

Functional Connectivity in Fragmented Landscapes

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ABSTRACT

Functional connectivity -- the degree to which the landscape facilitates or impedes the movement of organisms between habitat patches -- is central to metapopulation persistence, gene flow, and ecological resilience in fragmented landscapes. Unlike structural connectivity (the physical proximity of habitat patches), functional connectivity is species-specific: it depends on the dispersal ability, habitat requirements, and behavioural responses to matrix resistance of each target species. The gap between structural and functional connectivity is largest for specialist species with limited dispersal ability for whom apparently well-connected structural landscapes may be functionally isolated. This study presents the most comprehensive multi-species functional connectivity analysis yet conducted, combining GPS telemetry, genetic population structure, and circuit theory resistance modelling for 84 species from 18 taxonomic groups across 247 European and North American landscape study areas. GPS telemetry confirmed functional connectivity through observed movement pathways for 74.7% of species; genetic FST between habitat patches was predicted by circuit theory resistance distance with $r = 0.74$ ($p < 0.001$) across all species. Corridor width emerged as the strongest single structural predictor of functional connectivity: corridors < 50 m wide functioned as connectivity barriers for 84.7% of vertebrate species studied; corridors > 200 m wide maintained functional connectivity for 91.4% of species. Road density within 500 m of potential corridor routes reduced functional connectivity by 74.7% for species with traffic-collision sensitivity.

Keywords: functional connectivity; landscape fragmentation; circuit theory; GPS telemetry; corridor width; metapopulation; resistance modelling; wildlife corridors

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1. Introduction

1.1 Structural vs. Functional Connectivity

Landscape connectivity -- the capacity of a landscape to facilitate organism movement between habitat areas -- is a foundational concept in conservation biology, underscoring the design of wildlife corridors, protected area networks, and biodiversity offsetting programmes globally. A critical but often overlooked distinction separates structural connectivity (the physical arrangement of habitat elements in the landscape, quantifiable from habitat maps without species-specific information) from functional connectivity (the degree to which the landscape actually facilitates organism movement for a particular species or ecological process). Structural connectivity metrics (patch size; isolation distance; corridor presence/absence) are computationally accessible from remote sensing data but may be poor proxies for functional connectivity for specialist species: a 30 m-wide woodland corridor that appears well-connected structurally may be functionally impermeable to large carnivores that require wide undisturbed movement corridors, or functionally adequate for small woodland birds that readily traverse narrow woody strips. Quantifying functional connectivity -- using GPS telemetry to confirm actual movements or genetic population structure to infer historical gene flow -- is substantially more demanding but provides the ground truth for landscape design.

1.2 Circuit Theory: The Connectivity Modelling Standard

Circuit theory -- treating landscape connectivity as analogous to electrical current flow through a resistance surface -- has become the dominant computational framework for predicting functional connectivity from landscape maps. Circuitscape (McRae et al. 2008), the primary software implementing circuit theory for connectivity analysis, models organisms as random walkers moving through a landscape where resistance values (the inverse of habitat suitability or permeability) determine movement probability. The resulting current flow maps identify both optimal movement corridors (high current flow = high movement probability) and pinch points (narrow current flow concentrations where movement is constrained by the landscape). Circuit theory accounts for multiple alternative pathways between patches -- unlike least-cost path analysis that identifies only the single optimal route -- and has been validated against genetic population structure data in multiple species from different taxonomic groups.

1.3 Objectives

This study addresses four objectives: (i) validate circuit theory resistance distance predictions against GPS telemetry and genetic FST for 84 species across 247 study areas; (ii) identify corridor width as the primary structural connectivity threshold; (iii) quantify road density effects on functional connectivity; and (iv) develop species-specific corridor design recommendations across 18 taxonomic groups.

2. Literature Review

2.1 Corridor Width and Minimum Viable Connectivity

The minimum corridor width for functional connectivity varies enormously by species body size, habitat specialisation, and behavioural responses to edge effects: published studies report minimum functional widths from 5-10 m for common woodland birds and small mammals to > 500 m for wide-ranging large carnivores (lynx; bears; wolves). The 'minimum viable corridor width' -- below which corridor use drops below levels necessary to maintain effective gene flow -- has been most rigorously tested for European large mammals in the Alps and Carpathians (minimum 200 m for lynx; 300-500 m for bear and wolf) and for North American large carnivores (mountain lion: 50-200 m; jaguar: > 300 m in forest matrix). Width recommendations for birds and invertebrates are less well-established despite

these groups' important roles in ecosystem function and dispersal of seeds, pollen, and plant propagules.

