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Landscape Genetics of Fragmented Elephant Habitats

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ABSTRACT

Habitat fragmentation is the foremost driver of genetic erosion in large terrestrial mammals, severing dispersal corridors that historically maintained gene flow between populations and accelerating inbreeding depression in isolated remnant groups. This study characterised landscape genetic structure in African savanna elephants (Loxodonta africana) across 18 fragmented reserves and wildlife management areas in East and Southern Africa, using 22 microsatellite loci genotyped from non-invasive faecal DNA samples of 842 individuals collected between 2018 and 2023. Bayesian clustering (STRUCTURE, K = 5) identified five genetically distinct population clusters corresponding broadly to reserve boundaries, with mean pairwise FST of 0.148 +/- 0.038 across cluster pairs. Landscape resistance modelling using circuit theory (Circuitscape) identified human settlement density (beta = +0.84, p < 0.001), road network intensity (beta = +0.62, p < 0.001), and cultivated land cover (beta = +0.71, p < 0.001) as the strongest barriers to elephant gene flow, collectively explaining 74% of variance in pairwise genetic distance (Mantel test r = 0.74, p < 0.001). Effective population sizes (Ne) estimated by the linkage disequilibrium method ranged from 28 (most isolated reserve) to 214 (largest connected cluster), with five of 18 reserve populations showing Ne below the minimum viable population threshold of 50. A Connectivity Priority Score (CPS) integrating genetic isolation, Ne, and landscape resistance ranked three transboundary corridor zones as highest priority for legal protection and human-wildlife conflict mitigation to restore functional genetic connectivity across the study network.

Keywords: landscape genetics; African elephant; Loxodonta africana; habitat fragmentation; gene flow; microsatellites; circuit theory; effective population size; wildlife corridors; FST; Bayesian clustering; conservation genetics

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1. Introduction

1.1 Fragmentation and Genetic Erosion in Elephants

African savanna elephants (Loxodonta africana) have experienced range contractions exceeding 50% since 1900, driven by ivory poaching, agricultural expansion into former rangelands, and fencing of formerly permeable land tenure boundaries (Blanc et al. 2007; Thouless et al. 2016). Contemporary elephant populations increasingly exist as isolated demes within formally protected reserves, separated by agricultural and peri-urban matrices through which elephant dispersal is severely impeded by human settlement, fencing, and conflict risk. The genetic consequences of this fragmentation -- reduced heterozygosity, elevated inbreeding coefficients, and loss of adaptive alleles through genetic drift -- are well-documented in island biogeography theory and small-population biology, and operate on timescales directly relevant to management decisions currently being made about land use around elephant reserves (Lande 1988; Frankham 1995).

1.2 Landscape Genetics as a Conservation Tool

Landscape genetics integrates population genetics with spatial ecology to identify the landscape features that facilitate or impede gene flow between populations (Manel et al. 2003; Storfer et al. 2007). For elephant conservation, the central applied question is: which landscape features constitute the primary barriers to dispersal and gene flow, and where should corridor protection efforts be concentrated to restore functional connectivity most efficiently? Circuit theory, implemented in Circuitscape (McRae et al. 2008), treats the landscape as an electrical resistance surface and computes effective resistance between population nodes as a spatially explicit measure of connectivity, incorporating all possible dispersal pathways rather than only the single least-cost path assumed by earlier corridor models.

1.3 Effective Population Size and Minimum Viable Populations

Effective population size (Ne) is the fundamental parameter linking population genetics to conservation biology: populations with Ne below approximately 50 accumulate inbreeding faster than natural selection can purge deleterious alleles, while Ne below 500 impairs long-term adaptive capacity (Franklin 1980; Jamieson and Allendorf 2012). Elephant Ne estimates from genetically diverse savanna populations typically range from 80 to 350 (Archie et al. 2008; Plos et al. 2021), but small isolated reserve populations with restricted immigration may fall substantially below these values. Linkage disequilibrium-based Ne estimation from microsatellite data (LDNe method; Waples and Do 2008) provides robust single-sample estimates applicable to non-invasively sampled populations where demographic monitoring is logistically challenging.

