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Agriculture affects genetic diversity and functional connectivity in an ecologically flexible West African primate

Cristian Pizzigalli[1,2,3,4]✉, José Carlos Brito[1,2,3], Ahmed Tidjane Diop[5], Andack Saad Sow[6], Clive Barlow[7], Cecilia Montauban[8,9], Francesco Vittori[10], Hamidou Dieng[11], Helena Teixeira[12], Filipa Borges[1,2,13,14,15], Isa Aleixo-Pais[14,16], Mamadu Djaló[17], Mariama Sanneh[18], Nelson Fernandes[17], Ricardo Rocha[1,2,3], Tânia Minhós[15], Tom L. Jenkins[4], Victor Silva[1,2,3], Dietmar Zinner[19,20,21], Gisela H. Kopp[22,23,24], Raquel Godinho[1,2,3,25], Maria Joana Ferreira da Silva[1,2,26,27] and Orly Razgour[4,27]

Land-use changes in West Africa are threatening wildlife viability, yet their impacts on species' genetic diversity and connectivity remain poorly understood. We investigated the environmental drivers of genetic diversity and functional connectivity in the Near Threatened Guinea baboon (*Papio papio*) by genotyping 243 non-invasively collected faecal samples across its range and applying a landscape genetics framework. We identified distinct genetic clusters, with Gambian populations exhibiting the lowest genetic diversity and highest inbreeding. Genetic diversity was positively associated with shrublands and forest-savannah mosaics, highlighting the importance of these habitats for maintaining viable populations. Rivers, grasslands, and shrublands facilitate functional connectivity and act as dispersal corridors, whereas large waterbodies and intensive croplands serve as strong barriers. Notably, habitats constituted by mosaics of forest and croplands provide more permeable barriers to movement than strict monocultures. Our results suggest that intensive agricultural land use can reduce functional connectivity, whereas heterogeneous natural habitats and riverine networks sustain it. To ensure the long-term survival of Guinea baboons, conservation strategies must prioritize preserving riverine corridors and habitat heterogeneity. Furthermore, replacing monoculture farming with agroecological practices like agroforestry is crucial to support landscape connectivity and mitigate the adverse effects of agricultural expansion.

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INTRODUCTION

Anthropogenic transformation and exploitation of natural landscapes present significant challenges for wildlife (Newbold et al. 2015). Land-use change, primarily driven by agricultural intensification and urbanisation (Caro et al. 2022), is one of the main causes of the 73% decline in the global abundance of wildlife over the past 50 years (WWF 2024). As habitats are lost or fragmented, species survival is increasingly affected by the diminishing availability of essential resources and the disruption of dispersal and migration routes, thus reducing connectivity and gene flow between populations (Fahrig 2003; Haddad et al. 2015). The consequences of gene flow disruptions can be severe, potentially leading to reduced adaptability, reduced population viability, and an increased risk of local extinctions (Frankham 2002; Breed et al. 2019). Habitat loss driven by rapid land use changes has been particularly pronounced in tropical regions, which host the highest proportion of biodiversity and endemism (Temudo and Abrantes, 2013; Bellard et al. 2014; Laurance et al. 2014), and it is projected to increase in the near future (Alcamo et al. 2011; Bringezu et al. 2014; Herrmann et al. 2020). The rising demand for food to supply local human populations, together with the spreading of commodity crops, has become one of the main drivers of deforestation across West and Central Africa (Herrmann et al. 2020; Masolele et al. 2024). Cropland expansion often encroaches on pristine habitats, including forests and savannahs, diminishing the quality of habitats remaining for wildlife (Sasson 2012; Hansen et al. 2013; Hall et al. 2017; Akanmu et al. 2023; Masolele et al. 2024). This degradation of natural landscapes is further

[1]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal. [2]BIOPOLIS Program in Genomics, Departamento de Biologia, Universidade do Porto, Porto, Portugal. [3]Departamento de Biologia da Faculdade de Ciências, Universidade do Porto, Porto, Portugal. [4]Biosciences, Faculty of Health and Life Sciences, University of Exeter, Exeter, UK. [5]University of Manouba in the National School of Computer Science, Cité Ennasr, Tunisia. [6]Department of Biology, University of Nouakchott, Nouakchott, Mauritania. [7]Birds of Gambia, Brusubi Gardens, Gambia. [8]Department of Life Sciences, Imperial College London, Ascot, UK. [9]Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa. [10]Department of Human Science, University of Verona, Verona, Italy. [11]Faculty of Science and Techniques, University of Nouakchott, Nouakchott, Mauritania. [12]ISEM, University Montpellier, CNRS, IRD, Montpellier, France. [13]Centre for Ecology and Conservation, University of Exeter, Exeter, UK. [14]Anthropology Department, School of Social Sciences and Humanities, Universidade Nova de Lisboa (NOVA FCSH), Lisbon, Portugal. [15]Centre for Research in Anthropology (CRIA-NOVA FCSH/IN2PAST), Lisbon, Portugal. [16]CIMO, LA SusTEC, Instituto Politécnico de Bragança, Bragança, Portugal. [17]Primaction project, Bissau, Guinea-Bissau. [18]Gambian Department of Parks and Wildlife Management, Lamin, Gambia. [19]Cognitive Ethology Laboratory, Germany Primate Centre, Göttingen, Germany. [20]Department of Primate Cognition, Georg-August-Universität Göttingen, Göttingen, Germany. [21]Leibniz Science Campus Primate Cognition, Göttingen, Germany. [22]Zukunftskolleg, University of Konstanz, Konstanz, Germany. [23]Department of Biology, University of Konstanz, Konstanz, Germany. [24]Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Radolfzell, Germany. [25]Department of Zoology, Faculty of Sciences, University of Johannesburg, Auckland Park, South Africa. [26]Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, UK. [27]These authors contributed equally: Maria Joana Ferreira da Silva, Orly Razgour. Associate editor: Olivier Hardy
✉email: pizzigalli.cristian@gmail.com

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exacerbated by urbanization and the extraction of natural resources by, for instance, mining and logging (Edwards et al. 2014; Bousfield et al. 2020).

Guinea baboons (*Papio papio*) are ecological generalist primates endemic to West Africa. They occur across a variety of environmental conditions, from the northern arid areas of Mauritania with low human impact, to the southern tropical areas of the Republic of Guinea where human activities and land-use change are widespread (Pizzigalli et al. 2022; Wallis et al. 2020). Guinea baboons are classified as Near Threatened by the International Union for Conservation of Nature (IUCN) Red List (Wallis et al. 2020), and their main conservation threats are associated to agriculture, livestock farming, hunting for meat, and potential increase of anthroponotic disease transmission (Sá et al. 2012; Minhós et al. 2013; Wallis et al. 2020; Ferreira da Silva et al. 2021a; Ramon et al. 2026). Ecological niche modelling suggests that the occurrence of Guinea baboons depends on water availability in the most arid regions (the northern part of the distribution, Mauritania). In contrast, they are less likely to be present near croplands in other parts of their range (Vale et al. 2015). Additionally, spatial overlap with humans is increasing as large areas of natural habitats are being converted into agricultural fields across the species' range, also creating habitat loss and fragmentation (Galat et al. 1999; Wallis et al. 2020). This spatial overlap may have led to a 20–25% range contraction and a 20% population reduction over the past 30 years (Wallis et al. 2020; Brito et al. 2022). A decreasing trend that is likely to continue if the current rate of land-use changes and human population growth persists (Wallis et al. 2020).

The Guinea baboon is a long-lived species whose longevity could likely reach 27 years, as for other species of the same genus (Bronikowski et al. 2002). Although Guinea baboons exhibit female-biased dispersal (Fischer et al. 2017; Kopp et al. 2014, 2015), recent anthropogenic pressures on their habitat and hunting may have altered dispersal dynamics in some regions of their distribution (e.g., Guinea-Bissau; Ferreira da Silva et al. 2014, 2018). Moreover, at the northernmost limit of the species distribution in Mauritania, Guinea baboons are currently found scattered across three southern mountain massifs (i.e., Tagant, Assaba, and Afollé), and at a few sites along the Senegal River (Brito et al. 2022; Pizzigalli et al. 2022). In this arid region, Guinea baboons are found near temporary and permanent water bodies such as rivers and mountain rock pools (Vale et al. 2015; Pizzigalli et al. 2022). Gene flow patterns among Mauritanian populations inhabiting arid regions, and between these populations and neighbouring populations in Senegal and Mali, are currently unknown. Similarly, the environmental drivers of genetic diversity and the degree of connectivity across the species' range have not been characterized.

Landscape genetics has addressed the influence of landscape features on primate population structure and gene flow patterns (Westphal et al. 2021, and references herein), including on the African continent (Ruiz-Lopez et al. 2016). Yet, the effects of habitat fragmentation and land-use changes on functional connectivity in West Africa remain poorly understood. Functional connectivity refers to the degree to which landscape composition facilitates or impedes animal movement and genetic exchange between populations (Manel et al. 2003), and it is precisely this gap that limits our understanding of how Guinea baboon populations persist and interconnect across an increasingly altered landscape.

