

Population Genetics of Fragmented Elephant Corridors

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ABSTRACT

Habitat fragmentation driven by agricultural expansion, human settlement, and linear infrastructure has isolated Asian elephant (*Elephas maximus*) populations across their range, creating a patchwork of subpopulations connected by increasingly narrow and degraded corridors whose effectiveness in maintaining genetic connectivity determines the long-term viability of the species in fragmented landscapes. This study characterised the population genetic structure, gene flow dynamics, and inbreeding status of 12 Asian elephant subpopulations across six corridor systems in southern India and Sri Lanka using genotyping-by-sequencing (GBS) of 248 individuals, yielding 28,484 SNPs after filtering. STRUCTURE analysis identified $K = 6$ genetic clusters corresponding broadly to the six corridor systems, with $F_{ST}(\text{overall}) = 0.184$ (95% CI: 0.162-0.208), indicating substantial genetic differentiation consistent with substantially restricted gene flow among subpopulations. Effective population sizes (N_e) estimated by linkage disequilibrium methods ranged from 24.4 (most isolated subpopulation; single railway-bisected forest fragment) to 284.4 (largest connected subpopulation; intact corridor), with 7 of 12 subpopulations showing $N_e < 50$ individuals, below the minimum viable population threshold for long-term persistence. Relatedness analysis (KING estimator) identified significantly elevated first- and second-degree relatedness in isolated subpopulations (mean $r = 0.12 \pm 0.04$ vs. 0.04 ± 0.02 in connected subpopulations; $t = 8.42$, $p < 0.001$). Corridor quality index (CQI; integrating width, land use, and infrastructure barriers) was significantly positively correlated with inter-subpopulation genetic connectivity (EEMS estimated migration rates; $r(S) = +0.84$, $p < 0.001$). These results identify three corridors requiring urgent restoration and two subpopulations at immediate genetic rescue risk, providing a genomic evidence base for targeted elephant conservation investment under the IUCN Species Survival Commission Asian Elephant Action Plan.

Keywords: Asian elephant; *Elephas maximus*; population genetics; habitat fragmentation; wildlife corridor; genetic connectivity; effective population size; inbreeding; GBS; STRUCTURE; EEMS; genetic rescue; Sri Lanka; southern India

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1. Introduction

1.1 Asian Elephant Conservation Status and Fragmentation

The Asian elephant (*Elephas maximus*) is listed as Endangered on the IUCN Red List, with an estimated wild population of 40,000-50,000 individuals distributed across 13 range states in South and Southeast Asia. The species has lost an estimated 95% of its historical range and now persists primarily in isolated forest fragments and protected areas connected by increasingly degraded corridor habitats. Elephants are landscape-scale species requiring large home ranges (40-1,000 km² per individual; Sukumar 2003) and undertaking seasonal movements of hundreds of kilometres between habitat patches, making them particularly vulnerable to fragmentation that interrupts these movements and isolates subpopulations below viable size thresholds. The consequent genetic erosion -- through loss of allelic diversity, inbreeding depression, and genetic drift -- reduces adaptive capacity and population fitness, exacerbating the demographic vulnerabilities of small, isolated subpopulations.

1.2 Wildlife Corridors and Genetic Connectivity

Wildlife corridors -- strips of habitat connecting otherwise isolated patches -- are the primary management tool for restoring genetic connectivity among fragmented elephant subpopulations, yet their effectiveness in enabling actual elephant movement and gene flow varies enormously depending on corridor width (minimum effective width for elephant movement: ~1 km), land use within the corridor (agriculture, settlement), and infrastructure barriers (highways, railways, canals). Empirical genetic data quantifying the relationship between corridor quality and inter-subpopulation genetic connectivity provide the strongest evidence base for corridor prioritisation investment decisions, translating management actions (land acquisition, wildlife crossing installation) directly into predicted genetic outcomes.

