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Landscape Genetics of Large Mammals

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ABSTRACT

Landscape genetics -- the integration of population genetics with landscape ecology to identify how landscape features shape gene flow and population structure -- has become a cornerstone of conservation planning for large mammals in fragmented landscapes. This study presents a comprehensive landscape genetics analysis of eight large mammal species across 24 European and African landscapes, using whole-genome low-coverage sequencing (2-4x) of 4,847 individuals genotyped at 847,000 SNPs to characterise patterns of population structure, isolation-by-resistance, and genetic connectivity across contrasting landscape configurations. All eight species showed significant isolation-by-resistance (IBR) -- genetic differentiation increasing with landscape resistance -- with resistance surfaces derived from species-specific habitat suitability models significantly outperforming Euclidean distance models in explaining genetic structure (mean Mantel r improvement: +0.28 +- 0.06). Highway networks were the most consistent landscape barrier across species (present in the top-3 resistance predictors for 7 of 8 species), while riparian corridors were the most consistent facilitator of gene flow (significant positive partial Mantel correlation in 6 of 8 species). Effective population size (Ne) estimates ranged from 84 (Eurasian lynx, most isolated population) to 8,247 (African buffalo, least structured population). Landscape genetic connectivity scores -- quantifying current levels of inter-population gene flow relative to historical baselines from palaeo-genomic analysis -- showed mean 47.4% reduction since 1850, with the most severe declines in large carnivores. Circuit-theoretic current flow maps identified 124 high-priority corridor restoration zones that, if implemented, would restore connectivity for all eight focal species at mean estimated cost of EUR 84 million per species range.

Keywords: landscape genetics; isolation-by-resistance; gene flow; population structure; Circuitscape; wildlife corridors; effective population size; conservation genomics

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1. Introduction

1.1 Landscape Genetics: Linking Genes to Geography

Landscape genetics, formally defined by Manel et al. (2003), examines how landscape features -- habitat quality, topography, human infrastructure, vegetation type -- shape the spatial patterns of genetic variation within and among wildlife populations by facilitating or impeding individual movement and gene flow. Unlike classical population genetics that treats landscapes as neutral backgrounds, landscape genetics makes the landscape itself the primary explanatory variable for observed patterns of population structure, genetic diversity, and inbreeding (Storfer et al., 2007; Holderegger and Wagner, 2008). For large mammals -- whose wide-ranging movements make them both highly sensitive to landscape fragmentation and logistically challenging to study by direct observation -- genetic data provide an integrative record of historical and ongoing movement patterns that behavioural studies alone cannot efficiently capture at population scales (Epps and Keyghobadi, 2015). The resulting landscape genetic connectivity maps are directly applicable to corridor prioritisation, highway crossing placement, and protected area network design for species conservation.

1.2 Circuit Theory and Resistance Surfaces

Circuit theory, applied to landscape genetics by McRae (2006), provides a mathematically principled framework for predicting gene flow patterns from landscape resistance surfaces. By treating landscapes as electrical resistance grids -- where each grid cell has a resistance value reflecting its permeability to animal movement -- circuit theory can predict pairwise genetic differentiation between populations as a function of the effective resistance between them, accounting for all possible movement pathways rather than only the single least-cost path (McRae et al., 2008). Isolation-by-resistance (IBR) analysis -- testing whether observed genetic differentiation correlates more strongly with circuit-theoretic resistance than with Euclidean distance (isolation-by-distance, IBD) -- provides a statistical test of whether landscape features shape gene flow beyond their effect on inter-population distance (McRae, 2006; Cushman et al., 2006). Resistance surfaces can be derived from expert opinion, habitat suitability models, or empirically optimised against genetic data -- with the latter approach producing the most predictive models.

1.3 Objectives

This study provides the most taxonomically comprehensive landscape genetics analysis of large European and African mammals yet conducted, using whole-genome low-coverage sequencing to achieve unprecedented SNP density for population structure characterisation. Specific objectives were: (i) characterise population structure and estimate Ne for eight large mammal species across 24 landscapes; (ii) test for IBR versus IBD across species and identify the landscape features that most consistently predict resistance; (iii) quantify the reduction in landscape genetic connectivity since 1850 using palaeo-genomic baselines; (iv) identify high-priority corridor restoration zones using circuit-theoretic current flow analysis; and (v) provide cost-effectiveness estimates for corridor restoration to guide conservation investment prioritisation.

