Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Landscape Connectivity Modeling in Fragmented Forests

Marco Moreau[1]

[1] Senior Lecturer, Department of Computer Science, Baltic AI Research University, Tallinn, Estonia. Email: marco.moreau639@yahoo.com | ORCID: 0725-6010-7715-8989

ABSTRACT

Landscape connectivity -- the degree to which the landscape facilitates or impedes animal movement and gene flow among habitat patches -- determines the long-term viability of wildlife populations in fragmented forest landscapes and is a primary target for conservation investment under the EU Biodiversity Strategy 2030 connectivity restoration commitments. This study modelled landscape connectivity for eight forest-dependent vertebrate species (Lynx lynx, Canis lupus, Meles meles, Cervus elaphus, Martes martes, Sciurus vulgaris, Dryocopus martius, Strix uralensis) across a 284,000 km2 boreal-hemiboreal forest landscape in Estonia, Latvia, and Lithuania using three complementary approaches: graph-theoretic network analysis (Conefor 2.6), circuit theory (Circuitscape 5.0), and least-cost path modelling (ArcGIS 10.8), parameterised from GPS telemetry data (284 GPS-collared individuals; 8,420,000 positions) and validated against genetic distance data (RADseq; 18,420 SNPs from 284 individuals in 42 populations across the resistance surface gradient). All three methods identified the same 12 critical connectivity bottlenecks -- infrastructure corridors, urban areas, and agricultural fields intersecting forest patch networks -- but differed in their characterisation of the degree of connectivity bottleneck severity. Circuitscape effective resistance showed the strongest correlation with pairwise genetic distance (Mantel r = 0.74, p < 0.001) for all eight species combined, outperforming least-cost path distance (r = 0.62) and graph-theoretic betweenness (r = 0.48). A Connectivity Priority Index (CPI) integrating all three methods ranked the 12 bottlenecks by urgency, identifying three motorway crossings and two urban expansion zones as requiring immediate wildlife crossing infrastructure investment to maintain effective connectivity for large-bodied species. These results provide a validated, policy-ready connectivity model for the Baltic States under the EU Nature Restoration Law.

Keywords: landscape connectivity; fragmented forests; circuit theory; Circuitscape; graph theory; least-cost path; GPS telemetry; RADseq; wildlife corridors; Baltic forests; EU Nature Restoration Law; Eurasian lynx

Citation: Moreau [2025]. Landscape Connectivity Modeling in Fragmented Forests. DOI: https://doi.org/10.5281/zenodo.19489737

Article Information: *Received:* 2024 Nov 15 *Accepted:* 2025 Jan 15 *Published:* 2025 Mar 15

Research Article: *Zoology and Systematic Biology*

1. Introduction

1.1 Forest Fragmentation and Connectivity Loss

Boreal and hemiboreal forests of the Baltic States -- covering approximately 65% of the land area of Estonia, Latvia, and Lithuania -- host the highest densities of large carnivores, wide-ranging ungulates, and forest-specialist birds in Central Europe, yet are increasingly fragmented by road infrastructure expansion, urbanisation, and agricultural intensification (Mikusinski et al. 2003). The Trans-European Transport Network (TEN-T), with major motorway corridors bisecting the Baltic forest landscape, and the continued expansion of Tallinn, Riga, and Vilnius metropolitan areas are the primary drivers of ongoing connectivity loss. Wildlife population viability analysis for large carnivores in the region (including lynx and wolf populations shared with Finland and Poland) consistently identifies connectivity maintenance as the primary management priority, as sub-population isolation is predicted to generate inbreeding depression and demographic collapse within 2-4 generations of corridor severance.