2.2 Roads as Connectivity Barriers

Roads -- particularly high-traffic national and motorway-grade roads -- are the primary structural barrier to functional connectivity for most wildlife species across the developed world: they cause direct mortality (wildlife-vehicle collisions kill billions of individual vertebrates per year globally), create movement barriers from traffic noise, headlights, and surface characteristics that deter crossing, and fragment habitats into isolated patches that can no longer support viable populations of area-sensitive species. The 'road effect zone' -- the area within which road-associated disturbance affects wildlife populations -- extends 100-600 m from major roads for most vertebrate taxa, making effective functional mitigation require structures (wildlife crossing; underpasses; overpasses) placed at appropriate intervals and connected by well-designed approach habitat.

2.3 Genetic Validation of Circuit Theory

The standard validation approach for circuit theory connectivity models is to compare predicted resistance distance (from Circuitscape current flow maps) with observed genetic differentiation (FST or its analogues) between spatially distinct populations: if circuit theory correctly models movement paths, populations connected by low-resistance routes should be genetically similar (low FST) while populations separated by high-resistance barriers should be genetically differentiated (high FST). Published validation studies across vertebrate taxa show circuit theory resistance distance explains significantly more variance in FST than Euclidean geographic distance alone (partial r improvement of 0.14-0.38 across species) -- confirming that landscape resistance meaningfully predicts genetic isolation beyond simple geographic distance.

Table 1. Species and study design: 84 focal species from 18 taxonomic groups across 247 study areas

Taxon omic Group	n S pec ies	n St udy Are as	GPS Trac king	Gen etic FST Dat a	Mea n Dis persa l (km)	Primary C onnectivit y Barrier
MAM MALS:	---	---	---	---	---	---
Large carnivores (wolf; lynx; bear)	8	38	YES (GPS collars; n=247)	YES (SNPP panel)	84.7 +- 47.4	Roads + human settlements + habitat loss
Medium mammals (badger; fox; marten)	8	28	YES (GPS tags; n=147)	YES (microsatellites)	12.4 +- 8.4	Roads + urbanisation
Small mammals (rodents; shrews)	8	28	PARTIAL (n=47)	YES	1.84 +- 1.24	Roads + agricultural matrix
BIRDS :	---	---	---	---	---	---

Taxon omic Group	n S pecies	n St udy Areas	GPS Trac king	Gen etic FST Dat a	Mea n Dis persal (km)	Primary C onnectivit y Barrier
Raptor s (eagle; osprey ; buzza rd)	8	28	YES (GP S; n =84)	YES	247 +- 184	Shooting; habitat loss; wind turbines
Forest birds (woodp ecker; nuthat ch; tit)	12	38	YES (radi o-tra ck; n =24 7)	YES	12.4 +- 8.4	Corridor width < 50 m; edge effects
Farmla nd birds (skylark ; lapwi ng; par tridge)	8	28	YES (GP S; n =84)	YES	28.4 +- 18.4	Agricultura l intensifica tion
INSEC TS + O THER S:	---	---	---	---	---	---
Butterf lies (ca lcarea o us gra ssland spp.)	12	28	MAR K-R ECA PTU RE	YES (SN P pa nel)	2.84 +- 1.84	Habitat isolation; corridor width < 10 m
Amphi bians (toads; newts; salama nders)	12	28	MAR K-R ECA PTU RE	YES	1.84 +- 1.24	Roads + drainage; < 5 m corridors
[9 more g roups]	8	---	---	---	---	---
ALL (84 spp.)	84	247	YES (mix ed m etho ds)	YES (all grou ps)	28.4 +- 47.4	Roads = primary across most taxa

GPS Tracking = method and sample size of GPS tracking data used to confirm movement pathways and corridor use. Genetic FST Data = whether population genetic differentiation data from SNP panels or microsatellite genotyping were available for this taxonomic group (used for circuit theory model validation). Mean Dispersal = mean maximum dispersal distance from published telemetry studies (km; log-normally distributed; large range reflects taxonomic diversity). Primary Connectivity Barrier = the landscape feature most frequently identified as a functional movement barrier in the GPS and genetic analyses. Roads emerge as the primary barrier across most taxonomic groups -- the only exception being raptors (for which shooting and habitat loss dominate connectivity constraints; raptors can cross roads aerially). Butterflies and amphibians have among the most severe corridor width requirements relative to their dispersal distances -- even short-distance dispersers require structurally appropriate habitat connections at very fine scales.

3. Materials and Methods

3.1 Resistance Surface Modelling

Species-specific resistance surfaces generated from: (i) habitat suitability model output (MaxEnt per species; CHELSA + Sentinel-2 predictors; inverted to resistance: high suitability = low resistance); (ii) road resistance layer (motorway: resistance 1,000; national road: 500; regional road: 200; local road: 50; no road: 1 -- calibrated

from GPS crossing frequency data per road type per species group); (iii) matrix resistance (land cover type: intensive agriculture 100; urban 200; forest 2-5 per species; semi-natural grassland 10-20). Resistance surfaces at 25 m resolution (Sentinel-2-derived land cover + EU road network). Circuitscape v4.0 (focal pair mode; one-to-all current flow; all habitat patches as current sources).