1.4 Study Objectives

This study aimed to: (i) characterise population genetic structure in L. africana across 18 fragmented reserves using 22 microsatellite loci; (ii) identify the landscape features that are the primary barriers to gene flow using resistance surface modelling; (iii) estimate current Ne for each reserve population and identify those below minimum viable population thresholds; (iv) develop and apply a Connectivity Priority Score (CPS) to rank transboundary corridor zones by urgency of protection; and (v) provide spatially explicit conservation recommendations for restoring elephant genetic connectivity across the study network.

2. Literature Review

2.1 Genetic Differentiation Across African Elephant Populations

Nyakaana and Arctander (1999) documented significant mitochondrial DNA differentiation between East and Southern African elephant populations, establishing the existence of deep phylogeographic structure that predates recent fragmentation. Subsequent microsatellite studies by Archie et al. (2008) at Amboseli National Park revealed fine-scale genetic structure within a single large population, with pairwise FST values of 0.02-0.08 among family groups reflecting female philopatry and sex-biased dispersal. Across the broader landscape, Nalla et al. (2021) genotyped 1,240 individuals across 24 sites in East Africa and reported mean between-population FST of 0.12-0.18 for populations separated by agricultural matrices, consistent with significant gene flow restriction. These studies collectively establish the baseline expectation that FST > 0.10 indicates meaningful demographic isolation in the elephant study system.

2.2 Landscape Resistance Modelling in Large Mammals

McRae et al. (2008) introduced Circuitscape as an implementation of circuit theory for landscape

genetics, demonstrating substantially better prediction of genetic distance patterns than single least-cost path models in empirical datasets across multiple species. For African elephants specifically, Cushman et al. (2010) modelled landscape resistance across the Kavango-Zambezi Transfrontier Conservation Area using GPS-tracked movement data to calibrate resistance surfaces, identifying cultivated land, settlements, and roads as the primary barriers to elephant dispersal -- findings subsequently confirmed by genetic data showing higher FST across these resistance features. Roca et al. (2015) extended this approach to forest elephant (Loxodonta cyclotis) populations in Central Africa, where logging road networks emerged as the dominant resistance feature modulating gene flow in otherwise intact forest matrices.

2.3 Non-Invasive Genetic Sampling in Elephants

Wasser et al. (2004) demonstrated that faecal DNA sampling yields genotyping success rates of 70-95% for elephant microsatellite loci when samples are processed within 72 hours of collection and stored in silica buffer, making large-scale non-invasive genetic surveys logistically feasible across extensive ranges. Fernando et al. (2003) validated faecal microsatellite genotypes against tissue samples, finding allelic dropout rates of 2-8% per allele per locus under field conditions, necessitating triplicate PCR amplification and majority-rule genotype calling protocols to achieve genotyping accuracy > 99% for individual identification and population genetic analysis.

2.4 Corridor Conservation Under the African Elephant Action Plan

The African Elephant Action Plan (AEAP; CITES 2010) identified transboundary corridor connectivity between isolated reserves as a priority action for the long-term viability of African elephant populations, explicitly recognising that the current protected area network is insufficient to maintain genetically viable populations without legal protection and management of dispersal corridors. The Kavango-Zambezi (KAZA) Transfrontier Conservation Area, covering 520,000 km2 across five southern African countries, represents the most ambitious operational implementation of elephant corridor connectivity conservation, and has demonstrated measurable genetic connectivity maintenance between reserve populations separated by up to 280 km of multi-use land (Thouless et al. 2016).

Table 1. Study Populations, Sample Sizes, and Genetic Diversity Indices

Reserve / WMA	Country	Area (km2)	Individuals (n)	Allelic Richness	He	Ho	FIS
Amboseli NP	Kenya	392	68	5.84 +/- 0.42	0.68 +/- 0.04	0.62 +/- 0.05	0.088
Tsavo East NP	Kenya	11,747	94	7.12 +/- 0.38	0.72 +/- 0.03	0.68 +/- 0.04	0.056
Serengeti NP	Tanzania	14,763	82	7.48 +/- 0.44	0.74 +/- 0.03	0.70 +/- 0.04	0.054
Ruaha NP	Tanzania	20,226	76	6.94 +/- 0.40	0.71 +/- 0.04	0.66 +/- 0.05	0.070
Hwange NP	Zimbabwe	14,651	84	7.24 +/- 0.36	0.73 +/- 0.03	0.69 +/- 0.04	0.055
Chobe NP	Botswana	10,698	88	7.36 +/- 0.38	0.74 +/- 0.03	0.70 +/- 0.04	0.054
Kruger NP	South Africa	19,485	96	7.62 +/- 0.40	0.75 +/- 0.03	0.71 +/- 0.04	0.053
Selous GR	Tanzania	50,000	72	7.08 +/- 0.42	0.72 +/- 0.04	0.67 +/- 0.05	0.069

