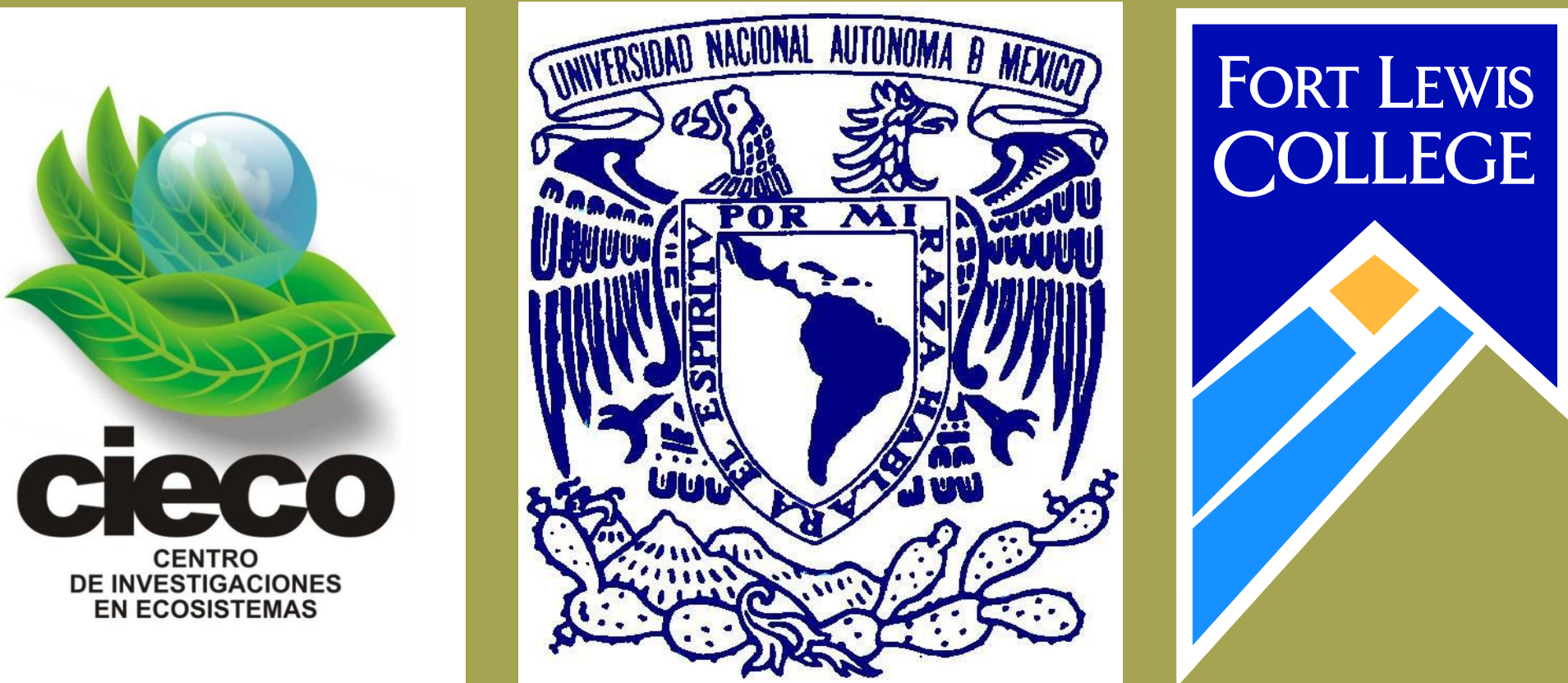




Genetic Structure and Speciation in a Lineage of Mexican Red Oaks: A Phylogeographic Study of *Quercus* Section *Lobatae* Subsection *Racemiflorae*

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INTRODUCTION

With approximately 160 species, Mexico is one of the primary centers of species diversification of the genus *Quercus* (Nixon, 1993). It has been postulated that varying physical factors from multiple complex orogenies, the interface of north temperate and subtropical climates and range shifts from glaciation have combined with the propensity for interspecific gene exchange resulting in the complex patterns of biodiversity seen today (Bacon & Spellenberg, 1996.)

If these processes are acting on oak species there should be contemporary evidence supporting this. Outside of specific studies focusing on hybridizing species pairs there have been no studies focusing on speciation in a phylogeographic context within the group in Mexico.

