

Geographic distance rather than climate shapes genetic differentiation in *Acacia senegal* in Niger

Abdel Kader Naino Jika

kader.jika@gmail.com

Université Abdou Moumouni

Aichatou Assoumane

Université Abdou Moumouni

Yves Vigouroux

DIADÉ, Univ. Montpellier, IRD, CIRAD

Research Article

Keywords: *Acacia senegal*, climatic heterogeneity, genetic differentiation, isolation by distance, landscape genetics, Sahel

Posted Date: October 28th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11376310/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Geographic distance and environmental heterogeneity can both generate genetic differentiation among natural populations, but their respective contributions are difficult to separate when climate varies along a geographic gradient. We examined the relative associations of geographic and climatic distance with genetic differentiation among eight natural populations of *Acacia senegal* (L.) Willd distributed along a west-to-east aridity and temperature gradient in Niger. Pairwise genetic differentiation was strongly associated with geographic distance and more weakly with climatic distance. When both predictors were fitted simultaneously, the geographic coefficient remained large whereas the climatic coefficient did not differ from zero. This result was consistent across the climatic distance definitions used and all eight leave-one-population-out iterations. Distance-based variance partitioning attributed 56.0% of adjusted genetic variation uniquely to geography and a smaller but statistically supported fraction of 12.1% uniquely to climate. Geographic separation is therefore the dominant factor structuring genetic differentiation. We hypothesize that the observed pattern reflects a strong isolation by distance pattern.

1 INTRODUCTION

The spatial distribution of genetic variation within a species results from the combined action of gene flow, genetic drift, demographic history, and natural selection. Under isolation by distance (IBD), gene exchange between populations declines as spatial separation increases, genetic differences accumulate locally, and genetic differentiation therefore increases with geographic distance (Wright, 1943; Rousset, 1997). Under isolation by environment (IBE), gene flow is restricted between ecologically dissimilar sites, or divergent selection acts against immigrants from contrasting habitats, producing a positive relationship between genetic and environmental distance (Wang, 2013; Wang & Bradburd, 2014). The two processes are not mutually exclusive, and both signatures are frequently recovered within the same species (Bradburd et al., 2013; Sexton et al., 2014). It is therefore difficult to separate their respective contributions.

Populations located far apart tend to experience different climates whether or not environmental dissimilarity itself restricts gene flow. A correlation between genetic and climatic distance is therefore not sufficient evidence of IBE. Simple and partial Mantel tests have long been used to examine such relationships, but partial Mantel tests can produce inflated type I error rates when the underlying data are spatially structured (Guillot & Rousset, 2013; Legendre et al., 2015). Multiple matrix regression with randomization (MMRR) offers an alternative framework in which the associations of geographic and ecological distance with genetic differentiation are estimated simultaneously and tested by joint permutation of the response matrix (Wang, 2013). Distance-based variance partitioning provides a further, ordination-based view of the same question, at the cost of stronger assumptions about how genetic, geographic, and environmental structure are represented.

Acacia senegal (L.) Willd. (syn. *Senegalia senegal* (L.) Britton) is a multipurpose tree of the drylands of sub-Saharan Africa. It is the main source of gum arabic, contributes to soil stabilization and to nitrogen

inputs in low-input dryland systems, and is a component of farmer-managed parklands across the Sahel (Fagg & Allison, 2004; Diatta et al., 2021). In Niger, mean annual rainfall decreases steeply from the south-west to the north-east, and natural *A. senegal* populations occur along this gradient in three recognized gum arabic production areas. The species therefore grows under conditions in which geographic position and climatic conditions are, by construction, strongly aligned. This alignment is precisely what makes a formal separation of geographic and climatic effects necessary in order to interpret the differentiation between populations as evidence of climatic adaptation or as evidence of restriction of gene flow linked to geographical distance.

A recent population-genomic study of 81 trees from eight populations from Niger, identified three genetic groups corresponding broadly to the western, central, and eastern gum arabic production areas, with low pairwise F_{ST} within areas and substantially higher values between western and eastern populations. The same study detected six SNPs associated with minimum temperature of the coldest month (BIO6), providing locus-specific evidence of genotype-climate associations (Assoumane et al., 2026). Whether climatic differentiation also contributes detectably to genome-wide population differentiation independently of geographic separation, however, was not tested. Earlier work based on nuclear microsatellites also recovered geographically structured groups among Nigerien populations of the species (Elhadji et al., 2017), and rangewide studies have shown that *A. senegal* retains marked spatial genetic structure across Africa despite the potential for long-distance gene flow (Odee et al., 2012, 2015; Omondi et al., 2023). The Nigerien populations thus provide a tractable system for asking whether differentiation along the Sahelian gradient is associated primarily with geographic separation, with climatic dissimilarity, or with both.

Here we combined pairwise F_{ST} estimates reported in Assoumane et al. (2026) and sampling coordinates for eight *A. senegal* populations with an independent climatic characterization derived from CHELSA V2.1 and CHELSA-BIOCLIM+ data. Our objectives were to (a) characterize climatic differentiation among the sampled populations, (b) estimate the independent associations of geographic and climatic distance with genetic differentiation, and (c) evaluate how stable these associations are under alternative distance definitions and to the removal of individual populations. Multiple matrix regression with randomization (MMRR) was used as the primary inferential framework (Wang, 2013), and Mantel tests (Guillot & Rousset, 2013; Legendre et al., 2015) together with distance-based variance partitioning were used to examine whether the same conclusion is reached under different statistical representations of the same data.

2 MATERIALS AND METHODS

2.1 Population data

Population-level genetic and geographic data were obtained from a previous population-genomic study of *A. senegal* in Niger (Assoumane et al., 2026). That study initially sampled 95 trees from nine natural populations distributed across three gum arabic production areas. One western population and four

individuals from another western population were excluded following the initial genetic structure analyses. The final dataset comprised 81 individuals from eight populations, with 6 to 12 individuals per population, and 4,446 filtered biallelic SNPs. Two populations were located in the western area, three in the central area, and three in the eastern area (Table 1).

Table 1
Sampling summary of the eight *Acacia senegal* populations analyzed in this study. Population identifiers, production areas, sample sizes, and coordinates follow Assoumane et al. (2026).

Population ID	Population	Area	n	Latitude (°N)	Longitude (°E)
P1	Begorou	West	6	14.0511	0.6495
P2	Kokoye	West	9	13.9862	0.7431
P3	Aseye	Center	12	15.0462	6.4149
P4	Bader	Center	11	14.7221	7.2341
P5	Dakoro	Center	10	14.5286	6.7148
P6	Goure	East	10	13.9686	10.2259
P7	Malan Mainari	East	11	13.2906	12.3081
P8	N’guel Kolo	East	12	13.4901	12.3478

The present study was conducted entirely at the population level. The underlying individual genotype matrix was not reanalyzed. Pairwise F_{ST} values and geographic coordinates were taken from the population-level data reported in Assoumane et al. (2026), and all subsequent computations were performed on these matrices.