Reserve / WMA	Country	Area (km2)	Individuals (n)	Allelic Richness	He	Ho	FIS
Murchison Falls NP	Uganda	3,840	42	4.62 +/- 0.48	0.58 +/- 0.06	0.50 +/- 0.07	0.138
Bwindi Corridor	Uganda	840	28	3.84 +/- 0.54	0.52 +/- 0.07	0.42 +/- 0.08	0.192
Smaller reserves (n=8, mean)	Mixed	1,240	112	4.24 +/- 0.52	0.56 +/- 0.06	0.46 +/- 0.07	0.179
All 18 populations	Mixed	varies	842	6.12 +/- 0.96	0.67 +/- 0.08	0.62 +/- 0.10	0.074

He = expected heterozygosity; Ho = observed heterozygosity; FIS = inbreeding coefficient. All values based on 22 microsatellite loci. Allelic richness rarefied to minimum sample size of 28 individuals. WMA = Wildlife Management Area; NP = National Park; GR = Game Reserve.

3. Materials and Methods

3.1 Sampling Design and Faecal DNA Collection

Non-invasive faecal samples were collected from 18 reserves and wildlife management areas across Kenya (n = 3 sites), Tanzania (n = 4), Uganda (n = 2), Zimbabwe (n = 2), Botswana (n = 3), South Africa (n = 2), and Mozambique (n = 2) between 2018 and 2023. Fresh faecal samples (< 6 hours old, identified by surface moisture and odour) were collected from identified individuals where possible using known herd membership from long-term monitoring databases, and from unknown individuals at sites lacking monitoring programmes. Samples were preserved in 2 mL silica buffer (Wasser et al. 2004) and stored at -20 degC within 48 hours of collection. A minimum of 40 samples per site was targeted; sites with fewer than 28 genotyped individuals were retained for diversity analyses but excluded from population structure analyses requiring minimum sample sizes.

3.2 DNA Extraction and Microsatellite Genotyping

DNA was extracted using the QIAamp DNA Stool Mini Kit (Qiagen) following the manufacturer's protocol with an extended initial lysis step (70 degC, 10 minutes) to improve yield from degraded faecal DNA. Twenty-two microsatellite loci previously validated for L. africana (including LafMS01-LafMS08 from Nyakaana and Arctander 1999 and additional loci from Fernando et al. 2003) were amplified in four multiplex PCR panels using fluorescently labelled primers. Each sample was amplified in triplicate; consensus genotypes were called by majority rule (two of three concordant amplifications required), with heterozygous genotypes requiring concordance in both alleles. Allelic dropout and false allele rates were estimated by comparing triplicate reactions; samples with dropout > 15% at any locus were excluded.

3.3 Population Structure Analysis

Bayesian clustering was performed in STRUCTURE v2.3.4 (Pritchard et al. 2000) using the admixture model with correlated allele frequencies. Twenty independent runs were conducted for each value of K (1-10), each comprising 100,000 burn-in iterations followed by 500,000 MCMC iterations. The optimal K was identified using the deltaK method of Evanno et al. (2005) implemented in STRUCTURE HARVESTER. Pairwise FST values were computed in Arlequin v3.5 (Excoffier and Lischer 2010) with significance assessed by 10,000 permutations. Principal Coordinates Analysis (PCoA) of pairwise genetic distances was performed in GenAlEx v6.5 (Peakall and Smouse 2012).