To better understand the patterns of historical phylogeography in the genus we examined the genetic structure of a wide-ranging complex of four taxa endemic to the Sierra Madre Occidental and Southern Cordillera of Mexico. The *Racemiflorae* is a natural lineage of Red Oaks united by the characteristic of producing acorns on racemose inflorescences (Trelease, 1921; Spellenberg & Bacon, 1996). Additionally the group shows varied patterns of disjunction and sympatry and is thus likely to be representative of the processes of gene exchange and habitat isolation that ultimately lead to speciation.

SPECIFIC AIMS

- Contrast patterns of chloroplast and nuclear DNA structure across the range of the four taxa
- Relate observed patterns of genetic structure to proposed processes leading to species diversification.

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METHODS

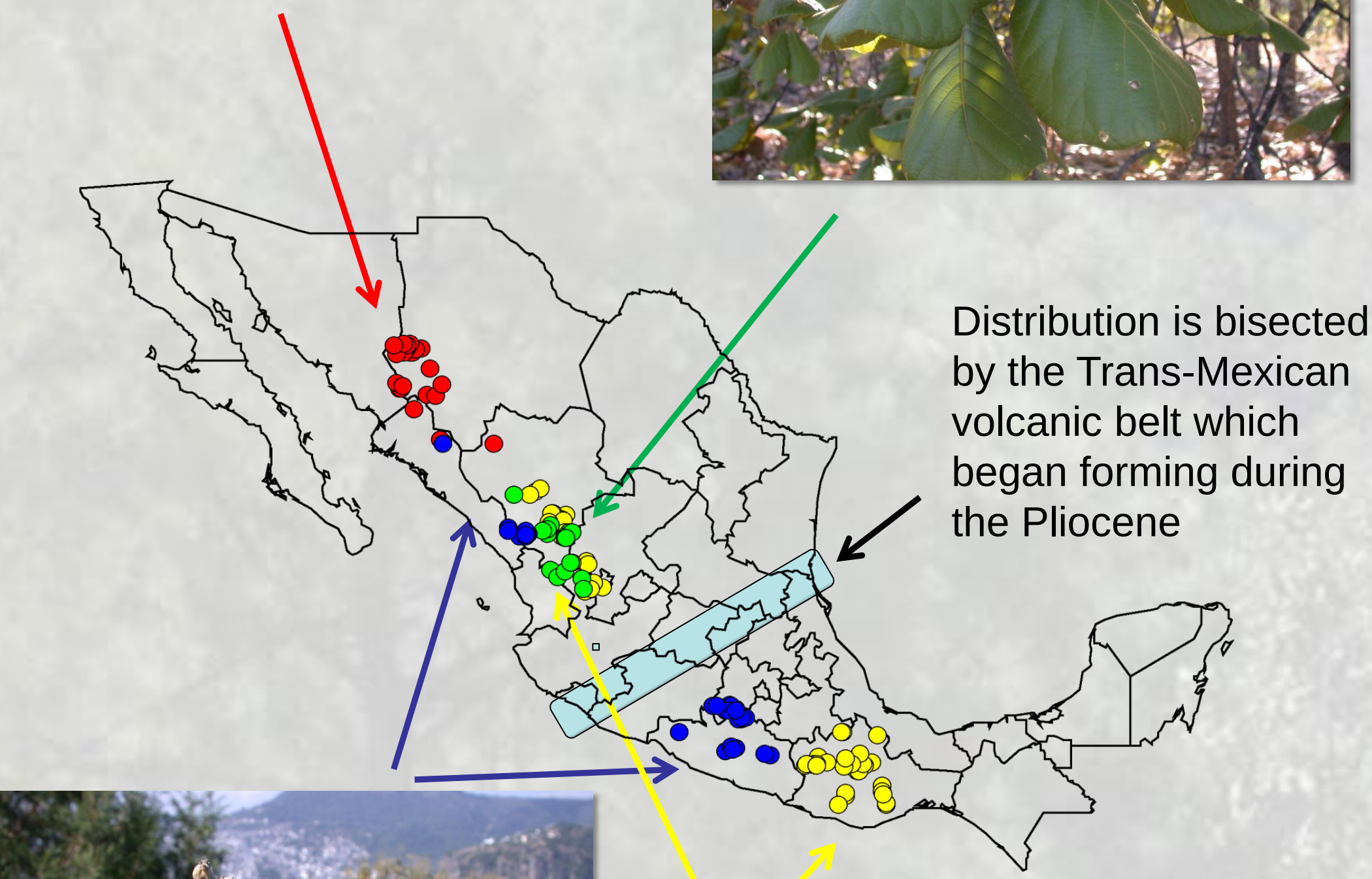
- Sampling of 490 individuals in 49 populations across the range of the four species.
- Genotyping by amplification of 7 mono- and dinucleotide cpSSR and 7 dinucleotide nuclear SSR loci.
- Determination of haplotype (chlorotype) diversity and structuring using Spatial Analysis of Molecular Variance (SAMOVA).
- Panbiogeographical track analysis to depict haplotype migration and infer centers of origin.
- Clustering of populations using UPGMA, Bayesian STRUCTURE analysis, and SAMOVA of nuclear SSR data at differing spatial scales to investigate species distinctions in regions of both sympatry and allopatry.



