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Delineating Functional Corridors Linking Leopard Habitat in the Eastern and Western Cape, South Africa

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Abstract: Natural landscapes are increasingly fragmented due to human activity. This contributes to isolation and inadequate gene flow among wildlife populations. These threats intensify where populations are already low, and gene flow is compromised. Ensuring habitat connectivity despite transformed landscapes can mitigate these risks. Leopards are associated with high levels of biodiversity and are the last widely occurring, free-roaming apex predator in South Africa. Although highly adaptable, leopard survival is reduced by human-caused mortality and habitat destruction. We aimed to assess the connectivity of leopard habitat in the Eastern Cape and Western Cape, South Africa. We predicted leopard habitat by correlating GPS data from 31 leopards to environmental features that included human-associated and natural landscapes. We used circuit theory to delineate corridors linking known leopard populations. Finally, using camera traps, we tested whether five predicted corridors were used by leopards. Leopard habitat was strongly correlated to moderate slopes and areas of natural land-cover and plantations, highlighting mountainous areas as important habitat with high connectivity probability. While most habitat patches showed some level of connectivity, leopards avoided highly transformed landscapes, potentially isolating some populations. Where corridors are not functional, active conservation measures for species connectivity becomes important.

Keywords: carnivore conservation; connectivity; circuit theory; habitat selection; Maxent; *Panthera* pardus

1. Introduction

Major threats to ecosystem functioning include the loss of biodiversity and habitat fragmentation due to human activities [1]. As a result, wildlife populations may become increasingly isolated from one another [2–4], increasing the likelihood of inbreeding and genetic drift-induced differentiation [2,4,5]. Broader ecological impacts of isolation include higher levels of intra- and interspecific competition in isolated habitat patches [6,7], and a resulting displacement of individuals into high-risk areas with increased anthropogenic effects [8,9].

Ensuring inter-patch connectivity in fragmented environments is paramount to mitigating the effects of isolation and improving species survival [3]. Two broad definitions of connectivity exist: structural and functional [10]. A structural corridor describes the physical environment and excludes the behavioural response of individuals [10]. Alternatively, a corridor becomes functional when it enables individuals to move along these corridors, promoting inter-path connectivity and enhancing genetic exchange [10–12]. Therefore, the ability of individuals to move across the landscape depends on complex interactions. For example, human-associated landscapes often contain barriers to animal movement such as linear transport lines [13], transformed landscapes (e.g., cultivated areas [14]) and human-caused mortality, either accidentally (e.g., vehicle collisions) or intentionally

(e.g., hunting, human–wildlife conflict; [15,16]). Similarly, natural landscapes can also contain barriers (e.g., steep ravines, large lakes [17]), while prey availability and distribution also contribute to species distribution (e.g., resource dispersion hypothesis, [18]).

Understanding the factors driving habitat selection provides opportunities to predict species distribution, and to identify potential functional corridors linking populations [19]. We used a multivariate approach, maximum entropy (Maxent), to correlate species presence data and environmental covariates to predict habitat distribution of species across the landscape [20]. The isolation by resistance hypothesis (IBR) [21] predicts a positive correlation between the isolation of populations and the level of resistance separating these populations. Low-quality habitat and non-habitat may have scarce resources and a high mortality risk, resulting in landscapes with higher resistance, while high-quality habitat contains abundant resources and low mortality risk, providing a permeable landscape. By incorporating species habitat distribution, derived using data from the target species, as a resistance landscape into corridor modelling, functional corridors can be delineated using circuit theory [21,22]. Circuit theory considers movement based on random walk algorithms and assumes the individual has no insight into landscape heterogeneity, thereby predicting many potential routes for current flow where there is the least resistance [21,22]. Incorporating spatial heterogeneity of landscapes along with random walk considerations gives IBR a strong theoretical foundation for predicting functional corridors [19,23,24].

Their large spatial requirements, low reproductive rates, strong association with high species richness, and their regularity roles in terrestrial ecosystems make large carnivores a useful focal species to predict landscape connectivity at regional scale for sympatric species [25–27]. Despite being highly adaptable and able to occupy a wide range of environments, leopard (*Panthera pardus*) survival is threatened by habitat loss and fragmentation [15,25]. These threats are further compounded by human-caused mortality due to human-carnivore conflict, and hunting [15,28,29]. Leopards in the Eastern and Western Cape provinces of South Africa are reported to have a discrete population structure, low population densities, and are persecuted due to high levels of human-carnivore conflict [4,30–32]. In the face of these threats, identifying corridors connecting habitat patches and reducing human–carnivore conflict can promote gene flow and the long-term survival of the leopard and sympatric species. In this study, we aim to identify leopard habitat, predict potential landscape corridors linking habitat patches, and test functionality between predicted habitat patches to determine whether leopard populations in the region can connect despite modified landscapes. First, we evaluate the relationship between leopard presence and anthropogenic and natural covariates, and use the model with the best fit to predict leopard habitat. Second, we employ circuit theory [33], to predict potential corridors linking 14 known leopard populations using the modelled leopard habitat distribution as a surface layer. Finally, while incorporating leopard occurrence data to random walk algorithms using circuit theory improves the identification of functional corridors [21], we used camera trap surveys to validate and test the functionality of five predicted corridors linking potentially isolated leopard populations in the Western Cape.