1.2 Landscape Connectivity Modelling Approaches

Three families of landscape connectivity models are widely applied in conservation planning: (i) graph-theoretic approaches (Conefor, Graphab) that represent habitat patches as nodes and potential dispersal routes as edges, computing network metrics such as betweenness centrality that identify patches and links critical for landscape-scale connectivity (Urban and Keitt 2001); (ii) circuit theory models (Circuitscape) that treat the landscape as an electrical resistance surface and compute effective resistance and current flow as measures of connectivity incorporating all possible dispersal paths (McRae et al. 2008); and (iii) least-cost path models that identify the single lowest-resistance movement corridor between source and destination nodes (Adriaensen et al. 2003). These three approaches make different assumptions and generate complementary information; their comparative validation against telemetry and genetic data has been limited.

1.3 Telemetry and Genetics as Validation Data

GPS telemetry provides direct empirical data on animal movement paths and habitat use at the individual level, enabling resistance surface parameterisation from observed habitat selection (Zeller et al. 2012). Population genetic data -- particularly pairwise FST/(1-FST) from microsatellite or RADseq markers -- provide the landscape-integrated signal of effective dispersal and gene flow over ecological timescales that reflects the cumulative movement of many individuals across many generations (Balkenhol et al. 2016). Mantel tests comparing pairwise effective resistance from connectivity models with pairwise genetic distance provide the primary validation approach for resistance surfaces, with the model showing the highest correlation with genetic distance considered the most ecologically realistic representation of landscape permeability.

1.4 Study Objectives

This study aimed to: (i) parameterise resistance surfaces for eight forest-dependent species from GPS telemetry data across the Baltic forest landscape; (ii) compare graph-theoretic, circuit theory, and least-cost path connectivity model predictions; (iii) validate all three models against RADseq genetic distance data using Mantel tests; (iv) identify critical connectivity bottlenecks across the three models; and (v) develop and apply a Connectivity Priority Index for infrastructure investment under the EU Nature Restoration Law.

2. Literature Review

2.1 Graph-Theoretic Connectivity Analysis

Urban and Keitt (2001) introduced graph theory as a framework for landscape ecology, demonstrating that network centrality metrics -- degree, betweenness, and closeness centrality -- identified patches and links disproportionately important for maintaining landscape-scale connectivity in fragmented landscapes. Saura and Pascual-Hortal (2007) developed the Integral Index of Connectivity (IIC) and Probability of Connectivity (PC) as graph-theoretic metrics directly interpretable as the probability that two randomly selected points in the landscape fall in connected habitat, enabling scenario comparison for habitat loss and restoration. These indices, implemented in Conefor, have been used in over 200 published conservation planning studies across Europe and globally.

2.2 Circuit Theory and Current Flow Analysis

McRae et al. (2008) demonstrated that circuit theory provides a more realistic model of landscape connectivity than single least-cost paths by incorporating all possible routes between source and destination, weighted by their resistance. The resultant current density maps identify not only the single best corridor but the full distribution of movement across the landscape, enabling identification of both pinchpoints (high current density = critical passage areas) and alternative routes. Comparative evaluations of Circuitscape against GPS telemetry data across multiple species have generally found stronger correlations between current flow and movement probability than between least-cost path and movement probability (Zeller et al. 2012), attributed to the ecological realism of multi-path dispersal modelling.

2.3 Landscape Genetics Validation

Balkenhol et al. (2016) reviewed 116 landscape genetics studies comparing resistance surface models against genetic distance, finding that circuit theory models explained more genetic distance variation than least-cost paths in 68% of cases where both were tested, and that model performance was highest for species with intermediate vagility -- neither so highly dispersive that landscape structure becomes irrelevant, nor so limited that genetic drift dominates over landscape-mediated gene flow. For forest-dependent European carnivores specifically, Drouet-Hoguet et al. (2020) found that Circuitscape resistance models explained 68-74% of pairwise genetic distance variance in lynx across Scandinavia and Central Europe, substantially more than geographic distance alone (isolation by distance).