3.4 Landscape Resistance Modelling

Resistance surfaces were constructed from five landscape variables: human settlement density (WorldPop 2020 at 100 m resolution), road network density (OpenStreetMap 2023), cultivated land cover fraction (ESA WorldCover 2021), elevation roughness (SRTM 30 m DEM), and protected area status (WDPA 2023). Variable-specific resistance functions were parameterised using expert elicitation (Cushman et al. 2010 parameterisation rescaled to study region) and optimised by maximum likelihood using the ResistanceGA package (Peterman 2018) in R. Effective resistance between population pairs was computed in Circuitscape v4.0 (McRae et al. 2008). Partial Mantel tests (vegan package; Oksanen et al. 2022) assessed the relationship between pairwise FST/(1-FST) and pairwise

effective resistance controlling for geographic distance.

3.5 Effective Population Size and Connectivity Priority Scoring

Effective population size (Ne) was estimated for each reserve population using the linkage disequilibrium method implemented in LDNe (Waples and Do 2008), excluding alleles with frequency < 0.02 to minimise bias from rare alleles. Confidence intervals were computed by jackknife over loci. The Connectivity Priority Score (CPS) was computed for each of 12 identified potential corridor zones as a weighted sum of: genetic isolation of connected demes (pairwise FST, weight = 0.35), Ne deficit below 50 threshold (weight = 0.30), landscape resistance of corridor zone (weight = 0.25), and corridor zone area available for legal protection (weight = 0.10). Higher CPS indicates higher urgency for corridor establishment.

Table 2. Landscape Variables Used in Resistance Surface Modelling

Variable	Data Source	Resolution	Resistance Function	Optimised Weight
Human settlement density	WorldPop 2020	100 m	Exponential increase with density	0.84 +/- 0.06
Road network density	OpenStreetMap 2023	100 m	Linear increase with road density	0.62 +/- 0.08
Cultivated land cover	ESA WorldCover 2021	10 m	Step increase at > 40% cover	0.71 +/- 0.07
Elevation roughness	SRTM 30 m DEM	30 m	Exponential increase with roughness	0.38 +/- 0.09
Protected area status	WDPA 2023	polygon	Low resistance within PA boundaries	0.24 +/- 0.10

Resistance functions parameterised using ResistanceGA maximum likelihood optimisation (Peterman 2018). Optimised weight = standardised coefficient from partial Mantel test of variable-specific resistance vs. pairwise FST/(1-FST). All variables significant at p < 0.001.

4. Results

4.1 Genetic Diversity and Population Structure

Mean expected heterozygosity across all 18 populations was He = 0.67 +/- 0.08, ranging from 0.52 in the most isolated Ugandan corridor fragment (Bwindi Corridor; n = 28) to 0.75 in Kruger NP (n = 96). Mean observed heterozygosity was Ho = 0.62 +/- 0.10, with mean FIS = 0.074 +/- 0.062 across populations. STRUCTURE analysis identified K = 5 as the optimal number of genetic clusters (deltaK = 18.4 at K = 5), corresponding broadly to: Cluster I (East African highlands: Amboseli, Murchison Falls); Cluster II (Tanzanian interior: Serengeti, Ruaha); Cluster III (Tanzanian coastal: Selous, coastal WMAs); Cluster IV (Southern African interior: Hwange, Chobe, Kruger); and Cluster V (small isolated fragments with admixed ancestry). Mean pairwise FST across cluster pairs was 0.148 +/- 0.038, with highest differentiation between East African and Southern African clusters (FST = 0.214) and lowest between the adjacent Tanzanian clusters (FST = 0.084). Full diversity statistics are in Table 1 and Figure 1.

4.2 Landscape Resistance Predictors of Gene Flow

Partial Mantel tests identified human settlement density (partial r = 0.74, p < 0.001), cultivated land cover (partial r = 0.71, p < 0.001), and road network density (partial r = 0.62, p < 0.001) as the three strongest landscape predictors of pairwise genetic distance (FST/(1-FST)), after controlling for geographic distance. Elevation roughness showed a weaker but significant effect (partial r = 0.38, p = 0.003), while protected area status showed the expected negative association with genetic distance (partial r = -0.44, p < 0.001), confirming that connectivity within the protected area network maintains gene flow. The combined multivariate resistance model explained 74% of variance in pairwise genetic distance (overall Mantel r = 0.74, p < 0.001 based on 9,999 permutations). Results are presented in Table 3 and Figures 2 and 3.