Q. radiata
Specialist on compacted volcanic ash, 2000-2600m, Central and S. Sierra Madre Occidental



Q. tarahumara
Specialist on hydrothermally altered soils, 1020-2200m, N. Sierra Madre Occidental



Distribution is bisected by the Trans-Mexican volcanic belt which began forming during the Pliocene



Q. conzattii
Generalist between 1700-2600m with bicentric distribution in Central and S. Sierra Madre Occidental and Sierra Madre del Sur.



Q. urbanii
Specialist on igneous soils, 1600-2580m, bicentric distribution from western Sierra Madre Occidental and the northern Balsas Upland of the Sierra Madre del Sur.

RESULTS

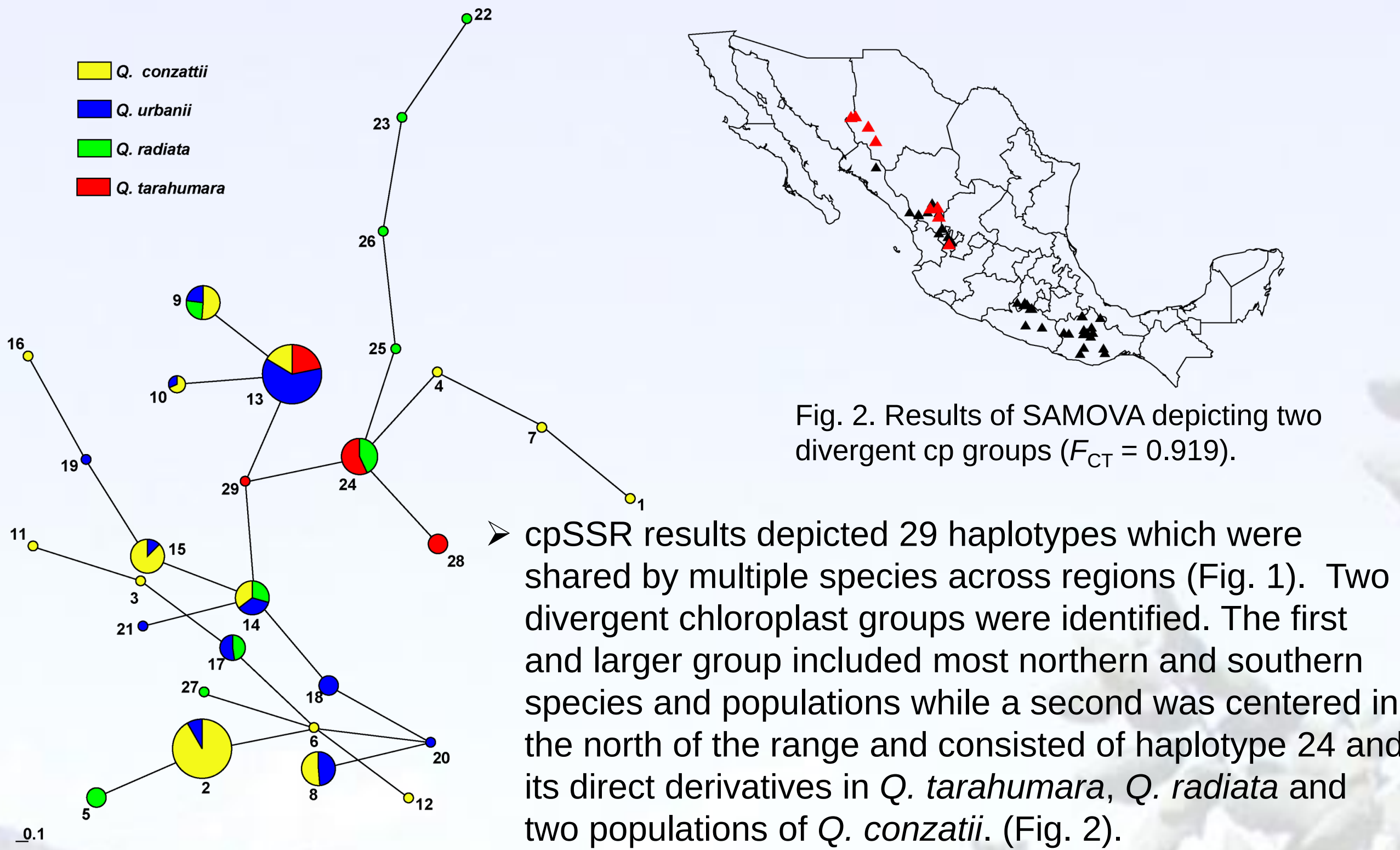


Fig. 1. MST of chloroplast haplotypes. Species designation indicated by color; haplotype frequency by size of marker.

- Analysis of individual haplotype distributions showed that most were shared across biogeographic regions, spanning the large disjunction of the group and were distributed widely. This is indicative of a wider continuous origin for the group prior to the Pliocene. Few haplotypes showed specific regional occurrences suggesting a later origin either through hybridization (H24) or mutation (Fig. 3).