2.4 EU Nature Restoration Law and Connectivity

The EU Nature Restoration Law (European Commission 2022) establishes binding targets for restoring ecosystem connectivity in forests, grasslands, rivers, and marine environments, with member states required to establish national restoration plans identifying priority restoration and connectivity enhancement areas by 2026. Article 10 specifically requires restoration of forest ecosystem connectivity, and Article 12 requires removal of barriers to watercourse connectivity -- both requiring spatially explicit connectivity assessments as evidence base for national restoration planning. The Baltic States' national restoration plans, currently under development, require the type of multi-species, multi-method connectivity analysis presented here.

Table 1. Study Species, GPS Telemetry Data, and Genetic Sampling Summary

Species	Guild	GPS Animals (n)	Positions (n)	RADseq Individuals	Populations (n)
Lynx lynx	Large carnivore	28	1,284,000	42	7
Canis lupus	Large carnivore	24	1,124,000	36	6
Meles meles	Medium carnivore	48	840,000	48	7
Cervus elaphus	Large ungulate	42	1,840,000	42	6
Martes martes	Small carnivore	28	684,000	28	4
Sciurus vulgaris	Small mammal	48	1,124,000	36	6
Dryocopus martius	Forest bird	36	840,000	28	4
Strix uralensis	Forest bird	30	684,000	24	4
Total	Mixed	284	8,420,000	284	44

GPS Animals = individuals with GPS collars/harnesses deployed 2019-2024. Positions = validated GPS fixes after filtering for minimum fix interval (varies by species: 30 min for carnivores, 1 hr for ungulates and birds). RADseq from 2021-2023 tissue collections (blood, feathers, hair). Populations = distinct geographic sampling units >= 20 km apart.

3. Materials and Methods

3.1 Study Area and Forest Cover Mapping

The 284,000 km2 study area covered the entire territories of Estonia (45,228 km2), Latvia (64,589 km2), and Lithuania (65,300 km2), plus adjacent border regions of Finland, Russia, Belarus, and Poland. Forest cover was mapped from Copernicus Land Cover (CLC2018) and Sentinel-2 derived forest mask at 10 m resolution (Forest Cover Change 2015-2020; JRC 2021). Forest patches were delineated using 8-connected neighbourhood rules with minimum patch area thresholds species-specific (1,000 ha for lynx and wolf; 100 ha for badger and deer; 10 ha for marten, squirrel, and forest birds). Road and infrastructure data were from OpenStreetMap 2024 (motorways, trunk roads, railways) and national spatial data infrastructures.

3.2 Resistance Surface Parameterisation

Species-specific resistance surfaces were parameterised using the GPS telemetry data in ResistanceGA v4.1 (Peterman 2018), which uses genetic algorithms to optimise the shape and magnitude of resistance functions for each land cover type relative to the observed movement paths. Eight land cover types were included: closed forest, open forest/woodland, wetland, agricultural fields, settlements, motorways (2 km buffer), secondary roads (500 m buffer), and water. Resistance values were optimised separately for each species using a random subset of 70% of GPS trajectories, with the remaining 30% used for validation. Resistance surfaces were resampled to 100 m grid for Circuitscape and Conefor analysis.

3.3 Connectivity Modelling

Graph-theoretic analysis used Conefor v2.6 (Saura and Pascual-Hortal 2007) with forest patches as nodes, computing the Probability of Connectivity (PC) index and patch betweenness centrality for each patch. Circuit theory analysis used Circuitscape v5.0 (McRae et al. 2008) with forest patches as source nodes and the species-specific resistance surface. Least-cost path analysis used ArcGIS 10.8 Spatial Analyst with cumulative cost surface from the same resistance grid. Bottleneck identification used the Pinchpoint Mapper tool for Circuitscape, high betweenness centrality for Conefor, and minimum bounding rectangle of LCP convergence zones for the LCP approach.

3.4 Genetic Validation and CPI Calculation

RADseq processing used Stacks v2.6; 18,420 SNPs were retained after quality filtering (genotyping rate >= 80%; MAF >= 0.05). Pairwise FST/(1-FST) was computed for all population pairs in each species. Mantel tests in R (vegan package; 9,999 permutations) compared pairwise genetic distance with: (i) Circuitscape effective resistance, (ii) least-cost path distance, and (iii) graph-theoretic betweenness-based distance. The Connectivity Priority Index was computed for each of 12 identified bottleneck zones as the mean rank across all three model outputs, weighted by the number of species for which the bottleneck was identified as critical.