2. Materials and Methods

2.1. Study Area

Located in South Africa, our study took place in the Eastern and Western Cape provinces (Figure 1). The two provinces together make up approximately 298,428 km^2 and host heterogeneous land uses, including dense urban zones, agriculture (e.g., cultivated, rangeland livestock, game farms), protected areas, and forestry. Vegetation biomes vary throughout the area and include Fynbos, Succulent Karoo, Nama Karoo, Albany Thicket, and Forest [34]. Elevation ranges from sea level and low valleys less than 500 m above sea level, to tall mountain peaks reaching over 1600 m along the Cape Fold Mountain range. The climate is moderate with annual rainfall ranging from 208 mm to 943 mm between the arid northern reaches and mesic southern regions [35]. Predominantly winter rainfall

patterns occur in the west, becoming increasingly summer rainfall toward the east and north [34].
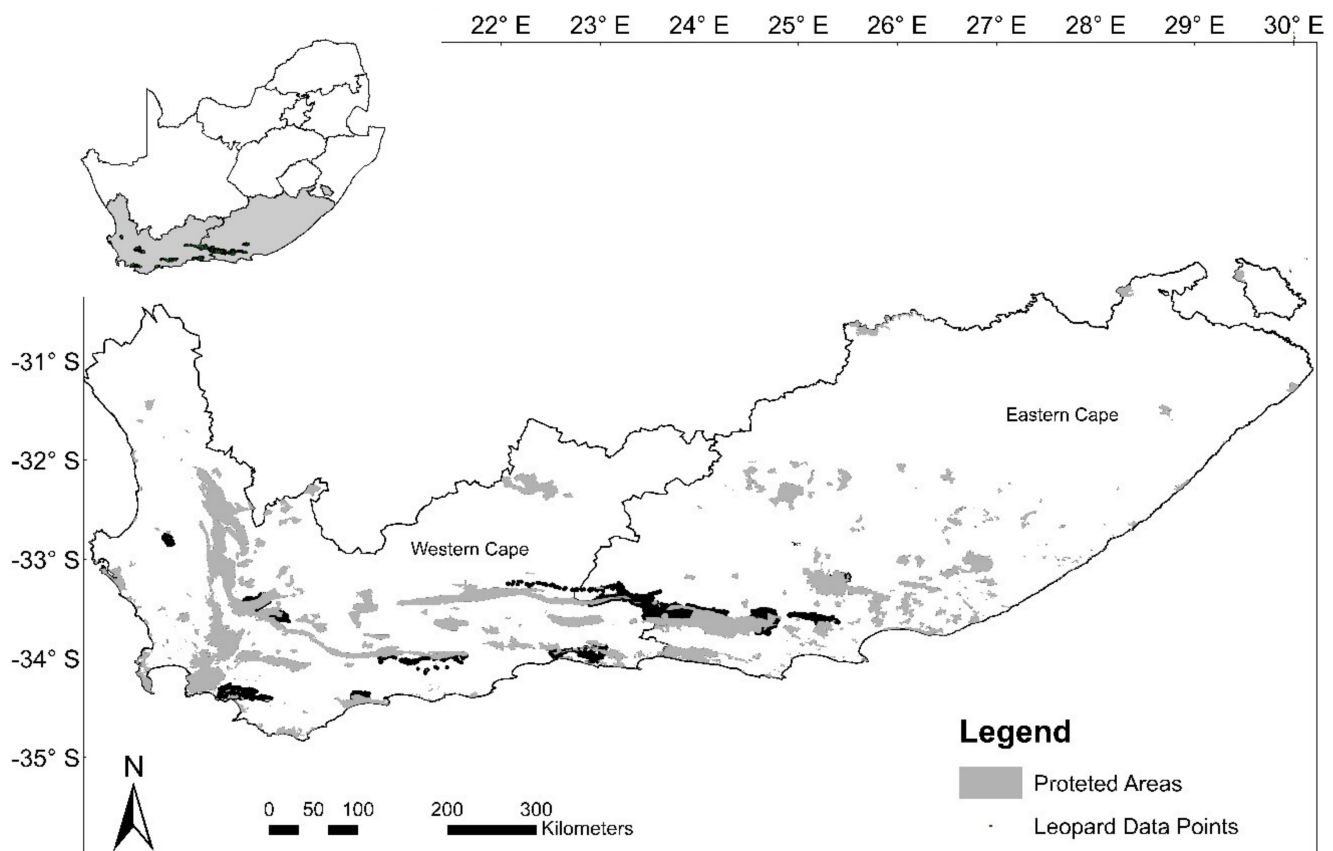

Figure 1. Study area and distribution of leopard occurrence data used to predict leopard habitat distribution models. The insert indicates the location of the study within South Africa.