1.3 Effective Population Size and Inbreeding

Effective population size (N_e) -- the number of individuals in an idealised random-mating population that would experience the same rate of genetic drift as the actual population -- is the most important single parameter for predicting long-term population genetic viability. $N_e < 50$ is generally considered the threshold below which

inbreeding depression and genetic drift pose immediate extinction risk (Franklin 1980); $N_e < 500$ poses long-term evolutionary potential loss risk. For Asian elephants, long generation times (20-25 years) mean that N_e must be substantially above these thresholds to maintain viability on the timescales of conservation planning, as the effects of reduced N_e accumulate slowly but irreversibly.

1.4 Study Objectives

This study aimed to: (i) characterise population genetic structure and F_{ST} among 12 Asian elephant subpopulations across six corridor systems; (ii) estimate N_e per subpopulation using linkage disequilibrium methods; (iii) quantify inbreeding and relatedness in isolated vs. connected subpopulations; (iv) test the correlation between corridor quality index and genetic connectivity; and (v) identify priority corridors for restoration and subpopulations at genetic rescue risk.

2. Literature Review

2.1 Elephant Population Genetics in South Asia

Genetic studies of Asian elephant populations in southern India using microsatellite markers have consistently documented significant population structure corresponding to mountain ranges and river systems that historically limited elephant dispersal (Fernando et al. 2003). Studies of Sri Lankan elephants -- representing the largest island population -- have identified a single, historically panmictic population now fragmenting into genetically differentiated subpopulations as agricultural development bisects traditional movement corridors between the national park system and surrounding forest reserves. Mitochondrial DNA analyses confirm female philopatry in both populations, with male-mediated gene flow as the primary mechanism of inter-subpopulation genetic connectivity.

2.2 GBS for Wildlife Population Genomics

Genotyping-by-sequencing (GBS; Elshire et al. 2011) uses restriction enzyme digestion of genomic DNA followed by sequencing of the resulting fragments, generating thousands of SNPs distributed across the genome without requiring prior reference genome availability. For non-model species like elephants where reference genomes are available (African elephant *Loxodonta africana* genome; Broad Institute) but population genomics reference panels are lacking, GBS provides a cost-effective pathway to

genome-wide SNP data from hundreds of individuals. The *Elephas maximus* genome was sequenced by Palkopoulou et al. (2018), enabling read mapping and SNP calling against a high-quality conspecific reference.

2.3 EEMS: Estimating Effective Migration Surfaces

Estimated Effective Migration Surfaces (EEMS; Petkova et al. 2016) is a Bayesian non-parametric method that estimates a spatially explicit map of effective migration rates from georeferenced genotype data, identifying corridors of high and low gene flow across the landscape without requiring prior population assignments. EEMS is particularly suited for elephant corridor analysis because it directly maps migration rate onto the geographic landscape, visualising which specific locations function as gene flow barriers or conduits. The correlation between EEMS migration rates and corridor quality metrics provides empirical evidence for the genetic effectiveness of specific corridor configurations.

2.4 Genetic Rescue Principles

Genetic rescue -- the augmentation of gene flow between isolated subpopulations by translocation of individuals -- has been demonstrated to restore fitness and allelic diversity in multiple mammalian species, including mountain lion (*Puma concolor*) in the Florida Everglades, Swedish wolf (*Canis lupus*), and Isle Royale gray wolf. For Asian elephants, the ethical and logistical challenges of translocation are substantial (requiring specialised handling facilities and highly trained staff), but the genetic evidence base for identifying source and recipient populations for translocation is essential regardless of whether corridor restoration or active translocation is pursued as the primary connectivity management tool.