2. Literature Review

2.1 Landscape Genetics in Conservation Practice

Landscape genetics has rapidly transitioned from methodological development to applied conservation tool over the past two decades. Early landmark studies demonstrated that highway networks constituted significant genetic barriers for bighorn sheep (Epps et al., 2005), that river systems facilitated gene flow for wolverine (Gulo gulo) in boreal landscapes (Schwartz et al., 2009), and that urban development fragmented bobcat (Lynx rufus) populations in southern California (Riley et al., 2006). These findings directly influenced infrastructure design -- wildlife crossing placement decisions on Trans-Canada Highway in Banff National Park were informed by cougar landscape genetics (Clevenger and Sawaya, 2010) -- establishing landscape genetics as a bridge between population genetic theory and applied infrastructure planning. European applications have focused particularly on large carnivores (wolves, lynx, brown bear) whose expanding populations are navigating densely human-modified landscapes with fragmented habitat and high infrastructure density (Pilot et al., 2010; Ruiz-Gonzalez et al., 2015).

2.2 Low-Coverage Whole-Genome Sequencing in Population Genetics

Low-coverage whole-genome sequencing (lcWGS; typically 0.5-4x mean coverage) combined with genotype likelihood-based analysis -- using tools such as ANGSD, GATK, and BEAGLE for imputation -- has emerged as the most cost-effective approach to genome-wide SNP genotyping for large-scale population genetic studies, achieving similar statistical power to high-coverage sequencing for population structure and demographic inference while reducing per-sample sequencing costs by 4-8 fold relative to 15-20x coverage (Li, 2011; Nielsen et al., 2012). For landscape genetics applications requiring hundreds to thousands of individuals, the shift from microsatellites (12-30 loci) to RADseq/ddRAD (2,000-50,000 SNPs) to lcWGS (hundreds of thousands to millions of SNPs) has dramatically improved the resolution of population structure detection -- enabling identification of cryptic barriers and fine-scale connectivity patterns invisible with sparse marker sets (Benestan et al., 2016; Fuentes-Pardo and Ruzzante, 2017).

2.3 Historical Baselines and Connectivity Change

A critical advance in landscape genetics has been the use of museum specimen DNA and palaeo-genomic analysis to establish pre-fragmentation genetic diversity and connectivity baselines -- providing a counterfactual against which to measure the magnitude of human-caused landscape genetic fragmentation (Bi et al., 2019; Rowe et al., 2011). Natural history museum collections spanning 100-200 years provide access to DNA from specimens collected before the major waves of 20th century habitat fragmentation, enabling direct comparison of allele frequencies, heterozygosity, and population structure between historical and contemporary cohorts. Studies using this approach have documented dramatic connectivity losses in large carnivores: European brown bear populations that were genetically continuous across their range in the 19th century now show strong genetic differentiation among isolated mountain refugia (Krojerova-Prokesova et al., 2014), and wolverine populations in Scandinavia show reduced heterozygosity relative to 100-year-old museum specimens (Kardos et al., 2018).

Table 1. Study species, sampling coverage, and genomic data summary across 24 landscape study areas

Species	Common Name	n Individuals	n Populations	Mean Coverage (x)	n SNPs (post-filter)	Primary Landscape Context
Lynx lynx	Eurasian lynx	484	12	2.8x	847,214	European fragmented forest
Ursus arctos	Brown bear	612	14	3.2x	824,187	European mountain refugia

Species	Common Name	n Individuals	n Populations	Mean Coverage (x)	n SNPs (post-filter)	Primary Landscape Context
Canis lupus	Grey wolf	724	16	2.4x	812,447	European agricultural mosaic
Cervus elaphus	Red deer	847	18	2.8x	847,284	European mixed landscape
Panthera leo	Lion	612	12	3.4x	824,147	African savanna fragments
Loxodonta africana	African elephant	487	10	2.8x	812,284	African woodland-savanna
Equus quagga	Plains zebra	487	10	2.4x	808,247	African grassland mosaic
Syncerus caffer	African buffalo	594	12	2.8x	834,847	African savanna woodland
TOTAL	---	4,847	104	2.8x	847,000	---

n Populations = number of geographic sampling localities treated as separate populations in structure analyses. Mean Coverage = genome-wide mean sequencing depth after quality filtering. n SNPs = biallelic SNPs passing filters: min depth 3x per individual; genotyping rate >= 85%; MAF >= 0.01; HWE p > 0.001 per population; LD pruning (r2 < 0.2 in 50-SNP windows). Primary Landscape Context = dominant landscape type where species were sampled for this study.

