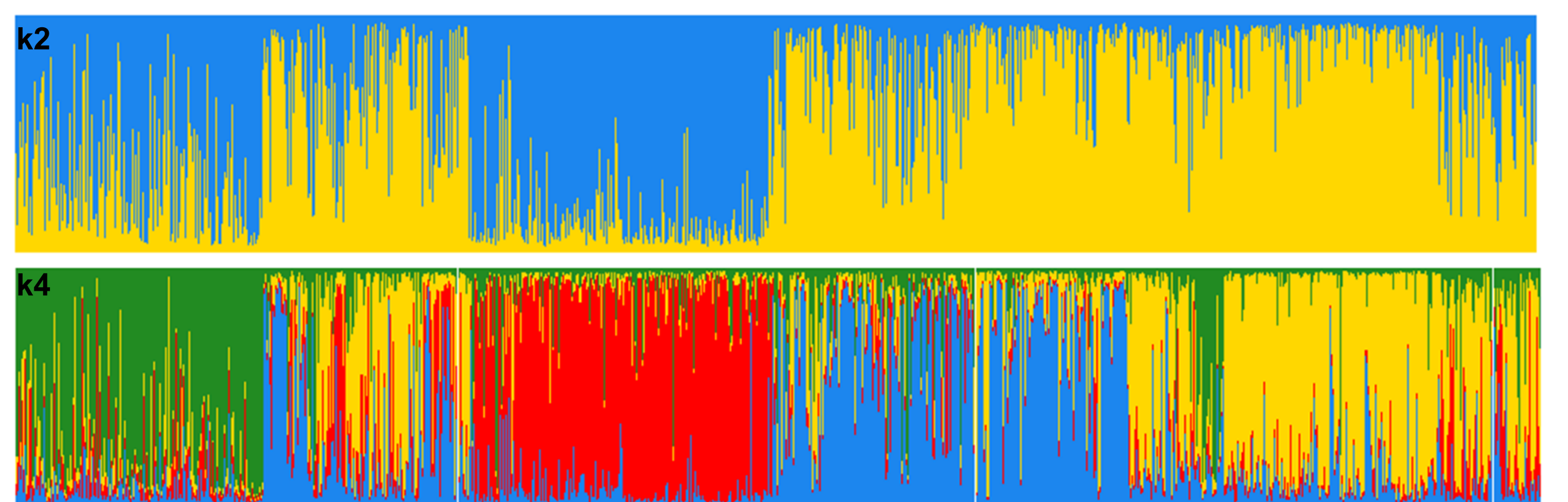
- Min Fst = 3% (between blue and yellow clusters)

- Max Fst = 10% (between blue and red clusters)

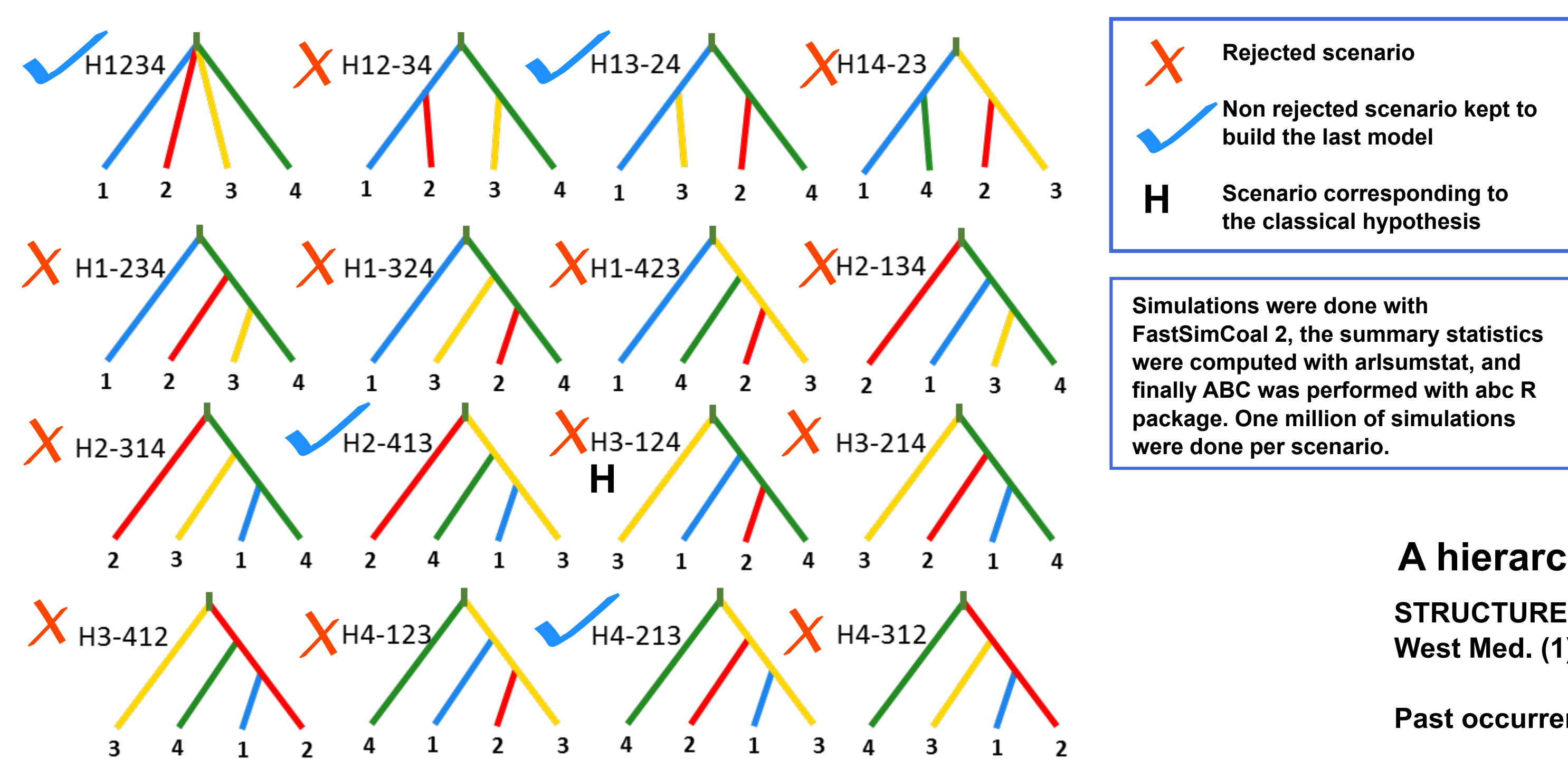
Genetic diversity structure of the carob tree