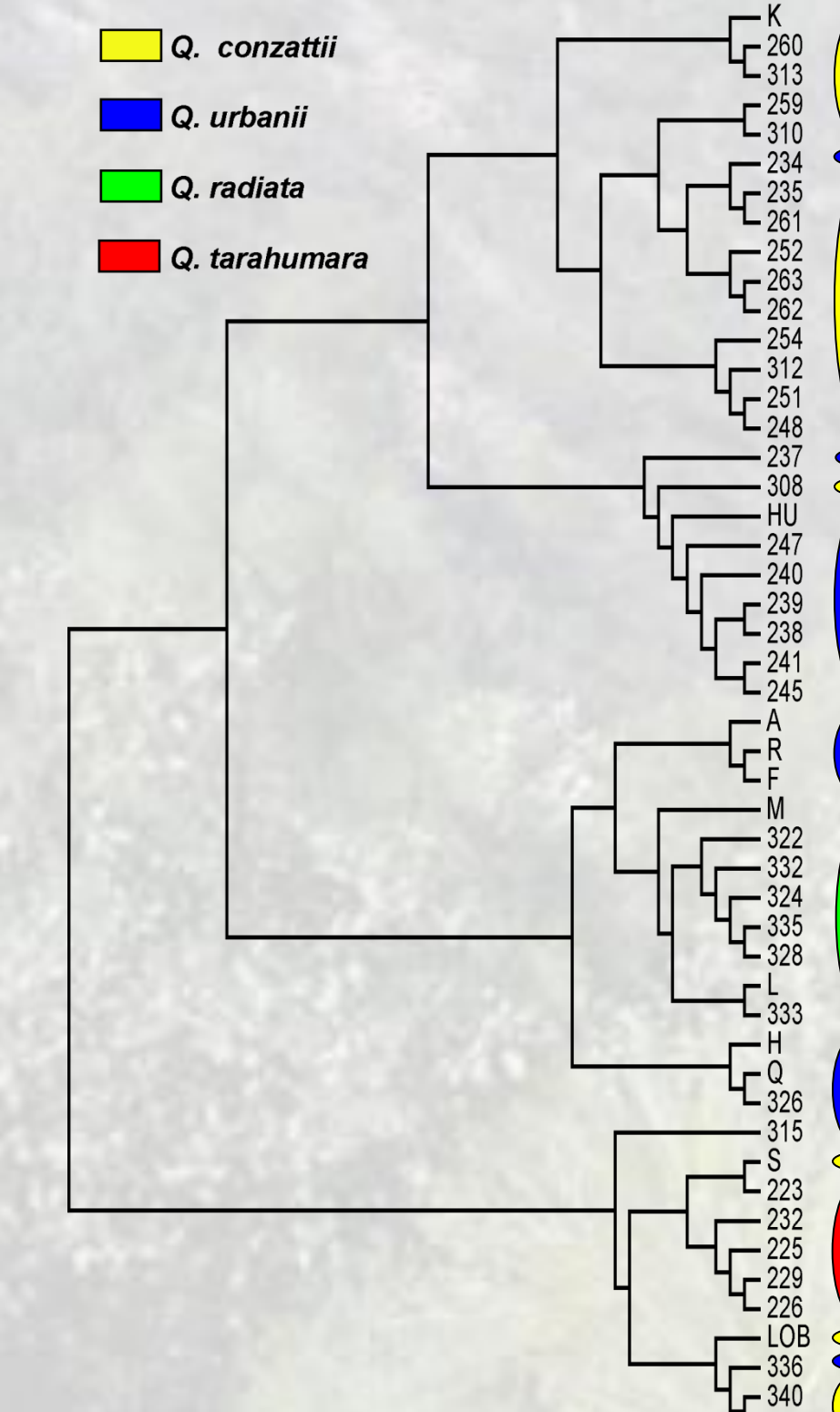


Fig. 4. UPGMA dendrogram of relationship among 49 populations based on Nei's D_s.

- SAMOVA showed the greatest differentiation occurred across two distinct groups, a larger group consisting of the majority of the section and two populations of *Q. tarahumara* at the northern extreme of the range of *Racemiflorae*. These populations corresponded to those exhibiting the highest proportion of cp haplotype 24 and are likely divergent due to recent hybrid origin.