2.2 Genetic distance

Pairwise genetic differentiation was expressed as $F_{ST}/(1 - F_{ST})$ following Rousset (1997), and values were computed for the 28 population pairs. The resulting matrix was symmetric with zero diagonal. Linearized values were checked independently against the original F_{ST} matrix; the maximum absolute numerical discrepancy was 5×10^{-11} .

2.3 Geographic distance

Geographic distances between populations were calculated as great-circle distances from the sampling coordinates using the Haversine formula with a mean Earth radius of 6371.0088 km.

The sampling configuration is strongly elongated from west to east, extending more than 1200 km longitudinally but approximately 195 km latitudinally (Figure S1). Raw geographic distance was therefore used as the primary geographic predictor, which is consistent with the distinction drawn by Rousset (1997) between approximately linear and two-dimensional population configurations. Because the

effective spatial geometry of gene flow cannot be established from eight sampling locations, $\log_{10}$ -transformed geographic distance was also analyzed as a predefined sensitivity specification.

2.4 Climatic variables

Climatic conditions at each population were characterized using CHELSA V2.1 and CHELSA-BIOCLIM+ climatologies at 30 arc-second resolution for the 1981–2010 period (Karger et al., 2017, 2021; Brun et al., 2022). Six bioclimatic variables were extracted from CHELSA V2.1: annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual temperature range (BIO7), annual precipitation (BIO12), and precipitation seasonality (BIO15). Three additional variables were obtained from CHELSA-BIOCLIM+: climate moisture index (CMI), potential evapotranspiration (PET), and vapor pressure deficit (VPD). For CMI, PET, and VPD, annual values were computed as the arithmetic mean of the 12 monthly climatological layers.

Five variables were retained for the climatic analysis: BIO5, BIO7, BIO12, CMI, and VPD. They represent, respectively, heat extremes, annual thermal range, moisture supply, climatic water balance, and atmospheric evaporative demand (Table 2). BIO1, BIO6, BIO15, and PET were excluded from the climatic distance calculation for redundancy with the other variables. PET enters directly into the computation of CMI and was strongly correlated with CMI across the eight populations ($r = -0.96$). BIO1, BIO6, and BIO15 were also highly correlated with the other retained variables ($|r| \geq 0.95$).

Table 2
Climatic variables extracted from CHELSA V2.1 and CHELSA-BIOCLIM + at the eight population coordinates. Retained variables were used to compute climatic distance; descriptive variables were excluded because of redundancy.

Variable	Description	Role	Mean ± SD
BIO1	Annual mean temperature (°C)	Descriptive	28.36 ± 0.80
BIO5	Maximum temperature of warmest month (°C)	Retained	40.19 ± 0.43
BIO6	Minimum temperature of coldest month (°C)	Descriptive	13.90 ± 1.57
BIO7	Annual temperature range (°C)	Retained	26.29 ± 1.21
BIO12	Annual precipitation (mm)	Retained	325.5 ± 44.7
BIO15	Precipitation seasonality (CV, %)	Descriptive	154.1 ± 8.4
CMI	Climate moisture index ($\text{kg m}^{-2} \text{ month}^{-1}$)	Retained	-172.8 ± 12.9
PET	Potential evapotranspiration ($\text{kg m}^{-2} \text{ month}^{-1}$)	Descriptive	199.1 ± 12.4
VPD	Vapor pressure deficit (Pa)	Retained	2326.3 ± 68.9

2.5 Climatic distance

The five retained variables were standardized to zero mean and unit variance and analyzed by principal component analysis (PCA). The number of components used to define climatic distance was fixed in advance as the minimum number required to explain at least 80% of total climatic variance. Euclidean distances among population scores on the retained axes formed the primary climatic distance matrix.

We also assessed whether calculating climatic distances directly from the climatic variables, without PCA, affected the results. We constructed a climatic distance matrix using Euclidean distances based on the five standardized variables. We also constructed a climatic water-stress distance matrix using Euclidean distances based on standardized CMI and VPD.

2.6 Mantel tests and MMRR

Simple Mantel tests were used to examine the association between genetic and geographic distance, between genetic and climatic distance, and between geographic and climatic distance (Guillot & Rousset, 2013; Legendre et al., 2015). Partial Mantel tests were then used to test the genetic-geographic association while controlling for climate, and the genetic-climatic association while controlling for geography. All Mantel tests used Pearson correlations and 9999 permutations as implemented in the R package *vegan* version 2.7-5. Because partial Mantel tests can be unreliable under spatially structured data (Guillot & Rousset, 2013; Legendre et al., 2015), we also used multiple matrix regression with randomization (MMRR; Wang, 2013). Using a scripted R implementation, genetic distance was regressed simultaneously on geographic and climatic distance: the lower triangular elements of each matrix were unfolded and ordinary least-squares regression was fitted to the resulting vectors. Significance was assessed by jointly permuting the row and column labels of the genetic distance matrix 9999 times and recomputing the regression coefficients. All distance matrices were standardized before analysis so that the geographic and climatic coefficients are directly comparable.

2.7 Sensitivity and leave-one-population-out analyses

Three sensitivity analyses were defined in advance, each modifying a single component of the primary MMRR specification. The first replaced raw geographic distance by $\log_{10}$ -transformed distance. The second replaced the PCA-based climatic distance by Euclidean distance computed directly from the five standardized variables. The third used the climatic distance based only on CMI and VPD.

A leave-one-population-out analysis was also performed: the primary MMRR model was refitted eight times, excluding one population at each iteration. Climatic PCA axes were retained from the complete eight-population dataset so that coefficients remained comparable across iterations. Stability was assessed from the sign and magnitude of the geographic and climatic coefficients and from changes in model R^2 .

2.8 Distance-based variance partitioning

Because geographic and climatic distances were correlated, an exploratory distance-based redundancy analysis (db-RDA) was used to partition genetic variation into unique geographic, unique climatic, shared, and unexplained fractions. Principal coordinates were computed from the geographic distance matrix,

and the minimum number of axes explaining at least 80% of geographic variation was retained; a single axis met this criterion and captured 98.7% of geographic variation. Climatic structure was represented by the PCA axes retained in the main climatic analysis. Principal coordinates derived from the genetic $F_{ST}/(1 - F_{ST})$ matrix were used as the response. Adjusted R^2 fractions were computed following Peres-Neto et al. (2006), and the unique geographic and climatic fractions were tested by partial db-RDA with 9999 permutations.

With eight populations, three explanatory axes, and few residual degrees of freedom, this analysis is underpowered relative to the MMRR framework, and it operates on ordination axes rather than on pairwise distances. It is therefore reported as an exploratory complement and not as an alternative estimate of the same quantity.