We implement a landscape genetics framework (Manel et al. 2003; Razgour et al. 2024) and used a geographically extensive genetic dataset to fill these gaps and to investigate population connectivity in Guinea baboons throughout their range. Specifically, the objectives of this research are to: (i) assess patterns of functional connectivity and identify isolated populations; (ii) investigate the association between environmental features and the observed genetic diversity; and (iii) identify landscape features related to functional connectivity among Guinea baboon populations.

Based on established evidence that Guinea baboons are negatively affected by anthropogenic activity (Minhós et al. 2013; Vale et al. 2015; Ferreira da Silva et al. 2018; Wallis et al. 2020), we hypothesized that genetic diversity would be negatively correlated with human-dominated landscapes and positively correlated with natural habitats such as forests and savannahs. Riverine landscapes (e.g., gallery forest), and roads may play an important role as preferred dispersal corridors connecting Guinea baboon populations (Pizzigalli et al. 2022). These "linear structures" can facilitate foraging movement to feeding sites and/or water sources shared by other social groups, and therefore facilitate dispersal and movement between populations. Hence, we hypothesize that these features are positively related to functional connectivity, while large waterbodies represent barriers. Previous studies in long-term monitored populations from Niokolo-Koba National Park (southeast Senegal) have shown that Guinea baboons use all available habitats but spend significant time in gallery forests (Sharman, 1981; Zinner et al. 2021; Ohrndorf et al. 2024). Therefore, we also tested the hypothesis that natural open areas and forests may either promote or hinder functional connectivity. Crop-raiding behaviours often result in direct persecution and hunting by farmers (Amador et al. 2015; Wallis et al. 2020; Ferreira da Silva et al. 2021b; Bersacola et al. 2022), and a negative association between baboon occurrence and human activities has been reported in a previous modelling study (Vale et al. 2015). We therefore hypothesize that croplands and areas dominated by human activity harm functional connectivity between Guinea baboon populations.

MATERIALS AND METHODS

Study area

The study area spans the known distribution of Guinea baboons (Wallis et al. 2020) (Fig. 1). This region encompasses three major biogeographic realms: the Sahel (Sahelian Acacia Savannah), the Sub-Sahelian Savannah (West Sudanian Savannah), and the Afrotropic, which includes Western Guinean forest-savannah mosaics, mangroves, montane forest, and lowland forests (Burgess et al. 2004; Vale et al. 2015; Dinerstein et al. 2017). In the most arid part of the study area stand the Tagant, the Assaba, and the Afollé mountain massifs, the former two and the latter separated latitudinally by the Karakoro River valley, which remains dry for most the year (Campos et al. 2012). The Fouta Djallon, rising in the Republic of Guinea, is the highest mountain in the region (1538 m), whose central plateau is the source of several major rivers, including Gambia, Senegal (via Bafing and Bakoy), Corubal, Koliba, Kolenté (Great Scarcies), Kaba (Little Scarcies), and Konkouré. The Fouta Djallon's eastern slopes contribute to the Niger River tributaries, while the Niger River's source is located in the southeastern extension of the Guinea Highlands. Another major river is the Casamance River, located in the Casamance region (Senegal) between Gambia and Guinea-Bissau, flowing westwards to the Atlantic Ocean (Fig. 1).

Genetic data production

We used genetic data from previous works produced from 2010 to 2017 (Teixeira 2016; Kopp 2015; Ferreira da Silva et al. 2014), and autosomal multi-locus microsatellite loci genotypes generated from non-invasive faecal samples collected in Mauritania and Gambia between 2019 and 2022. The generation time (mean age of parents at offspring birth) for wild Guinea baboons is currently unknown, but it is likely comparable to closely related species. Based on data from yellow baboons (*P. cynocephalus* from Amboseli, Kenya) (Altmann and Alberts, 2003) and olive baboons (*P. anubis* from Gombe National Park, Tanzania) (Bronikowski et al. 2002; Swedell, 2011), baboon generation time ranges from 6 to 11 years, with a wild lifespan of approximately 30 years (Bronikowski et al. 2002). Thus, our dataset likely integrates genetic data representing between 1.1 and 2 baboon generations. All genetic data were obtained from faecal samples collected non-invasively and preserved using a two-step method (Roeder et al. 2004; Nsubuga et al. 2004), which location of each sample was recorded using a Geographic Positioning System (GPS) receiver.

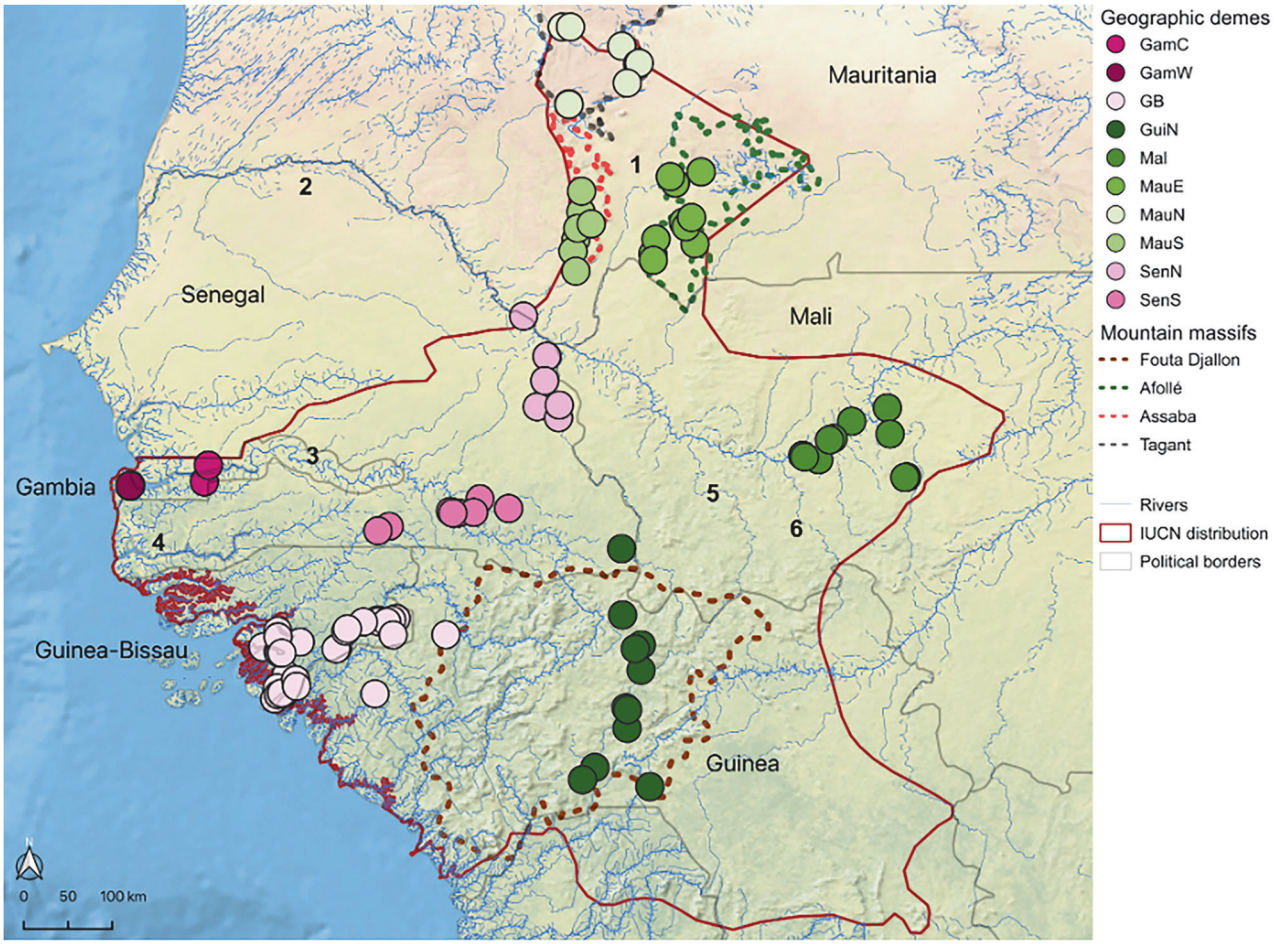

Fig. 1 Geographic distribution of the 243 unique Guinea baboons (*Papio papio*) genotypes from West Africa used in the analyses. Different colours relate to different geographic demes. The red line represents the known distribution of the species according to the International Union for Conservation of Nature Red List of Threatened Species (Wallis et. al., 2020). Numbers in the map represent: (1) the Karakoro Valley; (2) the Senegal River; (3) Gambia River; (4) the Casamance River; (5) the Bafing River; (6) the Bakoy River.

