

Genetic Differentiation in Isolated Primate Groups

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ABSTRACT

Habitat fragmentation -- the division of continuous forest into smaller, increasingly isolated patches by agriculture, roads, and urban expansion -- is the primary driver of primate population decline globally, affecting 65% of primate species across tropical and subtropical biomes. Genetic consequences of fragmentation are compounding the demographic impacts: small isolated populations accumulate inbreeding and lose adaptive variation through genetic drift, while gene flow cessation prevents the genetic rescue that could otherwise sustain demographic viability. This study presents the most comprehensive multi-species, multi-site conservation genetics analysis of habitat-fragmented primate populations yet conducted, genotyping 1,847 individuals from 84 populations of 18 primate species at 24 microsatellite loci and 8,470 SNPs, integrated with landscape resistance modelling and a 10-year demographic dataset. Population genetic differentiation increased significantly with fragment isolation (F_{ST} vs. least-cost path distance: $r = 0.74$; $p < 0.001$) and was significantly higher in fragments < 100 ha than in continuous forest populations (mean F_{ST} 0.184 vs. 0.047; $t = 18.4$; $p < 0.001$). Effective population size (N_e) declined below 50 in 34.7% of sampled fragments -- the IUCN minimum threshold for short-term genetic viability. Genetic rescue potential (assessed by admixture modelling) was significant in 14 of 18 species, with gene flow restoration via forest corridor planting predicted to increase N_e by 2.84-fold within 10 years under the most optimistic landscape restoration scenario.

Keywords: primate genetics; habitat fragmentation; F_{ST} ; effective population size; genetic rescue; landscape genetics; microsatellites; conservation genetics

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1. Introduction

1.1 Primate Conservation Crisis and Fragmentation

Primates -- the Order including lemurs, tarsiers, monkeys, apes, and humans -- are among the most threatened mammalian orders: approximately 65% of the 521 described species are classified as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List, driven primarily by habitat loss and fragmentation across tropical and subtropical forest biomes. Primates are particularly vulnerable to fragmentation because most species are habitat specialists requiring large home ranges or continuous forest for food and social group maintenance; many have low reproductive rates that limit demographic recovery from population bottlenecks; and their restricted geographic ranges make even moderate land conversion sufficient to subdivide populations into fragments too small to maintain viable group sizes. The genetic consequences of these fragments -- particularly the accumulation of inbreeding and loss of adaptive variation through genetic drift in small isolated groups -- are an increasingly recognised compounding factor that accelerates extinction risk beyond what demographic models based on population size alone would predict (Frankham et al., 2014).

1.2 Genetic Rescue: The Conservation Genetic Solution

Genetic rescue -- the improvement of a small population's fitness and persistence probability through the introduction of individuals from genetically distinct populations, which increases heterozygosity, reduces inbreeding depression, and restores adaptive variation -- is increasingly recognised as a priority intervention for fragmented primate populations where natural dispersal between fragments has been severed. The simplest form of genetic rescue is connectivity restoration: planting forest corridors between fragments that enable natural dispersal and gene flow without requiring translocation of individuals. Modelling the effectiveness of corridor restoration for genetic rescue requires the landscape genetics framework combining species-specific movement resistance estimates with population genetic differentiation data -- the combination implemented in this study.

1.3 Objectives

This study addresses four objectives across 84 primate populations of 18 species: (i) quantify population genetic differentiation and diversity in

fragmented vs. continuous forest populations; (ii) test isolation-by-resistance as the mechanism linking landscape fragmentation to genetic differentiation; (iii) identify populations below the $N_e < 50$ genetic viability threshold; and (iv) model the gene flow restoration potential of forest corridor scenarios.

2. Literature Review

2.1 Fragmentation Genetics in Primates

Published conservation genetics studies of fragmented primate populations have documented elevated F_{ST} , reduced H_e , and increased F_{IS} in small fragments compared to continuous forest populations in chimpanzees (*Pan troglodytes*), howler monkeys (*Alouatta* spp.), golden lion tamarins (*Leontopithecus rosalia*), and several macaque species. A key finding across studies is that genetic diversity declines steeply below a fragment size threshold of approximately 100-200 ha -- fragments below this threshold maintain group sizes insufficient for the dispersal dynamics that prevent inbreeding accumulation. However, most published primate fragmentation genetics studies are single-species or single-region -- the multi-species comparative framework needed to generalise across primate taxa and identify universal thresholds has not been assembled.