2.9 Statistical analyses and reproducibility

All analyses were performed in R 4.6.1 using terra version 1.9–34, vegan version 2.7-5, and base R functions. All permutation procedures used 9999 permutations with fixed random seeds. The analytical pipeline was rerun through the results audit, and checksum verification confirmed that the source data remained unchanged.

3 RESULTS

3.1 Geographic and climatic differentiation

Pairwise geographic distances among the eight *A. senegal* populations ranged from 12.4 to 1264.8 km. The first two principal components of the five retained climatic variables explained 83.1% of total climatic variation and therefore satisfied the predefined 80% retention criterion; PC1 explained 66.2% and PC2 16.9% (Fig. 1). PC1 separated populations mainly according to thermal and precipitation conditions, whereas PC2 was strongly associated with climate moisture index.

Population scores indicated substantial climatic differentiation among the three production areas. The two western populations were separated from most central and eastern populations along PC1. Malan Mainari, although geographically located in the eastern area, occupied a climatic position closer to the central populations than to the other eastern populations. Pairwise climatic distances ranged from 0.33 to 4.61, and geographic and climatic distances were significantly correlated (Mantel $r = 0.606$, $p = 0.0325$; Fig. 2c).

3.2 Geographic and climatic associations with genetic differentiation

Genetic differentiation showed a strong positive association with geographic distance (Mantel $r = 0.986$, $p = 0.0001$; Fig. 2a). It was also positively associated with climatic distance, although the correlation was considerably weaker ($r = 0.604$, $p = 0.0322$; Fig. 2b).

Partial Mantel tests gave contrasting results for the two predictors. The genetic-geographic relationship remained strong after controlling for climatic distance ($r = 0.978$, $p = 0.0001$), whereas the genetic-climatic association was weak and nonsignificant after controlling for geography ($r = 0.051$, $p = 0.381$).

The primary MMRR analysis produced the same pattern. The geographic coefficient was large and significant ($\beta_{\text{geo}} = 0.980$, $p = 0.0001$), whereas the climatic coefficient was close to zero and nonsignificant ($\beta_{\text{clim}} = 0.011$, $p = 0.772$). The two-predictor model accounted for 97.3% of the variation in the unfolded genetic distance matrix ($R^2 = 0.973$; global $p = 0.0001$; Table 3).

Table 3

Associations of genetic differentiation with geographic and climatic distance under the primary MMRR model, three sensitivity analyses, Mantel and partial Mantel tests, and exploratory distance-based variance partitioning. All permutation tests used 9999 permutations.

Analysis	Geographic definition	Climatic definition	Geographic effect	Climatic effect	R^2
MMRR primary	raw km	PCA PC1 + PC2	$\beta = .980$, $p = .0001$	$\beta = .011$, $p = .772$	.973
MMRR S1	$\log_{10}$ km	PCA PC1 + PC2	$\beta = .752$, $p = .0020$	$\beta = .130$, $p = .317$	.705
MMRR S2	raw km	five variables, no PCA	$\beta = .989$, $p = .0001$	$\beta = -.003$, $p = .941$	.973
MMRR S3	raw km	CMI + VPD	$\beta = .996$, $p = .0001$	$\beta = -.021$, $p = .598$	.973
Mantel (genetic vs. geographic)	raw km	–	$r = .986$, $p = .0001$	–	–
Mantel (genetic vs. climatic)	–	PCA	–	$r = .604$, $p = .0322$	–
Partial Mantel, geographic climatic	raw km	PCA	$r = .978$, $p = .0001$	–	–
Partial Mantel, climatic geographic	raw km	PCA	–	$r = .051$, $p = .381$	–
db-RDA (exploratory)	geographic PCoA	climatic PCA	unique = 56.0%, $p = .0003$	unique = 12.1%, $p = .0135$	.843 ^a

^a Adjusted R^2 of the full geographic-climatic db-RDA model. Shared fraction = 16.1%; unexplained fraction = 15.7%.

3.3 Sensitivity analyses

All three sensitivity analyses retained a positive and statistically supported geographic coefficient together with a small, nonsignificant climatic coefficient (Table 3; Fig. 3).

With $\log_{10}$ -transformed geographic distance, the geographic coefficient decreased to .752 but remained significant ($p = .0020$), the climatic coefficient increased to .130 but remained nonsignificant ($p = .317$), and model fit decreased to $R^2 = .705$. With Euclidean climatic distance computed from the five standardized variables without PCA, the coefficients were $\beta_{\text{geo}} = .989$ ($p = .0001$) and $\beta_{\text{clim}} = -.003$ ($p = .941$), with $R^2 = .973$. With climatic distance based only on CMI and VPD, the coefficients were $\beta_{\text{geo}} = .996$ ($p = .0001$) and $\beta_{\text{clim}} = -.021$ ($p = .598$), with $R^2 = .973$.

3.4 Leave-one-population-out analysis

The geographic association remained stable when populations were removed sequentially (Table 4; Fig. 4). Geographic coefficients ranged from .944 to .999 and were significant in all eight analyses ($p \leq .0035$). Climatic coefficients ranged from $-.021$ to .061, changed sign depending on which population was omitted, and were nonsignificant in every iteration ($p \geq .302$).

Removal of Malan Mainari produced the largest departure from the complete model ($\beta_{\text{geo}} = .944$, $\beta_{\text{clim}} = .061$), which is consistent with its intermediate position in climatic space, but the overall pattern was unchanged.

Table 4
Stability of the primary MMRR model under sequential exclusion of each population. Climatic principal component axes were retained from the complete eight-population dataset so that coefficients remain comparable across iterations.

Population omitted	β_{geo}	p_{geo}	β_{clim}	p_{clim}	R^2
P1 Begorou	.977	.0004	.022	.699	.980
P2 Kokoye	.994	.0009	-.014	.834	.973
P3 Aseye	.999	.0009	-.021	.634	.972
P4 Bader	.989	.0011	-.004	.902	.974
P5 Dakoro	.965	.0009	.033	.435	.971
P6 Goure	.978	.0035	.023	.401	.982
P7 Malan Mainari	.944	.0012	.061	.302	.975
P8 N'guel Kolo	.992	.0008	-.013	.791	.969
Full sample	.980	.0001	.011	.772	.973

3.5 Distance-based variance partitioning

The exploratory db-RDA partition attributed 56.0% of adjusted genetic variation uniquely to geography and 12.1% uniquely to climate; a further 16.1% was shared between the two sets of predictors and 15.7% remained unexplained (Fig. 5). Both the unique geographic fraction ($p = .0003$) and the unique climatic fraction ($p = .0135$) were significant. The full geographic-climatic model had an adjusted R^2 of .843.