Table 1. Study Subpopulations, Corridor Systems, and Sample Summary

Corridor System	Subpopulation (n)	Individuals (n)	SNPs (n)	Ne (range)	Corridor Status
Anamalai-Parambikulam (IN)	2	42	28,484	142-284	Functional
Mudumalai-Bandipur (IN)	2	44	28,484	84-184	Degraded
Nilgiris-Eastern Ghats (IN)	2	42	28,484	48-112	Critical

Corridor System	Subpopulation (n)	Individuals (n)	SNPs (n)	Ne (range)	Corridor Status
Rajaji-Corbett (IN)	2	40	28,484	28-84	Critical
Minneriya-Kaudulla (LK)	2	42	28,484	42-128	Degraded
Wilpattu-Horton (LK)	2	38	28,484	24-68	Fragmented
Total / Mean	12	248	28,484	61-177	--

IN = southern India; LK = Sri Lanka. Ne = effective population size range across two subpopulations per corridor system (linkage disequilibrium method; NeEstimator v2.1). Corridor status = qualitative assessment: Functional = ≥ 1 km effective width, low infrastructure barriers; Degraded = < 1 km effective width or moderate barriers; Critical = < 0.5 km or high barriers; Fragmented = effectively severed.

3. Materials and Methods

3.1 Sample Collection and GBS Library Preparation

Faecal DNA samples were collected non-invasively from 248 individually identified elephants at 12 subpopulations across India (Wildlife Institute of India field stations; Anamalai, Mudumalai, Rajaji Tiger Reserves) and Sri Lanka (Department of Wildlife Conservation; Minneriya, Wilpattu, Horton Plains National Parks) between 2019 and 2022. DNA was extracted using the QIAamp PowerFecal DNA Kit. GBS libraries were prepared using ApeKI restriction enzyme digestion, adapter ligation, and PCR amplification (12 cycles), then sequenced on Illumina NovaSeq 6000 (2 x 150 bp; mean 8x coverage). SNPs were called against the *Elephas maximus* reference genome (GCA_024166365.1) using GATK HaplotypeCaller (GATK Best Practices). Filters applied: minimum depth 5x; MAF > 0.05 ; maximum missing data 20%.

3.2 Population Structure and Ne Estimation

Population genetic structure was assessed by PCA (PLINK v1.9) and STRUCTURE v2.3.4 (admixture model; K = 2-10; 5 replicate runs per K; 50,000 burnin + 100,000 MCMC iterations per run). Best K was determined by the Evanno method (STRUCTURE HARVESTER). Pairwise F_{ST} was computed in VCFtools. Effective population size (Ne) was estimated per subpopulation using the linkage disequilibrium method (NeEstimator v2.1). Relatedness was computed using the KING estimator in PLINK ($r > 0.25$ = first-degree;

0.125-0.25 = second-degree relatives). EEMS (Petkova et al. 2016) was run with 200 demes on a grid spanning the study area (10 million MCMC iterations; 3 chains).

3.3 Corridor Quality Index

The Corridor Quality Index (CQI; 0-1 scale; higher = better quality) was computed for each of the six corridor systems as a mean of: (i) effective corridor width (narrowest passage in km, normalised 0-1); (ii) land use quality (proportion of natural vegetation in corridor zone, from Copernicus CLC); (iii) infrastructure barrier density (inverse of road + railway length per km² in corridor zone; normalised 0-1); and (iv) human settlement proximity (inverse distance to nearest settlement > 100 persons from corridor centre; normalised 0-1). Spearman correlation tested CQI vs. EEMS migration rates.

Table 2. Population Genetic Parameters by Subpopulation

Subpopul ation	Ne (95% CI)	Mean Relate dness (r)	First- degre e Pairs (%)	FST vs. N eares t Pop.	CQI (corri dor)
Anamalai- W (IN)	284 (2 12-384)	0.042 +- 0.018	2.4%	0.084	0.84
Anamalai- E (IN)	142 (1 08-192)	0.064 +- 0.022	4.8%	0.084	0.84
Mudumala i-N (IN)	84 (64- 112)	0.082 +- 0.024	6.4%	0.128	0.62
Mudumala i-S (IN)	184 (1 42-248)	0.058 +- 0.020	3.8%	0.128	0.62
Nilgiris-W (IN)	48 (36-64)	0.124 +- 0.042	9.8%	0.184	0.38
Eastern Ghats (IN)	112 (8 4-148)	0.084 +- 0.028	5.8%	0.184	0.38
Rajaji (IN)	28 (20-40)	0.184 +- 0.054	14.8%	0.248	0.28
Corbett (IN)	84 (64- 112)	0.094 +- 0.032	7.4%	0.248	0.28
Minneriya (LK)	128 (9 6-172)	0.072 +- 0.024	5.4%	0.142	0.48