2.2. Leopard Occurrence Data

We used GPS data from 31 free-roaming adult leopards (19 males and 12 females; Table 1) collared (GPS collars, Vectronic aerospace, Berlin, Germany; Satellite collars, AWT, Johannesburg, South Africa; Followit AB, Lindesberg, Sweden) between 2007 and 2021 in the Eastern Cape and Western Cape (Table 1; Figure 1). Each leopard was monitored for an average of 259 (±160) days, with males monitored for 253 (±149) days, and females 269 (±182) days on average (Table 1). Collars were set to obtain fixes between 4 and 6 h intervals. Leopards were captured in walk-in, fall-door traps.

Using telemetry data in species distribution modelling can cause severe spatial bias in the results, with some areas being over-represented due to spatial data clusters such as kill sites, or resting sites [36]. To limit spatial autocorrelation, we spatially filtered the leopard occurrence data [36,37]. We first created a 1 km^2 fish-net grid using the Data Management Tool in ArcGIS 10.4 software (ESRI, 2016) for the extent of the Eastern Cape and Western Cape. We then used the Spatial Join function in ArcGIS 10.4 to join the 1 km^2 grid cells to the leopard occurrence points, thereby reducing the GPS points per grid cell. We used the spatially filtered leopard occurrence points (4149), where 3219 occurrence points represented 19 male leopards and 930 points represented 12 female leopards, to generate the leopard distribution map (Figure 1).

Table 1. Summary of GPS collar data collected from individual male and female leopards collected between 2007 and 2021 used to predict leopard habitat.

Number.	Male ID	GPS Points	Monitoring Period		Collar Type	Days Monitored	Female ID	GPS Points	Monitoring Period		Collar Type	Days Monitored
1	111	106	8 September 2017	8 April 2018	AWT	212	1412	132	17 September 2014	2 January 2016	AWT	472
2	115	230	13 June 2015	21 November 2015	AWT	161	3704	91	27 September 2007	10 November 2008	Vectronic	410
3	2996	135	8 December 2006	7 December 2007	Vectronic	364	3710	78	2 August 2007	11 December 2007	Vectronic	131
4	2997	170	15 June 2007	13 August 2008	Vectronic	425	3805	185	7 January 2009	21 October 2010	Vectronic	652
5	6596	126	22 June 2021	1 October 2021	Followit	101	6775	49	11 April 2009	26 July 2009	Vectronic	106
6	6666	181	11 March 2009	17 May 2010	Vectronic	432	6777	27	22 June 2009	1 January 2010	Vectronic	193
7	6667	214	31 December 2008	28 May 2010	Vectronic	513	6875	68	1 June 2020	1 September 2020	Vectronic	92
8	6773	154	21 February 2020	24 June 2020	Followit	124	6896	17	10 February 2021	11 March 2021	Followit	29
9	6774	56	1 January 2020	10 February 2020	Followit	40	8183	43	30 May 2010	11 June 2011	Followit	377
10	6776	63	5 May 2009	13 August 2010	Vectronic	465	8294	121	4 March 2011	20 November 2011	Vectronic	261
11	6867	108	31 May 2020	27 December 2020	Followit	210	8642	36	24 January 2011	29 November 2011	Vectronic	309
12	8182	141	13 June 2010	23 February 2011	Vectronic	255	38092	83	21 September 2009	8 April 2010	Vectronic	199
13	8578	301	2 October 2010	18 August 2011	Vectronic	320						
14	8677	111	1 May 2014	15 June 2014	Vectronic	45						
15	9536	177	11 June 2011	24 September 2011	Vectronic	105						
16	9648	95	27 February 2012	17 June 2012	Vectronic	111						
17	29971	105	1 October 2009	25 July 2010	Vectronic	297						
18	38051	343	21 September 2012	21 April 2013	Vectronic	212						
19	85781	403	30 September 2014	14 November 2015	Vectronic	410						