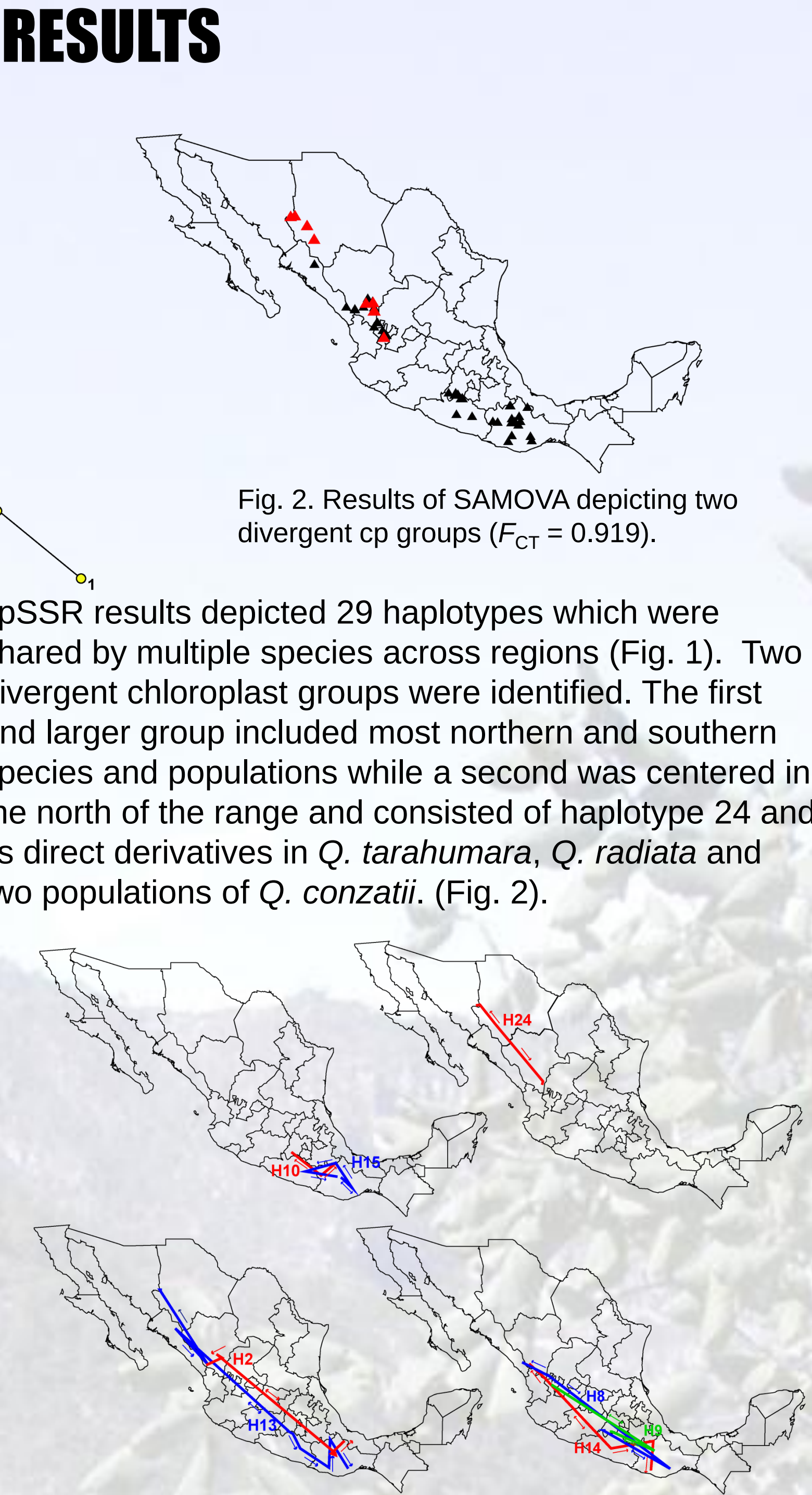


Fig. 2. Results of SAMOVA depicting two divergent cp groups ($F_{CT} = 0.919$).