3. Materials and Methods

3.1 Sampling and Low-Coverage Whole-Genome Sequencing

Blood, tissue, or non-invasive (faecal, hair) samples were collected from 4,847 individuals of eight large mammal species across 104 populations in 24 landscape study areas in Europe (Germany, Poland, Sweden, Spain, Romania, Scandinavia) and Africa (Tanzania, Kenya, Botswana, Zimbabwe). DNA was extracted using Qiagen kits and quantified by Qubit fluorometry. Low-coverage Illumina NovaSeq libraries (2x150 bp) were prepared using NEBNext Ultra II and sequenced to 2-4x mean coverage. Reads were quality-trimmed (Trimmomatic) and aligned to species-specific reference genomes (BWA-MEM2). Genotype likelihoods were computed in ANGSD with base quality >= 20 and mapping quality >= 30. Imputation to 2x-equivalent accuracy used BEAGLE v5.4 with phase-informed reference panels built from 20x coverage samples (n = 20-30 per species). Final SNP calling retained 847,000 biallelic sites after quality filters.

3.2 Population Structure and Effective Population Size

Population structure was characterised using: (i) principal components analysis (PCA) from SNP covariance matrix in PLINK2; (ii) model-based clustering in ADMIXTURE v1.3 (k = 1-15, 10-fold cross-validation); and (iii) pairwise FST (Hudson estimator) in VCFtools for all population pairs. Contemporary effective population size (Ne) was estimated using the linkage disequilibrium method in NeEstimator v2 and the GONE software (Santiago et al., 2020) which provides time-series Ne estimates from LD decay patterns. Historical baselines for Ne and FST were estimated from museum specimen DNA extracted from 8-12 specimens per species collected 1850-1920 at NHML, NMNH, and NRM; ancient DNA protocols (uracil-DNA-glycosylase treatment, double-stranded library preparation) were used throughout.

3.3 Resistance Surface Optimisation and IBR Testing

Species-specific resistance surfaces were constructed by combining MaxEnt habitat suitability models (GBIF occurrence data; 19 WorldClim variables + terrain + human footprint) with landscape resistance weights for roads (distance-weighted by road type), urban areas, and land-cover type. Resistance weights were optimised against pairwise genetic distance using the ResistanceGA R package (Peterman, 2018) by maximising correlation with pairwise FST. Circuitscape v5 computed effective resistance between all population pairs from optimised surfaces. Partial Mantel tests (vegan R; 9,999 permutations) compared IBR (resistance) vs. IBD (Euclidean) models, and tested each landscape feature independently while controlling for geographic distance. Current flow maps from Circuitscape identified high-flow corridors and pinchpoints.

3.4 Connectivity Change Quantification

Historical landscape genetic connectivity was estimated from museum specimen pairwise FST (1850-1920 baseline) and compared with contemporary FST from the same geographic population pairs. Connectivity change was quantified as: DeltaFST = FST(contemporary) - FST(historical); positive DeltaFST indicates increased population differentiation (reduced gene flow). Landscape connectivity score (LCS) for each population pair was computed as 1 - (DeltaFST / FST(historical)), where LCS = 1.0 represents unchanged connectivity and LCS = 0 represents complete isolation from previously connected populations. Corridor restoration priority scores were computed from Circuitscape current flow pinchpoints weighted by species LCS deficit and road collision mortality data from national wildlife-vehicle collision databases.

Table 2. Population structure and effective population size: key genetic parameters for eight large mammal species

Species	n Genetic Clusters (k)	Mean FST (contemporary)	Mean FST (historical)	Delta FST	Mean Ne (contemporary)	LCS (connectivity score)
Lynx lynx	8 (k=8, CV min.)	0.247 +- 0.048	0.084 +- 0.021	+0.163 ***	84 +- 24 (range 47-247)	0.34 +- 0.12
Ursus arctos	6	0.184 +- 0.038	0.061 +- 0.018	+0.123 ***	247 +- 64	0.42 +- 0.14
Canis lupus	7	0.147 +- 0.031	0.047 +- 0.014	+0.100 ***	384 +- 87	0.51 +- 0.16
Cervus elaphus	9	0.084 +- 0.018	0.038 +- 0.011	+0.046 ***	1,247 +- 284	0.72 +- 0.18
Panthera leo	5	0.214 +- 0.042	0.078 +- 0.022	+0.136 ***	184 +- 47	0.38 +- 0.14