4 DISCUSSION

4.1 Geographic distance is the dominant correlate of genetic differentiation

This pattern is consistent with the spatial structure already described among the western, central, and eastern populations of the species in Niger. The source genomic study recovered three genetic clusters broadly matching these areas, with low differentiation within areas and the highest F_{ST} values between western and eastern populations (Assoumane et al., 2026). Earlier microsatellite analysis of partly overlapping populations also identified three geographically structured groups and reduced estimated gene flow among distant populations (Elhadji et al., 2017). Agreement between two independent marker systems suggests that geographic structuring is a repeatable property of *A. senegal* in Niger rather than an artifact of a particular dataset.

Spatial genetic structure has likewise been reported across the broader African range of the species. Phylogeographic work indicates that historical population processes and large-scale geographic structure have contributed to differentiation within *A. senegal* (Odee et al., 2012, 2015), although substantial long-distance gene flow can occur in some populations (Omondi et al., 2023). The strong spatial pattern observed in Niger therefore probably reflects contemporary dispersal limitation, historical population structure, and geographic separation acting together.

The correlation should not, however, be read as evidence for a single dispersal mechanism. The eight populations fall into three geographically ordered regions, and differentiation between regions contributes a large share of the overall distance relationship. The available design cannot distinguish a continuous decline in gene exchange with distance from hierarchical regional differentiation of historical origin: with two western, three central, and three eastern populations, only seven of the 28 pairs are within-region comparisons, and the within-region distance range is too narrow to test the slope independently. Denser sampling in the intervals between production areas would be required to determine whether a continuous IBD process operates within the Nigerien range.

The geographic transformation had a measurable influence on model fit. Raw distance produced a stronger relationship than $\log_{10}$ -transformed distance ($R^2 = 0.973$ versus 0.705), which is compatible with the strongly elongated west-east geometry of the sampling design and with theoretical expectations for approximately linear population configurations (Rousset, 1997). The effective geometry of dispersal cannot be inferred from the sampling envelope alone, so this result is better described as an

empirical property of the present dataset than as evidence that the species occupies a one-dimensional dispersal habitat.

The climatic PCA showed that geographic areas do not map exactly onto climatic space. Malan Mainari is geographically eastern but climatically closer to the central populations, and its exclusion produced the largest change in MMRR coefficients, although the geographic effect remained strong and the climatic effect nonsignificant. Populations of this type, where geographic and climatic position are decoupled, carry more information for separating the two effects than additional populations sampled along the main gradient, and they should be prioritized in future sampling.

4.2 The climatic association is weaker and method-dependent

Climatic distance was associated with genetic differentiation in the simple Mantel analysis, but this relationship largely disappeared once geographic distance was taken into account. The climatic MMRR coefficient was close to zero in the primary model and remained small and nonsignificant in every sensitivity and leave-one-population-out analysis, including the specification restricted to water-balance variables.

Much of the apparent genetic-climatic relationship therefore reflects the spatial organization of climate across Niger. Populations that are geographically distant also experience different thermal and water-balance conditions, so a simple genetic-climatic correlation cannot separate a direct climatic contribution from a geographic pattern with which climate covaries. This is the situation for which MMRR and variance partitioning were developed (Bradburd et al., 2013; Wang, 2013), and it is one in which partial Mantel tests alone would provide weak evidence in either direction (Guillot & Rousset, 2013; Legendre et al., 2015).

The exploratory db-RDA gave a more qualified result. After separation of the shared geographic-climatic component, 12.1% of adjusted genetic variation was uniquely associated with climate, compared with 56.0% uniquely associated with geography, and the climatic fraction was statistically supported despite the absence of a climatic effect in MMRR and partial Mantel analyses. We do not treat this as a contradiction between methods. MMRR relates unfolded pairwise distances simultaneously, whereas db-RDA represents genetic, geographic, and climatic structure in ordination space and partitions the corresponding components of variation; the two approaches do not estimate the same quantity. With eight populations, the db-RDA also has few residual degrees of freedom, and adjusted fractions estimated under these conditions carry wide uncertainty. The climatic fraction is best read as an indication that a smaller climatic component may persist after geographic structure is accounted for, and not as a replacement for the primary MMRR result.

A comparable methodological contrast has been reported in *Cephalotaxus oliveri*. Liu et al. (2023) found significant simple associations of genetic differentiation with both geographic and environmental distance, whereas the environmental effect became nonsignificant in partial Mantel and simultaneous

MMRR analyses; their RDA-based partition nevertheless identified an environmental fraction independent of geography. The biological systems, marker types, and explanatory variables differ substantially between that study and ours, but both illustrate that inference about IBE depends strongly on how shared spatial and environmental structure is represented statistically. Other tree species show simultaneous but unequal contributions of geography and environment: geographic isolation and climatic variability both contributed to differentiation in fragmented *Pinus cembra* populations of the western Alps (Tóth et al., 2019), whereas geographic distance dominated and environmental effects were comparatively weak in *Sequoiadendron giganteum* (DeSilva & Dodd, 2020). Across the wider literature, IBE signatures are common but far from universal (Sexton et al., 2014). Their relative importance appears to vary with species, landscape, history, and analytical framework, which argues for reporting several frameworks rather than selecting the one that yields the expected answer.

4.3 Relationship with previous evidence of climatic association in *Acacia senegal*

The genomic study from which the pairwise F_{ST} values were obtained detected six SNPs associated with minimum temperature of the coldest month using Bayenv2 (Assoumane et al., 2026). That result and the present analyses address different levels of genetic variation. The previous study tested environmental associations at individual loci, whereas the present study asks whether genome-wide population differentiation covaries with climatic dissimilarity independently of geographic distance.

Local adaptation at a limited number of loci can occur while genome-wide differentiation remains structured primarily by geography. These population-level results neither confirm nor challenge the locus-specific BIO6 associations reported previously. The climatic fraction detected by db-RDA is also compatible with a smaller contribution of climatic heterogeneity that is not captured consistently across analytical frameworks.

4.4 Limitations

The main limitation is the small number of populations. Eight populations generate 28 pairwise comparisons, but these are not statistically independent observations. Permutation procedures account for matrix structure when significance is assessed; they do not create additional biological replication. Statistical power to detect a moderate climatic contribution therefore remains limited, and the near-perfect model fit obtained here reflects the strength of the spatial gradient rather than a large effective sample.

Working from pairwise F_{ST} values reported in Assoumane et al. (2026) also restricts what can be estimated. Individual-level genomic data would allow allele frequencies, population structure, spatial eigenfunctions, and genotype-environment relationships to be modeled within a single framework, and would be particularly useful for testing whether the climatic fraction detected by db-RDA persists once finer-scale spatial structure is modeled explicitly.

The climatic characterization is a further limitation. Five variables were selected to summarize temperature extremes, rainfall, climatic water balance, and atmospheric evaporative demand. They capture major dimensions of Sahelian climate but not the full environment experienced by *A. senegal*. Soil texture and fertility, groundwater accessibility, topographic position, land use, vegetation structure, and local disturbance may all contribute to differentiation, and several of these are known to vary at scales far finer than the climatic grid. The present analysis therefore concerns climatic heterogeneity specifically, not IBE in its broader ecological sense.