For the samples collected between 2019 and 2022 in Mauritania and Gambia, we extracted DNA following the protocol of Gerloff et al. (1995). Since more than one species of primate inhabit the area, we firstly identified samples to the species level using the hypervariable region I (HVRI) d-loop of the mitochondrial DNA (mtDNA) (Kopp et al. 2014). We amplified mitochondrial DNA using Polymerase Chain Reaction (PCR) and forward and reverse primers by Hapke et al. (2001). We conducted amplifications using a MyCycler Bio-Rad Thermal Cycler at CIBIO, University of Porto, Portugal. We checked the quality of DNA visually for errors using Codon-Code Aligner v. 2.0.6 (Richterich, 2004). The consensus sequences had a final length of 341 base pairs (bp). We used BLASTn (Altschul et al. 1990) to compare our query sequences with the reference sequence database, and samples were confirmed as Guinea baboons when the percentage of identity exceeded 98%.

We selected DNA extracts confirmed to be from Guinea baboons for genotyping using 11 human-derived microsatellite loci that cross-amplify in *Papio* sp. (Bayes et al. 2000; e.g., Ferreira da Silva et al. 2014), to address sampling gaps across the species range from previously published datasets. We determined sex molecularly following the protocols described in Kopp et al. (2015). We amplified microsatellite loci in four PCR multiplex reactions with three to four loci each (Ferreira da Silva et al. 2014). We performed PCRs with 1–2 µl of DNA template, 5 µl of QIAGEN Multiplex PCR Master Mix, 1 µl of primer mix, and RNase-free water to a final volume of 10 µl. We carried out all PCRs in a MyCycler Bio-Rad Thermal Cycler (see Table S1 for details). We performed extractions and PCRs in non-invasive DNA dedicated facilities at CIBIO, using negative controls to monitor potential contamination with human DNA or cross-contamination. We analysed PCR products on an ABI3130xl Genetic Analyzer (Applied Biosystems) using CTM (Centro Testagem Molecular, at CIBIO) fragment analysis service, and determined allele sizes using the GeneScanTM 500 LIZ® size standard.

Genotyping followed a modified "multi-tubes" approach (Taberlet et al. 1996). We estimated the number of replicates across loci necessary to obtain reliable consensus genotypes following the approach implemented in Ferreira da Silva et al. (2014). We carried out a minimum of four amplifications per locus per sample and quantified the reliability of consensus genotypes across loci using the "Quality Index" (QI), discerting genotypes showing a QI below 0.55 (Miquel et al. 2006). We estimated the probability that two individuals sampled randomly from the same population share identical genotypes across all typed loci (Probability of Identity, pID) and the probability of identity among siblings (pIDsib) (Taberlet and Luikart 1999; Waits et al. 2001) for the full locus panel using GenAlEx v.6.503 (Peakall and Smouse 2006). We ranked loci by their individual pIDsib values, and calculated cumulative pIDsib across loci to determine the minimum number of markers required to achieve discriminatory thresholds of pIDsib < 0.01 and pIDsib < 0.001. This analysis confirmed that five to eight loci were sufficient to reach a > 99.9% probability of distinguishing full siblings. We removed from the dataset samples possibly belonging to the same individual. We used Micro-checker v2.2.3 (Van Oosterhout et al. 2004) to detect genotyping errors due to non-amplified alleles (null alleles), large allele dropout, and scoring of stutter peaks. To merge the dataset generated from faecal samples collected in Mauritania and Gambia between 2019 and 2022 with previously published data, we calibrated the allele sizes by re-genotyping six reference samples present in each of the published datasets at the same conditions of the new samples.

Population genetic structure and diversity

To gain a preliminary understanding of the number of genetic clusters, we performed a Principal Component Analysis (PCA) using the function *dudi.pca* of the package *ade4* (Chessel et al. 2004) and a discriminant analysis of principal components (DAPC) using the function *dapc* of the *mapmixture* package (Jenkins 2024) in R v4.3.0 (R Development Core Team 2021). We run the DAPC considering an equal number of PCs as our expected K (10) minus 1 (Thia, 2023).

We estimated the population structure using the individual-based Bayesian software STRUCTURE v2.3.4 (Pritchard et al. 2000). To avoid bias in the number of clusters estimated by STRUCTURE due to related individuals (Devloo-Delva et al. 2019; Parreira et al. 2020), we used the function *coancestry* in the *related* R package (Pew et al. 2015) to identify and exclude closely related individuals from our dataset. To select the most appropriate relatedness estimator for our data, we performed simulations based on our empirical allele frequencies using the *familysim* and *coancestry* functions in the *related* package. Based on these simulations, Wang's (2002) estimator demonstrated the highest accuracy and was therefore chosen to calculate pairwise relatedness. We divided the dataset by countries (i.e., Mauritania, Mali, Senegal, Gambia, Guinea-Bissau, and the Republic of Guinea), and analysed separately each subset. We excluded from further analyses one individual from each dyad exceeding the relatedness threshold of 0.6, prioritising the exclusion of individuals with a larger amount of missing data. We tested the final dataset (Table S2 and Fig. 1) for linkage disequilibrium and deviation from Hardy–Weinberg equilibrium (HWE) in GENEPOP v4.7.5 (Rousset 2008) using default parameters and the false discovery rate with an alpha of 0.05 to detect type-1 errors (Storey and Tibshirani 2003). We used the dataset without highly related individuals and ran five independent simulations in STRUCTURE with 1,000,000 Markov Chain Monte Carlo (MCMC) steps following a burn-in of 100,000 iterations, with the maximum number of potential clusters (*K*) set as eight. Since the final dataset included an unequal number of individuals among sampling sites, we used parameter combinations of the alternative ancestry prior, an initial ALPHA value of 0.2, and the uncorrelated allele frequency model (Wang 2017). In all runs, the "admixture model" was assumed as an allele frequency model (Falush et al. 2003). We estimated the most probable number of *K* by the highest log-likelihood [Ln P(X/*K*)] and using the statistic ΔK developed by Evanno et al. (2005). We then used STRUCTURE HARVESTER v6.8 (Earl and Von Holdt, 2012) to process STRUCTURE results.

To present levels of admixture within each geographic deme, we used the *mapmixture* package (Jenkins 2024) in R v4.3.0 (R Development Core Team 2021), which uses multi-coloured pie charts to display the average admixture proportion of each STRUCTURE cluster across all individuals in a population/site.

For population-level analyses, we divided the genetic dataset into ten geographic demes (Fig. 1): three in Mauritania (MauN, MauS, MauE, representing the Tagant, Assaba, and Afollé mountain massifs respectively); two in Senegal (SenN and SenS, spanning between the Mauritania-Senegal border and Niokolo-Koba National Park respectively); two in Gambia (GamW and GamC, representing Makasutu forest and the central region); and one each in Mali (Mal, representing the Kongassambougou Reserve), one in Guinea-Bissau (GB), and in the Republic of Guinea (Gui). We assigned individuals to the same geographic deme if they were located within a defined geographic distance, following the approach in Kopp et al. (2014). This was done in order to reduce potential biases in the estimation of genetic diversity levels when different numbers of social groups are included in the geographic demes (Parreira and Chikhi 2015). We tested different distance buffers (i.e., 50, 70, and 150 km radius around each geographic deme) to group samples into geographically distinct populations, considering the distribution of sampling sites across the study area. We found that genetic differentiation would increase beyond 50 km and that using a 70 km radius to define geographic demes provided the best balance between sample size per deme and the delimitation of geographically distinct populations, in line with the findings of Kopp (2015) and Kopp et al. (2014). To further validate the 70 km distance threshold as a biologically meaningful boundary for delineating population demes, we assessed the spatial distribution of genetically close individuals using two complementary approaches implemented in R. First, we identified individuals sharing identical multi-locus genotypes (MLGs) in our dataset including related individuals using the package *poppr* (Kamvar et al. 2014). Identical MLGs in diploid organisms indicate either recaptured individuals or first-degree relatives at the same site, providing a conservative estimate of within-deme site fidelity. Second, using the Wang (2002) pairwise relatedness estimates generated previously, we applied a conservative threshold of $r \geq 0.60$ to identify putative first-order relatives (parent-offspring and full-sibling dyads), minimising false-positive assignments. We assigned each individual to its nearest geographic deme, and computed pairwise distances between individuals using the *geosphere* package (Hijmans 2022). We computed bootstrapped means and 95% percentile confidence intervals (5000 replicates) for pairwise distances among identical-MLG pairs and putative first-order kin dyads, both across the full dataset and restricted to dyads within the same deme. We evaluated the results against the 70 km threshold to assess whether the spatial scale of kinship and site fidelity was consistent with the proposed deme boundaries. We then calculated the extent of genetic differentiation between geographic deme pairs using F_{ST} using the function *genet.dist* in the *hierfstat* R package (Goudet 2005) and Jost's *D*, using the function *pairwise_D* in the *mmod* R package (Winter 2012).