2.3. Habitat Covariates

We selected factors known to influence leopard habitat selection as covariates in our statistical models [29,32,38–40]. We obtained environmental covariates from various sources (Table 2). These included human-associated covariates (distance to roads, land-cover, human population density) and natural covariates (distance to rivers, slope, elevation, and land-cover; Figure 2; Table 2). We used the South African Level 2 land-cover classes of 2018 (a categorical variable) [41], so that similar environments were grouped together resulting in reduced fragmentation of the results. The static variables such as land cover of 2018 and road infrastructure covariate from 1998 were appropriate to use for our temporal leopard location data collection between 2007 and 2021 (Table 1), as there were no major road developments during this time, and the land cover appeared to adequately represent landcover for the period of data collection. We estimated the distance to rivers and roads as the Euclidian distance to the respective covariates using QGIS 3.12.1 (QGIS.org, 2021. QGIS Geographic Information System. QGIS Association. http://www.qgis.org, last accessed on 1 November 2021). While natural prey density and availability influence predator habitat predictions [42], such data do not exist at regional scale in South Africa. Therefore, we created a potential prey species distribution layer using camera trap data from published [26,30,31] and unpublished data (Appendix A). Potential prey included free-roaming ungulate species found to contribute to the broad dietary niche of leopard in the region [43–45] including bushbuck (*Tragelaphus scriptus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), Cape grysbok (*Raphicerus melanotis*) and grey rhebok (*Pelea capreolus*), along with smaller species, including hares (*Lepus* sp.), rock hyrax (*Procavia capensis*) and Cape porcupine (*Hystrix africaeaustralis*) (Table A1; Appendix A). We detected potential prey species at 244 of the 258 camera trap stations set across five survey areas (Appendix A). As carnivores are generally associated with high mammalian species diversity [26], we used the same habitat variables to determine both the prey species distribution modelling and the leopard habitat distribution modelling (Appendix A). Following Swanepoel et al. [39], we did not restrict the extent of the subsampled background region because both leopard and the prey species we focused on occur widely throughout the two provinces and are not specifically restricted across the region [31,32,38,39].

We converted all environmental covariates to the same extent and resolution, approximately 1 km^2, using QGIS 3.12.1, to predict a fine-scale resolution habitat suitability map. Mapping was performed using the Albers Conical Equal Area projection system. All covariates were masked by the Eastern Cape and Western Cape for the modelling process. We tested the collinearity of the environmental covariates using the variance inflation factor (VIF, [46]) before including them in the models.

Table 2. Source of environmental variables used and methods of layer manipulation for habitat prediction modelling.

Variable Name	Description	Origin	QGIS Operation	Original Raster Resolution (Degrees)	Rescaled Resolution (Degrees)	Source
Elevation	Digital Elevation Model (DEM) from Shuttle Radar Topography Mission (SRTM).	National Geospatial-Intelligence Agency and the NASA (National Aeronautics and Space Administration)	Rescaled (average)	0.0003	0.0083	a
Human Population Density	Constrained population map of South Africa 2020	WorldPop, School of Geography and Environmental Science, University of Southampton	Rescaled (average)	0.00083	0.0083	b
Land Cover	South Africa National Landcover—Level 2 categories 2018	Department of Environment, Forestry and Fisheries (DEFF), South Africa.	Rescaled (mode)	0.0002	0.0083	c
Prey	Distribution of potential prey (ungulates and rodents)	Camera trap data (Published and Unpublished)	N/A		0.0083	N/A
Rivers	Euclidean distance to rivers 2018	Council for Scientific and Industrial Research (CSIR), South Africa.	Raster file of Euclidean distance to rivers created using GDAL Proximity. Rescaled (average)	0.0003	0.0083	d
Roads	Euclidean distance to all major roads 1998	National Geospatial Information (NGI), South Africa, Cape Town. Department of Land Affairs, South Africa.	Raster file of Euclidean distance to roads created using GDAL Proximity. Rescaled (average)	0.0003	0.0083	e
Slope	Ground slope derived from DEM.	Slope derived from DEM from SRTM	Slope created from SRTM using GDAL Slope (z = 96405.94). Rescaled (average)	0.0003	0.0083	N/A

Data Source: (a) http://geoportal.rcmrd.org/layers/servir%3Asouth_africa_srmt30meters (accessed 8 August 2021), (b) https://www.worldpop.org/geodata/summary?id=49663 (Accessed 8 August 2021); (c) https://egis.environment.gov.za/sa_national_land_cover_datasets (accessed 23 October 2021); (d) http://bgis.sanbi.org/Projects/Detail/217 (accessed 8 August 2021); (e) http://daffarcgis.nda.agric.za/portal/home/item.html?id=dcd4481173bd439bbe1dbc0977830e3f (accessed 8 August 2021).