Finally, climatic values were derived from long-term gridded climatologies at the population coordinates. Such data describe average conditions over a 30-year window. They do not describe the microsites occupied by individual trees, the environments that prevailed when the current adult cohorts established, or the interannual extremes that impose episodic selection in Sahelian systems, where a single failed rainy season can determine recruitment for a decade.

4.5 Implications for conservation and germplasm sampling

Despite these limitations, the geographic signal was exceptionally stable: it persisted across alternative representations of both geographic and climatic distance and was not driven by any single population. Two practical consequences follow. First, geographic coverage across the Nigerien range should remain a primary criterion when *A. senegal* populations are sampled for conservation collections or for gum arabic plantation material, because a substantial part of the differentiation among populations is organized along the west-east axis. Second, geographic differentiation should not by itself be treated as evidence of local climatic adaptation. Delineating adaptive populations or seed-transfer zones would require denser sampling, individual-level genotype-environment analysis, and, ultimately, provenance trials in which fitness is measured under contrasting Sahelian conditions. Provenance responses to rainfall at the site of origin have been documented elsewhere in the species (Diatta et al., 2021), which makes such trials a realistic next step rather than a distant prospect.

5 CONCLUSIONS

Genetic differentiation among eight natural populations of *Acacia senegal* across Niger was strongly associated with geographic distance. The relationship held after climatic distance was included in the same model, under alternative definitions of both distances, and after sequential removal of individual populations. Climatic dissimilarity was associated with genetic differentiation when considered alone, but this association was not independently supported by MMRR or by partial Mantel analysis once geography was controlled, although exploratory variance partitioning identified a smaller climatic component alongside the dominant geographic fraction.

Geographic structure is therefore the most stable correlate of genetic differentiation in the sampled populations, while a weaker climatic contribution remains possible. Denser geographic sampling and individual-level genomic analyses will be needed to separate continuous isolation by distance from

regional population history, and to determine whether climatic heterogeneity contributes directly to adaptive differentiation.

Declarations

Funding

The genomic data reanalysed in this study were generated in a study funded by the IRD JEAI program. The present analysis received no specific funding.

Competing Interests

The authors declare that there are no conflicts of interest.

Author contributions

A. K. Naino Jika: conceptualization, methodology, formal analysis, writing of the original draft. A. Assoumane: data curation, validation, review and editing. Y. Vigouroux: validation, review and editing. All authors read and approved the final manuscript.

Data Availability

The pairwise F_{ST} estimates and sampling coordinates used in this study are available in Assoumane et al. (2026). Additional data and R scripts supporting the analyses are available from the corresponding author upon reasonable request.

References

1. Assoumane, A., Abdoulaye, A. A., Naino Jika, A. K., Tidjani, M., Moussa, D., Berthoul-Salazar, C., & Vigouroux, Y. (2026). Population genomics of *Acacia senegal* (L.) Willd: Adaptive variation in its natural range in Niger. *Research Square* [preprint]. <https://doi.org/10.21203/rs.3.rs-8339114/v1>
2. Bradburd, G. S., Ralph, P. L., & Coop, G. M. (2013). Disentangling the effects of geographic and ecological isolation on genetic differentiation. *Evolution*, 67, 3258–3273. <https://doi.org/10.1111/evo.12193>
3. Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L., & Karger, D. N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*, 14, 5573–5603. <https://doi.org/10.5194/essd-14-5573-2022>
4. DeSilva, R., & Dodd, R. S. (2020). Fragmented and isolated: Limited gene flow coupled with weak isolation by environment in the paleoendemic giant sequoia (*Sequoiadendron giganteum*). *American Journal of Botany*, 107, 45–55. <https://doi.org/10.1002/ajb2.1406>
5. Diatta, O., Sarr, M. S., Hansen, J. K., Diallo, A. M., Nielsen, L. R., Ræbild, A., & Kjær, E. D. (2021). Survival and growth of *Acacia senegal* (L.) Willd. (*Senegalia senegal* (L.) Britton) provenances depend

- on the rainfall at the site of origin. *Annals of Forest Science*, 78, 25. <https://doi.org/10.1007/s13595-021-01098-5>
6. Elhadji, S. D., Assoumane, A., Abdou, M. M., Hassane, I. B., Moussa, D., Tidjani, M., & Alzouma, M. Z. (2017). Exploring genetic diversity and structure of *Acacia senegal* (L.) Willd. to improve its conservation in Niger. *African Journal of Biotechnology*, 16, 1650–1659. <https://doi.org/10.5897/AJB2016.15846>
 7. Fagg, C. W., & Allison, G. E. (2004). *Acacia senegal and the gum arabic trade: Monograph and annotated bibliography*. Oxford Forestry Institute.
 8. Guillot, G., & Rousset, F. (2013). Dismantling the Mantel tests. *Methods in Ecology and Evolution*, 4, 336–344. <https://doi.org/10.1111/2041-210X.12018>
 9. Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. <https://doi.org/10.1038/sdata.2017.122>
 10. Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2021). *Climatologies at high resolution for the earth's land surface areas (CHELSA V2.1)* [Data set]. EnviDat. <https://doi.org/10.16904/envidat.228>
 11. Legendre, P., Fortin, M.-J., Borcard, D., & Peres-Neto, P. (2015). Should the Mantel test be used in spatial analysis? *Methods in Ecology and Evolution*, 6, 1239–1247. <https://doi.org/10.1111/2041-210X.12425>
 12. Liu, H., Wang, Z., Zhang, Y., Li, M., Wang, T., & Su, Y. (2023). Geographic isolation and environmental heterogeneity contribute to genetic differentiation in *Cephalotaxus oliveri*. *Ecology and Evolution*, 13, e9869. <https://doi.org/10.1002/ece3.9869>
 13. Odee, D. W., Telford, A., Wilson, J., Gaye, A., & Cavers, S. (2012). Plio-Pleistocene history and phylogeography of *Acacia senegal* in dry woodlands and savannahs of sub-Saharan tropical Africa. *Heredity*, 109, 372–382. <https://doi.org/10.1038/hdy.2012.52>
 14. Odee, D. W., Wilson, J., Omondi, S., Perry, A., & Cavers, S. (2015). Rangewide ploidy variation and evolution in *Acacia senegal*: A north-south divide? *AoB Plants*, 7, plv011. <https://doi.org/10.1093/aobpla/plv011>
 15. Omondi, S. F., Githae, E. W., & Khasa, D. P. (2023). Long-distance gene flow in *Acacia senegal*: Hope for disturbed and fragmented populations. *Ecology and Evolution*, 13, e10292. <https://doi.org/10.1002/ece3.10292>
 16. Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, 87, 2614–2625. [https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2)
 17. Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, 145, 1219–1228. <https://doi.org/10.1093/genetics/145.4.1219>
 18. Sexton, J. P., Hangartner, S. B., & Hoffmann, A. A. (2014). Genetic isolation by environment or distance: Which pattern of gene flow is most common? *Evolution*, 68, 1–15.