The genetic differentiation of carob tree is weak to moderate at the Mediterranean level but it is strongly structured by geography. According to Evanno's method, 2 or 4 genetic clusters are optimal whereas according to Mavrik4 4 clusters would be the optimal partition. The ordination based on pairwise Fst is congruent with the results of STRUCTURE.

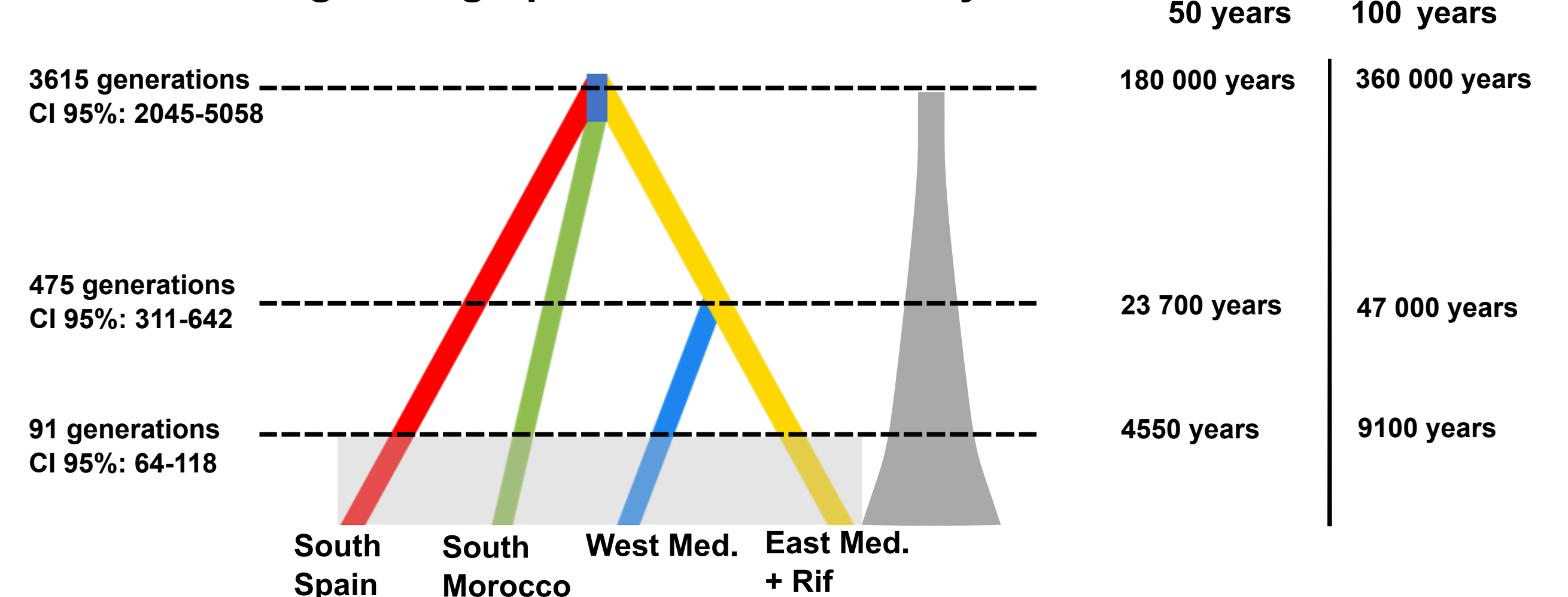
Mantel tests and multiple regression analyses based on pairwise distance matrices between populations found a significant isolation by distance at the finest and coarsest scales but not at intermediate distances, and failed to find any isolation by climate (current or past) despite significant climatic differences among the genetic clusters.



