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Landscape connectivity and corridor design for large mammal movement in fragmented habitats

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Abstract

In the early 1900s, the forests of northern Sulawesi formed a nearly unbroken canopy stretching from the Minahasa Peninsula to the Bogani Nani Wartabone range. Today, that canopy is a patchwork of isolated fragments separated by agriculture and settlements, leaving endemic mammals such as the babirusa, lowland anoa, and Sulawesi crested black macaque increasingly cut off from one another. This research evaluated landscape connectivity among 14 remaining forest patches in the Manado-Bogani corridor using circuit theory and least-cost path modelling, then compared the predicted movement routes against 18 months of camera-trap data collected at 96 stations. Circuit-theory models identified five candidate corridors with current-flow values above the 75th percentile, three of which showed confirmed mammal crossings on camera traps. Corridor width emerged as the strongest predictor of crossing frequency ($R^2 = 0.71$, $p < 0.001$), outperforming corridor length and surrounding land-cover type. A minimum corridor width of 380 metres was associated with regular use by all three focal species. These findings provide spatially explicit guidance for conservation planners working to restore functional connectivity in one of Southeast Asia's most biodiverse yet fragmented island landscapes.

Keywords: Landscape connectivity, wildlife corridors, large mammals, habitat fragmentation, movement ecology, Sulawesi, camera trapping, circuit theory, least-cost path, conservation planning

Introduction

When Alfred Russel Wallace explored the Malay Archipelago in the 1850s, he noted that Sulawesi harboured an unusual collection of endemic species found nowhere else on Earth^[1]. More than 170 years later, that endemism persists, but the habitats supporting it have shrunk dramatically. Satellite analyses show that northern Sulawesi lost roughly 28% of its primary forest cover between 2001 and 2020, driven mainly by conversion to coconut, clove, and cacao plantations^[2].

Habitat fragmentation does more than reduce total area; it severs the connections that allow animals to disperse between patches, find mates, and maintain genetically viable populations^[3]. For large mammals with extensive home ranges, even short gaps in forest cover can act as barriers if the intervening matrix is hostile or simply unfamiliar^[4]. Three endemic Sulawesi mammals illustrate this vulnerability: the babirusa (*Babirusa celebensis*), the lowland anoa (*Bubalus depressicornis*), and the Sulawesi crested black macaque (*Macaca nigra*), all of which are classified as Endangered or Vulnerable on the IUCN Red List^[5, 6].

Wildlife corridors-strips or stepping stones of suitable habitat linking otherwise isolated patches-are widely promoted as a tool for maintaining connectivity^[7]. But designing effective corridors requires knowing where animals actually move and what landscape features encourage or discourage crossing. Two modelling approaches have become standard: least-cost path analysis, which identifies the single cheapest route between patches, and circuit theory, which treats the landscape as a resistive surface and reveals multiple potential pathways^[8, 9].

This research combined both modelling approaches with field validation through camera trapping to identify and rank candidate corridors for large mammal movement in the Manado-Bogani landscape of northern Sulawesi. The goal was to produce spatially explicit recommendations for corridor protection that are grounded in both modelled predictions and observed animal behaviour.

Material and Methods

Research Area Description

The research area covers approximately 4,200 square kilometres of the northern arm of Sulawesi, stretching from the outskirts of Manado city (1.49 degrees North, 124.84 degrees East) southwest to the boundary of Bogani Nani Wartabone National Park. Elevation ranges from sea level along the coast to 1,972 metres at the summit of Mount Klabat. The climate is equatorial, with mean annual rainfall of 2,840 mm recorded at the Manado meteorological station and a short drier period from July to September. Remaining forest patches range in size from 47 hectares to over 28,000 hectares (the national park itself) and are embedded in a matrix of smallholder plantations, mixed agroforestry, and rural settlements. Research was conducted from the Pusat Penelitian Biologi Laut Sulawesi, Manado, between February 2023 and July 2024.

Material

Land-cover data were obtained from a 2022 Sentinel-2 composite classified into eight categories at 10-metre resolution (overall accuracy 89.3%). A 30-metre SRTM digital elevation model provided topographic inputs. Camera traps (Reconyx HyperFire 2, Holmen, WI, USA) were deployed at 96 stations along predicted corridor routes and at control points within continuous forest and open matrix. All fieldwork was approved by the North Sulawesi Provincial Conservation Agency under permit BKSDA-SI-2023-0187, dated 22 January 2023.