<https://doi.org/10.1111/evo.12258>

19. Tóth, E. G., Tremblay, F., Housset, J. M., Bergeron, Y., & Carcaillet, C. (2019). Geographic isolation and climatic variability contribute to genetic differentiation in fragmented populations of the long-lived subalpine conifer *Pinus cembra* L. in the western Alps. *BMC Evolutionary Biology*, 19, 190. <https://doi.org/10.1186/s12862-019-1510-4>
20. Wang, I. J. (2013). Examining the full effects of landscape heterogeneity on spatial genetic variation: A multiple matrix regression approach for quantifying geographic and ecological isolation. *Evolution*, 67, 3403–3411. <https://doi.org/10.1111/evo.12134>
21. Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, 23, 5649–5662. <https://doi.org/10.1111/mec.12938>
22. Wright, S. (1943). Isolation by distance. *Genetics*, 28, 114–138. <https://doi.org/10.1093/genetics/28.2.114>

Figures

Environmental PCA biplot (5 main standardized variables)

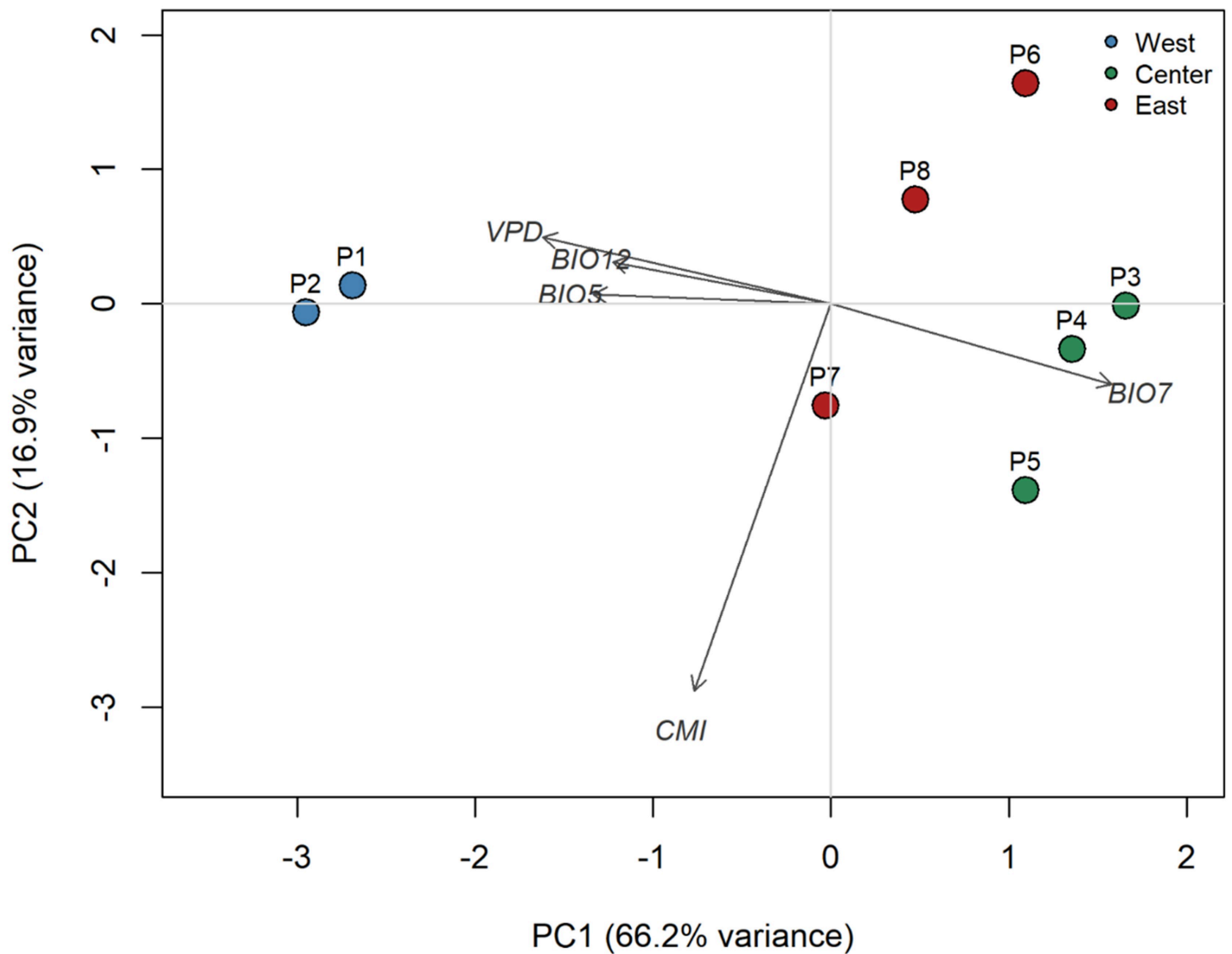


Figure 1

Climatic principal component analysis of the eight *Acacia senegal* populations. Population scores on the first two principal components computed from five standardized climatic variables (BIO5, BIO7, BIO12, CMI, VPD). PC1 and PC2 explain 66.2% and 16.9% of total climatic variation, respectively. Vectors represent variable loadings; Colors distinguish the western, central, and eastern production areas.