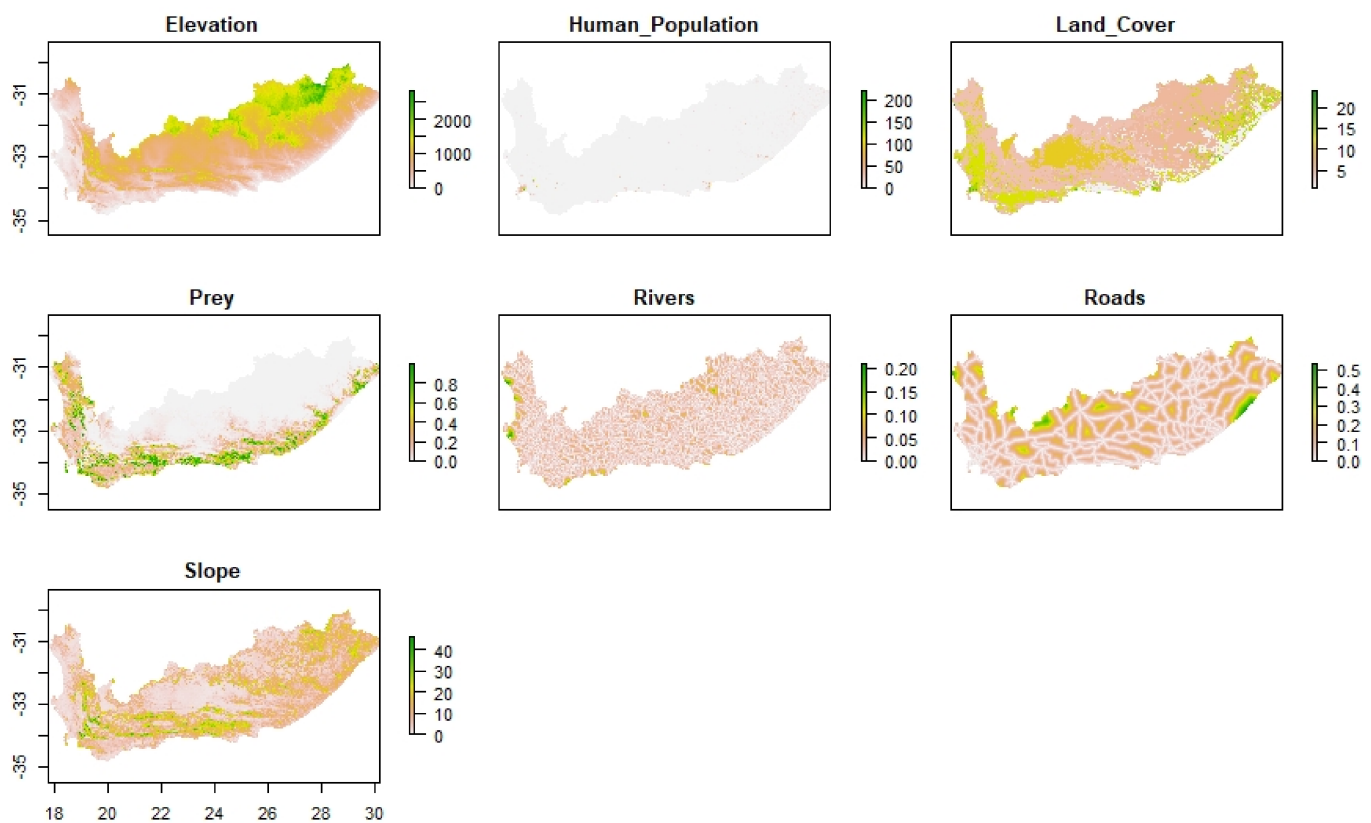**Figure 2.** Environmental covariates used to predict leopard habitat distribution.

2.4. Modelling

We modelled leopard habitat and the potential prey distribution using Maxent (version 3.4.4, [47]). We used the following parameters in our leopard habitat models: random seed, write plot data, regularized multiplier (0.1), 41,500 maximum number of background points, and ran 10-fold cross-validated model replicates with the maximum iterations set to 5000, with a convergence threshold of 0.00001. We selected a 10:1 available: presence points ratio in selecting the maximum number of background points to ensure available points were adequately represented in our models as this improves model prediction [48]. As true absence data are difficult to obtain and known locations are limited to sampling efforts, there can be a negative impact of spatial bias in predicting species distribution [49]. However, this concern diminishes with wide-ranging species such as the leopard, spatial thinning of presence data, a relatively widely distributed sample collection across the region, and the high ratio of background to presence data selected [48,49].

A random subset of the data (430 test data points) was used for each of the ten replicate runs and compared to the trained model (3719 points). The model outputs were averaged over the ten replicate runs. To avoid overfitting, we selected linear and quadratic features [50,51]. We used the same parameters for the potential prey distribution model, but restricted background points to the default 10,000. We used the Jackknife approach to evaluate the contribution that each variable provided to the geographic distribution models. During this process, Maxent generated three models: first, each covariate was excluded in turn and a model created with the remaining variables to check which was the most informative. Second, a model was created by individually using each covariate to detect which variable had the most information not featuring in the other variables. Finally, a model was generated based on all covariates. We plotted the response curves derived from univariate models to identify how each covariate correlated to presence probability. We evaluated the model fit using the area under the receiver operating characteristic curve (AUC), based on independent test data sets for each cross-validated run [52]. The AUC

assesses the ability of each model to discriminate between true and false positives. Its value ranges from 0 to 1 with values closer to one (1) indicating a better fit while values closer to 0.5 indicating a fit no better than random [53]. Each of the ten replicates produced a predicted habitat distribution raster file, of which the arithmetic mean was used to produce the final habitat distribution map. We were interested in identifying leopard habitat and potential barriers to habitat; therefore, we evaluated three models: (1) human-associated model, (2) natural features model, and (3) the full model, which included all variables.