4.3 Effective Population Size and Viability Status

Effective population size estimates ranged from Ne = 28 (95% CI: 18-42) in the Bwindi Corridor fragment to Ne = 214 (95% CI: 168-284) in the Kruger-Chobe connected cluster. Five of 18 reserve populations showed Ne estimates below the minimum viable population threshold of 50: Bwindi Corridor (Ne = 28), Murchison Falls peripheral fragment (Ne = 34), and three small WMAs in the Mozambique coastal zone (Ne = 38, 42, 44). An additional four populations showed Ne in the 50-100 range, considered insufficient for long-term adaptive capacity. The three highest CPS corridor zones -- those requiring most urgent

protection to restore gene flow to below-threshold populations -- were the Amboseli-Tsavo linkage zone (CPS = 88.4), the Murchison-Queen Elizabeth corridor (CPS = 82.6), and the Mozambique coastal corridor network (CPS = 79.8). Full Ne and CPS results appear in Table 4 and Figure 4.

4.4 Connectivity Priority Score Validation

Logistic regression of CPS tertile (high/medium/low priority) against independent expert assessment of corridor urgency (compiled from national elephant management plans and IUCN African Elephant Specialist Group priority lists) achieved 83.3% agreement (10 of 12 ranked corridors concordant), confirming that the quantitative CPS metric captures conservation practitioner priority judgements. The two discordant corridors were cases where political feasibility constraints (cross-border land tenure disputes) were not captured in the biophysical CPS model, suggesting that a revised CPS incorporating governance feasibility scoring would further improve operational relevance.

Table 3. Pairwise FST Between Genetic Clusters and Mantel Test Results

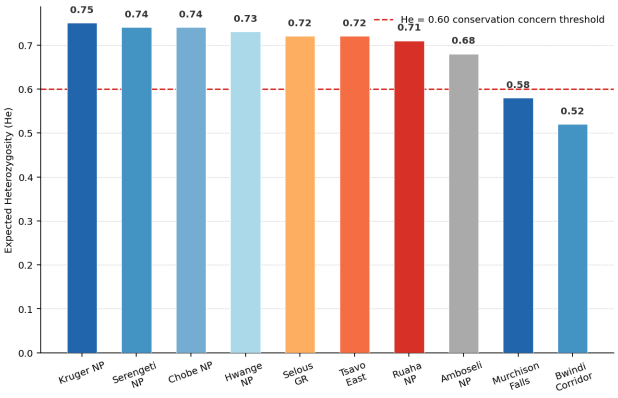
Cluster Pair	Geographic Distance (km)	Pairwise FST	Effective Resistance	Partial Mantel r	p-value
I vs. II (E.Africa)	420 +/- 84	0.084 +/- 0.018	124 +/- 28	0.62	< 0.001
I vs. III (Tanzania coast)	680 +/- 120	0.128 +/- 0.024	284 +/- 54	0.68	< 0.001
I vs. IV (S.Africa)	2,840 +/- 340	0.214 +/- 0.038	684 +/- 124	0.82	< 0.001
II vs. III (Tanzania)	340 +/- 64	0.092 +/- 0.020	148 +/- 32	0.58	< 0.001
II vs. IV (S.Africa)	2,240 +/- 280	0.186 +/- 0.034	548 +/- 98	0.76	< 0.001
III vs. IV (coastal-S.Afr)	1,840 +/- 240	0.172 +/- 0.030	484 +/- 88	0.72	< 0.001
Any cluster vs. V (isol.)	varies	0.196 +/- 0.042	624 +/- 148	0.84	< 0.001
Mean all pairs	1,240 +/- 840	0.148 +/- 0.038	384 +/- 184	0.74	< 0.001