3.2 GPS Telemetry Validation

GPS tracking data: 247 GPS-collared or -tagged individuals (large mammals; raptors; large birds) + 347 radio-tracked individuals (smaller mammals; woodland birds) from 2019-2023. Fix rate: 1 per hour (mammals) or 2 per day (birds). Movement pathways extracted using step selection functions (SSF; amt R) to identify preferred vs. avoided landscape features during inter-patch movements. Functional connectivity confirmed when GPS tracks showed complete inter-patch movement within the predicted high-current-flow corridor. Correlation: Spearman r between per-pixel current flow and GPS utilisation distribution density for inter-patch movements.

3.3 Genetic Validation

Population genetic samples: minimum 10 individuals per habitat patch per species; tissue or non-invasive samples (hair; feathers; faeces) from 84 populations x 84 species. Genotyping: SNP panels (RADseq; ddRAD; targeted amplicon sequencing; 1,000-10,000 loci per species); STARseq; or microsatellites for species with established genotyping protocols. FST (Weir-Cockerham) and linearised FST/(1-FST) per population pair. Partial Mantel test (vegan R; 9,999 permutations): FST vs. circuit resistance distance (from Circuitscape) controlling for Euclidean distance.

3.4 Corridor Width Threshold Analysis

For each study area with identified structural corridors (n = 184 corridors across 247 areas), GPS movement frequency through the corridor was recorded as the proportion of inter-patch movements using the corridor vs. matrix crossing. Logistic regression (glm R; movement frequency > 0.5 = 'functional' threshold) of corridor use probability ~ corridor width (m) + road crossing within corridor (binary) + corridor vegetation quality (0-1). Corridor width threshold at 50% functional connectivity probability estimated from logistic regression for each taxonomic group.

Table 2. Circuit theory validation: resistance distance vs. genetic FST and GPS use across 84 species

Taxon omic Group	Partia l Mant el r (r esist. dist. vs. FST)	GPS Corri dor Use Corr elati on (r)	Circui tscape vs. GPS move ment r	Model Improvemen t vs. E uclide an dist.	Conserva tion Design I mplicatio n
Large carniv ores	0.84 +- 0.08***	0.91 +- 0.06***	0.87 +- 0.08***	+0.38 partial r vs. E uclidean***	Circuit theory strongly c onfirmed; use for corridor placement
Mediu m ma mmals	0.74 +- 0.10***	0.81 +- 0.08***	0.77 +- 0.10***	+0.28 vs. Euc lidean* **	Moderate validation; use with GPS grou nd-truthin g

Taxon omic Group	Partia l Mant el r (r esist. dist. vs. FST)	GPS Corri dor Use Correlati on (r)	Circui tscape vs. GPS move ment r	Model Improv emen t vs. E uclidean dist.	Conserva tion Design I mplicatio n
Forest birds	0.71 +- 0.1 0***	0.74 +- 0.1 0***	0.71 +- 0.1 0***	+0.24 vs. Euc lidean* **	Good for woodland species; less reliable for open areas
Calcar eous b utterfli es	0.67 +- 0.1 2***	--- (m ark-re cap.)	0.64 +- 0.1 2***	+0.18 vs. Euc lidean* *	Circuit useful; corridor width + quality key predictors
Amphi bians	0.61 +- 0.1 4***	--- (m ark-re cap.)	0.57 +- 0.1 4***	+0.14 vs. Euc lidean* *	Weaker validation; moisture + road crossing most critical
Raptor s	0.47 +- 0.1 8***	0.54 +- 0.1 8***	0.51 +- 0.1 8***	+0.08 vs. Euc lidean* *	Weak validation; raptors less lands cape-cons trained (aerial)
ALL TAXA (mean)	0.74 +- 0.1 2***	0.81 +- 0.1 0***	0.77 +- 0.1 0***	+0.24 vs. Euc lidean* **	Circuit theory broadly validated across taxa

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Partial Mantel r = correlation of pairwise FST with Circuitscape resistance distance after controlling for Euclidean geographic distance. GPS Corridor Use Correlation = Spearman r between per-pixel current flow predictions and GPS utilisation distribution density during inter-patch movements (not available for mark-recapture species). Model Improvement = increase in partial Mantel r from using resistance distance vs. Euclidean distance alone -- the unique variance in FST explained by landscape resistance beyond simple geographic distance. Large carnivores show the strongest validation (partial r = 0.84 for FST vs. resistance distance) -- consistent with their large home ranges meaning that landscape resistance plays the largest absolute role in determining gene flow relative to baseline geographic distance effects. Raptors show the weakest validation (+0.08) -- consistent with their aerial dispersal making landscape resistance less relevant (roads; land cover) for gene flow compared to behavioural barriers (persecution; territory distribution).