We calculated observed (H_o) and expected heterozygosities (H_e) for each geographic deme using the *hierfstat* R package (Goudet 2005). We computed allelic richness (A_r) and number of private alleles (P_{rA}) using the functions *allelic.richness* and *private_alleles* of the *adegenet* R package (Jombart et al. 2018), which applies rarefaction to standardize allelic richness and private alleles across demes to ensure that comparisons are not biased by differences in sample size. As a descriptive measure of within-deme kin structure, we calculated the mean multilocus relatedness coefficient for each deme, using individual-level estimates derived from the Triadic Maximum Likelihood (*TrioML*) estimator in the *Coancestry* package (Wang 2011). To obtain unbiased estimates of the inbreeding coefficient (F_{IS}) while accounting for the presence of null alleles and genotyping failures, we used the Individual Inbreeding Model (IIM) implemented in INEst v2.3 (Chybicki and Burczyk 2009). For each deme, the Bayesian Markov Chain Monte Carlo (MCMC) sampler run for 500,000 iterations, with a burn-in of 50,000 and a thinning interval of 50, using the full model ('nfb').

Landscape genetics analysis

Based on our own expertise in the species ecology and insights from the literature (e.g., Vale et al. 2015; Wallis et al. 2020; Zinner et al. 2021; Ohrndorf et al. 2024), we selected a set of 17 variables as potential environmental drivers of genetic diversity. (i) Six bioclimatic variables: aridity index (Zomer et al. 2022), annual ambient temperature (BIO1), annual precipitation (BIO12), precipitation seasonality (BIO15) (Fick and Hijmans, 2017), and mean monthly climate moisture index (Brun et al. 2022); and, (ii) 10 land cover variables: croplands, mosaic of forest and croplands, forests, mosaic of forest and savannah, shrublands, grasslands, flooded forests, bare areas, urban areas, and permanent water-bodies (derived from the GlobCover project, and reclassified as in Table S3; Bicheron et al. 2011). We additionally included a human footprint index (downloaded from the Last of the Wild V3 NASA project, Venter et al., 2018) as a proxy of human activities and facilities. The corresponding raster file included the extent of urban areas, croplands, pastures, human population density, night-time lights, railways, roads, and navigable waterways. All variables were projected to WGS 1984, at a resolution of approximately 1 km, and clipped to the study area with the R package *terra* (Hijmans et al. 2022). Because land cover and human footprint layers represent conditions around 2009, they are temporally close to our genetic sampling period (2010–2022) and provide a reasonable approximation of the landscape configuration during the period over which contemporary gene flow occurred.

We then calculated the average of each bioclimatic variable and the percentage of each land cover in an area of 70 km radius around the centroid of each geographic deme. We used a Spearman's rank correlation coefficient to test for multicollinearity between environmental variables. For variables with $r > 0.70$ and p-values < 0.05 (Schober et al. 2018), only one of the variables was kept for downstream analysis. To test for associations between genetic diversity metrics and retained environmental variables, while accounting for spatial autocorrelation, we applied Moran Spectral Randomization (MSR), following Wagner and Dray (2015). Geographic coordinates defined a spatial weights matrix (distance threshold: 5°), from which MSR generated spatially constrained surrogate environmental variables preserving multiscale spatial structure. Observed correlations (Pearson or Spearman based on residual normality diagnostics) were tested against this spatial null distribution to derive permutation-based p-values.

We used a landscape genetics approach (Manel et al. 2003) to test which environmental features were related to functional connectivity between Guinea baboon geographic demes. The approach is based on generating

resistance surfaces representing hypothesised relationships between landscape features and genetic connectivity (Spear et al. 2010). Measures of genetic connectivity were based on levels of genetic differentiation (F_{ST}) between demes, with the assumption that gene flow occurs between genetically similar (less differentiated) demes, while recognising that F_{ST} reflects a balance between drift and gene flow and may retain a signature of older demographic processes. We set the study area as the extent of the Guinea baboon's IUCN distribution polygon (Wallis et al. 2020), adding a buffer of 150 km around the distribution limits as in Vale et al. (2015). We created a total of 59 resistance surfaces to test our hypotheses by assigning landscape resistance costs based on expert knowledge of the species ecology and on the information available in the literature (e.g., Vale et al. 2015; Wallis et al. 2020; Zinner et al. 2021). In addition, we tested the impact of each environmental variable on connectivity by assigning different resistance costs in the tested landscape scenarios (Table S4), explicitly evaluating alternative resistance values to account for their potential effect as either a facilitator (resistance = 1) or a barrier to movement (resistance = 25, 50, 75, and 100).

To test the hypothesis of isolation by distance, we calculated Euclidean distances in R v4.3.0 (R Development Core Team 2021) between the centroid of all pairs of geographic demes. We also used these centroids as focal points to estimate pairwise resistance distances between them based on the different landscape resistance cost surfaces using Circuitscape v4.0.5 (McRae 2006). We used a Multiple Regression on Distance Matrices (MRDM; implemented in the *ecodist* package in R; Goslee et al. 2020) to relate measures of genetic differentiation (F_{ST}) with measures of Euclidean distance and landscape resistance. We selected the most representative cost surface for each hypothesis based on $R^2 > 0.25$ and p-values < 0.05. We fitted Maximum Likelihood Population Effect models (MLPE; Van Strien et al. 2012) for each hypothesis and the null model with the R packages *lme4* (Bates et al. 2015) and *usdm* (Naimi et al. 2014). Because we identified a weak positive correlation between geographic and genetic distance, this variable was included in the MLPE analyses. To reduce collinearity, we only included variables with a VIF (variable inflation factor) < 4 in models with more than one landscape variable. The best supported models were identified based on the Akaike Information Criterion corrected for small sample sizes (AICc) and Bayesian information criterion (BIC) evidence weights. We created movement density maps in Circuitscape v4.0.5 (McRae 2006) for the best supported models to visualise areas with high and low connectivity in our study region.

Research ethics statement

All fieldwork and sample collection complied with the legal and ethical requirements of the countries in which the research was conducted and followed relevant national legislation and guidelines for research on wild non-human primates. Non-invasive faecal samples from wild Guinea baboons (*Papio papio*) were collected without capturing, immobilising or otherwise handling individuals. This study did not involve human participants, human material or human data.

RESULTS

Data production, screening and filtering

Of the 527 novel samples collected for this study, 415 (308 from Mauritania and 107 from Gambia) were identified as Guinea baboons. From these 415 samples, 94 were selected to fill gaps in the geographic distribution of the existing data. Of these 94 samples, 70 were successfully genotyped. These genotypes were then merged to previously published data (Teixeira 2016; Kopp 2015; Ferreira da Silva et al. 2014), originating a dataset of 779 multi-locus genotypes formed by 372 males, 379 females, and 28 individuals of undetermined sex. We further excluded 38 genotypes with > 25% missing data, seven duplicated genotypes, and 491 genotypes identified as potential full siblings or parent-offspring to other individuals. This resulted in a final dataset of 243 unique genotypes (Fig. 1 and Table S2) used for statistical analyses.

To validate the 70 km geographic threshold used to aggregate individuals into distinct demes, we analyzed the spatial distribution of putative first-order kin (Wang's $r \geq 0.60$) identified prior to the final relatedness filtering step. Across the entire study area, the mean geographic distance separating first-order relatives was 50.8 km (95% CI: 39.1–64.8 km), significantly below the 70 km boundary. Furthermore, the vast majority of these close kin dyads (92.8%, $n = 854$) were successfully assigned to the same focal-point deme. Within these demes, kin pairs clustered tightly at a mean distance of 20.4 km (95% CI: 18.5–22.3 km). Individuals sharing identical multi-locus genotypes ($n = 7$ dyads), representing likely resampled individuals, were separated by a mean distance of 0.49 km (95% CI: 0–1.46 km). Together, these spatial kinship patterns confirm that the 70 km radius effectively represents the functional scale of recent gene flow and close kinship, justifying its use for delineating population boundaries.

Microchecker suggested the possible presence of null-alleles due to an excess of homozygosity for loci D14s306 (Gui, MauE, and MauS), D3s1768 (Mal, MauN, and MauS), D6s501 (Mal), D10s611 (MauE), and D13s765 (Mal). We decided to retain all loci because the presence of a null allele for these loci was recorded in less than a third of all populations and because these results could be related to undetected population structure. However, we interpret heterozygosity-based metrics with caution, particularly observed heterozygosity (Ho), which is more sensitive to null alleles and inbreeding effects. No allele scoring errors, linkage disequilibrium, or deviation from Hardy-Weinberg equilibrium were found in any of the geographic demes.