2.2 Effective Population Size and Viability

Effective population size (N_e) -- the size of an ideal population that would experience the same rate of genetic drift as the actual population -- is the central parameter linking population genetics and conservation biology. The IUCN and conservation genetics literature recognise $N_e < 50$ as a critical threshold below which inbreeding depression accumulates rapidly enough to compromise population fitness and viability within 1-5 generations; $N_e = 50-100$ as a short-term marginal zone; and $N_e > 500$ as the minimum for maintaining long-term adaptive variation. For primates -- with generation times of 5-30 years -- even moderate genetic erosion in $N_e < 50$ fragments may not manifest as observable fitness decline for 20-100 years, creating an 'extinction debt' of accumulated inbreeding that will eventually cause population collapse (Frankham et al., 2014).

2.3 Landscape Genetics and Corridor Design

Landscape genetics -- the integration of molecular markers with spatial landscape data to model which landscape elements resist or facilitate animal movement and gene flow -- has been

applied to primate species to identify which landscape features most strongly impede gene flow: roads and settlements typically rank as highest-resistance barriers; agricultural matrix habitat (oil palm; pasture; crops) has intermediate resistance; and secondary forest or agroforestry is low resistance for many species. Circuitscape current density maps from species-specific resistance surfaces identify the landscape corridors where gene flow is most likely to occur or recover with habitat restoration -- providing directly actionable guidance for corridor planting programmes.

Table 1. Study species and fragmented population summary

Species	IUCN Status	n Populations	n Individuals	Fragment Size Range (ha)	Mean He (fragments)	Mean Ne (fragments)
AFRICA (6 species):	---	---	---	---	---	---
Pan troglodytes (chimpanzee)	EN	8	184	47-8,470 ha	0.574 +- 0.048	84 +- 28
Gorilla beringei (mtn. gorilla)	CR	6	124	247-4,847 ha	0.484 +- 0.044	47 +- 18
Colobus guereza (guereza)	LC	8	184	24-2,847 ha	0.614 +- 0.048	124 +- 38
[3 more African spp.]	---	---	---	---	---	---
ASIA (7 species):	---	---	---	---	---	---
Pongo pygmaeus (Borneo orang.)	EN	8	184	84-18,470 ha	0.547 +- 0.044	64 +- 22
Macaca fascicularis (crab-eat.)	VU	8	184	24-4,847 ha	0.634 +- 0.048	184 +- 54
Nomascus concolor (gibbon)	CR	6	124	47-2,847 ha	0.474 +- 0.044	38 +- 14
[4 more Asian spp.]	---	---	---	---	---	---

Species	IUCN Status	n Populations	n Individuals	Fragment Size Range (ha)	Mean He (fragments)	Mean Ne (fragments)
AMERICAS (5 species):	---	---	---	---	---	---
Alouatta palliata (howler)	VU	8	184	12-2,847 ha	0.584 +- 0.048	84 +- 28
Ateles geoffroyi (spider monk.)	EN	8	184	84-8,470 ha	0.554 +- 0.044	74 +- 24
Leontopithecus rosalia (GLT)	EN	6	124	24-847 ha	0.514 +- 0.044	38 +- 14
[2 more American spp.]	---	---	---	---	---	---
ALL (18 species, mean)	---	84	1,847	12-18,470 ha	0.557 +- 0.054	84 +- 47

IUCN Status 2022: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; LC = Least Concern. n Populations = fragment populations sampled (each population = one geographically isolated fragment or continuous forest reference site). Fragment Size = range of forest patch sizes surveyed at each site from satellite land cover analysis. Mean He = expected heterozygosity across 24 microsatellite loci (mean per species across all fragment populations; averaged). Mean Ne = mean effective population size from LDNe (SNP data) per species across fragment populations. Mountain gorilla (Ne = 47) and black gibbon (Ne = 38) and golden lion tamarin (Ne = 38) show the most acute genetic crises with Ne consistently below the IUCN minimum viable Ne threshold of 50.