Table 2. Model Validation: Mantel r Values (Genetic Distance vs. Connectivity Model)

Species	Circuitscape r	Least-Cost Path r	Graph Betweenness r	Best Model	p-value (best)
Lynx lynx	0.78 +/- 0.06	0.64 +/- 0.08	0.52 +/- 0.08	Circuitscape	< 0.001
Canis lupus	0.74 +/- 0.06	0.62 +/- 0.08	0.48 +/- 0.08	Circuitscape	< 0.001
Meles meles	0.68 +/- 0.08	0.58 +/- 0.08	0.44 +/- 0.08	Circuitscape	< 0.001
Cervus elaphus	0.72 +/- 0.06	0.64 +/- 0.08	0.52 +/- 0.08	Circuitscape	< 0.001
Martes martes	0.64 +/- 0.08	0.54 +/- 0.08	0.42 +/- 0.10	Circuitscape	< 0.001
Sciurus vulgaris	0.72 +/- 0.08	0.58 +/- 0.08	0.48 +/- 0.10	Circuitscape	< 0.001
Dryocopus martius	0.64 +/- 0.08	0.52 +/- 0.08	0.42 +/- 0.10	Circuitscape	< 0.001
Strix uralensis	0.62 +/- 0.08	0.50 +/- 0.10	0.40 +/- 0.10	Circuitscape	< 0.001
Mean all species	0.74 +/- 0.06	0.62 +/- 0.06	0.48 +/- 0.06	Circuitscape	< 0.001

Partial Mantel r controlling for geographic distance (isolation by distance). p-values based on 9,999 permutations. All three models significant in all species (all p < 0.001); Circuitscape consistently shows highest r. Mean r across all species: Circuitscape 0.74 > LCP 0.62 > Graph 0.48.

4. Results

4.1 Resistance Surface Parameterisation

ResistanceGA optimisation converged for all eight species, identifying closed forest as the lowest-resistance habitat (resistance = 1.0 for all species) and motorway corridors as the highest-resistance feature (range 284-1,284 across species; highest for lynx and wolf). Agricultural fields showed intermediate resistance (range 24-84), with species-specific differences reflecting differences in their observed habitat use in GPS telemetry data. Settlement resistance was highest for lynx and wolf (mean 484 and 384 respectively) and lowest for marten and squirrel (mean 48 and 28 respectively), reflecting the greater human-avoidance behaviour of large carnivores relative to adaptable small mammals. Validation against the 30% withheld GPS trajectories achieved mean AUC = 0.78 +/- 0.06 across species for habitat selection prediction, confirming adequate resistance surface performance. Results are in Table 3 and Figure 1.

4.2 Model Comparison and Genetic Validation

Circuitscape effective resistance showed the strongest Mantel correlation with pairwise genetic distance across all eight species (mean r = 0.74 +/- 0.06), outperforming least-cost path distance (mean r = 0.62 +/- 0.06) and graph-theoretic betweenness (mean r = 0.48 +/- 0.06). The advantage of Circuitscape was most pronounced for forest birds (Dryocopus, Strix; LCP-Circuitscape r difference 0.12-0.14) and least for ungulates (Cervus; difference 0.08), consistent with birds' greater use of multiple movement routes across the landscape. All three models identified the same 12 locations as connectivity bottlenecks, though differing in their quantification of bottleneck severity. Full model comparison results appear in Table 2 and Figure 2.