Population genetic structure and diversity

We found relatively high levels of admixture among geographic demes, despite distance and habitat heterogeneity. DAPC revealed considerable admixture and genetic proximity among clusters (Fig. S1), with only Mali (Mal) forming a clearly distinct and well-separated group. STRUCTURE analysis identified six genetic clusters as the most likely population structure (Fig. S2 and S3). Fewer than half of the individuals were successfully sexed (47% females, 43% males). Among sexed individuals, the only clear "mismatch" between sampling location and STRUCTURE assignment was a female sampled in Guinea-Bissau that was genetically assigned to the Guinea (Republic of Guinea) cluster. Most genotypes from Guinea-Bissau were grouped in Cluster 1 though with some admixture. All individuals from Gambia, along with admixed individuals from Guinea-Bissau, Guinea, Senegal, and Mauritania, were assigned to Cluster 2. Senegal individuals were included with admixed individuals from southern Mauritania, Mali, Guinea-Bissau and Guinea in Cluster 3. Individuals found mainly in northern and southern Mauritania and those admixed from northern Senegal formed Cluster 4. Individuals in Cluster 5 were formed almost exclusively from individuals from eastern Mauritania, with some admixed ones from northern Senegal and southern Mauritania. Individuals in Mali exclusively belonged to Cluster 6 (Figs. 2 and S3). We recorded the highest levels of genetic differentiation between Gambian and the remaining demes (min $F_{ST} = 0.112$ between GamC and Gui; max $F_{ST} = 0.205$ between GamC and Mal), and the lowest levels between the northern and southern Senegal populations ($F_{ST} = 0.025$) (Fig. S4).

Additionally, Gambian geographic demes showed the lowest levels of genetic diversity across all sampled populations (GamC: $N = 8$, $A_r = 2.81$, $H_o = 0.51$, $F_{IS} = 0.04$; GamW: $N = 12$, $A_r = 2.98$, $H_o = 0.43$, $F_{IS} = 0.05$), despite displaying the highest mean pairwise relatedness among all demes (GamW *TrioML rel.* = 0.15). Inbreeding coefficients were consistently low across all geographic demes (F_{IS} range: 0.01–0.07; Table 1), with Guinea recording the highest value (Gui: $F_{IS} = 0.07$). Mali and Guinea-Bissau each recorded the highest number of private alleles (Mal: $P_{rA} = 4$, $N = 34$; GB: $P_{rA} = 4$, $N = 22$), while eastern Mauritania recorded the highest allelic richness (MauE: $A_r = 4.39$, $N = 26$). Guinea showed the highest expected heterozygosity and lowest internal relatedness among all demes (Gui: $H_E = 0.69$, $N = 21$, *TrioML rel.* = 0.06). Southern Senegal displayed the highest observed heterozygosity and low levels of inbreeding (SenS: $N = 57$, $H_o = 0.67$, $F_{IS} = 0.01$; Table 1).

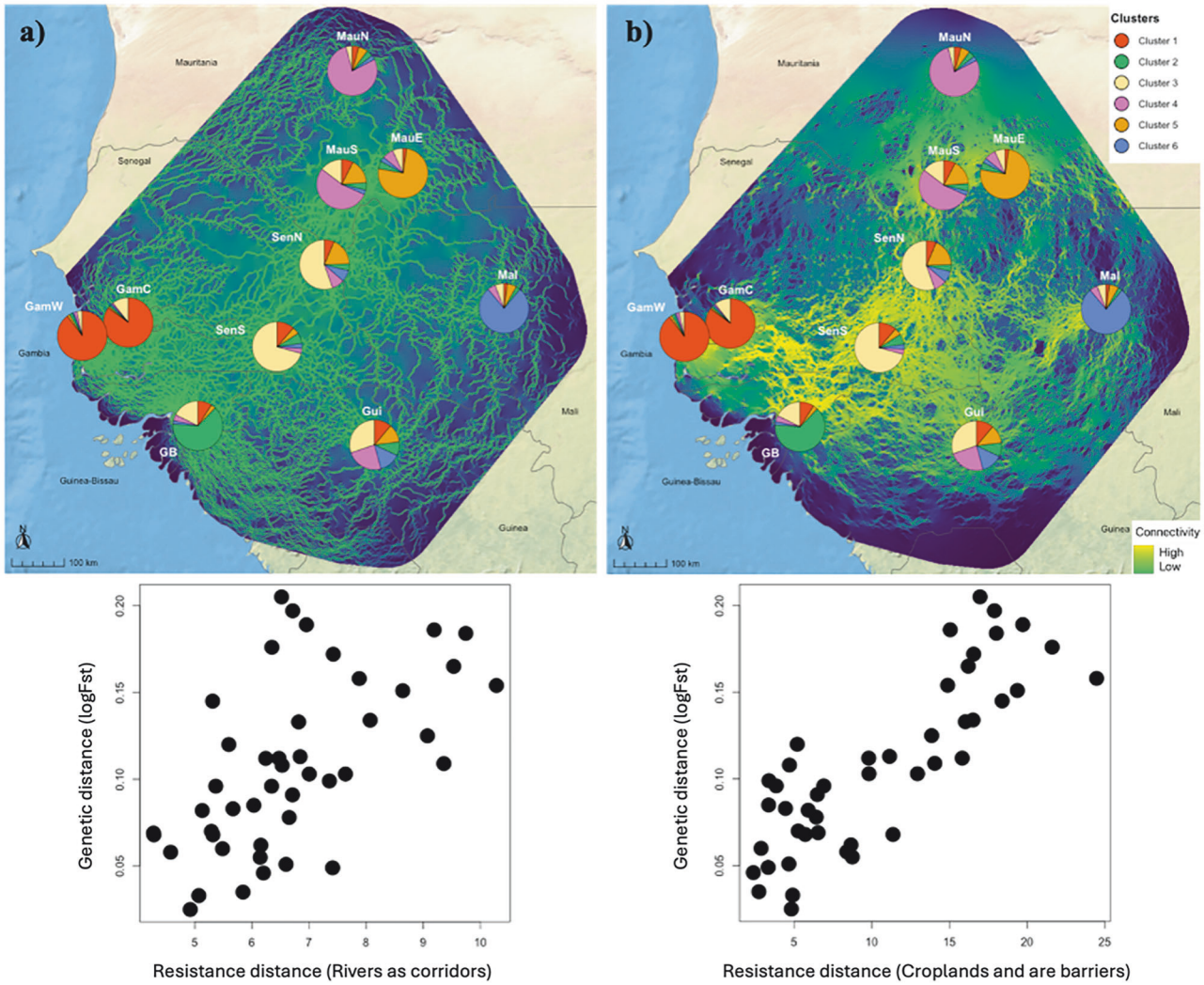

Fig. 2 Predicted movement density between geographic demes in landscape resistance scenarios where: **a** rivers are coded as corridors and large waterbodies as barriers; **b** croplands as strong barriers (resistance value = 100), forests and mosaics of croplands and natural habitats are permeable barriers (resistance value = 25 and 10, respectively), and natural habitats are facilitators for connectivity (resistance value = 1). Maps show electric currents crossing the matrix between pairs of demes based on the resistance surfaces generated for landscape variables included in the analysis. Colours represent the probability of movement across the landscape, ranging from low probability in dark blue to high probability in yellow. Population structure results are displayed by the pie charts, which represent the level of genetic admixture in each geographic deme for the six ancestral populations recorded. The acronyms GB, GamC, GamW, Gui, Mal, MauE, MauN, MauS, SenN, and SenS above the pie charts refer to the ten geographic demes. Plots under the maps show the relationship between genetic distance (F_{ST}) and landscape resistance distance.

Landscape genetics analyses

Twelve bioclimatic and landscape variables were highly correlated (Table S5). The environmental variables retained for downstream analyses were the percentage of croplands, forest, grasslands, mosaic of forest and savannah-like environments (shrubland and grasslands), shrublands, urban areas, and water bodies. Observed heterozygosity (H_o) was positively associated with the presence of shrublands ($R = 0.66$, $p\text{-value} = 0.02$). Observed heterozygosity (H_o) showed a positive association with shrublands ($R = 0.66$, $p = 0.02$; Table S6). Given the potential influence of null alleles and inbreeding on H_o, we consider this association less robust than those observed for allelic richness (A_r) and private alleles (P_{rA}). Allelic richness (A_r) and number of private alleles (P_{rA}) were positively associated with the mosaic of forested areas and savannah (A_r: $R = 0.67$, $p\text{-value} = 0.03$; P_{rA}: $R = 0.61$, $p\text{-value} = 0.05$) (Fig. S5 and Table S6). As values of genetic differentiation based on F_{ST} and Jost's D were highly correlated ($R^2 = 0.918$, $p\text{-value} = 0.001$), we only used the F_{ST} results in the landscape genetics analysis. Euclidean distance exhibited a weak correlation with genetic differentiation among geographic demes ($R^2 = 0.18$, $p\text{-value} = 0.003$; Fig. S6), and it was therefore included as one of the models in our model comparison analysis. We found that the landscape resistance scenarios most related to the genetic differentiation between demes were: (i) rivers as corridors for dispersal, while large waterbodies (i.e., lakes) as barriers; and (ii) croplands as strong barriers while forests and the mosaic of croplands and natural habitats as permeable barriers, and natural habitats (mosaic of forest and savannahs, bare areas, grasslands, and shrublands) as facilitators of functional connectivity (R + CFM; $R^2 = 0.724$, $p\text{-value} = 0.001$; AICcmin = 0.303, BICew = 0.303) (Table 2). The second-best supported model is identical to the previous one but without considering large water bodies as barriers, which had a nearly identical R^2 (0.723) and the second-highest evidence weights (AICcmin = 0.249, BICew = 0.264).