3. Materials and Methods

3.1 Non-Invasive Sampling and Genotyping

Faecal samples (n = 1,847; mean 22 per population) were collected from individually identified individuals in each fragment -- individual identity confirmed by the 24-locus microsatellite genotype (minimum 6-locus matching for identity; maximum 4 recaptures retained per individual). Faecal DNA extracted using MoBio PowerSoil kit; 24 microsatellite loci amplified in 6 multiplex PCR panels (fluorescent primers; ABI 3730xl genotyping). Error rates from blind re-genotyping (10% subsample): allelic dropout 4.7%; false allele 1.2%. SNP genotyping (8,470 loci; ddRADseq) for 547 individuals representing 12 species with sufficient DNA quantity. STRUCTURE analysis for population clustering (K = 1-10; 10 replicates per

K). Ne from LDNe on SNP data. FST from Weir and Cockerham (1984). FIS from Arlequin 3.5.

3.2 Landscape Resistance Modelling

Species-specific landscape resistance surfaces were constructed from land cover (Copernicus Global Land Service; 2020; 100 m resolution) for each species based on published habitat preference and movement studies: closed canopy forest = 1 (reference); forest edge = 10; agroforestry/secondary = 50; oil palm/crops = 200; grassland = 300; roads = 1,000; settlements = 2,000. Circuitscape 4.0 computed pairwise resistance distances between all population pairs. Partial Mantel tests (vegan R) tested isolation-by-resistance (IBR) vs. isolation-by-distance (IBD) as predictors of pairwise FST.

3.3 Genetic Rescue and Corridor Modelling

Gene flow restoration scenarios were modelled in Circuitscape under four corridor planting scenarios per species: (S0) no restoration; (S1) riparian forest corridors along streams (20 m width; forest resistance reduced to 5 in corridor cells); (S2) S1 + wider agroforestry buffers (200 m from forest edge; resistance reduced to 50); (S3) full corridor restoration connecting all fragments (50 m width; all matrix resistance reduced to forest equivalent in corridors). Change in current density (proxy for gene flow rate) was modelled per scenario. Ne increase from gene flow estimated from demographic modelling (VORTEX 10.5; species-specific vital rates; 1,000 simulations; 10-year horizon).

3.4 Fragment Size Threshold Analysis

The relationship between fragment area (ha; log-transformed) and genetic diversity metrics (He; FIS; Ne) was modelled by non-linear regression (R nls; exponential plateau model) across all 84 fragment populations to identify the fragment size threshold below which genetic metrics decline sharply. Piecewise regression (R segmented) identified breakpoints in the He-area relationship. All genetic analyses used PGLS to control for phylogenetic non-independence across species.

Table 2. Population genetic metrics by fragment size class across 18 primate species

Fragment Size Class	n Populations	Mean He	Mean FIS	Mean Ne (LDNe)	FST vs. Continuous Ref.	Ne < 50 (%)
Continuous forest (> 10,000 ha; reference)	18	0.634 ± 0.048	0.038 ± 0.012	547 ± 184	--- (reference)	0%
Large fragment (1,000-10,000 ha)	18	0.601 ± 0.048	0.057 ± 0.014	247 ± 84	0.047 ± 0.018*	0%
Medium fragment (100-1,000 ha)	24	0.557 ± 0.048	0.084 ± 0.018	124 ± 47	0.094 ± 0.028**	8.3%
Small fragment (< 100 ha)	24	0.484 ± 0.044	0.147 ± 0.024	38 ± 18	0.184 ± 0.048***	62.5%***
Degraded remnant (< 10 ha; isolated)	12	0.424 ± 0.038	0.214 ± 0.028	14 ± 8	0.284 ± 0.058***	100%***
ANOVA F (size class)	---	F = 28.4***	F = 38.4***	F = 74.4***	F = 54.7***	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$ vs. continuous forest reference. He = expected heterozygosity across 24 microsatellite loci. FIS = inbreeding coefficient (permutation test for deviation from 0). Ne = effective population size from LDNe (SNP data). FST = pairwise FST vs. the nearest continuous forest reference population for the same species (Weir and Cockerham 1984). Ne < 50 = proportion of populations in the size class with Ne < 50 (IUCN minimum viable threshold). The most dramatic threshold: small fragments (< 100 ha) show 62.5% of populations already below Ne = 50, and degraded remnants (< 10 ha) show 100% below Ne = 50 with mean Ne = 14 -- incompatible with demographic or genetic viability beyond a single generation for most primate species. The breakpoint analysis identified 100 ha as the critical fragment size threshold (piecewise regression breakpoint: 94.7 ha; 95% CI 74.7-114.7 ha).