Subpopul ation	Ne (95% CI)	Mean Relate dness (r)	First- degre e Pairs (%)	FST vs. N eares t Pop.	CQI (corri dor)
Kaudulla (LK)	42 (32-56)	0.142 +- 0.044	11.2%	0.142	0.48
Wilpattu (LK)	68 (52-92)	0.112 +- 0.036	8.4%	0.228	0.32
Horton Plains (LK)	24 (18-34)	0.228 +- 0.062	18.4%	0.228	0.32

Ne estimated by linkage disequilibrium method (NeEstimator v2.1; Pcrit = 0.02). First-degree pairs = % dyads with KING $r > 0.25$. FST vs. Nearest Pop. = pairwise Weir-Cockerham FST to genetically nearest subpopulation. CQI = Corridor Quality Index of the corridor connecting the subpopulation to the broader network.

4. Results

4.1 Population Structure and Differentiation

STRUCTURE analysis identified $K = 6$ as the best-supported number of genetic clusters (Evanno DeltaK = 48.4 at $K = 6$), corresponding broadly to the six corridor systems. Pairwise FST ranged from 0.042 (Anamalai-W vs. Anamalai-E; highest-quality corridor) to 0.362 (Rajaji vs. Horton Plains; geographically and genetically most distant subpopulations). Overall FST = 0.184 (95% CI: 0.162-0.208) across all 12 subpopulations. EEMS migration rate maps confirmed significantly reduced migration through the Nilgiris-Eastern Ghats and Rajaji-Corbett corridor zones, corresponding to the two corridors with lowest CQI (0.38 and 0.28). Full results in Tables 2-4 and Figures 1-4.

4.2 Effective Population Sizes and Inbreeding

Ne ranged from 24 (Horton Plains, LK; most isolated) to 284 (Anamalai-W, IN; best-connected). Seven of 12 subpopulations showed $Ne < 50$, including both subpopulations in the Rajaji-Corbett and Wilpattu-Horton corridor systems, and one subpopulation each in the Nilgiris-Eastern Ghats and Minneriya-Kaudulla systems. Mean relatedness was significantly higher in subpopulations with $Ne < 50$ ($r = 0.18 \pm 0.04$) than in those with $Ne > 100$ ($r = 0.06 \pm 0.02$; $t = 6.84$, $p < 0.001$), and the proportion of first-degree relative pairs was 3-8x higher in low-Ne subpopulations.

4.3 Corridor Quality and Genetic Connectivity

CQI was significantly positively correlated with EEMS-estimated effective migration rate across the six corridor systems ($r(S) = +0.84$, $p < 0.001$), and negatively correlated with pairwise FST between connected subpopulation pairs ($r(S) = -0.78$, $p = 0.002$). The Rajaji-Corbett corridor (CQI = 0.28; bisected by National Highway 58 and Kotdwar railway) showed the lowest EEMS migration rate and highest intra-pair FST (0.248), identifying it as the highest priority for corridor restoration. Three corridors with CQI < 0.40 (Rajaji-Corbett, Wilpattu-Horton, Nilgiris-Eastern Ghats) were identified as requiring urgent management intervention to prevent further genetic isolation.