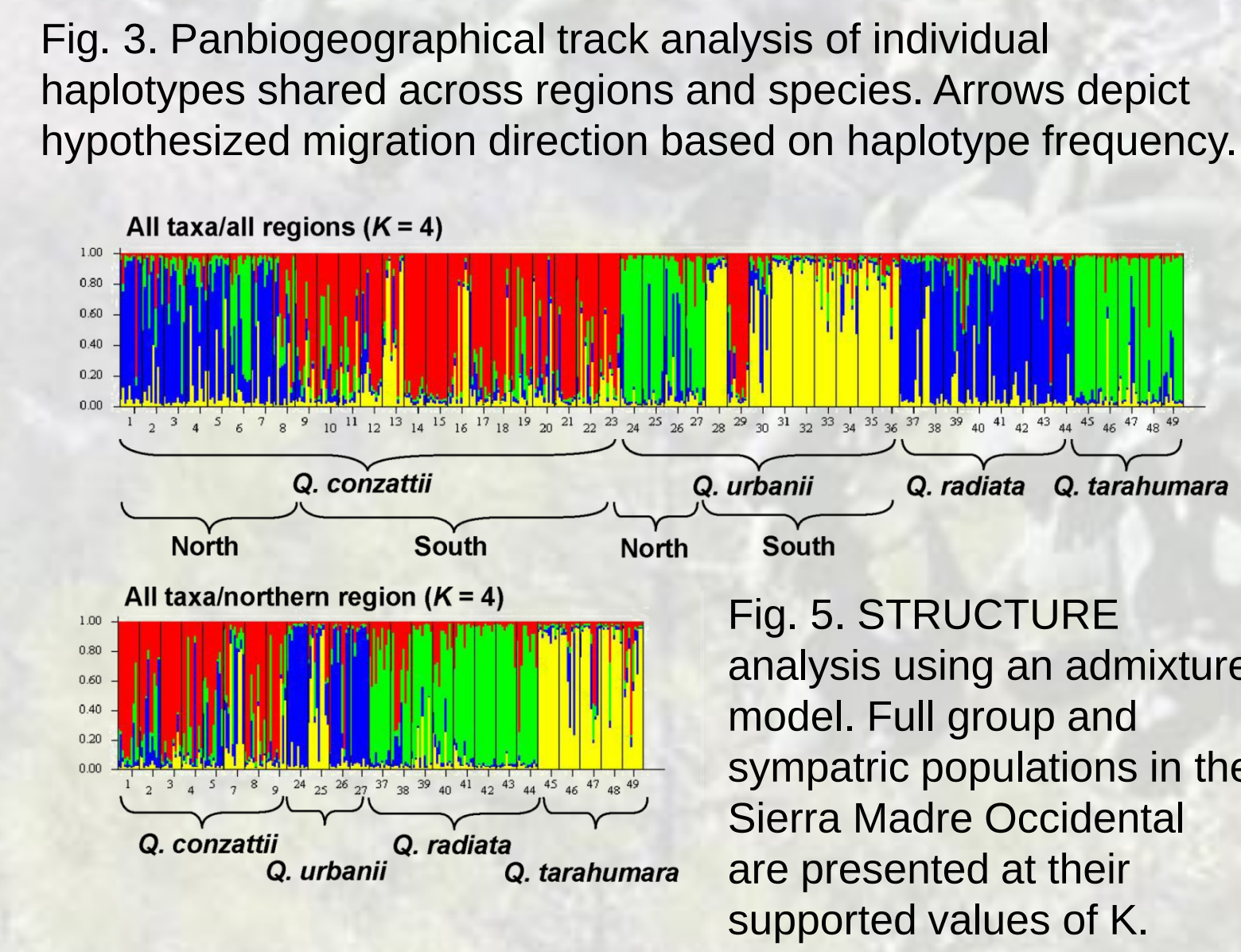


Fig. 3. Panbiogeographical track analysis of individual haplotypes shared across regions and species. Arrows depict hypothesized migration direction based on haplotype frequency.