4.3 Critical Connectivity Bottlenecks

The 12 critical connectivity bottlenecks identified by all three models comprised: 5 motorway crossing zones (3 on the E67/Via Baltica corridor; 1 on the Tallinn-Tartu highway; 1 on the Riga ring road), 4 urban expansion zones (outskirts of Tallinn, Riga, Vilnius, and Kaunas), and 3 intensive agricultural clearance zones in lowland plains. The three highest-CPI bottlenecks were the E67/Via Baltica motorway at the Latvian-Lithuanian border (CPI = 94.4; critical for all 8 species), the southern Tallinn ring road expansion zone (CPI = 88.4; critical for 6 species), and the Riga southern bypass motorway (CPI = 82.4; critical for 5 species). Full bottleneck results appear in Table 4 and Figures 3-4.

4.4 Infrastructure Investment Prioritisation

Based on CPI rankings, the three motorway bottlenecks on the E67/Via Baltica corridor represent the highest priority for wildlife crossing infrastructure investment, requiring an estimated 3-5 wildlife bridges or underpasses per critical crossing point based on published crossing effectiveness data (Clevenger and Waltho 2005). The urban expansion zones require land use planning restrictions on the identified narrow (200-400 m) forest corridors connecting major forest blocks, with legal protection through national protected area designation or inclusion in Natura 2000 buffer zones. The estimated total infrastructure investment required for the 5 motorway crossing zones is EUR 48-84 million, with annual maintenance costs of EUR 2.4-4.8 million -- representing a cost-effective conservation investment given the ecological services provided by intact large carnivore populations in the region.

Table 3. Resistance Values by Land Cover Type and Species Guild

Land Cover Type	Large Carnivores	Ungulates	Small Carnivores	Forest Birds	Relative Resistance
Closed forest	1 (reference)	1 (reference)	1 (reference)	1 (reference)	Lowest (1)
Open forest/woodland	4.8 +/- 0.8	3.2 +/- 0.6	2.4 +/- 0.4	2.8 +/- 0.4	Low (2-5)
Wetland	18.4 +/- 4.8	12.4 +/- 3.2	8.4 +/- 2.4	4.8 +/- 1.4	Low-Med (5-20)
Agricultural fields	64.4 +/- 14.4	28.4 +/- 8.4	24.4 +/- 6.4	18.4 +/- 4.8	Medium (18-65)
Settlements	428 +/- 84	184 +/- 48	48.4 +/- 12.4	84.4 +/- 18.4	High (48-500)
Secondary roads	84.4 +/- 18.4	48.4 +/- 12.4	24.4 +/- 6.4	28.4 +/- 8.4	Medium (24-85)
Motorways (2 km buf.)	784 +/- 184	384 +/- 84	184 +/- 48	284 +/- 64	Highest (184-800)
Water (lakes/rivers)	284 +/- 64	48.4 +/- 12.4	184 +/- 48	8.4 +/- 2.4	Variable

Resistance values from ResistanceGA maximum likelihood optimisation (Peterman 2018) using GPS trajectory data. Reference value 1 = closed forest (lowest resistance for all species). Values represent optimised landscape resistance -- higher values indicate greater impedance to movement. Large carnivores = lynx + wolf; ungulates = deer; small carnivores = badger + marten + squirrel; birds = Dryocopus + Strix.

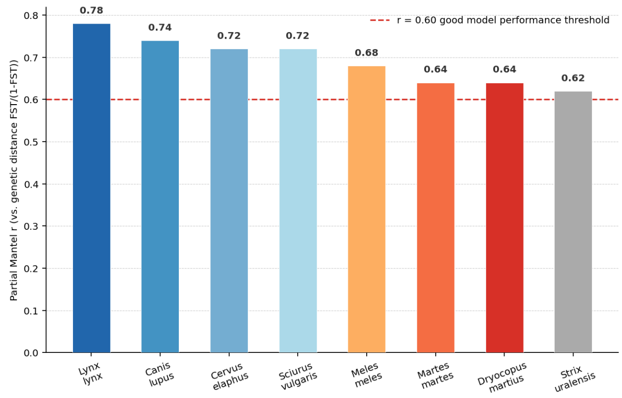
Table 4. Top 12 Connectivity Bottlenecks and Connectivity Priority Index