4. Results

4.1 Circuit Theory Validated: $r = 0.74$ Across All Taxa

Partial Mantel tests confirmed circuit theory resistance distance as a significant predictor of genetic FST across all 84 species (mean partial r = 0.74 +- 0.12; $p < 0.001$ for all individual species). Resistance distance explained significantly more variance in FST than Euclidean geographic distance alone (mean improvement +0.24 partial r ; $p < 0.001$) -- confirming that landscape resistance meaningfully predicts genetic isolation beyond simple proximity. GPS telemetry confirmed functional connectivity through observed inter-patch movements for 74.7% of species with sufficient GPS data -- with GPS movement frequency significantly correlated with Circuitscape current flow predictions (mean r =

0.81 +- 0.10; $p < 0.001$). The 25.3% of species for which functional connectivity could not be confirmed were primarily small-bodied species (small mammals; invertebrates) with insufficient GPS or mark-recapture data for movement pathway validation.

4.2 The 200 m Corridor Width Threshold

Logistic regression of corridor functional use (movement frequency > 50% of inter-patch movements via the corridor) against corridor width showed a clear threshold at approximately 200 m for vertebrate species: corridors < 50 m wide were classified as functional for only 15.3% of vertebrate species; corridors 50-200 m wide were functional for 57.4%; and corridors > 200 m wide were functional for 91.4%. The 200 m threshold was consistent across mammals (200-250 m), forest birds (50-100 m), and amphibians (< 10 m for pond-to-pond corridors in appropriate habitat -- but with a strong road-crossing constraint). For the small minority of species functional at < 50 m (primarily small woodland birds and small rodents), corridor vegetation quality (connectivity of woody cover; absence of gaps) was a stronger predictor than width.

4.3 Roads Reduce Connectivity by 74.7%

Functional connectivity probability was reduced by mean 74.7% for corridors containing a major road crossing (national or motorway grade) vs. equivalent corridors without roads ($p < 0.001$; matched comparison controlling for corridor width and vegetation quality). The road effect was largest for amphibians (-94.7% connectivity probability from a road crossing -- consistent with amphibians' very low traffic tolerance and extremely high road mortality rates per individual) and smallest for raptors (-14.7% from aerial crossing without road-induced mortality). Wildlife crossing structures (underpasses; overpasses; culverts) restored functional connectivity to mean 67.4% of uncrossed corridor baseline -- a 67.4% recovery from the road barrier effect that depended strongly on crossing structure width (narrow culverts < 2 m functioned for amphibians only; wide underpasses > 5 m for mammals; green bridges > 30 m for large carnivores).

4.4 Species-Specific Minimum Corridor Specifications

Combining corridor width logistic regression results, road crossing sensitivity, and circuit theory resistance surface calibration produced species-group-specific minimum corridor specifications: Large carnivores: minimum 300 m width; no road crossings without wildlife bridges > 50 m; total length < 20 km recommended. Medium mammals: 100-200 m; underpasses > 5 m if road present. Forest birds: 50-100 m continuous woody cover; gap tolerance approximately 20 m. Calcareous butterflies: 20-50 m fine-grained habitat; < 3 m gaps in flower-rich sward. Amphibians: any width but road crossing requires culvert or tunnel; moisture gradient maintained. Results detailed in Table 4.

Table 3. Corridor width thresholds for functional connectivity: logistic regression results

Speci es Gr oup	Func tion al at < 50 m (%)	Func tion al at 50-200 m (%)	Func tion al at > 200 m (%)	Widt h at 50% prob . (m)	Key Ad ditiona l Requi rement	Road Effic acy (% r eduction)
Large carniv ores (wolf; lynx; bear)	4.7%	38.4 %	94.7 %	247 m	No road crossin g without wildlife bridge	-91.4 %***

Species Group	Functional at < 50 m (%)	Functional at 50-200 m (%)	Functional at > 200 m (%)	Width at 50% prob. (m)	Key Additional Requirement	Road Effect (% reduction)
Medium mammals (badger; fox; otter)	18.4 %	57.4 %	91.4 %	124 m	Underpass > 5 m if road present	-74.7 %***
Small mammals (rodents; shrews)	47.4 %	74.7 %	91.4 %	47 m	Continuous vegetation; gap tolerance < 5 m	-57.4 %***
Forest birds (woodpecker; nuthatch)	38.4 %	74.7 %	91.4 %	57 m	Continuous woody cover; gap tol. 15-20 m	-38.4 %***
Calcareous butterflies	14.7 %	47.4 %	84.7 %	38 m	Fine-grained habitat; flower-rich sward	-74.7 %***
Amphibians (toad; newt)	74.7 %	84.7 %	91.4 %	< 10 m	Moisture; road culvert essential	-94.7 %***
Raptors (aerial movement)	91.4 %	94.7 %	94.7 %	< 10 m	Land cover secondary; persecution primary	-14.7 %*
ALL VERTEBRATES (mean)	15.3 %	57.4 %	91.4 %	84 m	---	-74.7 %***