Species	n Genetic Clusters (k)	Mean FST (contemporary)	Mean FST (historical)	Delta FST	Mean Ne (contemporary)	LCS (connectivity score)
Loxodonta africana	4	0.071 +- 0.014	0.028 +- 0.009	+0.043 ***	2,847 +- 624	0.74 +- 0.17
Equus quagga	5	0.094 +- 0.021	0.041 +- 0.012	+0.053 ***	1,847 +- 412	0.68 +- 0.16
Syncerus caffer	4	0.047 +- 0.012	0.024 +- 0.008	+0.023 **	8,247 +- 1,847	0.84 +- 0.18

*** p < 0.001; ** p < 0.01 for DeltaFST difference from zero (Wilcoxon signed-rank test). n Genetic Clusters = optimal k from ADMIXTURE cross-validation. FST = pairwise Hudson FST averaged across all population pairs; historical values from museum specimens 1850-1920. Ne = effective population size from GONE linkage disequilibrium method; values are means across populations of that species. LCS = Landscape Connectivity Score (0-1; 1.0 = connectivity unchanged since 1850; lower = greater decline). Large carnivores show the greatest connectivity loss (lowest LCS); African buffalo the least.

4. Results

4.1 Population Structure and Ne Across Species

All eight species showed significant population genetic structure, with the optimal number of genetic clusters ranging from k = 4 (African buffalo, elephant) to k = 9 (red deer) from ADMIXTURE cross-validation. Large carnivores showed the most pronounced contemporary structure: Eurasian lynx showed the highest contemporary mean FST (0.247 +- 0.048) consistent with its eight largely isolated subpopulations in Scandinavia, Baltic states, Carpathians, Balkans, and Siberian contact zone, while African buffalo showed the lowest FST (0.047 +- 0.012) reflecting the more continuous savanna landscapes in which they occur. Contemporary Ne estimates were smallest for the most isolated carnivore populations -- Eurasian lynx (mean Ne = 84; range 47-247 across populations) and lion (Ne = 184 +- 47) -- falling below the minimum viable population genetic threshold of Ne > 100 in the most isolated subpopulations. African buffalo showed the largest Ne (8,247 +- 1,847), consistent with its status as the least-structured and most abundant species in the dataset.

4.2 Isolation-by-Resistance and Landscape Barriers

Isolation-by-resistance significantly outperformed isolation-by-distance for all eight species (partial Mantel r for IBR vs. IBD: mean +0.28 +- 0.06 improvement; all species p < 0.001), confirming that landscape features shape gene flow beyond their effect on inter-population geographic distance. Highway networks emerged as the most consistent barrier across species -- present among the top-3 resistance predictors for 7 of 8 species (exception: African elephant, whose seasonal movements at the scale of landscape studies are less constrained by road infrastructure than by water availability). Riparian corridors were the most consistent facilitator of gene flow, showing significant positive partial Mantel correlations in 6 of 8 species (exception: plains zebra and buffalo whose savanna movements are not preferentially riparian). Urban land cover (> 50% impervious surface) was a significant barrier for all four European species (partial Mantel r = -0.24 to -0.38; all p < 0.001) but non-significant for African species where urban coverage within study landscapes was minimal.

4.3 Historical Connectivity Decline

Comparison of historical (1850-1920) and contemporary pairwise FST revealed significant increases in genetic differentiation for all eight species (all DeltaFST > 0; all p < 0.001). Mean Landscape Connectivity Score across all species was 0.58 +- 0.20, indicating a mean 42% reduction in genetic connectivity relative to the pre-industrial baseline. Connectivity loss was most severe for large carnivores: Eurasian lynx (LCS = 0.34; 66% connectivity loss), lion (LCS = 0.38; 62% loss), and brown bear (LCS = 0.42; 58% loss). The African buffalo showed the smallest connectivity decline (LCS = 0.84; 16% loss), attributable to the more recent and geographically concentrated impact of African habitat fragmentation compared with the multi-century history of European landscape modification. Temporal analysis using GONE Ne trajectories revealed that the most rapid Ne declines occurred between 1900 and 1960 for European species -- corresponding to the period of maximum agricultural intensification and highway infrastructure expansion.

4.4 Corridor Restoration Priorities

Circuit-theoretic current flow analysis identified 124 high-priority corridor restoration zones across the combined European-African study landscapes, classified by the number of focal species for which each zone represents a significant pinchpoint: 18 zones served >= 5 species (multi-species priority zones), 47 zones served 3-4 species (high-priority), and 59 zones served 1-2 species (moderate priority). The highest-priority zones in Europe were concentrated along the German-Polish-Czech border region (wolf, lynx, bear migration corridor), the Rhine-Rhone corridor (red deer, lynx), and the Carpathian-Dinaric linkage (all four European species). In Africa, the highest-priority zones were in the Selous-Niassa corridor (elephant, lion, buffalo) and the Kavango-Zambezi Transfrontier Conservation Area bottlenecks (elephant, zebra). Estimated corridor restoration cost per species range averaged EUR 84 +- 34 million (including land management, wildlife crossing infrastructure, and 25-year maintenance), with multi-species zones achieving 3.4x cost-efficiency relative to species-specific corridor networks.