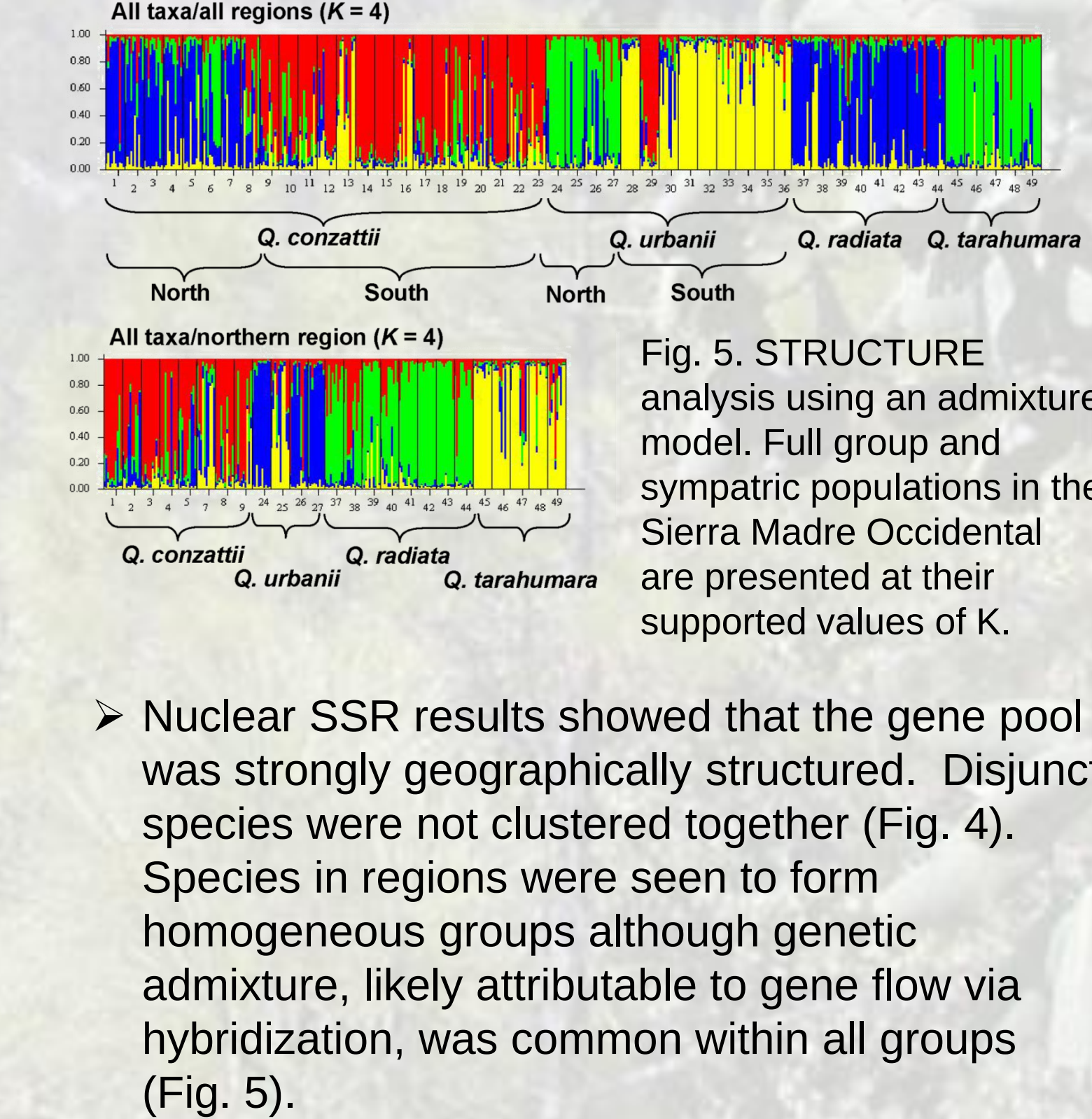


Fig. 5. STRUCTURE analysis using an admixture model. Full group and sympatric populations in the Sierra Madre Occidental are presented at their supported values of K.