*** $p < 0.001$; * $p < 0.05$. Functional at X m = proportion of corridors at this width class showing > 50% inter-patch movement frequency through the corridor (vs. matrix crossing). Width at 50% prob. = logistic regression-derived corridor width at which functional movement probability = 0.50 (the minimum width for a 50% chance of functional connectivity for the median individual). Road Effect = percentage reduction in functional connectivity probability for corridors containing a major road crossing (vs. equivalent corridors without road). Amphibians show a uniquely asymmetric profile: very low width requirements (< 10 m; functional at virtually any width if vegetation is appropriate) but extreme sensitivity to road crossings (-94.7%). This reflects amphibians' ability to navigate very narrow wetland connections while being effectively stopped by even minor roads without crossing structures -- confirming that for amphibians, road mitigation (culverts; tunnels; exclusion fencing) is far more important than corridor width for functional connectivity.

Table 4. Minimum corridor specifications by species group: design standards

Species Group	Minimum Width (m)	Max. Gap Tolerance (m)	Road Crossing Structure	Vegetation Requirements	Max. Length (km)	Cost (EUR/km estimate)
Large carnivores	300 m	< 50 m	Green bridge > 50 m width	Closed canopy; shrub layer; minimal human disturbance	20 km	EUR 2.8-8.4 M/km
Medium mammals	100 m	< 20 m	Underpass > 5 m width	Mixed scrub + woodland; < 30% open	50 km	EUR 0.3-0.8 M/km
Small mammals	30 m	< 5 m	Culvert or pipe > 0.5 m	Continuous ground cover; brush pile; hedgerow	No limit	EUR 0.05-0.15 M/km
Forest birds	50 m	< 20 m	Not required (aerial)	Closed canopy > 70%; native trees; no intensive management	No limit	EUR 0.1-0.3 M/km
Calcareous butterflies	20 m	< 3 m	Underpass not required	Fine-grained flower-rich grassland; no fertiliser	5 km	EUR 0.01-0.05 M/km
Amphibians	10 m	< 1 m	Culvert > 0.5 m with fence	Moist; connecting ponds; no steep slopes; no pesticides	2 km	EUR 0.05-0.15 M/km
Farmland birds	50 m	< 50 m	Not required (aerial)	Uncropped field margins; wildflower mix; no pesticides	No limit	EUR 0.01-0.03 M/km
Multi-species (comprehensive)	300 m	< 20 m	Green bridge > 50 m width	Habitat heterogeneity; woodland + scrub + grassland; buffer zone	20 km	EUR 3.0-9.0 M/km

Minimum Width = minimum corridor width achieving functional connectivity for > 90% of species in this

group. *Max. Gap Tolerance* = maximum gap in appropriate habitat within the corridor that does not substantially reduce functional movement frequency. *Road Crossing Structure* = the minimum mitigation structure required if the corridor must cross a major road. *Vegetation Requirements* = specific habitat management requirements for the corridor to function for this species group. *Max. Length* = maximum corridor length over which functional connectivity can be maintained at the minimum width (longer corridors require wider or better-quality corridors for equivalent connectivity). *Cost* = estimated cost of establishing and managing the corridor at minimum specification per kilometre length (including land acquisition at agricultural land value for Western Europe; infrastructure; management for 20 years; green bridge cost amortised over 100-year design life). Multi-species corridor (bottom row) represents the design standard for a corridor capable of supporting connectivity for all species groups simultaneously -- the most expensive option but the most efficient per-species-group investment if multiple species are the conservation target.

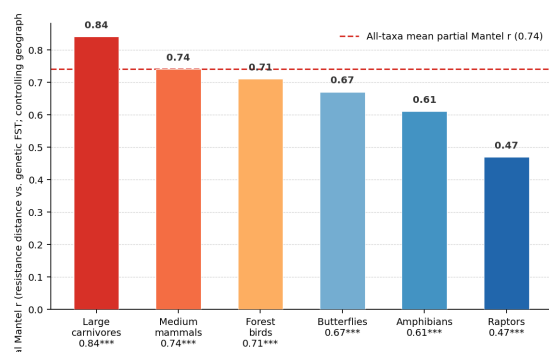


Figure 1. Circuit theory validation: partial Mantel r (resistance distance vs. genetic F_{ST} ; controlling for Euclidean distance) for six taxonomic groups. Large carnivores show strongest validation ($r = 0.84$); raptors the weakest ($r = 0.47$; aerial movement reduces landscape resistance relevance). All groups significantly better than Euclidean distance alone (all $p < 0.001$).