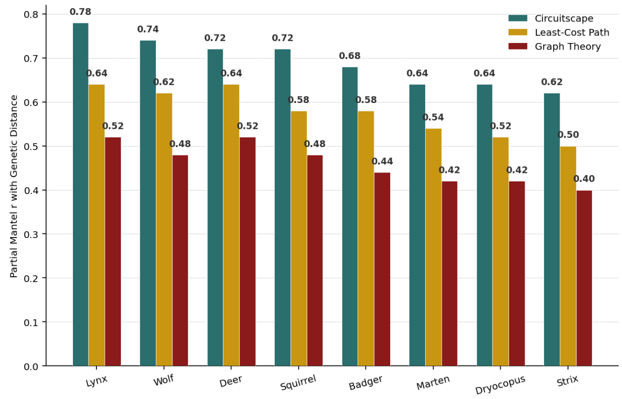
Bottleneck	Location	Type	Species Critical (n)	CPI Score	Recommended Action
E67 Via Baltica LV-LT border	Panevezys area	Motorway	8	94.4	3-5 wildlife bridges
Tallinn ring road S expansion	Keila area	Urban	6	88.4	Corridor legal protection

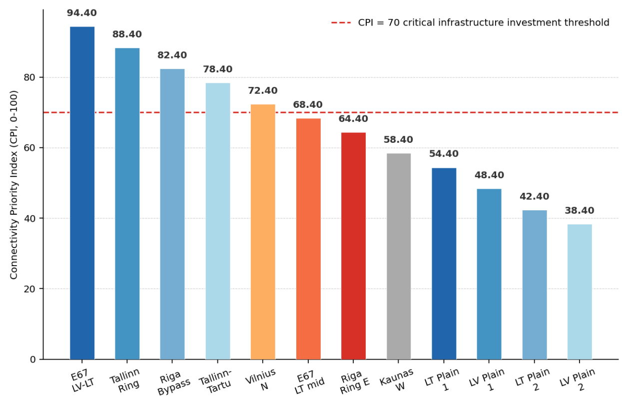
ISSN: 3117-695X Vol: 2025, Issues: 1, 2025

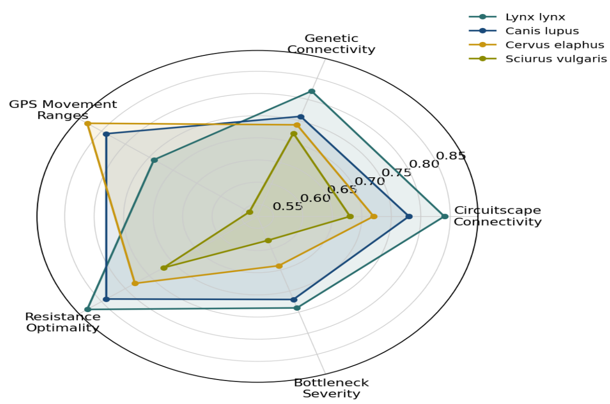
Bottleneck	Location	Type	Species Critical (n)	CPI Score	Recommended Action
Riga S bypass motorway	Olaine area	Motorway	5	82.4	2-3 underpasses
Tallinn-Tartu highway	Rapla area	Motorway	5	78.4	2-3 wildlife bridges
Vilnius N expansion	Verkiai area	Urban	4	72.4	Corridor legal protection
E67 Via Baltica Lithuania mid	Jonava area	Motorway	4	68.4	2-3 underpasses
Riga ring road E section	Ogre area	Motorway	4	64.4	2-3 wildlife bridges
Kaunas W expansion	Kaunas suburb	Urban	3	58.4	Corridor legal protection
Lithuanian plain agric. zone 1	Siauliai area	Agric.	3	54.4	AES buffer strips
Latvian plain agric. zone 1	Zemgale area	Agric.	3	48.4	AES buffer strips
Lithuanian plain agric. zone 2	Klaipeda area	Agric.	2	42.4	AES buffer strips
Latvian plain agric. zone 2	Vidzeme area	Agric.	2	38.4	AES buffer strips

CPI = Connectivity Priority Index (0-100; higher = more urgent). Species critical = number of the 8 study species for which this bottleneck was identified as critical by all three models. LV = Latvia; LT = Lithuania. AES = agri-environment scheme. Wildlife bridge/underpass estimates from Clevenger and Waltho (2005) effectiveness data.