Areas of high, low, and no movement probability between geographic demes are depicted in movement density maps based on (i) the presence of rivers and (ii) croplands, forests, and a mosaic of croplands and natural habitats (Figs. 2 and S7). The

Table 1. Genetic diversity in Guinea baboon geographic demes.

Geographic demes	*N*	P_{rA}	A_r	H_O	H_E	*TrioML*	F_{IS}
GamC	8	0	2.818	0.51	0.53	0.11	0.04
GamW	12	1	2.987	0.43	0.56	0.15	0.05
GB	22	4	3.847	0.6	0.64	0.13	0.02
Gui	21	0	4.264	0.57	0.69	0.07	0.07
Mal	34	4	4.254	0.61	0.67	0.09	0.03
MauE	26	2	4.392	0.57	0.67	0.11	0.03
MauN	29	1	3.914	0.58	0.67	0.12	0.02
MauS	13	1	4.175	0.5	0.62	0.1	0.04
SenN	21	2	3.953	0.61	0.65	0.09	0.02
SenS	57	3	3.873	0.67	0.63	0.12	0.01

Population IDs are the geographic demes retrieved (distribution depicted in Fig. 1). *N* is the number of unique genotypes, P_{rA} is the number of private alleles, A_r is the mean allelic richness per geographic deme across all loci, H_o is the mean observed heterozygosity per site, H_e is the mean expected heterozygosity per site, *TrioML* is the mean multilocus relatedness estimated using the TrioML estimator, F_{IS} is the mean inbreeding coefficient calculated as $F_{IS} = (1\text{-}(H_o/H_s))$. The acronyms GamC, GamW, GB, Gui, Mal, MauE, MauN, MauS, SenN, and SenS refer to the ten geographic demes.

connectivity maps show high landscape connectivity between central (SenN, SenS) and southern geographic demes (GB and Gui). In contrast, low connectivity was detected between the Mauritanian and all other geographic demes. We found connectivity between Gambian geographic demes and the other populations through potential corridors in the Casamance region (southern Senegal) linking Gambia, Guinea-Bissau, and southern Senegal (GB and SenS, respectively). High connectivity areas link the Malian geographic deme (Mal) with the remaining ones from the rest of the distribution, approximately overlapping with the course of the Bafing, the Bakoy, and the Senegal rivers.

DISCUSSION

We investigated the impacts of environmental factors on genetic diversity and functional connectivity of the Guinea baboon across its entire distribution. Our STRUCTURE and DAPC results suggest the presence of six genetic clusters, and pairwise significant F_{ST} values suggest substantial genetic differentiation between several geographic demes. We found higher levels of genetic diversity in geographic demes with a high proportion of shrublands and mosaic habitats of forest and savannah. We also found that rivers and open habitats (i.e., bare areas, grasslands, and shrublands) may represent corridors for functional connectivity and that areas with large-scale agriculture possibly act as a stronger barrier to gene flow, while forests and croplands and natural habitats mosaics represent barriers that are more permeable.

Patterns of functional connectivity

Our results are consistent with previous studies based on autosomal markers showing substantial genetic structure across the Guinea baboon distribution range, while also indicating gene flow among geographic regions (Kopp 2015). Guinea baboons often exhibit female-biased dispersal, and local-scale studies in Senegal have found stronger spatial genetic structuring in males than females, consistent with more restricted male-mediated gene flow at fine spatial scales (Kopp et al. 2014; Kopp, 2015). Females in Senegal have been observed moving between one-male units (OMUs), parties, or gangs (Goffe et al. 2016), whereas evidence from Guinea-Bissau suggests that the magnitude and direction of sex-biased gene flow can vary regionally and may be disrupted in fragmented, human-dominated landscapes (Ferreira da Silva et al. 2018). In our study, we found no clear evidence of sex-biased assignment to genetic clusters. Only one sexed individual showed a mismatch between sampling location and genetic assignment: a female sampled in Guinea-Bissau that was assigned to the Guinea genetic cluster. However, because sex was unavailable for more than half of our individuals, we could not formally assess sex-biased dispersal or gene flow. In particular, distinguishing pre- and post-dispersal individuals is necessary to avoid bias when inferring sex-specific dispersal patterns from spatial genetic data (Lawson Handley and Perrin 2007). Future studies combining larger samples of sexed individuals with sex-linked markers, particularly Y-linked markers that can be amplified from non-invasive samples, could provide a more direct assessment of sex-specific dispersal and gene flow in Guinea baboons (Mutti et al. 2023).

We disentangled the fine-scale landscape features that contribute to differences in functional connectivity. We found evidence of gene flow between northern and southern Mauritanian geographic demes, but limited admixture between these two and the eastern Mauritanian and Senegalese demes. Our genetic structure results suggest the presence of two clusters in Mauritania: cluster 4, distributed mostly in Tagant and Assaba, and cluster 5, which is almost exclusive to the Afollé mountain massif, with some admixed individuals in Assaba. The genetic admixture between the Tagant and Assaba can be explained by the geographic proximity of these two mountains, while the limited genetic admixture between the western and eastern Mauritanian clusters is possibly due to the presence of the Karakoro River valley. This north-south-oriented valley has a width of 70 km and has already been highlighted as a possible natural barrier between baboon populations from the Tagant-Assaba and the Afollé due to its lack of permanent surface water throughout most of the year (Campos et al. 2012; Vale et al. 2015). The connectivity between these two genetic clusters seems to increase in the area closer to the border between Mauritania and Mali, where more vegetation and water are available. However, this area is one of the most densely populated and with the highest levels of human impact in the country (Venter et al. 2018, Central Intelligence Agency 2024). Nevertheless, little is still known about the populations inhabiting southern Mauritania's mountain massifs, and future studies are needed to explore the potential genetic, ecological, and behavioural adaptations that may distinguish these "mountain" populations from their "lowland" counterparts in the more humid areas of the species' distribution. In parallel, future conservation management in Mauritania must prioritize the protection of change-prone ecosystems, particularly temporary rivers and mountain rock pools, coupled with local environmental education to prevent isolation and local extinctions driven by climate change and human impact (Pizzigalli et al. 2022).

Our analyses confirm the limited functional connectivity between the Mauritanian and Senegalese geographic demes, a

Table 2. Maximum likelihood population effect models in Guinea baboon populations, comparing resistance costs based on different landscape scenarios (See Table S4 for details of the models tested) to estimated genetic distance (F_{ST}) between geographic demes.

Models	R^2	*p-value*	AICc	BIC	AICcmin	BICew
RW + CFM	**0.724**	**0.001**	**−180.75**	**−173.26**	**0.238**	**0.231**
R + CFM	0.723	0.001	−180.46	−172.97	0.206	0.2
CFM	0.695	0.001	−180.28	−170.05	0.187	0.18
RW + CFM + HF	0.728	0.005	−180.15	−171.52	0.176	0.097
R + CFM + HF	0.726	0.005	−179.68	−171.05	0.139	0.077
CFM + HF	0.701	0.005	−177.78	−170.29	0.054	0.052
C	0.367	0.036	−143.08	−136.85	0	0
C + HF	0.543	0.037	−150.37	−142.87	0	0
CM	0.436	0.018	−145.03	−138.81	0	0
CM + HF	0.548	0.03	−149.94	−142.44	0	0
D	0.18	0.003	−153.14	−146.92	0	0
F	0.323	0.042	−147.81	−141.59	0	0
F + HF	0.547	0.024	−149.93	−142.43	0	0
HF	0.543	0.015	−152.46	−146.23	0	0
O	0.646	0.004	−161.81	−155.59	0	0
O + CM	0.646	0.009	−165.97	−158.47	0	0
O + F	0.652	0.006	−161.62	−154.13	0	0
R	0.724	0.001	−148.77	−142.55	0	0
R + C	0.416	0.072	−147.6	−140.11	0	0
R + C + HF	0.543	0.078	−148.22	−139.59	0	0
R + CM	0.548	0.064	−148.54	−141.05	0	0
R + CM + HF	0.387	0.092	−147.96	−139.33	0	0
R + F	0.473	0.038	−148.18	−140.69	0	0
R + F + HF	0.547	0.058	−147.98	−139.35	0	0
R + HF	0.543	0.027	−150.63	−143.13	0	0
R + O	0.65	0.006	−159.84	−152.35	0	0
RW	0.344	0.032	−149.67	−143.44	0	0
RW + C	0.429	0.066	−148.4	−140.9	0	0
RW + C + HF	0.544	0.075	−148.56	−139.94	0	0
RW + CM	0.483	0.034	−149.29	−141.8	0	0
RW + CM + HF	0.549	0.062	−148.36	−139.73	0	0
RW + F	0.402	0.079	−148.75	−141.26	0	0
RW + F + HF	0.547	0.056	−148.38	−139.76	0	0
RW + HF	0.544	0.025	−151.02	−143.53	0	0