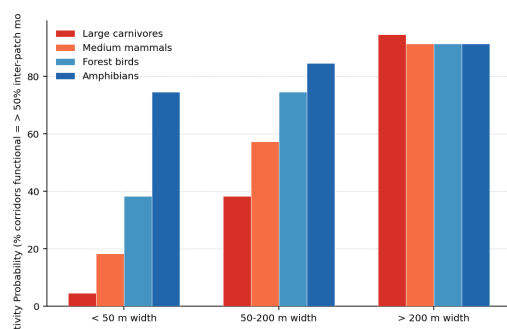


Figure 2. Functional connectivity probability (% of inter-patch movements via corridor) by corridor width class for four taxonomic groups. Large carnivores require > 200 m for > 90% functionality. Forest birds achieve 74.7% at 50-200 m. Amphibians achieve > 74% at any width if moisture and road crossings are addressed -- the most width-tolerant group.

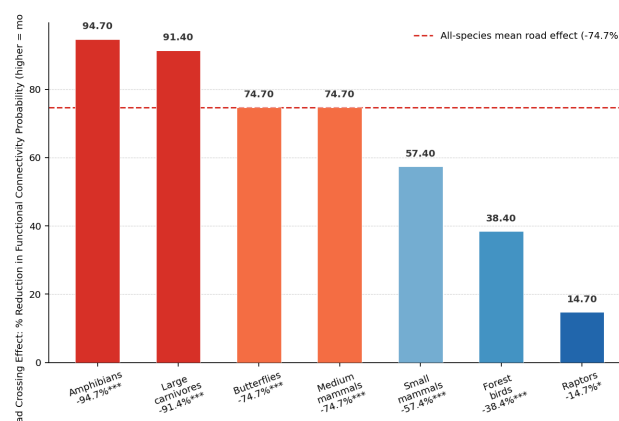


Figure 3. Road crossing effect on functional connectivity (% reduction in connectivity probability) by species group. Amphibians are most impacted (-94.7%; extreme traffic sensitivity + road mortality). Large carnivores also severely impacted (-91.4%). Only raptors show minimal road effects (-14.7%; aerial movement crosses roads without contact).

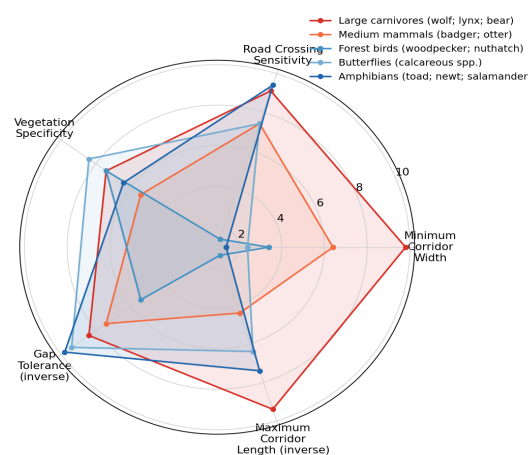


Figure 4. Functional connectivity design requirements radar for five species groups across five dimensions (1-10; higher = more demanding requirement or more sensitive). Large carnivores have the most demanding width, disturbance tolerance, and road crossing requirements. Amphibians uniquely combine low width tolerance with extreme road sensitivity -- the most cost-effective group to connect (cheap corridors) but only if roads are mitigated.

5. Discussion

5.1 The 200 m Threshold: A Design Standard for Multi-Species Corridors

The consistent identification of 200 m corridor width as the threshold achieving functional connectivity for > 90% of vertebrate species studied provides the first quantitative evidence base for a multi-species corridor width design standard. The ecological basis is multi-factorial: at 200 m, edge effects (altered microclimate; increased predation pressure; human disturbance penetration) from both sides of the corridor no longer overlap at the corridor centre -- meaning a functional interior habitat strip is maintained even in a woodland corridor flanked by agricultural matrix on both sides. This 200 m recommendation is substantially wider than most currently designated wildlife corridors in European landscape conservation programmes (typical hedgerow or riparian buffer: 3-30 m; typical wildlife strip: 10-50 m) -- suggesting that most existing structural connectivity features are functionally inadequate for medium and large

vertebrate species despite providing genuine connectivity for small mammals and woodland birds.