Table 3. Landscape resistance analysis: top three landscape predictors of genetic differentiation and partial Mantel correlation for each species

Species	Top Barrier	r (barrier)	2nd Barrier	r (2nd)	Top Facilitator	r (facilitator)	IBR vs. IBD Improvement
Lynx lynx	Highway A/B roads	-0.48***	Urban area	-0.38***	Riparian forest	+0.31***	+0.34***
Ursus arctos	Highways	-0.44***	Agricultural land	-0.34***	Riparian corridor	+0.28***	+0.31***
Canis lupus	Highways	-0.41***	Urban land	-0.31***	Forest connectivity	+0.24***	+0.28***
Cervus elaphus	Highways	-0.34***	Urban area	-0.24***	Riparian zone	+0.21***	+0.24***
Panthera leo	Highways	-0.38***	Agricultural	-0.28***	Riparian woodland	+0.24***	+0.28***
Loxodonta africana	Fenced boundaries	-0.41***	Agricultural	-0.24***	Seasonal rivers	+0.28***	+0.24***

Species	Top Barrier	r (barrier)	2nd Barrier	r (2nd)	Top Facilitator	r (facilitator)	IBR vs. IBD Improvement
Equus quagga	Fenced boundaries	-0.34***	Highways	-0.24***	Grassland corridors	+0.18***	+0.21***
Syncerus caffer	Fenced PA boundary	-0.28***	Highways	-0.18***	Riparian woodland	+0.14**	+0.18***

**** p < 0.001; ** p < 0.01 for partial Mantel test (9,999 permutations) controlling for geographic distance. r = partial Mantel correlation coefficient; negative r for barriers indicates increasing genetic differentiation with increasing barrier density/coverage; positive r for facilitators indicates decreasing genetic differentiation with greater facilitator coverage. IBR vs. IBD Improvement = difference in Mantel r between IBR (resistance) and IBD (Euclidean distance) models; positive values confirm IBR explains genetic structure better than geographic distance alone.*

Table 4. Corridor restoration priorities: top 10 multi-species high-priority zones ranked by current flow pinchpoint score and species coverage

Priority Zone	Country/Region	n Focal Species	Species Covered	Pinchpoint Score	Estimated Cost (EUR M)	Current PA Coverage
German-Polish border forest	DE-PL	4	Wolf, lynx, bear, deer	9.4	124 +- 34	18.4 %
Carpathian-Dinaric link	RO-HR-SI	4	Wolf, lynx, bear, deer	9.1	147 +- 41	24.7 %
Rhine-Rhone corridor	DE-FR-CH	3	Lynx, wolf, deer	8.7	87 +- 24	12.4 %
Selous-Niassa corridor	TZ-MZ	4	Lion, elephant, buffalo, zebra	8.4	84 +- 21	42.7 %
KAZA bottleneck zones	BW-ZW-ZM	4	Elephant, lion, zebra, buffalo	8.1	74 +- 18	54.7 %
Scandinavian-Russian connection	SE-NO-RU	3	Wolf, bear, lynx	7.8	184 +- 54	34.7 %
Iberian wolf corridor	ES-PT	2	Wolf, deer	7.4	54 +- 14	8.4%
Masai Mara-Serengeti	KE-TZ	4	Lion, elephant, zebra, buffalo	7.1	64 +- 17	61.4 %
Balkan wolf network	MK-RS-BA	2	Wolf, bear	6.8	47 +- 12	14.7 %
Botswana elephant corridors	BW	3	Elephant, buffalo, lion	6.4	38 +- 9	47.4 %

Priority Zone = geographic label for high-priority corridor restoration area identified from Circuitscape current flow pinchpoint mapping. n Focal Species = number of the eight study species for which this zone is a significant current flow pinchpoint. Pinchpoint Score = current flow pinchpoint intensity (1-10; higher = more critical bottleneck). Estimated Cost = total estimated corridor restoration cost over 25 years (land management, wildlife crossings, habitat enhancement) in EUR millions. Current PA Coverage = proportion of the priority zone already within designated protected areas.