2.5. Connectivity Model

We employed circuit theory using Circuitscape software (version 4.0, [33]) to identify potential corridors linking leopard populations. Circuit theory links populations through multiple possible pathways, with connectivity potential increasing according to the number of connected pathways [19,23,24,54]. The current-flow connectivity analyses use a resistance or conductive surface layer to assess connectivity between known resident populations. In a surface layer, each pixel is a resistor or conductor with an assigned resistance/conductance value derived from the predicted habitat modelling analyses. In addition to the surface layer, Circuitscape requires defining the core habitats or known populations (nodes), between which connectivity is measured. We identified source nodes based on known leopard presence from published and unpublished data [30–32,38,43,55,56]. The subjective shape of each node was guided by the shape of: (1) protected areas and (2) mountain ranges reported to host leopard [31–33,39,42,53], (3) leopard genetic structure [4], and (4) road networks separating nodes. We identified 14 discrete leopard habitat patches as source nodes. Connectivity among nodes was predicted to be a function of the surface layer [57]. We used the raw ASCII output of Maxents' habitat prediction model with the best fit as the conductance surface layer for Circuitscape analyses. We ran Circuitscape in the pairwise mode, and the focal node currents were set to zero [3,58,59]. The final current-flow map was reclassified into five categories using natural breaks (Jenks method), where 1 indicates most movement constrained category for leopard movement and 5 indicates the most permeable [40,59,60]. This highlights cells where current-flow has a greater value than the 80th percentile, allowing for the identification of high-quality areas for connectivity and better identification of important areas for *P. pardus* movements. Furthermore, these categories offer an easily interpretable cartographic product that conservation managers may use to rank conservation zones [40,59].

2.6. Functional Corridor Assessments

We used camera traps to test corridor functionality along five potential leopard corridors. The corridors were identified based on (1) preliminary Circuitscape analyses predicting permeability (>60th percentile), (2) the presence of remnant natural vegetation linking known leopard populations [31] and (3) the surrounding habitat was characterised by highly transformed landscapes (Figure 3). This provided an opportunity to test high-quality areas for leopard connectivity, surrounded by high resistances in the surroundings that could limit the flow of individuals across the landscape [40,59]. We aimed to validate these corridors by determining whether these areas facilitate leopard movement between known populations where low gene flow and low population density have been reported [4,31] (Figure 3). Four of these corridors (the Breede, Duiwenhoks, Goukou and Gourits rivers) had a linear shape that potentially facilitated leopard movement between known leopard habitat patches from the north to the south. The fifth site (Klein Swartberg) was considered a potential 'stepping-stone' rather than a linear corridor between leopard habitat patches (Figure 3). The average Euclidean distance to leopard habitat patches on either side of the linear corridors was 31.2 km, with the Breede river having the longest distance between habitat patches (41 km; Table 3). We placed 294 camera stations along these corridors between May 2015 and March 2021 (Figure 3; Table 3). All cameras were placed between 40 and 60 cm high, in areas considered most likely to detect leopard. Camera trap placements along the four linear corridors were placed in a transect fashion, whereby single