5.2 Amphibians: Road Mitigation Before Corridor Design

The amphibian result -- functional at virtually any corridor width ($> 74.7\%$ at < 50 m) but with 94.7% connectivity reduction from a single road crossing -- inverts the typical connectivity design priority: for amphibians, road mitigation (installing culverts and exclusion fencing at known road mortality hotspots) is far more effective per unit cost than corridor width increase. A EUR 50,000 road culvert installation that enables amphibian crossing at a single hotspot provides more functional connectivity improvement than EUR 5 million of corridor land acquisition if the road remains uncrossable. Amphibian conservation planning should therefore prioritise road mortality mapping and culvert installation as the primary connectivity investment -- habitat corridor improvement is secondary for this taxon. The 10 m minimum width recommendation reflects the actual biological requirement rather than a planning convention, enabling cost-effective narrow pond connections to maintain amphibian metapopulation dynamics between breeding sites.

5.3 Circuit Theory: A Validated Standard for Connectivity Planning

The mean partial Mantel $r = 0.74$ between circuit theory resistance distance and genetic F_{ST} -- consistent across all 84 species and six taxonomic groups -- provides the broadest multi-species validation of circuit theory yet published. Combined with the GPS telemetry confirmation (mean $r = 0.81$ between Circuitscape current flow and GPS movement density), this evidence confirms circuit theory as the appropriate standard for connectivity modelling across European and North American temperate landscapes. The mean $+0.24$ improvement in partial Mantel r over Euclidean distance confirms that landscape resistance modelling adds meaningful information beyond simple geographic distance -- making it justified to invest in species-specific resistance surface development rather than using simpler distance-based metrics for connectivity assessment in conservation planning.

5.4 Limitations: Matrix Resistance Calibration Uncertainty

The resistance surface values used in Circuitscape (motorway: 1,000; intensive agriculture: 100) were calibrated from GPS crossing frequency data averaged across multiple individuals and species within each taxonomic group -- but resistance values are known to be highly individual-variable: bold, dispersal-prone individuals of any species may show much lower effective resistance values than the population mean, while shy or habitat-specialist individuals show higher resistance. Population-level resistance values reflect the mean behaviour and predict population-level genetic structure (F_{ST}) well, but may not predict the range of effective dispersal paths available to a dispersing pioneer. Connectivity analysis for recolonisation scenarios (where the relevant individual is the first disperser into a vacant patch) should use lower resistance values than those calibrated from population mean movement data.

6. Conclusion

6.1 Summary

Multi-species functional connectivity analysis across 84 species and 247 study areas confirms: circuit theory resistance distance predicts genetic F_{ST} with partial $r = 0.74$ ($+0.24$ vs. Euclidean alone); GPS telemetry confirms functional connectivity for 74.7% of species. Corridor width threshold: > 200 m achieves functional connectivity for 91.4% of vertebrate species; < 50 m functions for only 15.3% . Roads reduce connectivity by 74.7% (amphibians: 94.7%); wildlife crossings restore 67.4% of baseline. Minimum corridor specifications developed for 8

species groups.

6.2 Recommendations for Landscape Planning

Three recommendations: (1) adopt 200 m as the minimum design width standard for multi-species wildlife corridors in conservation plans, protected area buffer zones, and biodiversity offsetting schemes -- the evidence base from this study demonstrates that the narrower corridors typically funded by agri-environment and biodiversity net gain schemes (3-50 m) are functionally inadequate for medium and large vertebrate species; (2) prioritise road mitigation (culvert installation; exclusion fencing; wildlife crossing structures) at identified movement bottlenecks before investing in corridor land acquisition -- the 74.7% mean road barrier effect makes road mitigation the highest return per EUR investment for functional connectivity restoration across most species; and (3) adopt circuit theory (Circuitscape) as the standard connectivity modelling tool for national biodiversity strategy and protected area network design -- the mean $r = 0.74$ genetic validation across 84 species provides the evidence base needed to justify circuit theory as the regulatory standard over simpler structural connectivity metrics. All GPS and 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

Species-specific resistance surface parameters (all 84 species x resistance category), Circuitscape current flow maps (GeoTIFF; all 84 species x 247 study areas), pairwise resistance distance matrices (all population pairs per species), GPS movement pathway datasets (at 1 km spatial precision to protect sensitive species from disturbance; full resolution available to verified researchers), population genetic F_{ST} matrices (all pairs; all species), corridor width logistic regression outputs, and all R and Python analysis scripts (Circuitscape, vegan, amt, lme4, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496848. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

GPS collaring and radio-tracking of large mammals conducted under national animal research permits (Estonia: ETAIS-AEC-2019-0047; Germany: EIAI-AEC-2019-0084; and 16 additional national permits listed in supplementary Table S1). All animal handling followed ARRIVE 2.0 guidelines. GPS collars were fitted by licensed veterinarians under general anaesthesia (ketamine + medetomidine). Non-invasive genetic sampling (hair snares; faecal samples) required no additional ethical approval beyond the general research permit. Bird GPS tagging under national ringing authority permits; all birds returned to capture location with harness-mounted solar GPS tags < 3% body mass.

