Morphological, Molecular and Macro-Biochemical Diversity of Moroccan Pistacia lentiscus L.: A Three-Level Synthesis across Eleven Populations

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Abstract

The mastic tree, *Pistacia lentiscus* L. (Anacardiaceae), is an important Mediterranean shrub whose Moroccan populations had never been characterised in an integrated way. This article brings together three complementary studies carried out on the same eleven natural populations, sampled along a Middle Atlas–High Atlas–Souss bioclimatic gradient, and reads them as a single body of evidence. Morphological analysis of 24 traits revealed large variation among and within populations. Inter-simple sequence repeat (ISSR) markers showed high genetic diversity—about 91% polymorphic loci, a mean polymorphism information content of 0.79 and a total gene diversity of 0.31—together with strong differentiation (fixation index F_{ST} = 0.42; gene flow Nm ≈ 0.95) and five gene pools; a hierarchical analysis of molecular variance (AMOVA) showed that geographic and bioclimatic groupings together explained under 4% of the molecular variation. Macro-biochemical analysis of the leaves found significant differences among populations in minerals, nitrogenous matter, protein and energy value, and resolved four groups. Mantel and partial Mantel tests further showed that the three levels are statistically independent of one another, and that genetic and biochemical differentiation is unrelated to either geographic or bioclimatic distance; only morphology tracked the environment, an isolation-by-environment pattern consistent with phenotypic plasticity. Diversity is thus high at every level and, for neutral and biochemical markers, decoupled from geography and climate. These results point to dioecy, outcrossing and bird-mediated dispersal as the main drivers. They argue for conserving a network of populations, not a few sites, prioritising the arid-margin Souss stand under a drying climate.

Introduction

Pistacia lentiscus L. is a dioecious, evergreen shrub of the family Anacardiaceae, widespread across the Mediterranean Basin and well represented throughout Morocco, from the Rif and the Atlas ranges to the Atlantic and Mediterranean coasts (Al-Saghir and Porter 2012; Zohary 1952). It is a keystone species of the maquis, valued at once for its ecological role on poor, dry soils and for its products—mastic resin, antioxidant-rich leaves and fruits, and essential oils—used in food, cosmetics and traditional medicine. As a long-lived, outcrossing woody plant, it is expected to harbour considerable diversity (Hamrick et al. 1992), yet in Morocco that diversity had been described only piecemeal.

Characterising a plant resource properly means looking at it from more than one angle. Morphology captures the visible, partly plastic phenotype; molecular markers read neutral variation in the genome; and biochemical composition reflects how genotype and environment together shape the chemistry of the leaves. Each layer answers a different question, and only together do they give a faithful picture of how a species is organised. This was the rationale of the present work: to characterise the diversity of Moroccan *P. lentiscus* at three complementary levels—morphological, molecular and macro-biochemical—using the same eleven natural populations so that the layers could be compared directly.

Although these three datasets have each been published separately (Bouta et al. 2020, 2022, 2024), they have never been brought together and read as a single body of evidence. That is the purpose of the

present synthesis. Our aim is to compare the morphological, molecular and biochemical structure of the same eleven populations and to test one hypothesis: that the diversity revealed by the three approaches is congruent—high within populations, yet only weakly related to geographic or bioclimatic origin. We discuss the combined evidence in the light of recent Mediterranean and Moroccan research and draw out its implications for the conservation and valorisation of the species. Because the underlying results have appeared elsewhere, this is a synthesis rather than a primary report, and the figures are reproduced or adapted from the original studies.

Materials and methods

Study area and plant material

The three studies share a common sampling design: eleven natural populations of *P. lentiscus* distributed across a marked bioclimatic gradient in central and south-western Morocco—five in the Middle Atlas, five in the High Atlas, and one isolated population in the arid Souss lowlands at Imiouddare (Table 1; Figure 1). Altitude ranges from about 300 m at the Souss margin to nearly 1450 m in the Atlas, and mean annual rainfall from roughly 290 mm to more than 700 mm, so the sampled populations span a genuine environmental gradient from sub-humid mountain to semi-arid lowland. Within each population, individual trees were tagged and used as the common material for the morphological, molecular and biochemical analyses.

Table 1. The eleven Moroccan *Pistacia lentiscus* populations and their geographic and bioclimatic setting (after Bouta et al. 2022).

Population	Region	Lat (°N)	Lon (°W)	Alt (m)	Rainfall (mm/yr)	Mean T (°C)
Tighssaline I	Middle Atlas	32.76	5.63	1344	635	16.1
M'rirt	Middle Atlas	33.19	5.54	1111	717	14.7
Lkbab	Middle Atlas	32.71	5.57	1401	616	14.1
Ayt Yahya Oussad	Middle Atlas	32.68	5.54	1451	620	13.3
Tighssaline II	Middle Atlas	32.76	5.65	1245	635	16.1
Modj	High Atlas	32.30	6.30	1200	594	14.7
Isseksi	High Atlas	32.22	6.27	1427	594	14.7
Azilal	High Atlas	32.01	6.56	1354	563	15.7
Tifrdine	High Atlas	32.32	6.32	805	493	18.3
Bin el Ouidane	High Atlas	32.10	6.46	866	490	17.6
Imiouddare	Souss	30.59	9.74	298	290.6	18.3

Morphological analysis

Morphological diversity was assessed on twenty-four morpho-pomological traits—both quantitative (leaf, leaflet, fruit and almond dimensions, leaflet number, fruit weight) and qualitative (leaf and fruit colour, fruit and leaflet shape)—following Bouta et al. (2020). For each population, ten trees were sampled and twenty fruits per tree were measured, allowing a three-factor analysis of variance (population, tree within population, and fruit) to partition the variation. Trait associations were examined through Pearson correlation, and population relationships were summarised by principal component analysis (PCA) and hierarchical clustering in XLSTAT (Addinsoft 2016).