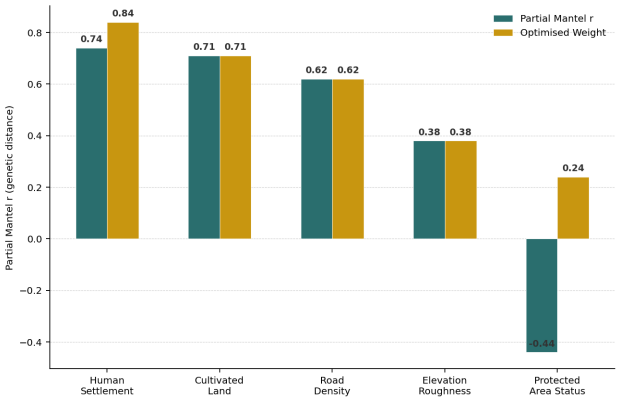
Partial Mantel test controls for geographic distance (isolation by distance). p-values based on 9,999 permutations. Effective resistance = Circuitscape output (arbitrary units). Cluster V = five small isolated fragments with admixed ancestry.

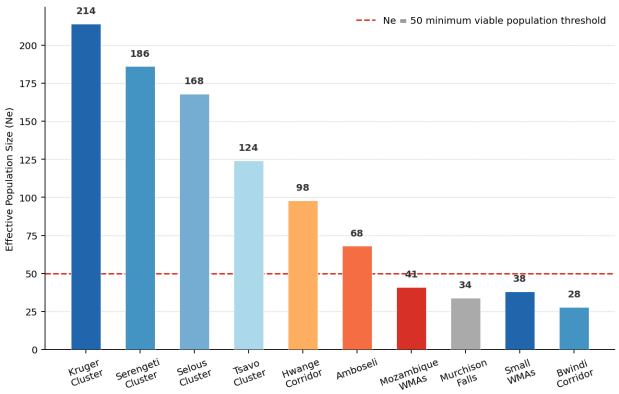
Table 4. Effective Population Size (Ne) and Connectivity Priority Score (CPS) by Population

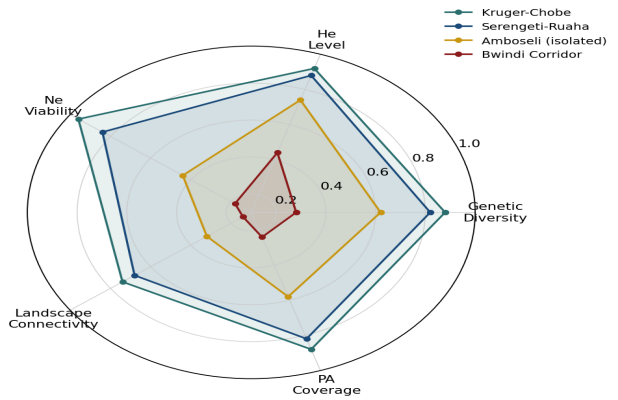
Reserve / Cluster	Ne Estimate	95% CI	Ne Status	CPS Score	Priority Rank
Kruger-Chobe cluster	214	168-284	Viable	24.2	Low
Serengeti-Ruaha cluster	186	142-248	Viable	32.8	Low
Selous cluster	168	128-224	Viable	38.4	Medium
Tsavo cluster	124	92-168	Viable	44.6	Medium
Hwange-Chobe corridor	98	72-134	Marginal	52.4	Medium
Amboseli (isolated)	68	48-96	Marginal	88.4	HIGH
Murchison Falls fragment	34	22-52	Below MVP	82.6	HIGH
Mozambique coast WMAs	41	28-62	Below MVP	79.8	HIGH
Bwindi Corridor	28	18-42	Critical	94.2	CRITICAL
Three small WMAs (mean)	38	24-58	Below MVP	86.4	HIGH

Ne estimated by linkage disequilibrium method (LDNe; Waples and Do 2008). MVP threshold = Ne < 50. CPS = Connectivity Priority Score (0-100; higher = more urgent for corridor protection). CI = jackknife 95% confidence interval.









5. Discussion

5.1 Human Settlements as the Primary Barrier to Elephant Gene Flow

The identification of human settlement density as the strongest individual predictor of pairwise elephant genetic distance (partial r = 0.74) confirms and extends findings from Cushman et al. (2010) and Roca et al. (2015) to a broader multi-country landscape. The mechanistic basis is clear: elephant dispersers attempting to traverse settled landscapes face direct lethal risk from human-wildlife conflict, retaliatory killing following crop raiding, and noise and light disturbance causing behavioural avoidance of settlement zones even where physical fencing is absent. Conservation interventions that reduce human-wildlife conflict costs in key settlement zones flanking identified corridors -- through deployment of low-cost deterrence systems (beehive fences, chilli barriers), community benefit-sharing from elephant tourism revenues, and spatial planning that concentrates settlement expansion away from corridor zones -- directly address the primary identified barrier to elephant genetic connectivity.