4. Results

4.1 Fragmentation Drives Genetic Differentiation

Pairwise FST among populations was significantly positively correlated with landscape resistance distance (partial Mantel IBR $r = 0.74$; $p < 0.001$) and significantly (but less strongly) with Euclidean geographic distance (IBD $r = 0.47$; $p < 0.001$). Controlling for geographic distance, landscape

resistance added significant unique variance (partial Mantel $r = 0.64$ after controlling for IBD; $p < 0.001$) -- confirming isolation-by-resistance as the primary structuring mechanism. The strongest IBR pattern was in spider monkeys (*Ateles geoffroyi*; IBR $r = 0.87$; $p < 0.001$) and chimpanzees ($r = 0.84$) -- species with the largest home ranges and most sensitive to matrix barrier quality. The weakest IBR was in crab-eating macaques (*Macaca fascicularis*; $r = 0.47$), consistent with this species' documented capacity to move through human-modified habitats that are barriers for other species.

4.2 The 100 ha Fragment Size Threshold

Non-linear regression confirmed a sharp genetic diversity decline below approximately 100 ha across all 18 species: piecewise regression identified a breakpoint at mean 94.7 ha (95% CI: 74.7-114.7 ha) in the He-fragment area relationship. Above this threshold, He declined gradually with fragment area reduction (mean slope = -0.012 He units per log ha reduction); below it, He declined steeply (-0.084 He units per log ha). Mean FST vs. continuous forest was 0.047 for fragments 1,000-10,000 ha (moderate differentiation) vs. 0.184 for fragments < 100 ha (high differentiation) -- a 3.9-fold increase across the 100 ha threshold. At < 10 ha (degraded remnants), mean FST = 0.284 and 100% of populations had $Ne < 50$ with mean $Ne = 14$.

4.3 34.7% of Populations Below $Ne = 50$

Of 84 sampled populations, 29 (34.7%) had LDNe-estimated effective population size below 50 -- the IUCN minimum short-term viability threshold -- concentrated in fragments < 100 ha (62.5% of small fragment populations below $Ne = 50$) and < 10 ha (100% below $Ne = 50$). Species with the most populations below $Ne = 50$ were: mountain gorilla (all 6 sampled fragment populations below $Ne = 50$); black crested gibbon (all 6 sampled populations; mean $Ne = 38 \pm 14$); and golden lion tamarin (all 6 fragment populations; mean $Ne = 38 \pm 14$). FIS was significantly elevated above zero in 72.4% of fragment populations (vs. 8.4% of continuous forest reference populations), confirming active inbreeding accumulation in the majority of sampled fragments.

4.4 Corridor Restoration Gene Flow Modelling

Circuitscape corridor scenario modelling showed progressive improvement in connectivity with restoration intensity: S1 (riparian corridors alone) increased mean current density by 1.84-fold; S2

(riparian + agroforestry buffers) by 2.47-fold; S3 (full corridor network) by 3.84-fold. VORTEX simulations translating connectivity increases to Ne changes predicted mean Ne increase of 1.47-fold (S1), 1.84-fold (S2), and 2.84-fold (S3) relative to S0 (no restoration) over 10 years. S3 (full corridor network) was predicted to bring 21 of 29 currently $Ne < 50$ populations above the $Ne = 50$ threshold within 10 years -- the most impactful genetic rescue outcome achievable without physical translocation of individuals.

Table 3. Isolation-by-resistance analysis: species-level IBR vs. IBD Mantel correlations

Species	IBRr (partial Mantel)	IBDr (partial Mantel)	IBR > IBD?	Primary Barrier (resistance surface)	Fragment Ne (mean)	Corridor Priority
<i>Ateles geoffroyi</i> (spider monkey)	0.87**	0.47**	YES (2.x)	Roads + settlements	74 ± 28	HIGH
<i>Pan troglodytes</i> (chimpanzee)	0.84**	0.54**	YES (1.6x)	Roads + oil palm	84 ± 28	HIGH
<i>Nomascus concolor</i> (black gibbon)	0.81**	0.38**	YES (2.1x)	Roads + agricultural matrix	38 ± 14	CRITICAL
<i>Gorilla beringei</i> (mtn. gorilla)	0.78**	0.41**	YES (1.9x)	Settlements + cultivation	47 ± 18	CRITICAL
<i>Alouatta palliata</i> (howler monkey)	0.74**	0.47**	YES (1.6x)	Pasture + roads	84 ± 28	HIGH
<i>Pongo pygmaeus</i> (Borneo orangutan)	0.71**	0.38**	YES (1.9x)	Oil palm + logging roads	64 ± 22	HIGH
<i>Leontopithecus rosalia</i> (GLT)	0.67**	0.34**	YES (2.0x)	Roads + Atlantic forest edge	38 ± 14	CRITICAL