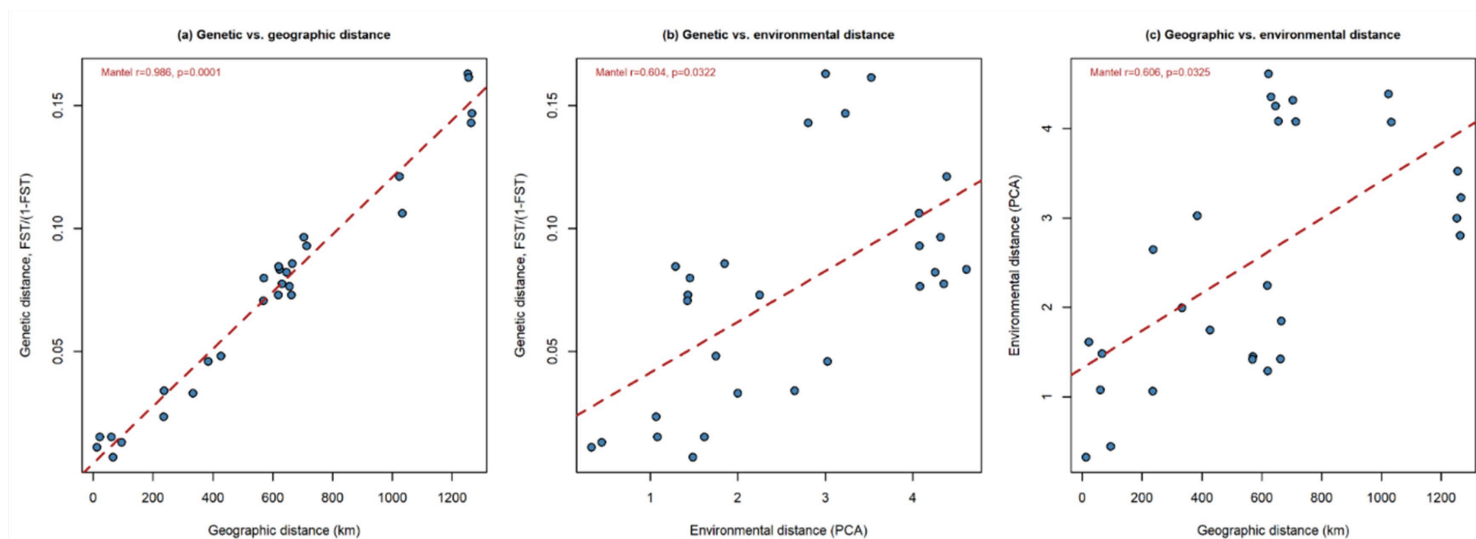


Figure 2

Pairwise distance relationships among the 28 population pairs.(a) Genetic vs. geographic distance, (b) genetic vs. environmental distance, (c) geographic vs. environmental distance. Dashed lines are descriptive ordinary-least-squares fits, not inferential; annotated statistics are the corresponding simple Mantel r and permutation p -value (9,999 permutations).

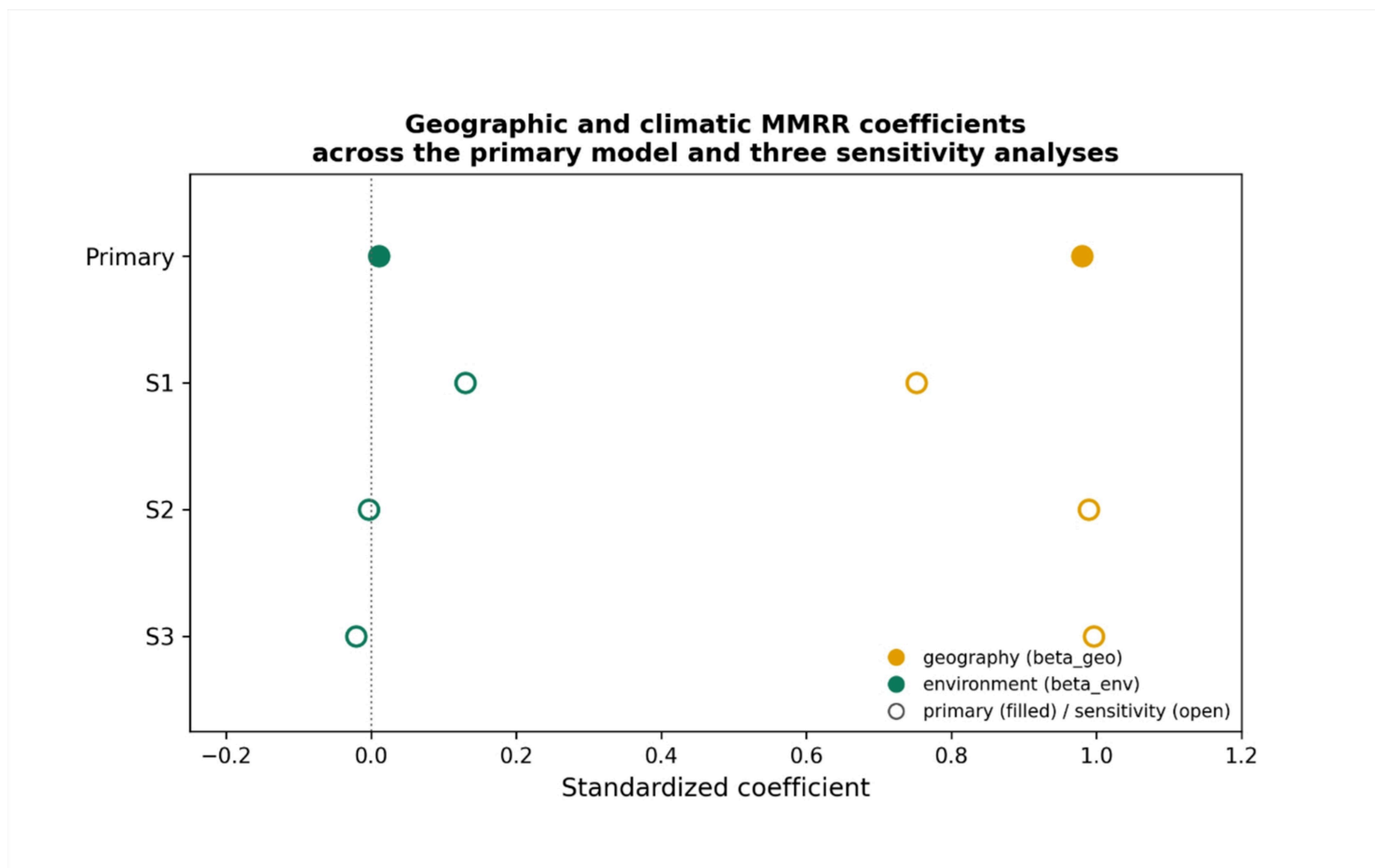


Figure 3

Robustness of standardized geographic and environmental coefficients across all tested model specifications. Filled circles denote the primary specification; open circles denote the three sensitivity analyses.