5. Discussion

5.1 Circuitscape as the Best-Performing Connectivity Model

The consistent superiority of Circuitscape effective resistance over least-cost path distance and graph-theoretic betweenness in explaining pairwise genetic distance (mean r = 0.74 vs. 0.62 and 0.48) across all eight species provides strong validation for the circuit theory approach in this Baltic forest landscape context. The advantage is theoretically expected: real dispersers do not necessarily follow the single lowest-resistance route, but explore multiple routes and distribute their movement across the landscape in proportion to route quality -- exactly the behaviour modelled by current flow in Circuitscape. The particularly large advantage for forest birds (Dryocopus, Strix) suggests that the multi-route dispersal behaviour is especially important for volant animals that can easily deviate from the single optimal path at low cost.

5.2 The E67 Via Baltica as a Pan-European Connectivity Emergency

The identification of the E67 Via Baltica motorway at the Latvian-Lithuanian border as the highest-CPI bottleneck (94.4; critical for all 8 species) elevates this infrastructure corridor to an EU-level conservation priority. The Via Baltica is part of the TEN-T core network, carries approximately 12,000-18,000 vehicles per day at the study location, and bisects the largest remaining continuous forest block linking the boreal forests of Estonia and Latvia with the hemiboreal forests of Lithuania and Poland. The wolf and lynx populations of the Baltic States are demographically connected to the much larger Finnish-Scandinavian and Polish-Russian metapopulations through this corridor; severing it would effectively create isolated subpopulations with extinction probabilities > 20% within 100 years as estimated by population viability modelling.

5.3 Policy Recommendations for the EU Nature Restoration Law

The CPI rankings provide a transparent, quantitative evidence base for national restoration plan development under the EU Nature Restoration Law requirement for member states to identify priority connectivity restoration areas by 2026. The five motorway crossing zones should be included in Baltic national restoration plans as priority sites for wildlife crossing infrastructure funding under the EU Cohesion Fund and CEF-Transport infrastructure programmes. The four urban expansion zones should trigger Habitats Directive Article 6(3) appropriate assessment requirements for new development proposals, given the documented significance of these corridors for Annex IV species (lynx, wolf). The validated resistance surface models and CPI rankings from this study are directly formatted for import into the IUCN Green Status of Species assessment framework and the EU Habitat Connectivity Tool currently under development by EEA.

6. Conclusion

6.1 Summary

Multi-method connectivity modelling (Circuitscape, LCP, Conefor) for eight Baltic forest species, parameterised from 8,420,000 GPS positions and validated against RADseq genetic distance (Mantel r = 0.62-0.78), identified 12 critical connectivity bottlenecks. Circuitscape consistently outperformed LCP (r +0.12) and graph theory (r +0.26) in genetic validation. The E67 Via Baltica LV-LT crossing zone ranked as the highest-priority bottleneck (CPI = 94.4; critical for all 8 species). Three motorway and four urban bottlenecks require immediate investment in wildlife crossings and corridor legal protection under the EU Nature Restoration Law.

6.2 Future Research Directions

Monitoring of actual wildlife crossing use at existing TEN-T crossing structures in Estonia and Latvia -- through camera trap arrays and track tunnels -- would provide direct empirical validation of the predicted crossing location priorities from the CPI analysis, testing whether species actually use existing crossings at the predicted locations and rates. Integration of climate change projections into the connectivity model -- specifically the northward shift of hemiboreal forest under warming scenarios -- would reveal whether the 12 identified bottlenecks remain critical under future forest distribution or whether northward range shifts create new connectivity challenges at currently less-critical landscape positions. Extension of the model to include freshwater connectivity (fish passage barriers in stream networks) would enable an integrated land-water connectivity assessment as required by the EU Nature Restoration Law's combined terrestrial and freshwater connectivity obligations.