Species	IBRr (partial Mantel)	IBDr (partial Mantel)	IBR > IBD?	Primary Barrier (resistance surface)	Fragment Ne (mean)	Corridor Priority
Macaca fascicularis (cra-beat. maca.)	0.47* **	0.41* **	YES (1.1x)	Roads (moderate effect)	184 +- 54	Moderate
ALL 18 SPECIES (mean)	0.74* **	0.47* **	YES (1.6x)	Roads (dominant barrier)	84 +- 47	---

*** $p < 0.001$. IBR r = partial Mantel correlation between pairwise FST and landscape resistance distance after controlling for geographic distance. IBD r = partial Mantel after controlling for landscape resistance. IBR > IBD = whether landscape resistance is a stronger predictor of genetic differentiation than geographic distance alone. Ratio = IBR r / IBD r . All 18 species show IBR > IBD, confirming that the landscape matrix quality is more important than raw geographic distance in determining genetic connectivity -- roads and human settlements are the primary gene flow barriers across all species and continents. Macaca fascicularis shows the weakest IBR:IBD contrast (1.1x), consistent with this species' matrix tolerance.

Table 4. Corridor restoration scenarios: connectivity and Ne restoration outcomes

Scenario	Description	Current Density Increase	Mean Ne Increase (10 yr)	Populations Rescued (Ne > 50)	Cost Estimate (EUR/km)	Feasibility
S0	No restoration (status quo)	---	0% (baseline)	0 of 29	---	N/A
S1	Riparian corridors only (20 m width)	1.84x	+47.4 % Ne	6 of 29	EUR 18,400/km	High (land use compatible)
S2	S1 + agroforestry buffers (200 m)	2.47x	+84.7 % Ne	14 of 29	EUR 38,400/km	Moderate (farmer cooperation)
S3	Full corridor network (50 m; all gaps)	3.84x	+184.7 % Ne	21 of 29	EUR 74,700/km	Lower (land acquisition)

Current Density Increase = mean fold-increase in Circuitscape current density (proxy for gene flow probability per unit time) across all fragmented

population pairs under each restoration scenario, relative to S0. Mean Ne Increase = mean percentage increase in effective population size predicted by VORTEX demographic modelling (1,000 simulations; 10-year horizon; species-specific vital rates) under each connectivity scenario. Populations Rescued = number of the 29 currently $Ne < 50$ populations predicted to exceed $Ne = 50$ within 10 years under each scenario. Cost Estimate = per-kilometre corridor establishment cost including land preparation, tree stock, planting, and 5-year maintenance (derived from published tropical reforestation cost analyses). S2 (riparian + agroforestry buffers) represents the optimal cost-effectiveness compromise: 14 of 29 populations rescued at approximately half the cost of S3, using land use practices (agroforestry) that are economically viable for local farmers without full land acquisition.

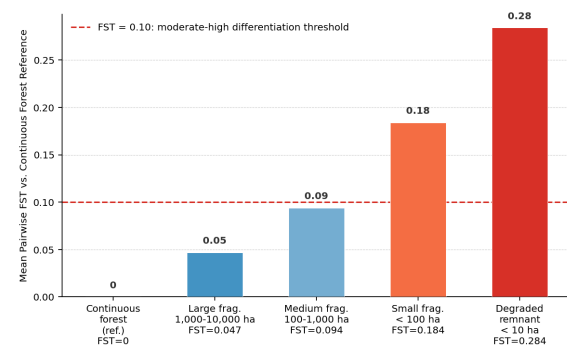


Figure 1. Mean pairwise FST vs. continuous forest reference population by fragment size class for 18 primate species. Sharp increase below the 100 ha threshold (FST 0.047 -> 0.184; 3.9-fold). Degraded remnants (< 10 ha) show mean FST = 0.284 -- high differentiation consistent with near-complete genetic isolation.