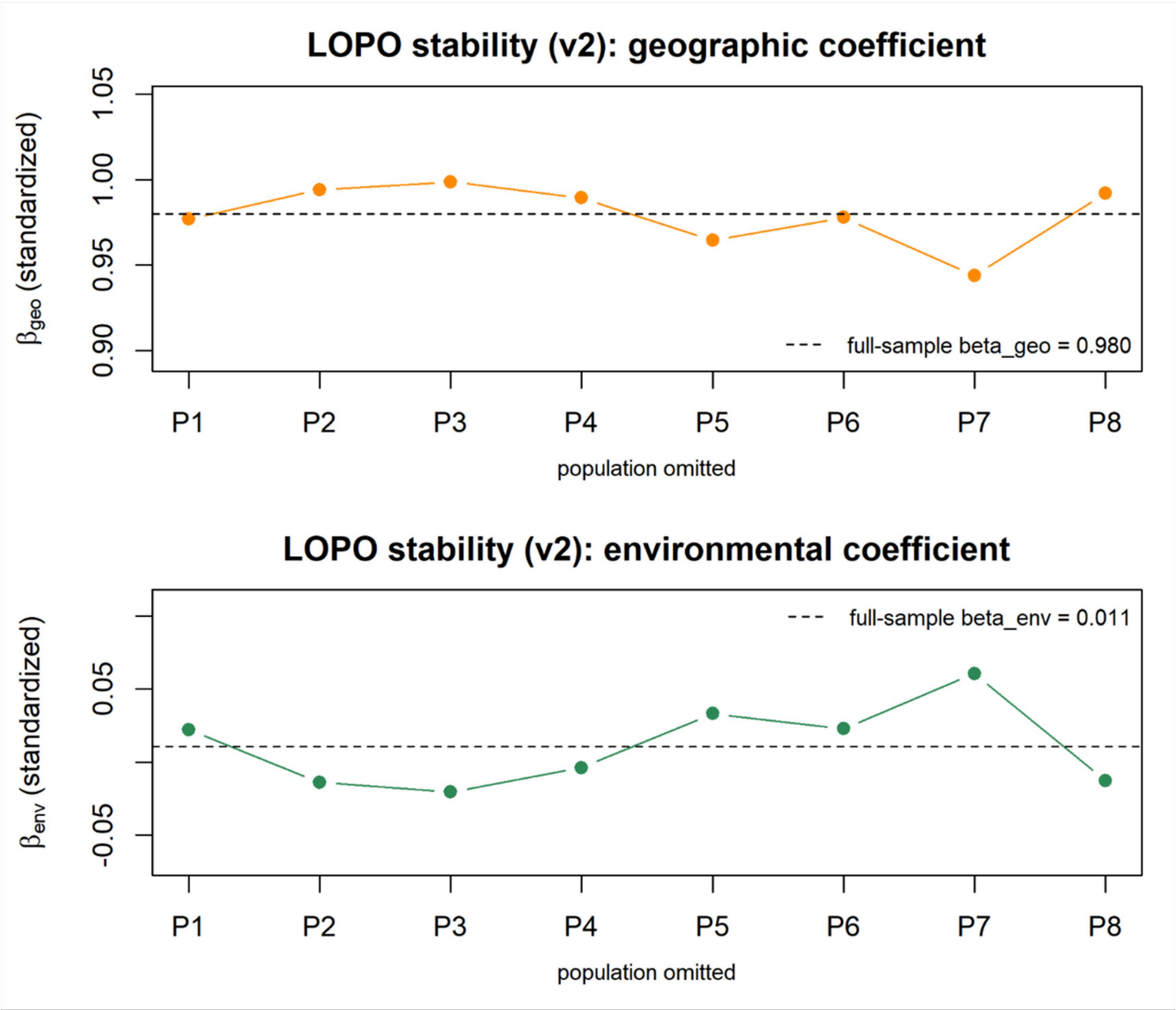


Figure 4

Leave-one-population-out stability of the primary MMRR model. Standardized geographic (top) and environmental (bottom) coefficients when each population is sequentially excluded; dashed line marks the full-sample (n=8) reference value.

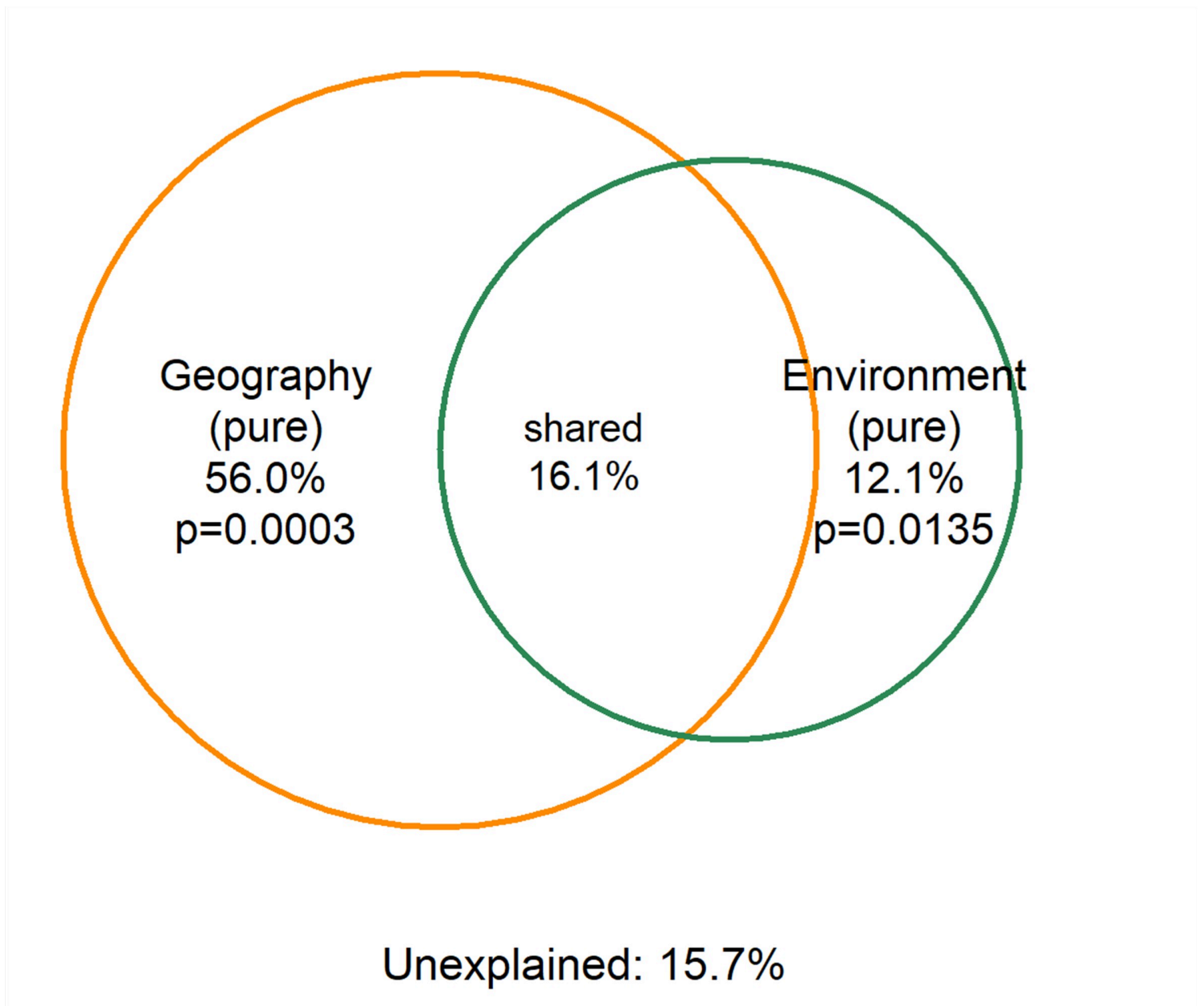


Figure 5

Distance-based redundancy analysis (db-RDA) variance partition. Fractions of adjusted R^2 of the genetic distance matrix uniquely attributable to geography, uniquely attributable to environment, shared between them, and unexplained (exploratory analysis, $n=8$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [supplementary.docx](#)