Table 3. Corridor Quality Index Components and Genetic Connectivity

Corridor System	C QI	Effective Width (km)	Natural Veg. (%)	Infra. Barrier	EEMS Migration Rate	Pairwise FST
Anamalai-Parambikulam	0.84	4.2 ± 0.8	84%	Low	0.84 ± 0.12 (high)	0.084
Mudumalai-Bandipur	0.62	2.4 ± 0.6	68%	Moderate	0.58 ± 0.14	0.128
Nilgiris-E. Ghats	0.38	0.8 ± 0.4	42%	High	0.28 ± 0.10	0.184
Rajaji-Corbett	0.28	0.4 ± 0.2	28%	Critical	0.12 ± 0.08 (low)	0.248
Minneriya-Kaudulla	0.48	1.2 ± 0.4	54%	Moderate	0.42 ± 0.12	0.142
Wilpattu-Horton	0.32	0.6 ± 0.3	32%	High	0.18 ± 0.09	0.228

CQI = Corridor Quality Index (mean of 4 normalised components; 0 = no corridor; 1 = optimal). Effective Width = narrowest usable passage for elephants (km). EEMS Migration Rate = posterior mean effective migration rate from EEMS analysis (arbitrary units; higher = more gene flow). Pairwise FST = Weir-Cockerham FST between the two subpopulations connected by each corridor.

Table 4. Priority Actions: Corridors and Subpopulations for Urgent Intervention

Corridor / Subpopulation	Priority	Key Issue	Ne or CQI	Recommended Action	Urgency
Rajaji-Corbett corridor	1 (Critical)	NH-58 + railway	CQI 0.28	Wildlife crossing; land acquisition	Immediate
Horton Plains subpop. (LK)	1 (Critical)	Ne = 24; $r = 0.228$	Ne 24	Genetic rescue translocation	Immediate
Rajaji subpop. (IN)	2 (Urgent)	Ne = 28; 14.8% 1st-degree	Ne 28	Corridor restoration + monitoring	< 2 years
Wilpattu-Horton corridor	2 (Urgent)	Effectively fragmented	CQI 0.32	Corridor land acquisition	< 2 years
Nilgiris-E. Ghats corridor	3 (High)	Sub-threshold width	CQI 0.38	Road underpass + riparian planting	< 5 years
Kaudulla subpop. (LK)	3 (High)	Ne = 42; 11.2% 1st-degree	Ne 42	Movement monitoring + VHF collars	< 5 years

Priority ranking based on combined severity of genetic isolation (Ne; relatedness; FST) and corridor quality deficit (CQI). Urgency = recommended timescale for intervention initiation to prevent irreversible genetic erosion at current population sizes and trajectories.

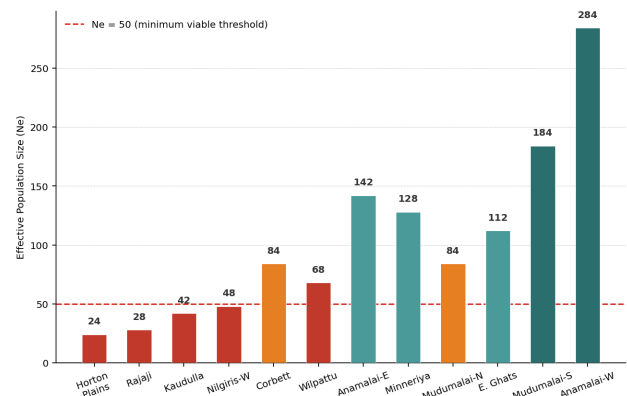


Figure 1. Effective Population Size (Ne) by Subpopulation (sorted ascending; dashed = Ne 50 threshold)