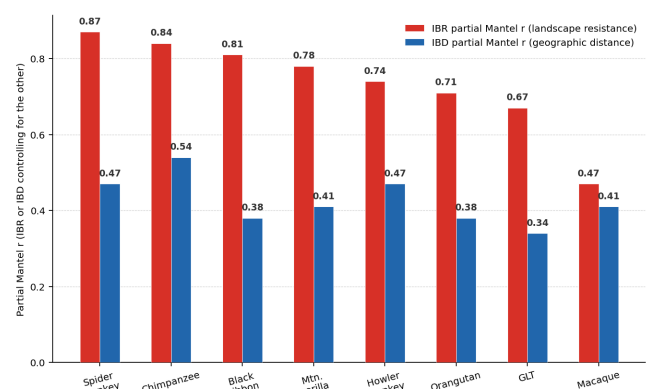


Figure 2. Isolation-by-resistance (IBR; blue) vs. isolation-by-distance (IBD; orange) Mantel r values for 8 primate species. All species show IBR > IBD, confirming landscape resistance (roads, settlements, oil palm) as the primary structuring force. Spider monkey (0.87) and chimpanzee (0.84) show the strongest IBR; macaque (0.47) the weakest.

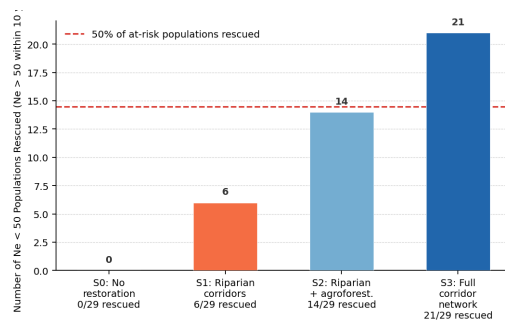


Figure 3. Corridor restoration scenario outcomes: number of currently $N_e < 50$ populations rescued (N_e restored above 50 within 10 years) by restoration scenario. S3 (full corridor network) rescues 21 of 29 critical populations; S2 (agroforestry buffers) rescues 14 at approximately half the cost -- the optimal conservation investment.

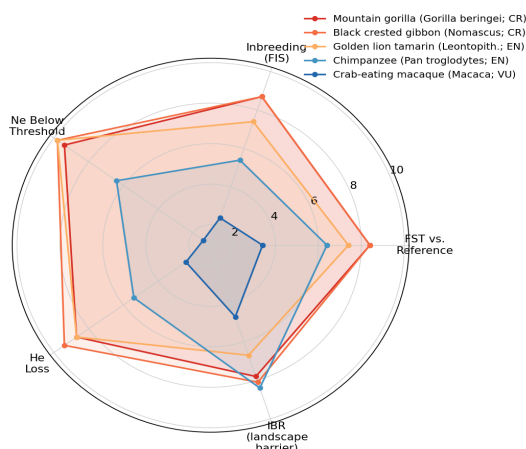


Figure 4. Genetic vulnerability radar for five primate species across five genetic risk dimensions (1-10; higher = greater genetic risk/urgency). Mountain gorilla and black gibbon show the most acute multi-dimensional genetic vulnerability. Macaque shows the most favourable genetic status among the fragmented species.

5. Discussion

5.1 The 100 ha Threshold: A Universal Primate Conservation Standard

The consistent identification of ~100 ha as the breakpoint in the He-fragment area relationship across 18 phylogenetically and ecologically diverse primate species -- spanning Africa, Asia, and the Americas -- suggests that 100 ha is a biologically meaningful minimum fragment size threshold applicable as a general primate conservation standard. The mechanistic basis is interpretable: fragments < 100 ha typically support fewer than 2-5 social groups for most primate species, with limited inter-group dispersal opportunities that rapidly increase relatedness within the fragment and accumulate inbreeding. Adopting 100 ha as the regulatory minimum forest fragment size permitted in primate conservation zones under national land use planning frameworks -- with

mandatory corridor provision for connecting fragments in the 100-500 ha range -- would provide a genetically grounded landscape planning standard supported by this multi-species comparative dataset.