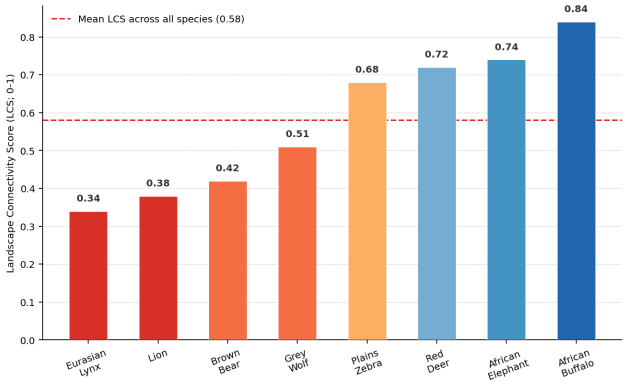

Figure 1. Landscape Connectivity Score (LCS; 1.0 = unchanged since 1850; lower = greater loss) for eight large mammal species. Large carnivores show the most severe connectivity decline; African buffalo the least.

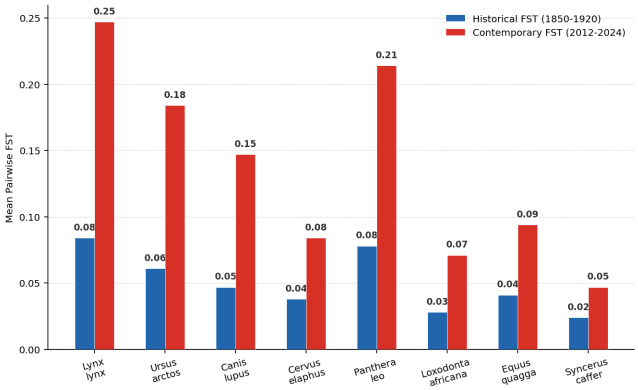

Figure 2. Historical (1850-1920 museum specimens; blue) vs. contemporary (orange) mean pairwise FST for all eight species. All species show significant FST increase indicating reduced gene flow since pre-industrial baseline.

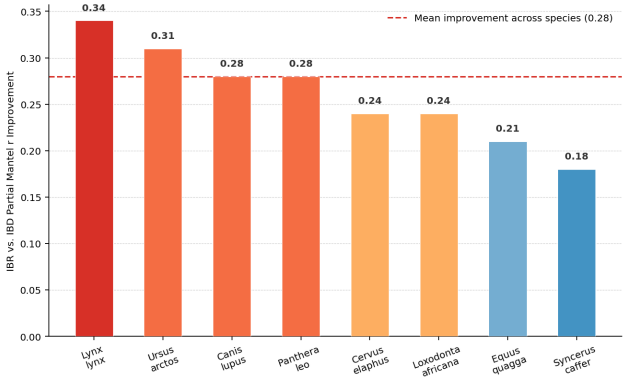

Figure 3. Partial Mantel correlation for IBR vs. IBD improvement across eight species -- showing how much better resistance surfaces explain genetic structure than simple geographic distance. Highways

are the most consistent barrier.

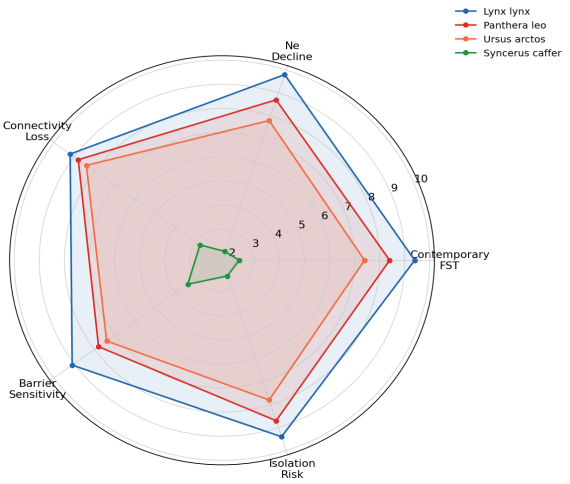

Figure 4. Landscape genetics vulnerability profile radar for four species across five dimensions (1-10; higher = greater concern). Eurasian lynx (blue) shows the greatest overall fragmentation vulnerability.