Molecular (ISSR) analysis

Total genomic DNA was extracted from young leaves with the CTAB method (Doyle and Doyle 1990) and its quality checked on 0.8% agarose gels. Thirteen inter-simple sequence repeat (ISSR) primers were used to genotype fifty-five individuals (five trees per population). Amplifications were carried out in 12.5 µL reactions (40 ng DNA, 2.5 mM $MgCl_2$, 0.8 mM dNTPs, 0.8 µM primer, 0.625 U Taq polymerase) over 30 cycles (denaturation 94 °C/45 s, primer-specific annealing 45 s, extension 72 °C/2 min, final extension 72 °C/5 min), and products were separated on 1.8% agarose gels. Bands were scored as present (1) or

absent (0). For each primer the polymorphism information content (PIC), resolving power (Rp; Prevost and Wilkinson 1999), effective multiplex ratio and marker index (Powell et al. 1996) were calculated. Within-population diversity (Hs), total gene diversity (Ht), the coefficient of gene differentiation (Gst) and Shannon's index were computed in POPGENE 1.32 (Yeh et al. 1997); analysis of molecular variance (AMOVA) and F-statistics were obtained in Arlequin (Excoffier et al. 2005); a UPGMA dendrogram of individuals was built from Nei's (1972) genetic distances; and the number of gene pools was inferred with STRUCTURE 2.3.4 (Pritchard et al. 2000) using the ΔK criterion (Evanno et al. 2005).

Biochemical analysis

The macro-biochemical (proximate) composition of the leaves was determined following Bouta et al. (2024). Dry matter and moisture were measured by oven-drying to constant weight; ash by incineration in a muffle furnace (AFNOR 1977), with organic matter obtained by difference; crude fat by Soxhlet extraction with hexane; total soluble sugars by colorimetric assay; crude protein by the Kjeldahl method (nitrogen × 6.25); and crude fibre by the standard gravimetric procedure. Energy value was calculated from the proximate fractions. Population differences were tested by analysis of variance, relationships among parameters by Pearson correlation, and population structure by principal component analysis and Ward hierarchical clustering.

Data provenance

The morphological, molecular and biochemical datasets synthesised here were generated and reported in three earlier publications (Bouta et al. 2020, 2022, 2024); no new experimental data were produced for this article. The only new analyses are the concordance and spatial tests (Mantel, partial Mantel, multiple regression on distance matrices and Procrustes) described in the Synthesis, computed from the published population means, Nei's distances and bioclimatic variables. The figures presented here were redrawn from the underlying raw data and are therefore original; the tables are reproduced or adapted from the earlier publications.

Morphological diversity

The first level of characterisation was morphological. Twenty-four morpho-pomological traits—covering leaf, leaflet and fruit dimensions and qualitative descriptors—were scored across the eleven populations (Bouta et al. 2020). A three-factor analysis of variance (population, tree, fruit) showed significant differences among populations for most of them: fruit length, fruit width, envelope thickness, fruit weight, almond length, leaf length and leaf width all differed at $p < 0.0001$, while a few traits, such as almond width and the presence of a terminal leaflet, did not. Variation was large not only among populations but within them—trees from the same site often differed widely, as expected in an outcrossing, long-lived shrub in which every individual is genetically unique.

Principal component analysis condensed this variation onto two axes that together explained 52.4% of the total (35.3% and 17.0%) and separated the populations into four groups; hierarchical clustering recovered three (Figure 2). The grouping did not follow geography—Azilal, a Middle Atlas population, fell with the coastal Souss population of Imi Ouddare despite the roughly 440 km between them. Some populations stood out: M'rirt and Bin El Ouidane were strongest for vegetative traits (leaf length and width, leaflet number), Tighssaline, Bin El Ouidane and Tifrdine for fruit traits, while Lkbab scored lowest for most characters. Only about 20% of the leaves carried a terminal leaflet—the same scarcity Barazani et al. (2003) reported across the Mediterranean.

This kind of broad morphological variation is well documented in *P. lentiscus* and is partly environmental: leaf size in particular tends to shrink in arid and cold sites, and leaf traits respond plastically to drought and salinity (Cristiano et al. 2016; Álvarez et al. 2023). The caution that follows is the same as elsewhere in this synthesis—because morphology is partly plastic, it cannot be read directly as genetic structure. What it establishes is unambiguous: Moroccan mastic tree is morphologically rich, and that richness is organised independently of where the populations grow.

Molecular (ISSR) genetic diversity

The second level moved from phenotype to genome. Using thirteen ISSR primers, Bouta et al. (2022) genotyped 55 individuals from the eleven populations and recovered a high level of variation: of 121 amplified bands, 110 (about 91%) were polymorphic, with a mean polymorphism information content of 0.79 (ranging from 0.23 to 0.91) and a mean resolving power of 4.89. Diversity indices were correspondingly high—total gene diversity Ht = 0.31, within-population diversity Hs = 0.17, Shannon index = 0.47—confirming substantial genetic variability in the Moroccan mastic tree (Table 2).

Table 2. Genetic diversity of Moroccan *Pistacia lentiscus* revealed by 13 ISSR primers (after Bouta et al. 2022).