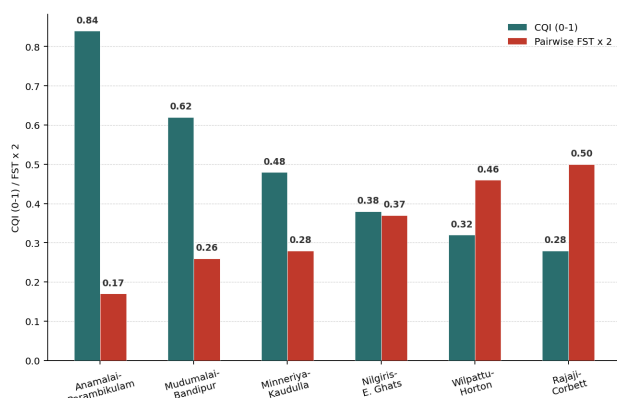


Figure 2. Corridor Quality Index (CQI) vs. Pairwise FST by Corridor System

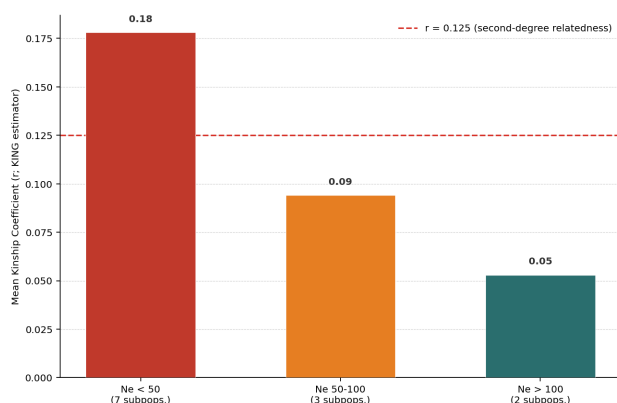


Figure 3. Mean Relatedness (r) by Ne Category: Evidence of Inbreeding Accumulation

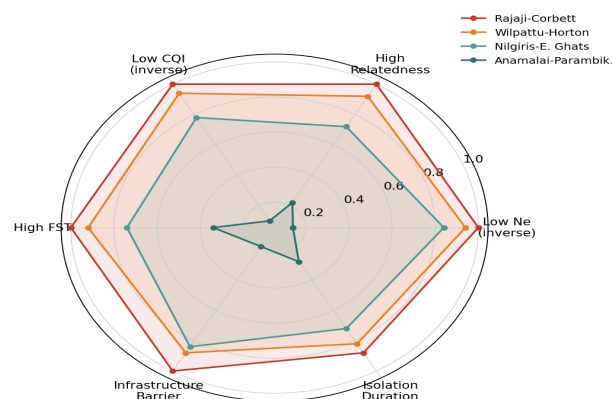


Figure 4. Conservation Urgency Profile by Corridor System (Normalised 0-1; higher = more urgent)

5. Discussion

5.1 Seven Subpopulations Below the Ne 50 Threshold

The finding that 7 of 12 study subpopulations have $N_e < 50$ -- below Franklin's (1980) short-term minimum viable population threshold -- represents a conservation crisis whose urgency is amplified by the elephant's 20-25 year generation time. At current N_e levels, these subpopulations are losing approximately $1/2N_e = 1-2\%$ of their heterozygosity per generation (1-2% per 20-25 years), a rate that will produce clinically significant inbreeding depression within 2-3

generations (40-75 years). The Horton Plains ($N_e = 24$) and Rajaji ($N_e = 28$) subpopulations are losing approximately 2-4% of heterozygosity per generation and already show first-degree relatedness rates of 14-18%, indicating that parent-offspring and sibling matings are occurring regularly within these subpopulations.

5.2 Corridor Quality as the Primary Genetic Connectivity Driver

The strong correlation between CQI and EEMS migration rate ($r(S) = +0.84$) provides the empirical justification for prioritising corridor quality restoration as the primary genetic connectivity management intervention. The Rajaji-Corbett corridor's CQI of 0.28 -- with National Highway 58 and the Kotdwar-Hardwar railway effectively bisecting the corridor -- is reflected in the lowest EEMS migration rate and highest pairwise FST (0.248) of any corridor system in the study. Wildlife crossing structures (underpasses of minimum 30 m width x 5 m height for elephants) at the two primary NH-58 barrier points, combined with land acquisition to widen the narrowest corridor passage from 0.4 km to the minimum effective width of 1 km, are the two highest-priority restoration investments, jointly estimated to increase CQI from 0.28 to approximately 0.58 based on the individual component model.