- Nuclear SSR results showed that the gene pool was strongly geographically structured. Disjunct species were not clustered together (Fig. 4). Species in regions were seen to form homogeneous groups although genetic admixture, likely attributable to gene flow via hybridization, was common within all groups (Fig. 5).

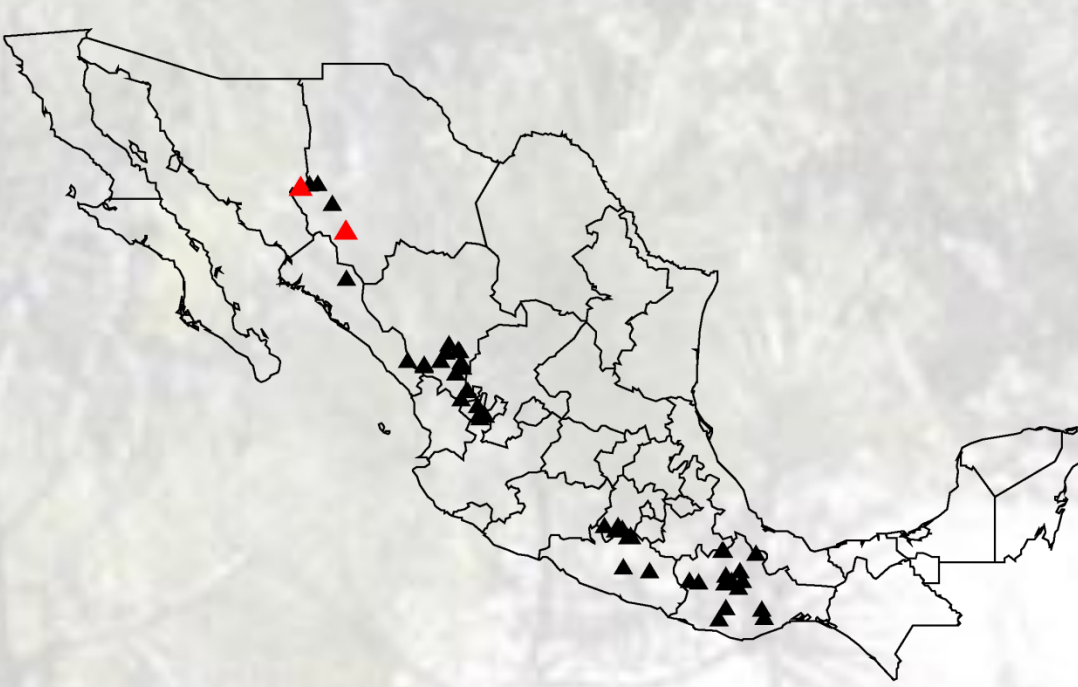


Fig. 6. Results of SAMOVA depicting two divergent nuclear groups ($F_{CT} = 0.31$).

DISCUSSION

Chloroplast and nuclear markers give distinctly different insights into evolutionary history. The independent patterns of history have been identified previously in *Quercus* (Whittemore & Schaal, 1991) and appear to be ubiquitous across the group. They both however show that gene exchange, either long-term coalescence of lineages and contemporary hybridization and genetic homogenization in geographic regions is a common trait.

In *Racemiflorae* the pattern of shared common chloroplast haplotypes across the Trans-Mexican volcanic belt disjunction suggests a one time continuous distribution for an ancestral *Racemiflorae*. The sharing and frequency of haplotypes however obscures the region of origin.

The occurrence of haplotype 24 in the north of the range indicates the evolutionarily recent incorporation of a lineage from outside the group. The common occurrence of this lineage within two of the more restricted specialist species, *Q. tarahumara* and *Q. radiata* suggests that their evolution may be more recent and in part a result of introduced evolutionary novelty (Arnold, 1997) through hybridization. While more is needed to prove the relationship we propose that this supports a general hypothesis of cyclic hybridization (Rattenbury, 1962) and generation of evolutionary novelty over time leading to the high levels of *Quercus* species diversity in Mexico.

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