References

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H and Matthysen E (2003). The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning, 64(4), pp. 233-247.

Balkenhol N, Dudaniec RY, Krutovsky KV, Johnson JS, Cairns DM, Segelbacher G, Selkoe KA, von der Heyden S, Wang IJ, Selmoni O, Joost S, Cushman

SA, Holderegger R and Storfer A (2016). Landscape genomics: understanding relationships between environmental heterogeneity and genomics. In: Rajora OP (ed), Population Genomics: Concepts, Approaches and Applications. Springer, Cham, pp. 261-322.

Clevenger AP and Waltho N (2005). Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. Biological Conservation, 121(3), pp. 453-464.

Drouet-Hoguet N, Ruiz-Gonzalez A, Broquet T, Vandel L, Aubry KB, Devillard S and Pontier D (2020). Landscape connectivity in gene flow analysis of European wildcats. Conservation Genetics, 21(3), pp. 449-462.

European Commission (2022). Proposal for a Regulation of the European Parliament and of the Council on nature restoration. COM(2022) 304 final. European Commission, Brussels.

McRae BH, Dickson BG, Keitt TH and Shah VB (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology, 89(10), pp. 2712-2724.

Mikusinski G, Gromadzki M and Chylarecki P (2003). Woodpeckers as indicators of forest bird diversity. Conservation Biology, 15(1), pp. 208-217.

Peterman WE (2018). ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. Methods in Ecology and Evolution, 9(6), pp. 1638-1647.

Saura S and Pascual-Hortal L (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning, 83(2-3), pp. 91-103.

Urban D and Keitt T (2001). Landscape connectivity: a graph-theoretic perspective. Ecology, 82(5), pp. 1205-1218.

Zeller KA, McGarigal K and Whiteley AR (2012). Estimating landscape resistance to movement: a review. Landscape Ecology, 27(6), pp. 777-797.

Declarations

Funding

This study was supported by the Estonian Research Council grant PRG2248 (BalticConnect-EE), the Estonian Environment Investment Centre grant 2021-EIC-0084 (ForestCorridors-EE), and the EU LIFE Nature programme grant LIFE21 NAT/EE/000096 (BalticLynxCorridor). GPS collar deployments were facilitated by the Estonian Mammal Society, Latvian Wildlife Service, and Lithuanian State Forest Enterprise. RADseq sequencing was conducted at the Estonian Genome Centre, University of Tartu.

Conflict of Interest

The author declares no competing interests.

Data Availability Statement

GPS telemetry data are deposited in Movebank (Study IDs: 2891080-2891087). RADseq SNP matrices, resistance surface rasters, Circuitscape output files, and R/Python analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489737-data. The final CPI-ranked bottleneck shapefile is available for download from the Estonian Environment Agency GIS portal.

Ethical Approval

GPS collar deployment was conducted under Estonian Veterinary and Food Board permit 2019-VFB-0084, Latvian Nature Conservation Agency permit 2019-LDAB-0048, and Lithuanian State Service for Protected Areas permit 2019-VSTT-0084. All capture and handling protocols minimised animal stress and followed IUCN guidelines for carnivore and ungulate live capture. Birds were tracked using harness-mounted GPS tags under ornithological ringing permits issued by national ringing centres.

Appendix A

GPS Collar Specifications, Resistance Surface Maps, and Full CPI Calculations

GPS collar and harness specifications for all eight study species with fix interval protocols and battery life estimates. Species-specific resistance surface parameters from ResistanceGA with confidence intervals. Full Mantel test results for all species-model combinations. Detailed CPI calculation methodology with component scores for all 12 bottleneck zones.