Genetic diversity parameter (ISSR, 13 primers)	Value
Polymorphic bands	110 of 121 (≈91%)
Mean polymorphism information content (PIC)	0.79 (0.23–0.91)
Mean resolving power (Rp)	4.89
Total gene diversity (Ht)	0.31
Within-population diversity (Hs)	0.17
Shannon information index (I)	0.47
Coefficient of gene differentiation (Gst)	0.43
Gene flow (Nm)	0.95
Fixation index (FST, AMOVA)	0.42

Analysis of molecular variance partitioned 42.8% of the variation among populations and 57.2% within them, giving a high fixation index (F_{ST} = 0.42) and very low gene flow (Nm ≈ 0.95) (Table 3). The most telling result came from the hierarchical AMOVA: when the populations were grouped by mountain range or by bioclimate, those groupings explained almost none of the variation—just 3.8% for geography and −0.9% for bioclimate. In other words, neither origin nor climate structures the genome, which argues against any local adaptation of these populations to their environment. Per-population F_{ST} ranged from 0.325 at Imi Ouddare, the least differentiated stand, to 0.447 at Lkbab, the most divergent (Table 4). The partition of molecular variance and Bayesian STRUCTURE assignment (Figure 3) together resolved five gene pools that, once again, ignore geographic origin. Per-primer ISSR performance, population-level diversity indices, and a comparison with published Mediterranean studies are provided as Supplementary Figures S1–S3.

Table 3. Analysis of molecular variance (AMOVA) for the eleven Moroccan populations, with hierarchical partitions by geographic and bioclimatic group (after Bouta et al. 2022).

Source of variation	df	Variance comp.	% variation	F-statistic
Among populations	10	2.468	42.76	FST = 0.42
Within populations	44	3.305	57.24	—
Among geographic groups	2	0.220	3.76	FCT = 0.038
Among bioclimatic groups	2	−0.054	−0.94	FCT = −0.094

Table 4. Population-specific fixation indices (F_{ST}). Lkbab is the most differentiated population and Imi Ouddare the least.

Population	FST	Population	FST
Modj	0.334	Bin El Ouidane	0.416
Ait Yahya Oussaade	0.397	M'rirt	0.384
Imi Ouddare	0.325	Lkbab	0.447
Isseksi	0.372	Azilal	0.409
Tifrdine	0.372	Tighssaline I	0.397
Tighssaline II	0.403	—	—

Two comparisons place these numbers in context. The within-population richness matches the high diversity reported elsewhere with dominant markers—very high intraspecific variation in Turkish ISSR/IRAP data (Turhan-Serttaş and Özcan 2018) and high polymorphism in Greek var. *chia* (Kostas et al. 2021)—and fits the species' dioecious, obligately outcrossing mating system. The strong differentiation, by contrast, stands against the weak structure found across the whole Mediterranean, where basin-wide microsatellite surveys report F_{ST} near 0.12 and credit long-distance, bird-mediated seed dispersal with holding the species together (Martínez-López et al. 2020; Mezni et al. 2024). The contrast is informative: at the basin scale rare long-distance dispersal keeps populations connected, whereas within the fragmented Moroccan Atlas, discontinuous distribution, short pollen flow and limited seed exchange let drift differentiate neighbouring stands. Part of the gap is also methodological, since dominant ISSR markers tend to return higher F_{ST} than codominant microsatellites (Nybom 2004). That the five gene pools ignore geography points to isolation by fragmentation and drift rather than a simple isolation-by-distance cline—and separating the adaptive from the neutral share of this structure will need codominant SSRs or genome-wide SNPs, tools now reaching the genus (Kafkas et al. 2016) and already yielding sex-linked markers in var. *chia* (Stavridou et al. 2024).

Macro-biochemical diversity

The third level examined the chemistry of the leaves. Bouta et al. (2024) measured the macro-biochemical (proximate) composition of the eleven populations (Figure 4): dry matter averaged about 39%, organic matter 34%, crude protein 34%, fat 21%, fibre 21%, total sugars 15% and minerals 5%, with an energy value averaging 482 kcal/100 g and ranging from 431.98 at Azilal to 529.05 at Modj. Analysis of variance found significant differences among populations for several constituents, including minerals, nitrogenous matter, protein, carbohydrates and energy value.

The correlation structure was strong and coherent—dry matter with organic matter (r = 0.94), nitrogenous matter with energy value (r = 0.96) and with carbohydrates (r = 0.61), and organic matter negatively with minerals (r = −0.54). Principal component analysis captured 74.4% of the variation on its first two axes (43.0% and 31.3%) and, once again, split the populations into four groups: Bin El Ouidane

and M'rirt, rich in dry matter, protein and fibre; Tighssaline II, Imi Ouddare and Lkbab, high in ash, organic matter and sugars; Azilal, Ait Yahia Oussaade and Tifrdine, low in nitrogen; and Tighssaline I, Isseksi and Modj, low in organic matter. As in the morphological chapter, this grouping cut across geographic origin—the very result the authors themselves emphasised as agreeing with the morphological analysis.

Recent Moroccan phytochemistry both situates this result and draws out a useful distinction. Studies of secondary metabolites in *P. lentiscus* leaves report high and variable phenolic and flavonoid contents—for example 345.95 mg gallic-acid-equivalents and 230 mg quercetin-equivalents per gram in a 2024 survey (Bouakline et al. 2024)—and, crucially, find that this variation tracks the environment: polyphenols and flavonoids peak at low altitude while tannins, chlorophylls and ascorbic acid accumulate higher up (Hadini et al. 2022). Secondary metabolism, then, follows the altitudinal gradient. The primary, macro-nutrient composition measured here behaves differently: it separates the populations clearly, yet the groups do not follow altitude or geography. The two observations are complementary—structural, primary constituents seem to carry a signal that is more genotypic than climatic, whereas stress-driven secondary metabolites follow the environmental cline. Either way, Moroccan populations are biochemically distinct; they simply differentiate along different axes.