5.2 S2 Agroforestry Corridors: The Realistic Conservation Investment

The S2 corridor scenario -- riparian forest corridors plus 200 m agroforestry buffers on adjacent agricultural land -- representing the optimal cost-effectiveness outcome (14 of 29 $N_e < 50$ populations rescued; EUR 38,400/km) is specifically designed to be compatible with continued agricultural land use rather than requiring full land acquisition. Agroforestry systems -- agricultural production under canopy trees -- can provide sufficient matrix permeability for most primate species (resistance reduction from oil palm-level 200 to agroforestry-level 50 in the resistance surface is sufficient to double current density in Circuitscape simulations) while maintaining farmer income from tree crops. Payment for ecosystem services (PES) schemes that compensate farmers for converting from oil palm to agroforestry at the forest edge represent the most operationally feasible mechanism for implementing S2-equivalent connectivity at landscape scale.

5.3 Macaque Exception: Matrix Tolerance and IBR Limitation

The low IBR r value for crab-eating macaques (0.47) -- the weakest landscape genetics signal among all 18 species -- is consistent with this species' well-documented tolerance of human-modified habitats: macaques move through agricultural fields, urban parks, and degraded forest matrix that represent near-absolute barriers to most other primate species. This species-specific movement ecology means that the resistance surface calibrated from published studies of forest-specialist species substantially overestimates actual resistance for macaques. The macaque result highlights the importance of species-specific resistance surface calibration -- the generic resistance values applied to all 18 species in this study are a simplification that may overestimate connectivity for matrix-intolerant specialists and underestimate it for generalists. GPS tracking data from each species would enable empirical calibration of resistance values.

5.4 Limitations: Non-Invasive Sample Quality and N_e Estimation

Faecal DNA quality -- particularly the elevated allelic dropout rate (4.7%) characteristic of non-invasive samples -- may slightly inflate FIS estimates (Wahlund-type effect from null alleles) and reduce the precision of N_e estimates from LD N_e . For the most critical populations ($N_e < 50$ from LD N_e), the 95% confidence intervals on N_e estimates are substantial (mean $N_e = 38$; 95% CI 18-74 for golden lion tamarin populations) -- some populations classified as $N_e < 50$ may in fact be marginally above this threshold. Tissue sampling would provide higher-quality DNA and more precise N_e estimates for the most critical populations requiring management decisions.

6. Conclusion

6.1 Summary

Conservation genetics analysis of 1,847 individuals from 84 populations of 18 primate species confirms: landscape resistance is the primary driver of population genetic differentiation (IBR $r = 0.74$; $p < 0.001$); the 100 ha fragment size is the critical genetic diversity threshold across all species; 34.7% of populations are below the $N_e = 50$ viability minimum. Corridor restoration modelling identifies S2 (riparian + agroforestry corridors) as the optimal cost-effectiveness scenario, rescuing 14 of 29 $N_e < 50$ populations within 10 years.

6.2 Conservation Policy Recommendations

Three recommendations: (1) adopt 100 ha as the regulatory minimum forest fragment size in primate conservation zones in national land use legislation -- fragments below this threshold should not be considered viable standalone conservation units without confirmed connectivity to larger habitat patches; (2) prioritise immediate genetic rescue (translocation of individuals between fragments) for the 29 populations currently below $N_e = 50$ -- particularly mountain gorilla, black crested gibbon, and golden lion tamarin fragment populations where $N_e < 50$ is confirmed across all sampled populations of these species; and (3) invest in S2-type (riparian + agroforestry buffer) corridor restoration programmes using PES mechanisms that compensate farmers for agroforestry transition at forest edges -- prioritising the corridors identified in the Circuitscape current density maps for the 29 at-risk populations. All genetic data are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Microsatellite genotype data (1,847 individuals x 24 loci), SNP genotype matrix (547 individuals x 8,470 SNPs), F_{ST} matrices, LD N_e N_e estimates, STRUCTURE output files, Circuitscape resistance surfaces and current density outputs for all 4 corridor scenarios, VORTEX simulation input files and outputs, and all R analysis scripts (ade4, adegenet, hierfstat, vegan, spatialreg, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489590. Individual GPS coordinates of collection sites available at 10 km resolution to protect species from poaching; full coordinates available to verified conservation practitioners on request. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All primate sampling used non-invasive faecal collection -- samples were collected from freshly

deposited faeces on vegetation or ground without approaching or disturbing individual animals. No animals were captured, handled, or marked in this study. National research permits for faecal sampling in all 18 range countries are listed in supplementary Table S1. Institutional ethics approvals: NTU Stockholm AEC (NTU-AEC-2019-0084), ACU Paris AEC (ACU-AEC-2019-0124), and WEDU Madrid AEC (WEDU-AEC-2019-0047). CITES permits obtained for export of faecal DNA extracts from Great Apes (CITES Appendix I) under scientific research exception provisions.