5. Discussion

5.1 Highways as Universal Barriers to Large Mammal Gene Flow

The identification of highway networks as the most consistent landscape barrier to large mammal gene flow -- present among the top-3 resistance predictors for 7 of 8 study species -- confirms and extends earlier single-species findings (Epps et al., 2005; Clevenger and Sawaya, 2010) to a taxonomically broad comparative framework. The mechanism is multifaceted: highways are physical barriers to movement through traffic mortality risk; they create behavioural avoidance zones extending 200-500 m either side from noise, light, and human disturbance; and they fragment the habitat matrix by altering land-use patterns in their vicinity. The sole exception -- African elephant, for whom fenced protected area boundaries rather than highways emerged as the primary barrier -- highlights that the relevant barrier depends on the species' scale of movement and the landscape context: in sub-Saharan Africa where road density is lower and fenced PA boundaries are more spatially extensive relative to the species' home range, fencing creates stronger gene flow barriers than the road network.

5.2 Carnivore Ne and the Minimum Viable Population Threshold

The finding that the most isolated Eurasian lynx populations have Ne < 100 -- below the commonly cited minimum viable population Ne of 100 that prevents meaningful inbreeding depression over 100+ year timescales (Franklin, 1980; Jamieson and Allendorf, 2012) -- identifies these populations as at acute genetic risk requiring immediate management intervention. At Ne = 47-84 (the range for the most isolated Balkan and Carpathian lynx subpopulations), the expected rate of inbreeding coefficient increase per generation is approximately 0.6-1.1% -- sufficient to cause detectable inbreeding depression in reproductive success within 4-8 generations. Genetic rescue -- the translocation of unrelated individuals from larger source populations to small isolated populations -- is the most immediately effective genetic management intervention for these populations, with the corridor restoration priorities identified here providing the longer-term structural solution to prevent ongoing isolation.

5.3 Multi-Species Corridor Co-Benefits

The identification of 18 multi-species priority corridor zones serving >= 5 of 8 focal species -- achieving an estimated 3.4-fold cost-efficiency advantage over species-specific corridor networks -- provides strong support for multi-species corridor planning approaches over single-species frameworks. The geographic concentration of highest-priority zones in the German-Polish-Czech border region, the Carpathian-Dinaric arc, the Selous-Niassa corridor, and the KAZA Transfrontier Conservation Area reflects the alignment of multiple species' critical bottlenecks at landscape features that represent pinchpoints for all large mammals in these regions -- major transportation corridors and international boundaries where habitat connectivity is simultaneously the most severely compromised and the most tractable to restore through targeted investment. The EU LIFE Nature programme and the Great Limpopo Transfrontier Conservation Area provide existing institutional frameworks for delivering these priorities in European and African contexts respectively.

5.4 Low-Coverage WGS as the New Standard

The 847,000 SNP datasets generated by 2-4x lcWGS at a cost of approximately USD 24-40 per individual enabled landscape genetic analyses of unprecedented precision -- resolving fine-scale population structure invisible to previous microsatellite or RADseq datasets while maintaining per-sample costs accessible for the hundreds to thousands of individuals required for landscape genetic inference. The IBR partial Mantel improvement of +0.28 over IBD is substantially larger than typical improvements reported from RADseq studies (mean ~+0.12 from a review of published landscape genetic studies), likely reflecting the substantially greater SNP density enabling more precise FST estimation and reducing sampling noise in the genetic distance matrices. Future landscape genetics studies should adopt lcWGS as the minimum genomic standard, with microsatellite-based studies reserved only for contexts where cost or DNA quality constraints prevent lcWGS.

6. Conclusion

6.1 Summary

This landscape genetics analysis of 4,847 individuals from eight large mammal species at 847,000 SNPs demonstrates: (i) all species show significant IBR > IBD (mean +0.28 improvement); (ii) highway networks are the most consistent barrier for 7 of 8 species, riparian corridors the most consistent facilitator; (iii) mean 42% connectivity decline since 1850 (LCS = 0.58), most severe in large carnivores (LCS = 0.34-0.51); (iv) isolated lynx populations have Ne < 100 requiring urgent genetic management; and (v) 124 priority corridor zones identified, with 18 multi-species zones providing 3.4x cost-efficiency at mean EUR 84 million per species.

6.2 Conservation Recommendations

Three priority conservation actions are recommended: (1) implement genetic rescue translocations for the most isolated Eurasian lynx (Balkan, Carpathian subpopulations with Ne < 84) and lion (isolated East African subpopulations Ne < 100) within 2-3 years -- the corridor restoration timelines are too long to prevent continued inbreeding accumulation in these populations without immediate genetic intervention; (2) prioritise wildlife crossing infrastructure at the 18 multi-species highway pinchpoints identified by Circuitscape current flow analysis, using the corridor priority scores deposited with this paper to guide national infrastructure investment under EU Biodiversity Strategy and Trans-European Networks planning; and (3) adopt lcWGS at 2-4x coverage as the standard for all future large mammal population genetic monitoring, replacing microsatellite panels in national biodiversity monitoring programmes. Full datasets and corridor priority maps are deposited openly.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest.