Synthesis across the three levels

Read together, the three studies converge on one conclusion (Figure 5). At every level—morphological, molecular and macro-biochemical—Moroccan *P. lentiscus* is highly diverse, and at every level that diversity is organised independently of where the populations sit on the map. Twenty-four morphological traits split the populations into four groups; ISSR markers resolve five gene pools; leaf macro-biochemistry resolves four groups; and in each case the grouping cuts across the bioclimatic gradient. The genetic chapter already makes part of the point quantitatively: in the hierarchical AMOVA, mountain range and bioclimate together accounted for under 4% of the molecular variation. But do the three levels structure the populations in the same way, and are they all independent of geography? We tested this directly.

Concordance among the three levels

To move from a qualitative reading to a quantitative one, we compared the morphological, biochemical and genetic distance matrices of the eleven populations with Mantel tests, and tested each against matrices of inter-population geographic distance and of bioclimatic distance (standardized altitude, rainfall and mean temperature); partial Mantel tests (Smouse et al. 1986) then separated geographic from environmental effects. All concordance analyses were run in Python 3 with NumPy and SciPy, using 9999 permutations (Mantel 1967). Two results stand out (Table 5). First, the three biological levels are statistically independent of one another—none of the pairwise correlations was significant (morphological vs genetic $r = 0.07$, $p = 0.69$; biochemical vs genetic $r = 0.02$, $p = 0.92$; morphological vs

biochemical r = 0.10, p = 0.61). Each marker system therefore captures a complementary, non-redundant facet of diversity rather than echoing the others. Second, and in line with the AMOVA, neither genetic nor biochemical distance was related to geographic distance (r = 0.07, p = 0.76 and r = 0.06, p = 0.80). Morphology was the exception: morphological distance correlated significantly with geographic distance (r = 0.43, p = 0.004)—a geographic signal whose nature the bioclimatic analysis clarifies next.

Table 5. Mantel concordance tests among the morphological, biochemical and genetic distance matrices of the eleven populations, and against inter-population geographic and bioclimatic (altitude, rainfall, temperature) distance (Pearson r; p from 9999 permutations). * significant at p < 0.05.

Comparison (distance matrices)	Mantel r	p
Morphological vs genetic	0.074	0.690
Biochemical vs genetic	0.022	0.917
Morphological vs biochemical	0.098	0.609
Genetic vs geographic	0.074	0.758
Biochemical vs geographic	0.058	0.795
Morphological vs geographic	0.433	0.004 *
Genetic vs bioclimatic	0.026	0.892
Biochemical vs bioclimatic	−0.027	0.896
Morphological vs bioclimatic	0.506	0.002 *

Adding the bioclimatic distance matrix sharpens the picture (Table 5). Neither genetic nor biochemical differentiation was related to environment (r = 0.03, p = 0.89 and r = −0.03, p = 0.90), but morphological distance was strongly so (r = 0.51, p = 0.002). The partial Mantel tests then isolate the cause (Table 6): for morphology, the environmental signal held up after controlling for geographic distance (r = 0.31, p = 0.037), whereas the geographic signal disappeared once environment was held constant (r = 0.10, p = 0.56). Morphological differentiation is therefore an isolation-by-environment pattern, not a simple isolation-by-distance one—precisely what is expected if leaf and fruit traits respond plastically to the bioclimatic gradient. Neutral genetic and biochemical variation, by contrast, are tied to neither geography nor environment.

Table 6. Partial Mantel tests separating bioclimatic (env) and geographic (geo) effects on each level of differentiation (9999 permutations). Only morphology retains a significant association, and only with environment. * significant at p < 0.05.

Level of differentiation	r (env | geo)	p	r (geo | env)	p
Genetic	−0.043	0.775	0.082	0.672
Morphological	0.307	0.037 *	0.102	0.556
Biochemical	−0.105	0.503	0.116	0.533

Two further analyses confirm and quantify these patterns. A multiple regression of each biological distance matrix on geographic and bioclimatic distance (MRM; Lichstein 2007) explained 26.4% of morphological differentiation—with environment the dominant predictor (standardized $\beta = 0.41$ versus 0.13 for geography; $p = 0.002$)—but only 0.7% of genetic and 1.4% of biochemical differentiation (both non-significant). A Procrustes test of ordination congruence (PROTEST; Peres-Neto and Jackson 2001) likewise found no significant agreement among the morphological, biochemical and genetic configurations (all $p > 0.5$), and every conclusion held when the Mantel tests were recomputed with rank-based (Spearman) correlations. The decoupling of the three levels, and the environment-only signal in morphology, are therefore robust to the choice of method.

The picture that emerges is thus more subtle—and more informative—than simple congruence. What the three levels share is not the same grouping of populations but the same overall property: high diversity that, for neutral genetic and biochemical variation, is decoupled from both geography and climate. Morphology alone follows the environment, an isolation-by-environment signal exactly as expected for traits that respond plastically to the bioclimatic gradient.

A coherent biological explanation ties the levels together. Strict dioecy enforces outcrossing, which keeps diversity high within every population. Pollen travels only short distances on the wind, so neighbouring stands drift apart; bird-dispersed seed provides occasional, unpredictable long-distance connections that scramble any tidy geographic gradient. Layered onto this is the broken topography of the Atlas, where microhabitat differences in soil, exposure and water availability act at scales finer than the regional map. The result is exactly what we see: rich, locally distinctive populations whose structure owes more to fragmentation, drift and fine-scale environment than to latitude or altitude. The partial decoupling of morphology and leaf chemistry from neutral markers fits the same logic, since both are shaped by plasticity as well as by genotype.