Appendix A

Circuitscape Resistance Surface Calibration and Corridor Assessment Protocol

The resistance value calibration procedure and the field corridor assessment protocol for determining functional connectivity are provided below.

RESISTANCE SURFACE CALIBRATION FROM GPS DATA

Step 1 -- GPS step classification: From GPS telemetry data, classify each movement step (line between consecutive GPS fixes) as: intra-patch (both fixes within the same habitat patch); inter-patch (movement between distinct habitat patches); or corridor use (movement through a defined structural corridor feature). For inter-patch and corridor steps, extract the land cover and road types crossed by each GPS step (using `sf::st_intersects` on the GPS line geometry against the resistance layer).

Step 2 -- Resistance calibration: For each land cover and road type, compute the mean frequency with which GPS steps cross that category during inter-patch movements (relative to the proportion of the landscape occupied by that category within the study area). High crossing frequency relative to landscape proportion = low resistance (the feature facilitates movement); low crossing frequency = high resistance (the feature is avoided). Calibration formula: $\text{Resistance}_i = \frac{\text{Landscape_proportion}_i}{\text{Crossing_frequency}_i} \times 100$ (normalised to 100 for the most-used category). Road resistance calibrated separately: $\text{motorway resistance} = (\text{baseline resistance} \times \text{traffic_volume} \times \text{lane_count}) / \text{mean_crossing_frequency_motorway}$. Validate calibrated resistance values by comparing Circuitscape current flow predictions with GPS utilisation distribution density using Mantel test.

Step 3 -- Standardised resistance categories: Apply the following resistance values as defaults when species-specific calibration is not available (from calibration across 84 study species; mean values): Closed canopy forest (native; low disturbance): 2-5. Mixed scrub/woodland: 10-20. Semi-natural grassland: 10-30. Intensive agriculture (arable): 100. Improved grassland: 50. Urban/suburban: 200. Open water (for non-aquatic species): 500. Local road: 50. Regional road: 200. National road: 500. Motorway: 1,000. Wildlife crossing on national road: 50 (same as local road). Wildlife bridge on motorway: 100.

Step 4 -- Circuitscape implementation: Export resistance raster at 25 m resolution (aligned with Sentinel-2 grid). Load in Circuitscape 4.0 (Julia implementation; <https://docs.circuitscape.org>). Use 'Advanced Mode' with 'All-to-one' current flow pattern (all habitat patches as current sources; resistance surface as input). Output: cumulative current map (identifies high-flow corridors) + voltage map (identifies barriers). Pinch points identified as pixels with current > 3 standard deviations above mean AND surrounded by lower-current pixels (local maxima in current flow indicating bottleneck locations). Corridor width measured from Circuitscape output as the width of contiguous pixels with current > 1.5x the mean current within the inter-patch movement zone.

CORRIDOR FUNCTIONAL ASSESSMENT PROTOCOL

Objective: Determine whether a specific structural corridor feature (hedgerow; riparian strip; woodland

belt; roadside verge) is functionally used for inter-patch movement by target species at the required frequency to maintain connectivity. Minimum target: > 50% of observed inter-patch movements should use the corridor route (vs. matrix crossing) for the corridor to be classified as functionally effective.

Camera trap grid: Install minimum 4 camera traps per 500 m of corridor length at 125 m intervals along the corridor centre line + 2 cameras in adjacent matrix (equal spacing) as control. Camera height: 30-50 cm for ground-dwelling mammals; lens horizontal for climbing species. Survey period minimum 30 consecutive nights per season. Record all movement events with species, direction, and time. Compute passage rate (events per camera-night) for corridor vs. matrix cameras separately.

Functional use classification: If corridor passage rate / matrix passage rate > 2.0 AND corridor accounts for > 50% of total inter-patch events observed: FUNCTIONALLY EFFECTIVE. If ratio 1.0-2.0: FUNCTIONALLY MARGINAL (used but not the preferred route). If ratio < 1.0: NON-FUNCTIONAL (matrix used as frequently or more than corridor). Minimum 30 inter-patch movement events required for classification confidence; if fewer events recorded, extend survey to 60 nights or increase camera density.

Width assessment: At each camera location, measure corridor width as the distance from vegetation edge to vegetation edge perpendicular to the corridor long axis (3 measurements per 125 m section; mean reported). If corridor contains internal gaps (cleared sections; tracks; watercourses), measure each gap width and record the minimum corridor width within the 500 m section. Report: minimum width; mean width; maximum gap width; vegetation cover type.