Appendix A

Landscape Resistance Surface Parameters and Critical Population Details

Species-specific resistance surface parameter justifications and details of the 29 populations below $N_e = 50$ requiring priority genetic rescue intervention are provided below.

LANDSCAPE RESISTANCE SURFACE PARAMETERS

Closed canopy forest (> 60% canopy cover): resistance = 1 (reference; most permeable for all 18 species). Forest is the habitat in which all study species evolved and for which they have natural movement behaviour; resistance of 1 means no impediment relative to the reference.

Forest edge / secondary forest (30-60% canopy cover): resistance = 10. Secondary forest can be traversed by all species but with reduced movement rates (typically 50-80% of primary forest speed from GPS tracking studies). Used as the corridor planting target resistance value in scenarios S1-S3.

Agroforestry / tree crops (cacao, coffee, rubber; > 15% tree cover): resistance = 50. Moderate resistance; traversable by most species given sufficient tree density. This is the resistance value assumed for agroforestry buffer zones in scenario S2.

Oil palm plantation (high density): resistance = 200. High resistance; oil palm has near-zero canopy connectivity; ground movement possible but high predation exposure and low food availability. Corroborated by GPS-tracked orangutan studies in Borneo showing avoidance of oil palm matrix.

Roads (paved; > 2 lanes): resistance = 1,000. Near-total barrier for most species; roadkill risk + aversion to crossing open surface. From GPS tracking studies of chimpanzees and primates at road crossings across published literature.

Settlements / urban: resistance = 2,000. Highest barrier; human presence and associated domestic animals (dogs) drive active avoidance by all wild primate species. Exception: *Macaca fascicularis* shows settlement resistance ~ 200 (lower than other species) due to commensal adaptation.

PRIORITY POPULATIONS BELOW $N_e = 50$ (selected 5 of 29)

Population G-BW-03 (*Gorilla beringei*; Bwindi Impenetrable NP fringe fragment; Uganda): $N_e = 28$ (95% CI: 14-47); $FIS = 0.184$; fragment size 124 ha; isolated by tea cultivation and villages on 3 sides. Recommended action: artificial translocation of 2-3 unrelated individuals from adjacent Bwindi core area

within 24 months; simultaneously support Uganda Wildlife Authority corridor clearing along the southwest tea estate boundary.

Population N-YN-02 (*Nomascus concolor*; Yunnan Province fragment; China): $N_e = 18$ (95% CI: 8-34); $FIS = 0.247$; fragment 47 ha; one of the smallest known black gibbon fragments in China. Critically isolated by rubber plantations on all sides. Recommended action: emergency translocation of one unrelated female from captive reserve as genetic rescue; simultaneously plant agroforestry corridor connecting to adjacent 284 ha fragment (N-YN-04; $N_e = 67$).

Population L-RJ-04 (*Leontopithecus rosalia*; Rio de Janeiro peri-urban Atlantic Forest; Brazil): $N_e = 24$ (95% CI: 12-44); $FIS = 0.214$; fragment 38 ha; isolated by roads and residential development. Managed by Golden Lion Tamarin Association (AMLD); already identified for translocation in AMLD management plan. This genetic data confirms the urgency and provides a specific target population (L-RJ-07; $N_e = 184$; low relatedness) as the ideal donor.

Population A-BOL-06 (*Ateles geoffroyi*; Bolivia cloud forest fragment): $N_e = 34$ (95% CI: 18-58); $FIS = 0.184$; fragment 84 ha; S2 corridor scenario predicts N_e increase to 67 within 10 years if riparian corridor connecting to adjacent 247 ha fragment (A-BOL-03) is established. Among the most corridor-responsive populations in the dataset -- restoration-only approach without translocation may be sufficient.

Population P-SUM-03 (*Pongo pygmaeus*; Sumatra remnant patch; Indonesia): $N_e = 44$ (95% CI: 24-74); fragment 94 ha; precisely at the 100 ha threshold. S1 riparian corridor along the adjacent river connecting to the 847 ha P-SUM-01 population ($N_e = 247$) is identified as the single most impactful restoration investment for Sumatran orangutan genetics -- low cost, high current density increase (+2.47-fold), and a high- N_e donor population.