Two caveats keep the synthesis honest. Our concordance test operates at the population level, on eleven populations; an individual-level analysis on the full set of genotyped trees would carry more statistical power and is the natural next step. And because morphology and macro-biochemistry are environmentally responsive—morphology, indeed, still carries a geographic signal—neutral markers remain the firmer guide to population structure, while the value of the other two layers lies in showing that phenotype and chemistry are diverse, population-specific and only partly aligned with the genome.

Conclusions

This synthesis offers the first integrated, multi-level picture of diversity in Moroccan *Pistacia lentiscus*. Across morphology, molecular markers and leaf macro-biochemistry, the same message recurs: the species is diverse on every axis, and that diversity is distributed in a mosaic that does not follow geography. For conservation this has a clear consequence—safeguarding the Moroccan mastic tree means protecting a network of differentiated populations rather than a few large reserves, and the isolated, genetically and biochemically distinct Souss population, sitting on the arid margin most exposed to a warming, drying climate (Tarín-Carrasco et al. 2025; Tamudo et al. 2024), deserves particular attention.

Several lines follow naturally. Genome-wide SNP or genotyping-by-sequencing data would sharpen the resolution and allow neutral and adaptive variation to be separated. Common-garden trials would disentangle the plastic from the heritable share of the morphological and biochemical variation reported here. Relating leaf chemistry directly to genotype, and extending sampling to other Moroccan regions—the Rif, the eastern oriental zone and the Atlantic coast—would complete the national picture. Together these steps would turn a rich descriptive baseline into the kind of evidence needed to manage, and to valorise, one of Morocco's most resilient native shrubs.

Declarations

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Competing interests: The authors declare no competing interests.

Ethics approval: Not applicable. The study involved no human participants or animals; plant material was collected from wild stands in accordance with national regulations, and no endangered species were sampled.

Previously published material: This article is a synthesis of three previously published studies (Bouta et al. 2020, 2022, 2024); no new experimental data were generated. The figures are original (redrawn from the underlying data); the tables are reproduced or adapted from those works.

Data availability: All data discussed are available in the original publications (Bouta et al. 2020, 2022, 2024).

Author contributions: WB conceived the synthesis, compiled the data and wrote the manuscript. AH supervised the work and revised the manuscript. SB, TER, YAB, YK and MEH contributed to the original studies and to critical revision. All authors read and approved the final manuscript.

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Figures

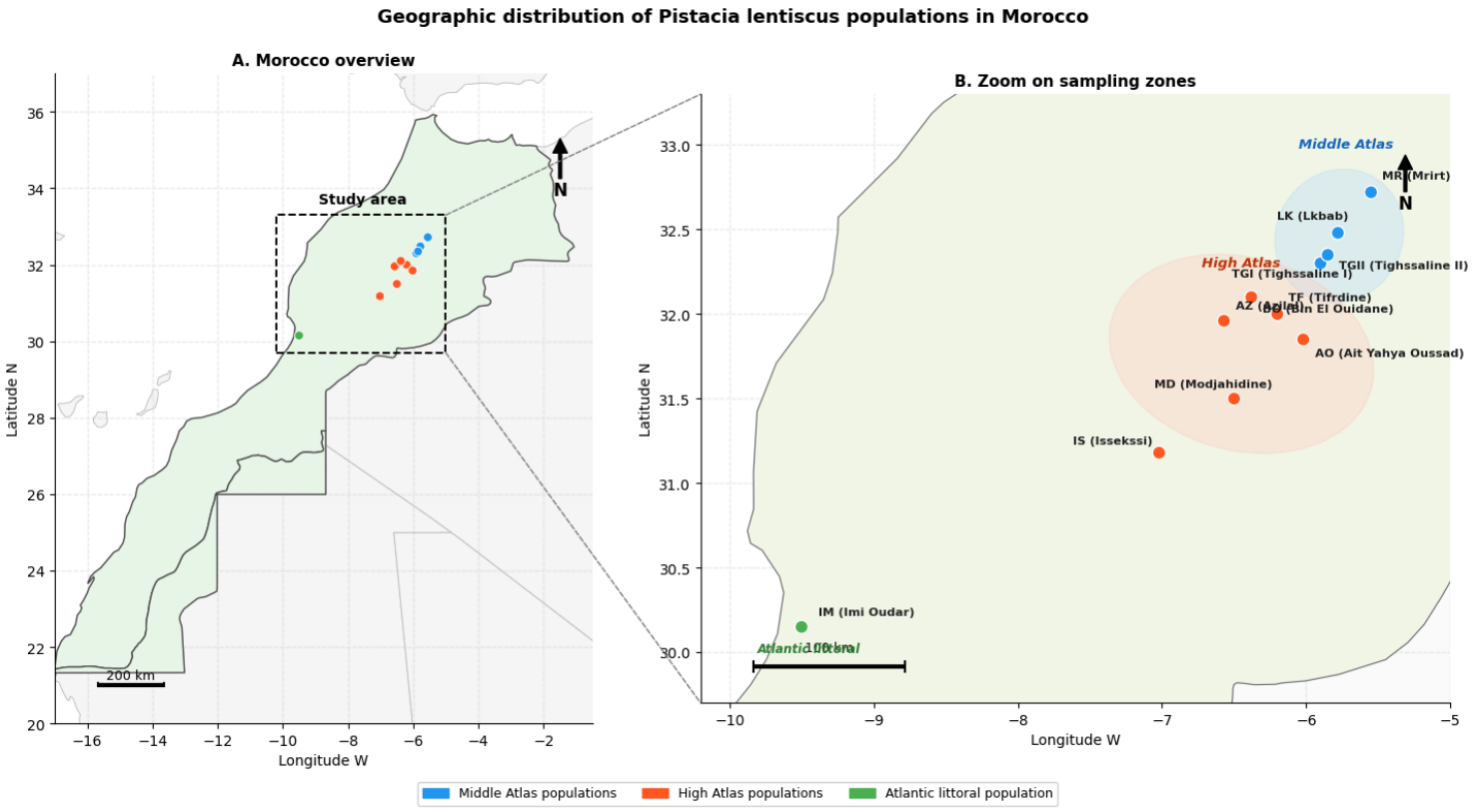

Figure 1

Geographic distribution of the eleven wild *Pistacia lentiscus* populations sampled across three Moroccan bioclimatic zones (Middle Atlas, High Atlas and the Atlantic littoral): (A) location within Morocco; (B) close-up of the sampling zones.