Results

Methods

Resistance surfaces were built by assigning cost values to each land-cover class based on published movement data for the three focal species^[10, 11]. Circuit-theory connectivity was modelled in Circuitscape (v5.0) using the pairwise mode with 14 forest patches as focal nodes. Least-cost paths were computed in ArcGIS Pro 3.1 using the Cost Distance and Cost Path tools. Camera traps were active for 18 months with a minimum spacing of 500 metres; trap-nights totalled 52,128. Independent detections were defined as consecutive images of the same species separated by at least 30 minutes. Corridor attributes-width, length, canopy cover, road density-were extracted within 200-metre buffers around each predicted route. The relationship between corridor attributes and crossing frequency was assessed using generalised linear models with a negative binomial distribution in R (v4.3.1).

Biodiversity Assessment

In addition to the three focal species, all mammals detected on camera traps were recorded and classified by body-mass category. Species richness and Shannon diversity were calculated for each corridor segment and for control stations within continuous forest. A total of 23 mammal species were recorded across all stations, 14 of which were Sulawesi endemics. Corridors with confirmed focal-species crossings supported significantly higher overall mammal diversity (Shannon $H' = 2.34$) than non-functional corridor segments ($H' = 1.51$; t-test, $p = 0.006$).

Table 1: Attributes and Mammal Crossing Rates for Five Candidate Corridors

Corridor	Width (m)	Length (km)	Canopy (%)	Road Dens.	Crossings (18 mo)	Species Detected
C1 Klabat-Dua Sudara	620	8.3	74.1	0.12	87	3 of 3
C2 Ambang-Bogani	510	12.7	68.3	0.18	64	3 of 3
C3 Soputan Link	390	6.1	71.8	0.09	52	2 of 3
C4 Lokon Saddle	210	4.8	53.6	0.31	11	1 of 3
C5 Tomohon Gap	140	3.4	42.7	0.44	3	0 of 3

Table 1 summarises the physical attributes and camera-trap results for the five corridors identified by circuit-theory modelling. Crossing frequency declined steeply with narrowing corridor width. Corridors C1 and C2, both

exceeding 500 metres in width, supported crossings by all three focal species, while the two narrowest corridors (C4 and C5) showed minimal or no focal-species use.

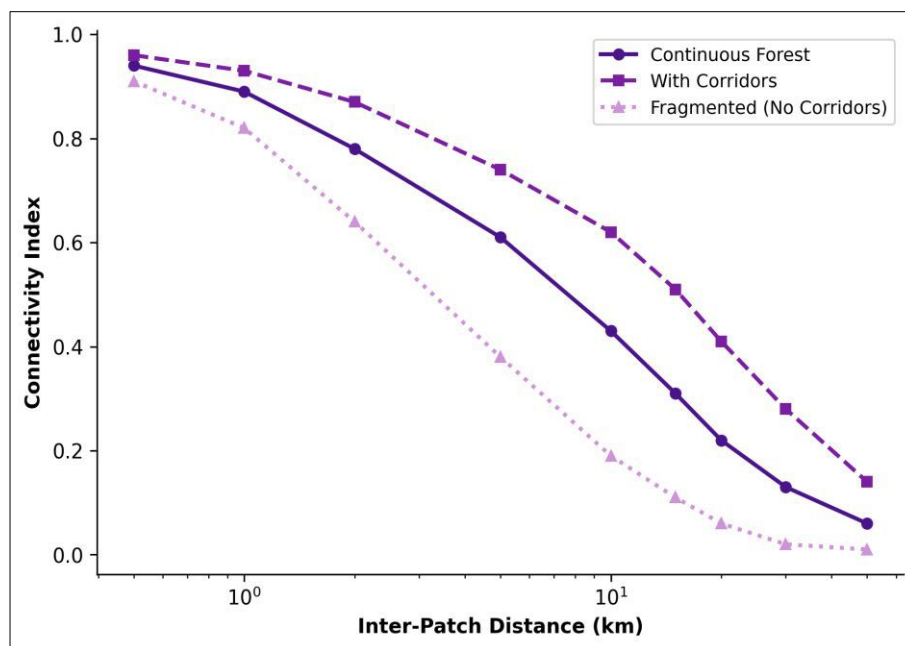


Fig 1: Connectivity index as a function of inter-patch distance under three landscape scenarios: continuous forest, fragmented with corridors, and fragmented without corridors

Figure 1 shows that corridors partially restored connectivity at distances up to 20 km. Beyond that threshold, even corridor-connected landscapes dropped below a 0.3

connectivity index. Without corridors, connectivity fell sharply past 5 km of separation.