Statistical phylogeography by approximate bayesian computing (ABC)



The best-fitting demographic model inferred by ABC



A hierarchical ABC approach

STRUCTURE output, constrained by the geographic patterns for rare exception (eg. Crete), was used to discern 4 genetic clusters: West Med. (1), Andalusia (2), East Med. with Rif (3), and South Morocco (4).

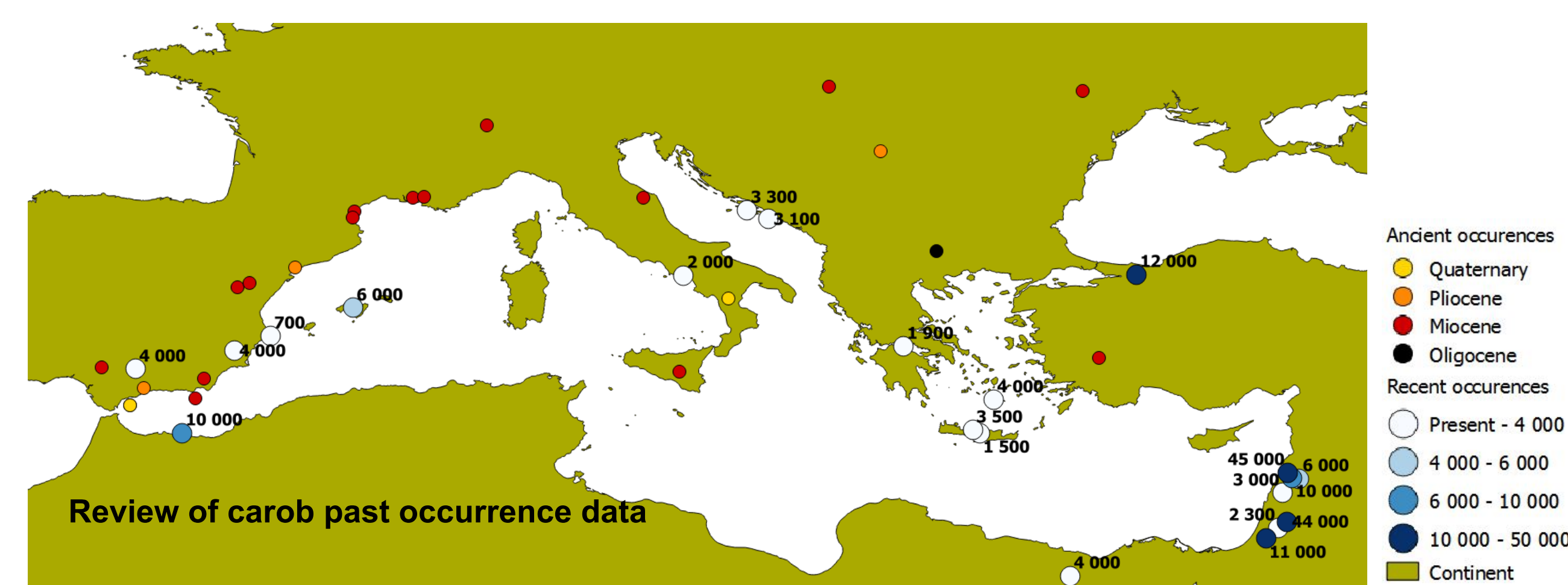
Past occurrence data did not allow to build a test of biogeographic hypotheses.

To explore a maximum of hypotheses, we decided to confront 16 scenarios. Twelve scenarios with very low posterior probability were rejected in a first round of analyses. To account for the 4 scenarios left, we added a 17th scenario to the analysis—the consensus tree of those 4 scenarios—which consists in a trifurcation between clusters 2, 4 and a third lineage, which then diverged into clusters 1 and 3. This scenario was found to be the most probable scenario, with the highest posterior probability (97%).

Then we used the selected topology and added gene flow, with or without demographic growth, both beginning at different timings. The timings considered are (1) the earliest realist date for carob tree domestication (6,000 BP i.e. 60 to 120 generations for carob), (2) the divergence between clusters 1 and 3 and (3) the ancestral divergence.

13 scenarios were confronted, and the selected scenario involves a demographic growth since the ancestral divergence, and gene flow since the potential domestication.

Our results refute the classical human-mediated dissemination hypothesis of carob tree, because the scenario matching to the classical hypothesis was rejected. Instead, our analyses determined that the carob was naturally distributed throughout the W Mediterranean long before any human settlement.



The highest genetic differentiation was found in the West Mediterranean, with three genetic clusters; meanwhile only one cluster occurs in the East.

Our inferences do not support the classical hypothesis of an exclusive East Mediterranean origin of carob tree followed by a westward human-mediated colonization.

The origin of the four lineages recognized within carob throughout the Mediterranean preceded its domestication.

The existence of multiple genetic groups with a strong geographic structure suggest that the domestication of carob occurred several times.