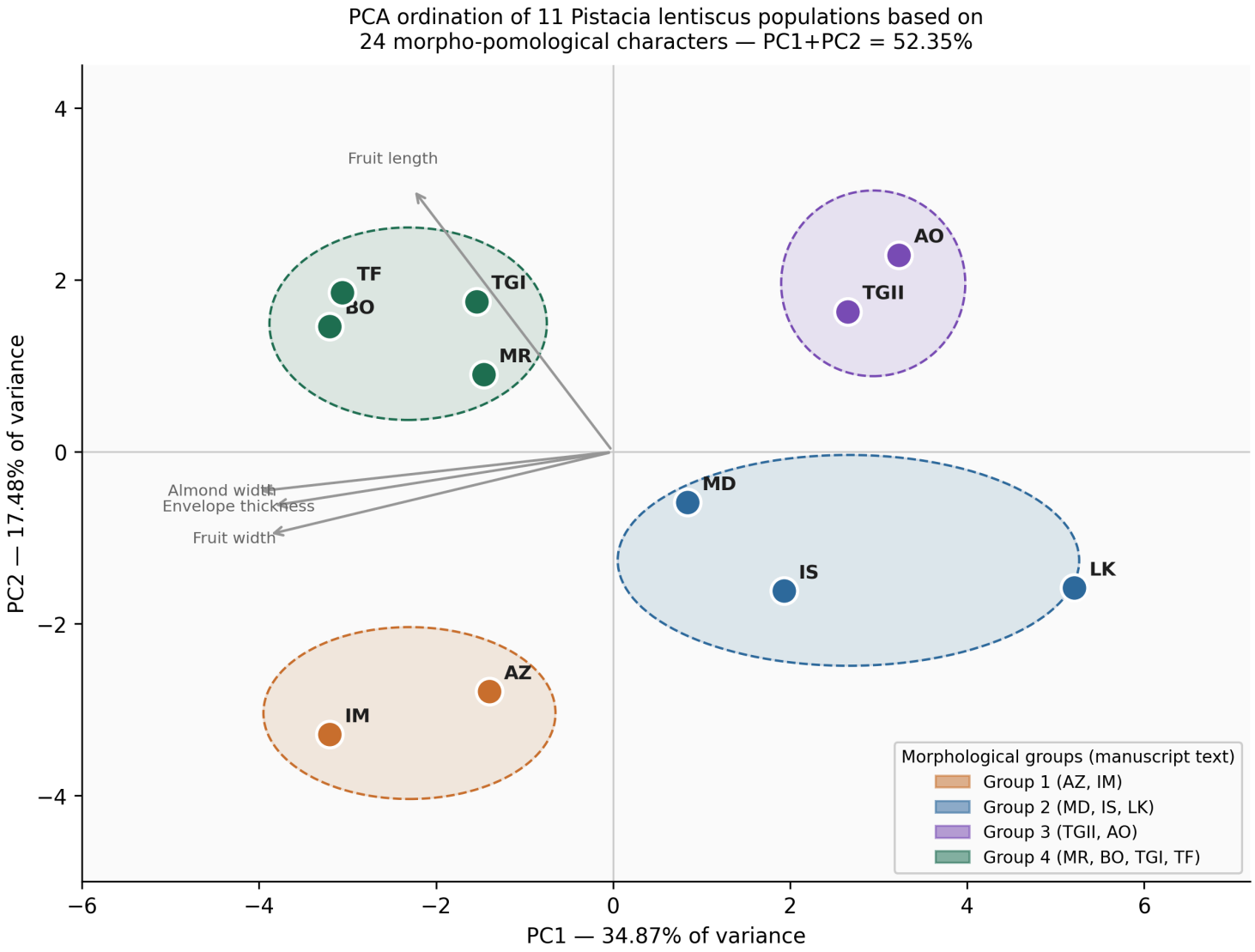

Figure 2

Principal component analysis of the eleven Moroccan *Pistacia lentiscus* populations based on 24 morpho-pomological characters (PC1 + PC2 = 52.35%). Four groups emerge that do not follow geographic origin—Azilal (AZ) groups with the distant coastal population of Imi Ouddare (IM). Arrows show the most influential character loadings (redrawn from the data of Bouta et al. 2020).