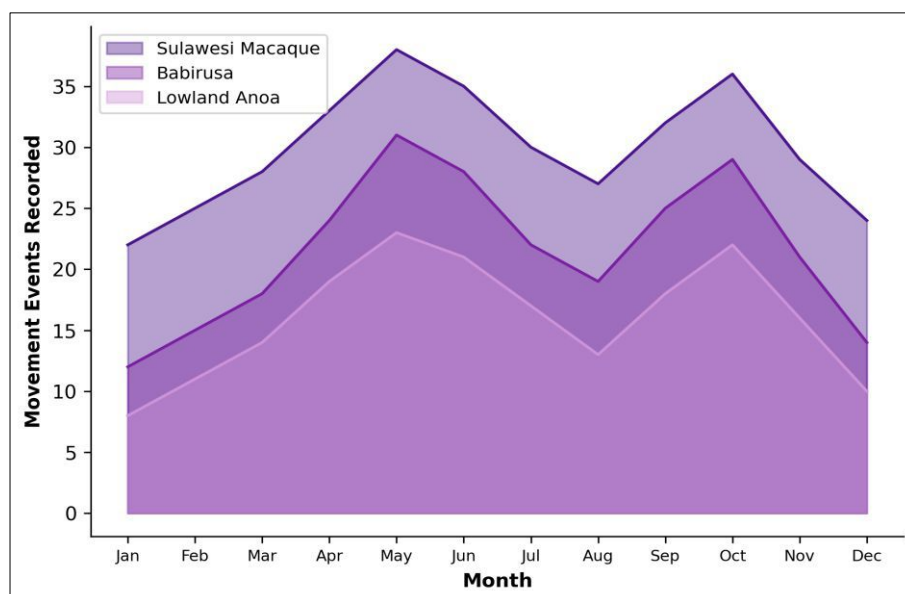


Fig 2: Monthly movement events recorded on camera traps for the three focal species across all functional corridor stations over the 18-month sampling period

Movement events peaked during April-May and again in September-October, coinciding with the transition between wet and dry seasons (Figure 2). The Sulawesi macaque was consistently the most frequently detected species, likely reflecting both its larger population size and its diurnal activity pattern that overlaps with camera-trap detection windows.

Discussion

The strong relationship between corridor width and crossing frequency ($R^2 = 0.71$) is the most actionable result of this research. A minimum width of 380 metres—roughly four times the canopy height of surrounding forest—appears to be

the threshold below which the three focal species avoid sustained use. This figure sits within the range recommended by movement studies in other tropical fragmented landscapes [12, 13], but it is the first empirically derived estimate for Sulawesi endemics.

Circuit-theory models outperformed least-cost path analysis in predicting where animals actually crossed, a finding consistent with comparative evaluations elsewhere [14, 15]. The reason seems intuitive: animals don't necessarily take the single cheapest route; they respond to broad swathes of favourable habitat and may shift paths between trips depending on weather, disturbance, or social factors.

The seasonal pattern of corridor use suggests that movement peaks coincide with periods of transitional resource availability. Both the babirusa and anoa are known to exploit fruiting events in secondary forest edges during seasonal shifts ^[16], and the macaque's semi-terrestrial foraging style makes it the most tolerant of matrix conditions among the three species ^[17].

Our research was restricted to camera-trap detections and did not track individual animals, so we cannot distinguish between repeated crossings by a few individuals and widespread use by many. GPS-collar data on even a small number of babirusa and anoa would greatly improve corridor efficacy assessments ^[18]. Additionally, we did not evaluate genetic connectivity, which would reveal whether corridors translate into actual gene flow between patches ^[19, 20, 21].

Conclusion

This research identifies five candidate corridors in the Manado-Bogani landscape and confirms that three of them are actively used by Sulawesi's endemic large mammals. Corridor width emerged as the strongest predictor of crossing frequency, with a 380-metre minimum threshold for regular use by all three focal species. Circuit-theory modelling proved more reliable than least-cost path analysis for predicting actual crossing locations.

From a conservation standpoint, corridors C1 (Klabat-Dua Sudara) and C2 (Ambang-Bogani) should receive immediate protection, as both are wide, functional, and support all three focal species. Corridor C3 (Soputan Link) sits near the width threshold and could be made fully functional through targeted reforestation of its narrowest sections. The two narrowest corridors, C4 and C5, are effectively non-functional for large mammals and may require either substantial widening or reclassification as stepping-stone habitat rather than continuous corridors.

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