Tested scenarios were: (i) Presence of rivers (R); (ii) Presence of rivers where large water bodies are considered barriers (RW); (iii) Open areas (O); (iv) Forests as corridors for dispersal (F); (v) croplands as strong barriers (resistance value = 100), forests and mosaics of croplands and natural habitats are permeable barriers (resistance value = 25 and 10, respectively) and natural habitats are facilitators for connectivity (resistance value = 1) (CFM); (vi) Large scale croplands as strong barriers (resistance value = 100) and mosaic of croplands and natural habitats as permeable barriers (resistance value = 10) (CM); (vii) Any type of cropland is a barrier (C); (viii) Human activities are barriers to dispersal (HF); (ix) Euclidean distance (D). Other than Euclidean distance ($R^2 = 0.18$), only landscape resistance models with $R^2 > 0.2$ and *p-value* < 0.05 were considered. The best model (RW + CFM) is highlighted in bold (CI 2.5%: −0.044; CI 97.5%: 0.038). Model fit is assessed using AICc (minimum value indicates the best model), BIC (penalizes model complexity more strongly than AICc), and BICcew (BIC-based relative evidence weights, where values near 1 indicate strong model support).

pattern previously suggested by mitochondrial DNA studies (Kopp et al. 2014) and species distribution models (Vale et al. 2015). The restricted, yet ongoing, gene flow between these demes is likely exacerbated by increasing anthropogenic pressure; notably, the 70 km stretch separating the southern Mauritanian and northern Senegalese populations is one of the most densely populated regions in Mauritania (Central Intelligence Agency 2024). In contrast to the broad admixture observed among other demes, the Malian deme forms the most clearly differentiated cluster in our DAPC results. This is consistent with the near-exclusive assignment of samples from the Kongassambougou Reserve to a single STRUCTURE cluster. This lack of admixture, combined with a relatively high number of private alleles despite geographical proximity to the Guinea-Bissau and Senegal demes, suggests reproductive isolation, local adaptation, or reduced recent gene flow. Furthermore, the Malian deme is located in a potential contact zone between Guinea and olive baboons (*P. anubis*), where hybridization has been hypothesized but remains undocumented (Kopp 2015). Consequently, its strong genetic differentiation and abundance of private alleles may reflect two possible scenarios: (i) long-term reproductive isolation and genetic drift of a Guinea baboon population, or (ii) ancient or recent admixture followed by reproductive isolation, during which introgressed olive baboon

alleles became fixed or enriched within the Malian population (Zinner et al. 2011; Jolly 2020; Roos et al. 2021). Ecological niche modelling further suggests that large parts of western Africa historically provided suitable habitat for olive baboons (Chala et al. 2019; Blinkhorn et al. 2025). Fine-scale whole genome sequencing and morphological assessment would be needed to test whether the Malian population carries diagnostic introgressed loci from olive baboons and to clarify the evolutionary history of this geographically marginal deme. Unfortunately, mostly due to the political instability of the region (Brito et al. 2018), this contact zone remains poorly investigated, and sampling gaps limit a comprehensive resolution of evolutionary history.

Contrastingly, the genetic signatures at the opposite western margin of the distribution suggest a very different evolutionary trajectory driven by demographic expansion rather than introgression. Gambian individuals were all assigned to a single cluster, which appears to have low admixture with other geographic demes, including the neighbouring Senegalese populations. This pattern, together with the lowest levels of genetic diversity and the highest levels of relatedness, could indicate signs of decreasing gene flow between Gambian populations and neighbouring ones, or that Gambian populations were subjected to more frequent events of past extinction and recolonization. As populations of Guinea baboons expanded into new territories, sequential founder events at the expansion wave may have caused "allele surfing" (Kopp 2015), a process in which rare alleles are propelled to high frequencies due to the joint effect of isolation by distance and geographic bottlenecks (Excoffier and Ray, 2008). The distinct clustering and low genetic diversity estimated for the Gambian population at the extreme western edge of the species' distribution are highly consistent with such a demographic history. This possible historical low diversity may now be further exacerbated by contemporary drivers of reduced gene-flow, such as the high human density and impactful activities characterising these areas, which likely contributed to breaks in habitat suitability, fragmenting the coastal, central, and eastern areas of the species' distribution (Vale et al. 2015). In line with this interpretation, our MLPE model selection showed that a model combining rivers and wetlands, croplands as a mosaic, and the human footprint was the 4th-best-supported model, with AICc values very similar to those of the top-ranking models. Previous studies also highlighted that coastal populations in Guinea-Bissau have lower levels of genetic diversity than those in the east (Ferreira da Silva et al. 2014). Increasing human activities, such as urbanization, hunting, and intensive agriculture (Sumberg and Giller, 2022; Mayhew et al. 2020), may have led to the isolation of demes. These pressures likely exacerbate the decrease in gene flow, particularly between populations in the western and central parts of the Guinea baboon's range.

Land use change and reduction of genetic diversity

Our results suggest that heterogeneous natural landscapes may contribute to the long-term maintenance of genetically diverse Guinea baboon populations. We found that allelic richness and private alleles were positively associated with mosaic of forests and savannah-like environments, highlighting the importance of heterogeneous natural landscapes for maintaining genetic diversity. Although observed heterozygosity was also positively associated with shrublands, this result should be interpreted cautiously because observed heterozygosity is more sensitive to null alleles and inbreeding than allelic richness. Moreover, this correlation between genetic diversity metrics and landscape variables should be interpreted just as exploratory since these analyses were conducted using only ten geographic demes, which limited the statistical power to detect robust relationship between genetic diversity and environmental drivers. Nevertheless, access to such diversity of habitat is in fact pivotal given the Guinea baboon's broad and seasonally adaptive diet (Sharman 1981; Zinner et al. 2021; Ohrndorf et al. 2024). By providing critical resources such as food, water, and sleeping sites, these natural habitats likely promote the persistence of large, well-connected populations. Although within deme genetic diversity is shaped by long-term demographic processes, including historical gene flow, maintaining habitat availability and connectivity is expected to help preserve effective population sizes and reduce future genetic erosion.

However, West Africa's accelerating human population growth, which has increased five-fold in the last 70 years (Herrmann et al. 2020), has placed immense pressure on land resources (Ouedraogo et al. 2010; Kleemann et al. 2017). This has driven extensive conversion of forests and savannahs into semi-arid farmlands (Brink et al. 2009; Brandt et al. 2018), leading to fragmentation of populations and a reduction in gene flow. Animal populations in human-modified landscapes often experience genetic erosion, evidenced by inbreeding depression and reduced heterozygosity (Almeida-Rocha et al. 2020; Minhós et al. 2022). Consistent with this interpretation, the western Gambia geographic deme, exhibited the lowest levels of genetic diversity and among the highest inbreeding levels. Gambia has one of the highest human footprint levels and the lowest percentage of natural habitats within our study area (Venter et al. 2018; Bicheron et al. 2011). Although some African mammals can persist in human-modified landscapes, they tend to favour areas with higher proportions of natural habitats and lower human disturbance (Bernard et al. 2024). Guinea baboons, despite their high ecological plasticity (Galat-Luong et al. 2006), show a marked decline in areas near cultivated lands (Vale et al. 2015; Ferreira da Silva et al. 2021a, 2021b). Encroaching agriculture not only degrades natural habitats but also increases the likelihood of negative human-wildlife interactions. The disappearance of savannah vegetation may induce baboons to feed on crops, which results in conflict with farmers and retaliation events (Hill, 2000; Wallis et al. 2020). The expansion of intensive agriculture may already be negatively affecting the persistence of the Guinea baboon directly and indirectly, in forms of habitat degradation, human-wildlife negative interactions, and by facilitating bushmeat hunting (Starin, 1989; Sá et al. 2012; Minhós et al. 2013; Ferreira da Silva et al. 2014; Wallis et al. 2020; Ferreira da Silva et al. 2021a, 2021b).

However, intensive agriculture remains the most widely funded agricultural method to date in West Africa (Biovision Foundation for Ecological Development and IPES-Food, 2020). Given the projected growth in human population and development across West Africa (Paul et al. 2017; Tilman et al. 2017), combining agroecological practices and techniques, like agroforestry and landscape mosaics, with wildlife conservation policies might be crucial to ensure long-term genetic health of wildlife populations and sustainable socio-economic development (Altieri et al. 2015; Perfecto and Vandermeer, 2008; Wezel et al. 2016).

Relationships between landscape and functional connectivity

Our model-selection results reveal a candidate set of similarly supported models rather than a single dominant scenario. However, all these models support the hypothesis that patterns of genetic connectivity in Guinea baboons' populations are likely driven by: (i) riverine landscapes acting as facilitators of movement, (ii) human activities, in particular croplands, functioning as strong barriers, and (iii) forests and mosaics of croplands and natural habitats serving as permeable barriers.