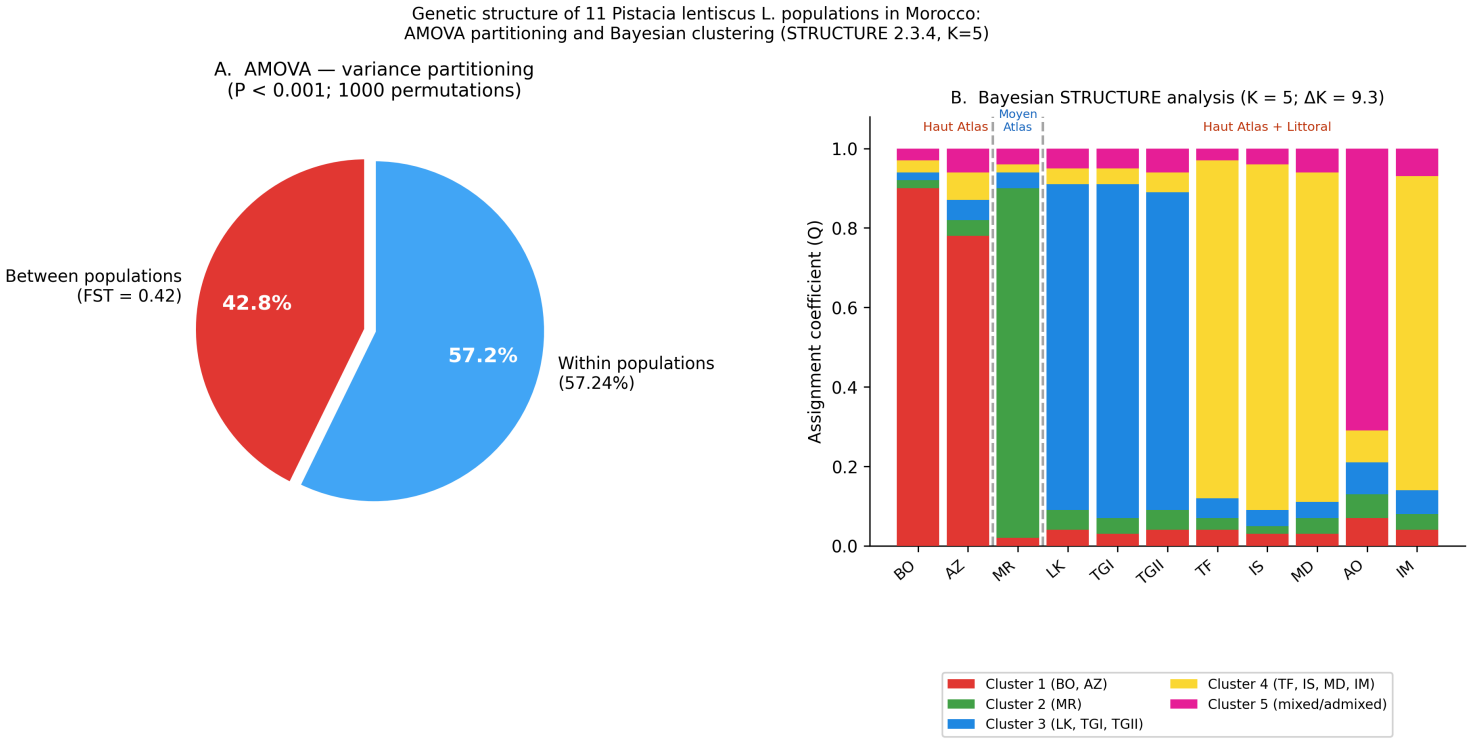

Figure 3

Population genetic structure of the eleven Moroccan *Pistacia lentiscus* populations. (A) Partition of molecular variance (AMOVA): 42.8% among and 57.2% within populations (F_{ST} = 0.42). (B) Bayesian STRUCTURE assignment (K = 5, ΔK = 9.3); each bar is an individual and colours show membership in the five gene pools, which do not follow geographic origin (redrawn from the data of Bouta et al. 2022).