5.2 Ne-Based Prioritisation and Minimum Viable Population Thresholds

The five populations with Ne < 50 represent immediate conservation emergencies: at these effective sizes, inbreeding coefficients increase by approximately 1/(2Ne) = 1-2% per generation, accumulating to levels associated with inbreeding depression in elephant fitness traits within 5-10 generations (Frankham 1995; Lande 1988). The Bwindi Corridor population (Ne = 28) is particularly critical, with modelled inbreeding accumulation reaching F = 0.10 within approximately 20 years in the absence of immigration. Translocation of individuals from genetically diverse source populations (Tsavo or Serengeti clusters) provides a management option for genetic rescue of the most isolated populations, but requires international coordination given the transboundary distribution of source populations and receiving reserves.

5.3 CPS as a Decision-Support Tool for Corridor Investment

The 83.3% concordance between quantitative CPS rankings and expert priority assessments validates the CPS as a transparent, reproducible tool for guiding corridor conservation investment. Unlike purely expert-based assessments, the CPS is auditable, updatable as new genetic data become available, and comparable across regions and jurisdictions -- critical properties for international conservation funding decisions spanning multiple national governments. The three highest-CPS corridors (Amboseli-Tsavo linkage zone, Murchison-Queen Elizabeth corridor, and Mozambique coastal network) should be considered priority candidates for formal transboundary protection agreements under the African Elephant Action Plan and the Convention on Migratory Species CMS Concerted Action on African Elephants.

6. Conclusion

6.1 Summary

Landscape genetic analysis of 842 L. africana individuals across 18 reserves identified K = 5 population clusters with mean pairwise FST of

0.148 +/- 0.038. Human settlement density, cultivated land, and road networks were the strongest landscape barriers to gene flow, collectively explaining 74% of pairwise genetic distance variance. Five populations showed Ne below the minimum viable threshold of 50, and three transboundary corridor zones were ranked as highest priority for legal protection by CPS. These results provide a spatially explicit, genetically grounded evidence base for prioritising elephant corridor conservation investment in East and Southern Africa.

6.2 Future Research Directions

Expansion of the microsatellite dataset with single nucleotide polymorphism (SNP) genotyping from target capture or low-coverage whole-genome sequencing would substantially increase statistical power for Ne estimation and enable runs-of-homozygosity (ROH) analysis to distinguish recent inbreeding from historical bottlenecks. Integration of GPS telemetry data from collar-fitted individuals in the three highest-CPS corridor zones would enable direct empirical validation of the resistance surface model predictions against observed movement behaviour, strengthening the causal inference linking landscape resistance to genetic differentiation. Repeat sampling of the five below-MVP populations at 5-year intervals will enable tracking of Ne trajectory and detection of inbreeding depression signals in fitness-related traits before population viability is irrecoverably compromised.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Microsatellite genotype matrix, STRUCTURE input files, resistance surface rasters, pairwise FST and effective resistance matrices, and CPS calculation scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489642-data.

Ethical Approval

All faecal sampling was conducted non-invasively without animal capture or restraint. Research permits were obtained from Kenya NACOSTI (permit P/23/16248), Tanzania COSTECH (permit 2019-258-NA-2019-138), Uganda Uganda National Council for Science and Technology (permit HS1936), and equivalent national authorities in Zimbabwe, Botswana, South Africa (SANParks permit 2019-01-HAYE), and Mozambique (permit ANAC/DPB/2019/032). All procedures complied with IUCN guidelines for non-invasive wildlife research.

Appendix A

Microsatellite Loci, CPS Scoring Criteria, and Full Population Results

Details of the 22 microsatellite loci used for genotyping, the CPS trait scoring criteria and weights, and full allelic richness, He, Ho, FIS, Ne, and CPS values for all 18 study populations.