Riverine landscapes have been suggested as possible connectivity corridors for Guinea baboons in the drier areas of the species distribution (Vale et al. 2015; Pizzigalli et al. 2022). Temporary dry riverbeds may provide pathways to reach permanent water sources (i.e., rock pools), with scattered surrounding vegetation offering year-round food resources. In

Senegal, Guinea baboons use various kinds of natural habitats for foraging, including gallery forests, forest-savannah mosaics, grasslands, and shrublands (Sharman, 1981; Galat-Luong et al. 2006; Zinner et al. 2021). Their dispersal movement is influenced by resource availability, travelling less when resources (i.e., food, water) and sleeping sites are abundant, and more when nearby resources diminish, mostly toward the end of the dry season and beginning of the rainy season (Zinner et al. 2021). This movement pattern highlights the importance of forest-savannah mosaics and heterogeneous habitats in shaping functional connectivity among Guinea baboon populations. Given this dependence, future human-induced climate-driven aridification and increased variability in rainfall in the region (Trisos et al. 2022) could further reduce the availability of surface water (e.g., seasonal pools and flow in smaller rivers) and suitable habitats for the species (i.e., heterogeneous landscapes), potentially intensifying isolation among Sahelian populations and weakening connectivity corridors identified here. Because our resistance surfaces represent contemporary landscape configuration, an important next step will be to couple landscape genetic inference with climate change and hydrological projections to test whether connectivity bottlenecks are likely to shift geographically over time, and whether corridors associated with river networks remain functional under plausible future scenarios.

Traditional agricultural methods, characterised by indigenous management techniques and developed over millennia of co-adaptation between humans and the surrounding ecosystem, have sustained thriving human population density (Fairhead and Leach, 1996). These traditional agriculture landscapes, made of a mosaic of cultivated land and natural habitats, resemble the structure of the savannah-forest mosaic habitat they have replaced, retaining their wild open-habitat flora and native African crop species (Akinola et al. 2020; Akanmu et al. 2023; Pashkevich et al. 2024; Silva et al. 2024). However, since the beginning of the 21st century, intensive agriculture in the form of monoculture plantations of non-indigenous species has been favoured in Sub-Saharan Africa due to their increasing value on the international market (Kumar 2007; Dendena and Corsi 2014; Minale et al. 2020; El Bilali 2021). These monocultures of commodity crops have lower structural complexity than natural forests or savannahs, resulting in the homogenisation of the landscape and a decline in species richness and composition compared to the habitats they have replaced (Rege and Lee 2023). This landscape homogenisation is likely causing reduced functional connectivity between Gambian and neighbouring populations, contributing to the low genetic diversity and high isolation observed in Gambian demes.

Because our analyses relate genetic diversity to land cover and human footprint layers from the early 2000s, they highlight associations between genetic structure and contemporary landscape configuration. While our focus is on the impact of these recent land-use changes, the observed genetic patterns may also retain signatures of older/or longer-term shifts. For instance, they may also reflect historical metapopulation dynamics involving colonisation, extinction, and recolonisation cycles (Van Nouhuys 2009), as well as the impacts of historical environmental changes, particularly in Mauritania's arid areas. In such Sahelian ecotone regions, natural climate fluctuations and habitat shifts have long driven population dynamics independent of human influence (Brito et al. 2014). In contrast, in areas such as along the Gambia River, where natural habitat fluctuations are less drastic than in the semi-arid north, the signatures of genetic isolation and low diversity are more likely to be related to the direct effects of anthropogenic landscape homogenisation and fragmentation over the past two decades. Thus, while historical processes may underlie genetic structure in northern populations, human activities could also be a major driver of reduced functional connectivity in the southern, more naturally stable parts of the species' range. Restoring natural habitats within human-dominated landscapes and promoting agroecological practices appear essential to maintain the genetic health and connectivity of wildlife populations in increasingly anthropogenic regions (Snapp et al. 2021). Adopting agroforestry practices in cultivated areas could offer a viable solution to balance wildlife conservation and socio-economic needs (Paul et al. 2017; Murthy et al. 2016). The inclusion of trees and bushes, especially from native species, in agricultural landscapes provides multiple ecosystem services, such as reducing soil erosion, boosting carbon sequestration, and improving water retention. These benefits offer additional, stable income sources for farmers (Lasco et al. 2014; Kovač et al. 2016; Torralba et al. 2016), while also supporting species that thrive in mosaic landscapes of forests and savannahs.

Landscape genetic studies on long-lived species such as Guinea baboons are particularly challenging, especially in regions like West Africa, where both high-quality genetic and environmental data are often scarce or difficult to obtain. Our resistance surfaces were parameterised uniformly across the study extent (i.e., the same cost scheme applied across regions), so the inferred resistance values represent a range-wide average and may not capture spatially varying responses to the same landscape feature. It is also important to note that the movement density maps depict potential dispersal pathways based on contemporary landscape resistance, whereas observed genetic structure reflects the cumulative outcome of historical gene flow, past demographic processes, and barriers not necessarily captured by our resistance models, which may explain apparent mismatches between predicted corridors and some cluster boundaries (e.g., the distinct genetic clustering of the Malian and Gambian demes despite high modelled connectivity). Despite these constraints, our study provides an important baseline for understanding the effects of landscape change on population connectivity in this species. Future research should aim to narrow these gaps by expanding the availability of molecular and environmental datasets and by integrating complementary approaches such as GPS tracking, telemetry, and remote sensing to better capture the spatial and temporal dynamics of habitat use and movement. In addition, because we used neutral microsatellite markers, this framework does not explicitly test for local adaptation; future landscape genomic analyses could evaluate whether functional connectivity drivers differ among major biogeographic regions or genetic clusters and test for local adaptation.

CONSERVATION IMPLICATIONS

Our study identifies low levels of genetic diversity and high levels of inbreeding in some populations occurring in areas with a high human footprint. Although these patterns cannot be directly attributed to current landscape characteristics, they are consistent with the long-term effects of habitat loss, fragmentation, and reduced connectivity on population genetic health. Previous studies have shown that Guinea baboons exhibit the lowest levels of mitochondrial and nuclear diversity among baboon species, and are among the primates with the lowest levels of genetic diversity (Kopp et al. 2023; Kuderna et al. 2023; Sørensen et al. 2023). These patterns likely result from historical bottlenecks or small founding populations (Jolly 2020), aligning with the evolutionary history hypothesized for the species (Kopp 2015; Jolly 2020). The reduced functional connectivity identified in this study may, over time, contribute to further losses in genetic diversity and increase the extinction risk for Guinea baboon populations. The decline in functional connectivity is primarily driven by the loss of natural habitats to agricultural expansion. Conservation strategies in West Africa should prioritise the preservation and restoration of natural habitats, including ecological corridors between key regions such as southern Mauritania and Senegal, within Gambia, and between Gambia and the Niokolo-Koba

National Park (Senegal). Implementing agroecological practices, such as agroforestry and creating mosaic landscapes of natural habitats and croplands, can enhance habitat availability and resilience. These measures offer a viable solution for balancing human development with the conservation of Guinea baboons and likely other primate species with similar ecological requirements. Additionally, future monitoring studies using molecular methods should be implemented to ensure reproductive connectivity between these populations, supporting their long-term survival and genetic viability.

The broader implications of our findings extend beyond Guinea baboons. The genetic connectivity patterns and impacts of land-use change observed in this species are likely relevant to other taxa that depend on forests, open areas, and/or heterogeneous landscapes. The expansion of monocultures poses significant threats to biodiversity (Chatham House Report 2021), leading to genetic erosion and increased vulnerability to environmental changes across species (Exposito-Alonso et al. 2022). Therefore, conservation strategies should not be species-specific but focus on maintaining habitat heterogeneity to boost connectivity and promoting sustainable land-use practices that benefit entire ecosystems, rather than being limited to species-specific approaches.

DATA AVAILABILITY

Data available at the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.14803545.

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AUTHOR CONTRIBUTIONS

CP, GHK, JCB, MJFS, OR, and RG contributed to the conceptualization, methodology, validation, formal analysis, investigation, data curation, and supervision of the project. CP, GHK, JCB, MJFS, OR, and RG were responsible for project administration and funding acquisition. CP, CM, GHK, JCB, MJFS, OR, RG, and TJ contributed to software development and/or original drafting of the manuscript. All authors, including ATD, ASS, CB, DZ, FB, FV, HT, IAP, MD, MS, NF, TM, and VS, provided resources and/or contributed to data curation and critical revision of the manuscript. All authors reviewed and approved the final version of the manuscript for publication.

COMPETING INTERESTS

The authors declare competing interests.

CONSENT FOR PUBLICATION

Our study brings together authors from several countries, including scientists based in the country where the study was conducted. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

ADDITIONAL INFORMATION

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Correspondence and requests for materials should be addressed to Cristian Pizzigalli.

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