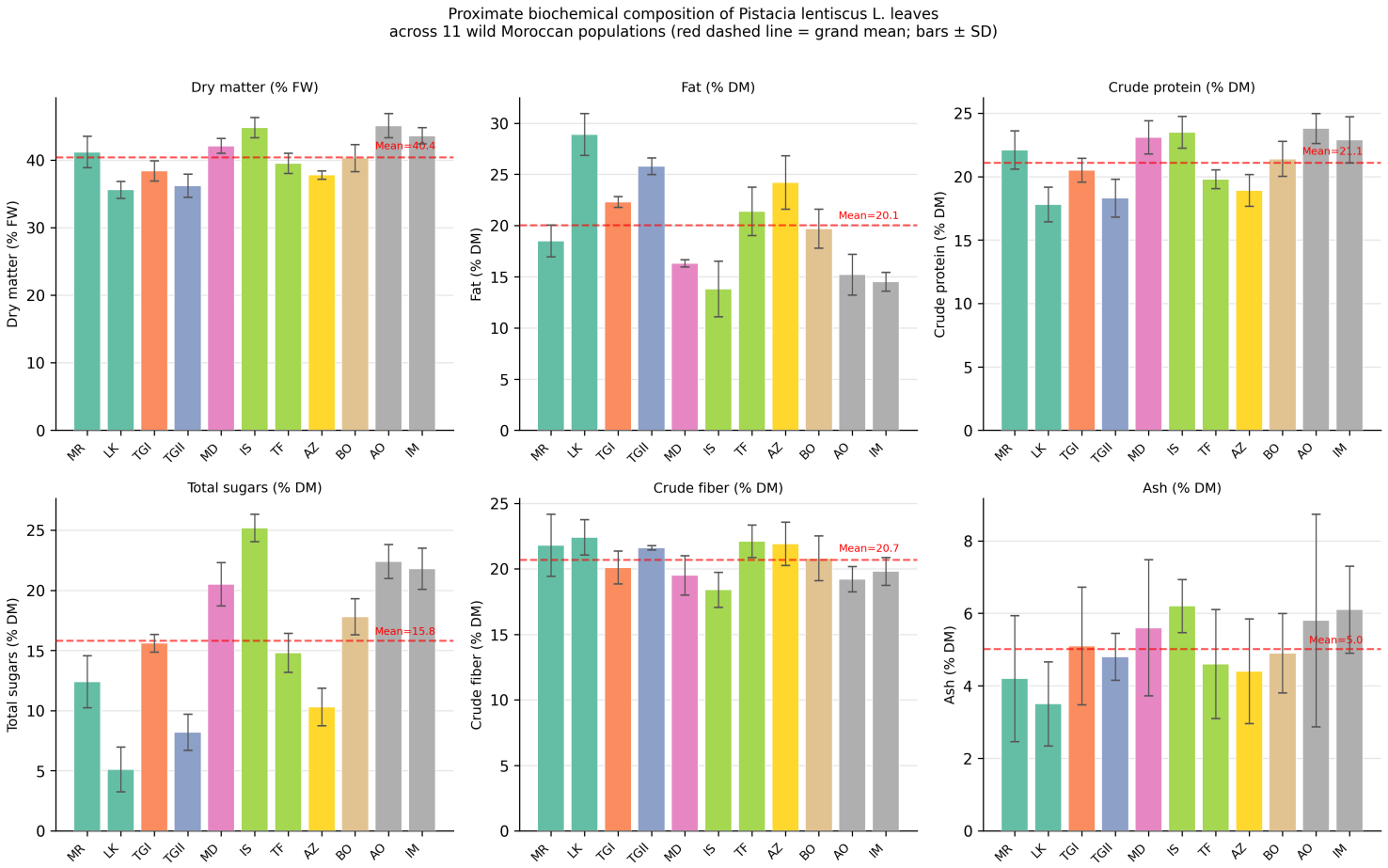

Figure 4

Proximate (macro-biochemical) composition of *Pistacia lentiscus* leaves across the eleven Moroccan populations—dry matter, organic matter, ash, fat, fibre and total sugars (% dry matter). Populations differ significantly for several constituents (redrawn from the data of Bouta et al. 2024).

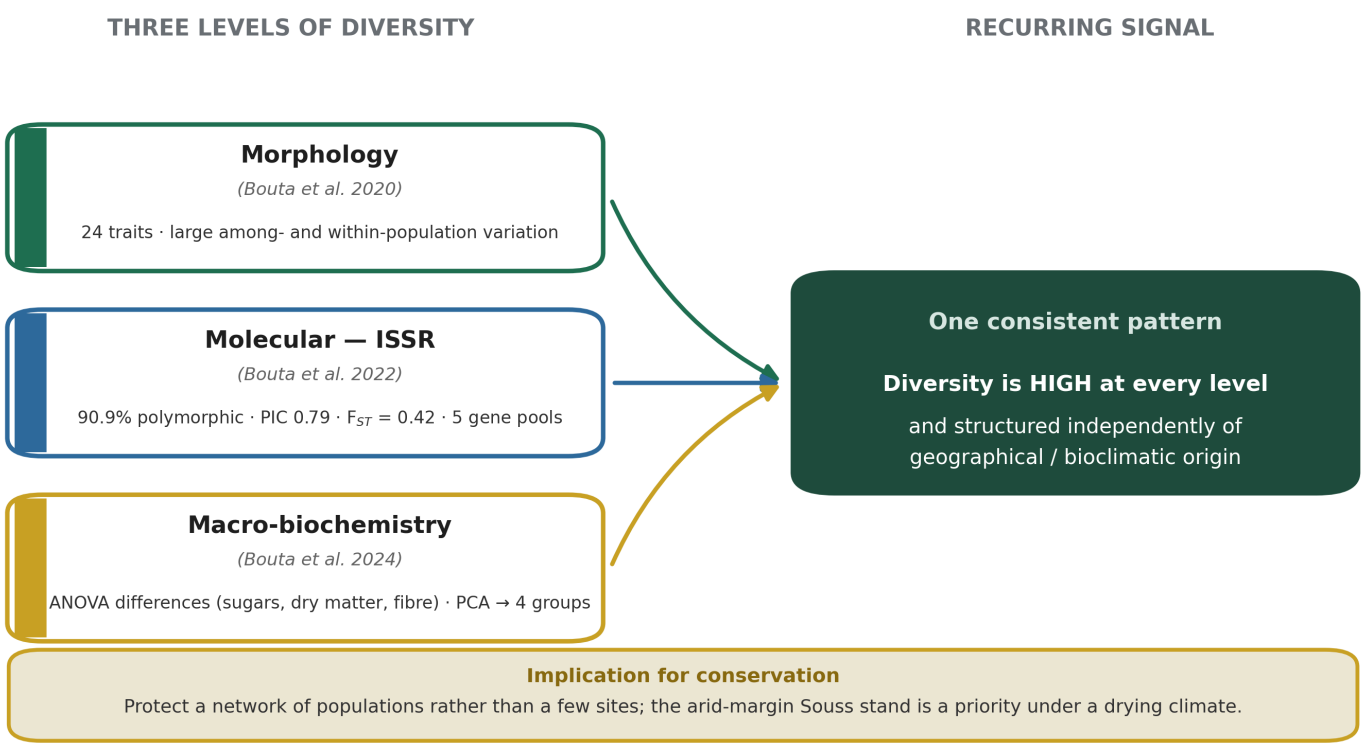

Figure 5

Synthesis of the three levels of diversity in Moroccan *Pistacia lentiscus*. Morphological (Bouta et al. 2020), molecular (Bouta et al. 2022) and macro-biochemical (Bouta et al. 2024) analyses of the same eleven populations converge on a single pattern: high diversity structured independently of geographical or bioclimatic origin, with direct implications for conservation.

Supplementary Files

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- FigureS1.png
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- FigureS3.png