cameras were placed across a section of approximately 500 m wide bands across the breadth of both sides of the rivers (Figure 3; Appendix A). The stepping-stone site allowed the placement of a pair of cameras facing each other in a grid fashion (Figure 3; Appendix A). For brevity, we provide more details on camera surveys along corridors in Appendix A. We analysed all camera trap data using digiKam version 7.2.0 (www.digikam.org, last accessed on 12 December 2021). We extracted data for each image (including date, time, all applied tags, and camera-related metadata) using the R package 'camtrapR' [61] in R statistical software, version 4.0.2 [46].
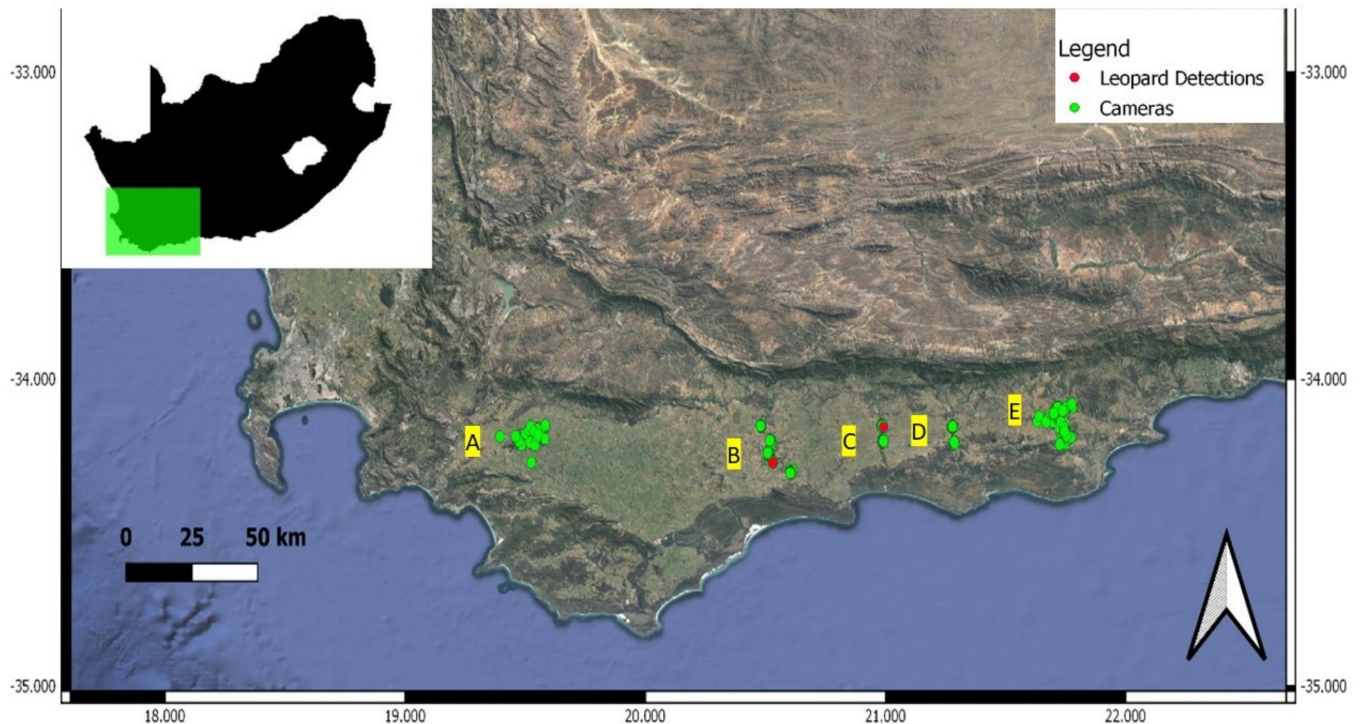
Figure 3. Five potential corridors, (**A**) Klein Swartberg, (**B**) Breede 1 and 2 (**C**), Duiwenhoks (**D**), Goukou, and (**E**) Gourits, tested for functionality using camera traps (green). Two corridors detected leopard presence (red). The insert indicates the location of the study (green shaded area) within South Africa.

Table 3. Summary of the camera trap survey to assess corridor functionality.

Start	End	Trap Nights	Leopard Captures	Total Images	Total Species	Total Wildlife Species	Total Distance Surveyed (km)	Euclidean Distance between Closest Known Leopard Habitat
29 April 2017	29 August 2018	27,882	1	44,363	29	23	34.9	41
21 August 2018	2 October 2019	21,052	0	62,930	36	27	36.2	41
27 January 2020	29 March 2021	9913	1	16,354	29	23	7.4	30
4 February 2020	2 April 2021	9866	0	15,506	27	23	7.3	24
25 October 2019	17 March 2021	22,979	0	55,509	41	32	39.0	20
15 May 2015	20 September 2016	7576	0	13,861	29	22	-	
		99,268	2	208,523			124.8	

3. Results

3.1. Habitat Prediction Model

None of the environmental variables showed strong collinearity (Appendix B) and all environmental covariates could be included in habitat prediction models. The model with the best fit explaining leopard distribution was the full model (AUC 0.90), followed by the natural model (0.88), and then the human-associated model (0.77: Table 4). While the full model had a better fit than the natural model, this difference was relatively low. Both the natural and human models had covariates with weak explanatory power when predicting leopard habitat. In the natural model, rivers had weakest explanatory power, while in the human model, human population density had the weakest explanatory power (Table 4). As each model hosted covariates that contributed to predicting leopard habitat differently, and due to the higher AUC, we employed the full model to predict leopard habitat. The covariate with the highest contribution to the full model was slope, followed by land-cover, prey distribution, elevation, and roads, while rivers and human population density had a low contribution to the model (4). Leopards appeared to select moderate slopes, land cover such as forested areas, fynbos and karoo shrublands, and planted forests, areas with higher predicted prey distribution, moderate elevation, intermediate distances to roads, areas close to rivers, and avoided areas with higher human density, (Appendix C). The modelled leopard habitat scores ranged from 0 (non-habitat) to 1 (high quality habitat) across the predicted leopard habitat (Figure 4).