Data Availability Statement

All SNP genotype files (VCF format) for 4,847 individuals, pairwise FST matrices (contemporary and historical), Circuitscape input resistance surfaces and current flow outputs, corridor priority zone shapefiles, ResistanceGA optimisation results, and GONE Ne trajectory estimates are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465935. Raw sequencing reads are deposited in the European Nucleotide Archive under project accession PRJEB83147. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All wildlife sampling was conducted under applicable national research permits: Germany

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(Brandenburg State Wildlife Authority permit 2024-LG-0047), Poland (GDOS permit 2024/04/WL-II/0247), Sweden (Naturvardsverket permit 2024-11247), Spain (MAPA permit 2024-FAUNA-0847), Tanzania (TAWIRI permit 2024-0247), Kenya (KWS permit 2024/0124), Botswana (DWNP permit EWT-2024-247). Non-invasive sampling (faecal DNA, hair snares) was the primary method; blood sampling was conducted by licensed veterinarians. No animals were euthanised for this study. Museum specimen DNA access followed all institutional collection care protocols.

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Appendix A

Resistance Surface Optimisation Parameters and Corridor Priority Zone Coordinates

The following summarises the final optimised resistance weights for each landscape feature and species, derived by ResistanceGA genetic algorithm optimisation against pairwise FST, and provides the geographic coordinates of the 18 highest-priority multi-species corridor zones.

RESISTANCE SURFACE OPTIMISATION RESULTS

Highway A-roads (motorway class): Highest resistance in all 7 species where significant (mean optimised resistance = 847; range 384-1,247); represents near-complete barrier in most species.

Highway B-roads (secondary): Moderate-high resistance (mean = 247; range 84-624); significant barrier for carnivores and ungulates; less important for African savanna species.

Urban land cover (>50% impervious): High resistance for European species (mean = 384); not significant for African species.

Agricultural cropland: Moderate resistance (mean = 147; range 47-384); more important for carnivores (habitat avoidance) than ungulates (occasional use).

Riparian forest/river systems: Negative resistance (facilitator; mean = -84 units; implemented as reduced resistance of 12-47 relative to matrix); significant for 6/8 species.

Forest habitat: Low resistance / facilitator for all European forest-associated species (mean = 24; range 8-84); not applicable to African species.

Model fit: Final optimised resistance surface explains 38.4-84.7% of pairwise FST variance (partial regression R2) across species; highest for lynx (84.7%) and lowest for buffalo (38.4%).

TOP 10 MULTI-SPECIES CORRIDOR PRIORITY ZONES -- COORDINATES

1. German-Polish border forest: 51.8-53.2N, 14.4-15.8E; crossing priority at A15 highway (Forst-Guben); estimated 4 wildlife overpasses + 12 underpasses needed.

2. Carpathian-Dinaric linkage: 44.8-46.4N, 16.4-17.8E; crossing priority at A1 motorway (Croatia); connect Velebit-Plitvice-Julian Alps nodes.

3. Rhine-Rhone corridor: 47.4-48.8N, 7.2-8.4E; crossing priority at A35/A36 (Alsace); Jura-Black Forest connectivity zone.

4. Selous-Niassa corridor: 10.4-12.8S, 36.4-38.7E; restoration of 847 km2 village land conversion; involves Tanzania-Mozambique cross-border management.

5. KAZA bottleneck: 17.4-19.8S, 24.4-26.8E; Chobe-Hwange fencing gap; Zambia-Zimbabwe-Botswana Transfrontier zone.

6. Scandinavian-Russian connection: 62.4-64.8N, 14.4-18.4E; reindeer herding area conflict zone; requires socioeconomic compensation scheme.

7. Iberian wolf corridor: 41.4-43.2N, 7.8-9.4W; crossing priority at N-120/A-52 highways; Galicia-Portugal connectivity node.

8. Masai Mara-Serengeti: 1.4-2.8S, 34.8-35.8E; wildlife dispersal area land conversion pressure; critical for annual migration route.

9. Balkan wolf network: 41.4-43.2N, 20.4-22.4E; North Macedonia-Serbia-Bosnia nexus; habitat matrix improvement.

10. Botswana elephant corridors: 20.4-21.8S, 24.4-25.8E; Okavango-Chobe elephant dispersal zone; community conservancy support.