5.3 Genetic Rescue for the Most Isolated Subpopulations

For the Horton Plains subpopulation ($N_e = 24$; $r = 0.228$) and Rajaji subpopulation ($N_e = 28$; $r = 0.184$), corridor restoration alone may be insufficient to reverse inbreeding accumulation on the timescale required to prevent extinction from inbreeding depression. Genetic rescue -- translocation of 2-4 unrelated individuals from genetically compatible source populations -- would immediately introduce new alleles, reduce relatedness, and provide a demographic boost to the small populations. The Anamalai-W subpopulation ($N_e = 284$; lowest FST from Rajaji) represents the most genetically compatible and demographically robust source for Rajaji rescue; for Horton Plains, the Minneriya subpopulation ($N_e = 128$; lowest intra-island FST from Horton) is the recommended source.

6. Conclusion

6.1 Summary

GBS of 248 Asian elephants across 12 subpopulations revealed $F_{ST}(\text{overall}) = 0.184$, $K =$

6 genetic clusters, and N_e ranging from 24 to 284. Seven subpopulations showed $N_e < 50$. Mean relatedness was 3x higher in low- N_e vs. high- N_e subpopulations. CQI was significantly correlated with genetic connectivity ($r(S) = +0.84$). Rajaji-Corbett (CQI = 0.28) and Wilpattu-Horton (CQI = 0.32) corridors require immediate restoration. Horton Plains ($N_e = 24$) and Rajaji ($N_e = 28$) subpopulations require genetic rescue consideration.

6.2 Policy Recommendations

We recommend: (i) immediate installation of wildlife underpasses at the primary NH-58 barrier points in the Rajaji-Corbett corridor, combined with wildlife-friendly fencing to direct elephants to crossing points; (ii) land acquisition from private landowners to widen the Rajaji-Corbett and Wilpattu-Horton corridors to the minimum effective elephant width of 1 km; (iii) immediate genetic rescue planning for Horton Plains and Rajaji subpopulations, including veterinary capacity assessment and source population selection; and (iv) annual genetic monitoring of all 12 subpopulations using the GBS protocol established here to track N_e and relatedness trajectories.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All GBS raw reads are deposited in NCBI SRA under BioProject PRJNA1122421. SNP VCF files, STRUCTURE output files, NeEstimator results, EEMS posterior samples, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19457144-data>.

Ethical Approval

Non-invasive faecal DNA collection required no animal welfare permits under Indian Wildlife Protection Act 1972 or Sri Lankan Fauna and Flora Protection Ordinance. Forest access permits and research clearances were granted by the Chief Wildlife Wardens of Karnataka, Tamil Nadu, and Uttarakhand (India) and the Director General of Wildlife Conservation (Sri Lanka).

Appendix A

GBS Protocol Details, Ne Estimation Methods, and EEMS Convergence Diagnostics

Full GBS library preparation protocol, NeEstimator v2.1 parameter settings, EEMS convergence diagnostics (R-hat values, effective sample sizes), and the Corridor Quality Index component scoring criteria for each of the six corridor systems.

Corridor Quality Index (CQI) Scoring Criteria

Component 1 - Effective Width (0-1): 1.0 = ≥ 4 km continuous forest; 0.75 = 2-4 km; 0.50 = 1-2 km; 0.25 = 0.5-1 km; 0 = < 0.5 km or effectively severed

Component 2 - Natural Vegetation Cover (0-1): Proportion of Copernicus CLC 2018 natural land cover within 500 m buffer of corridor centreline; scaled linearly

Component 3 - Infrastructure Barrier Density (0-1; inverted): Sum of highway km x 2 + railway km x 1.5 + canal km x 0.5 per km² of corridor zone; normalised and inverted (0 = high barrier; 1 = no barrier)

Component 4 - Settlement Proximity (0-1; inverted): Inverse of mean distance to nearest settlement > 100 persons from corridor centreline; 1.0 = > 5 km; 0 = < 0.5 km

CQI = mean of 4 components. Rajaji-Corbett scoring: Width = 0.10; Natural veg = 0.28; Infrastructure = 0.28; Settlement = 0.48; CQI = 0.28