Table 4. Summary of model fit to predict leopard habitat distribution, estimates of variable relative contributions, and the importance training gain of the environmental variables to the Maxent model.

Model Name	Variables	Contribution	Training Gain (Importance)	AUC
Human	Land cover	27.2	13.7	
	Human population	0.4	0.9	0.77
	Roads	3.8	6.5	
Natural	Elevation	4.2	22.2	
	Land cover	27.2	13.7	
	Rivers	0.7	0.9	0.88
	Slope	54.7	51.2	
	Prey	9.1	4.5	
Full	Human model variables			0.9
	Natural model variables			
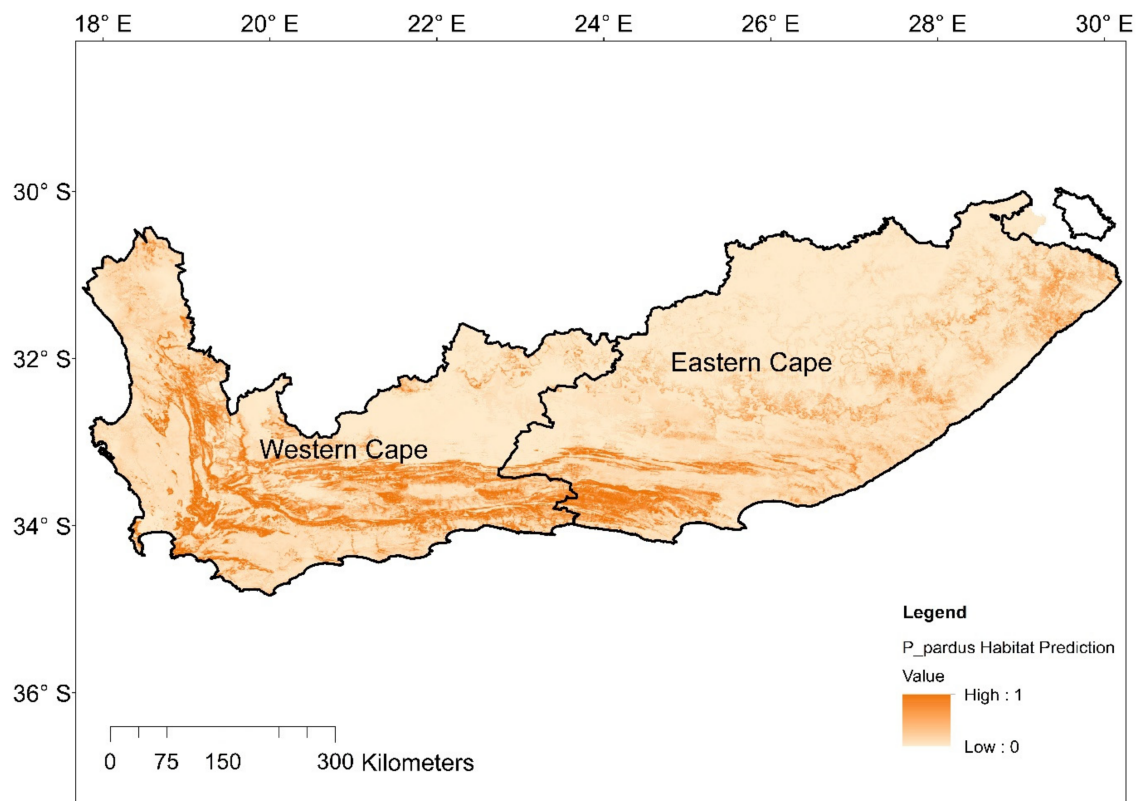
Figure 4. Predicted leopard habitat using the full model masked to the Eastern and Western Cape. Non-leopard habitat has value of 0 with predicted leopard habitat quality increasing to 1.

3.2. Connectivity Model

The source nodes (Figure 5) corresponded to leopard habitat identified by the habitat prediction model (Figure 4). Areas with high permeability (>80th percentile) appeared along the mid-regions of the Eastern Cape and Western Cape, where the high-quality habitat along mountain ranges appears to contribute to linking east and west populations (Figure 5). Connectivity between the Langeberg–Cederberg and Hermanus–Agulhas nodes showed very limited connectivity, where the cultivated landscape known as the Overberg appeared to restrict connectivity (Figure 5). Several potential narrow corridors linking habitat patches between the Langeberg–Cederberg and Duiwenhoks–Gourits nodes were identified as having moderate permeability (>60th percentile) (Figure 5). These long, narrow

corridors were represented by rivers and connectivity was limited due to the surrounding, highly transformed, cultivated landscapes (Figure 5). The eastern-most node representing the Greater Addo Elephant National Park (Addo) appeared to show no connectivity (<20 percentile) potential to the nearby Baviaanskloof node and to the Swartberg node to the west (Figure 5).
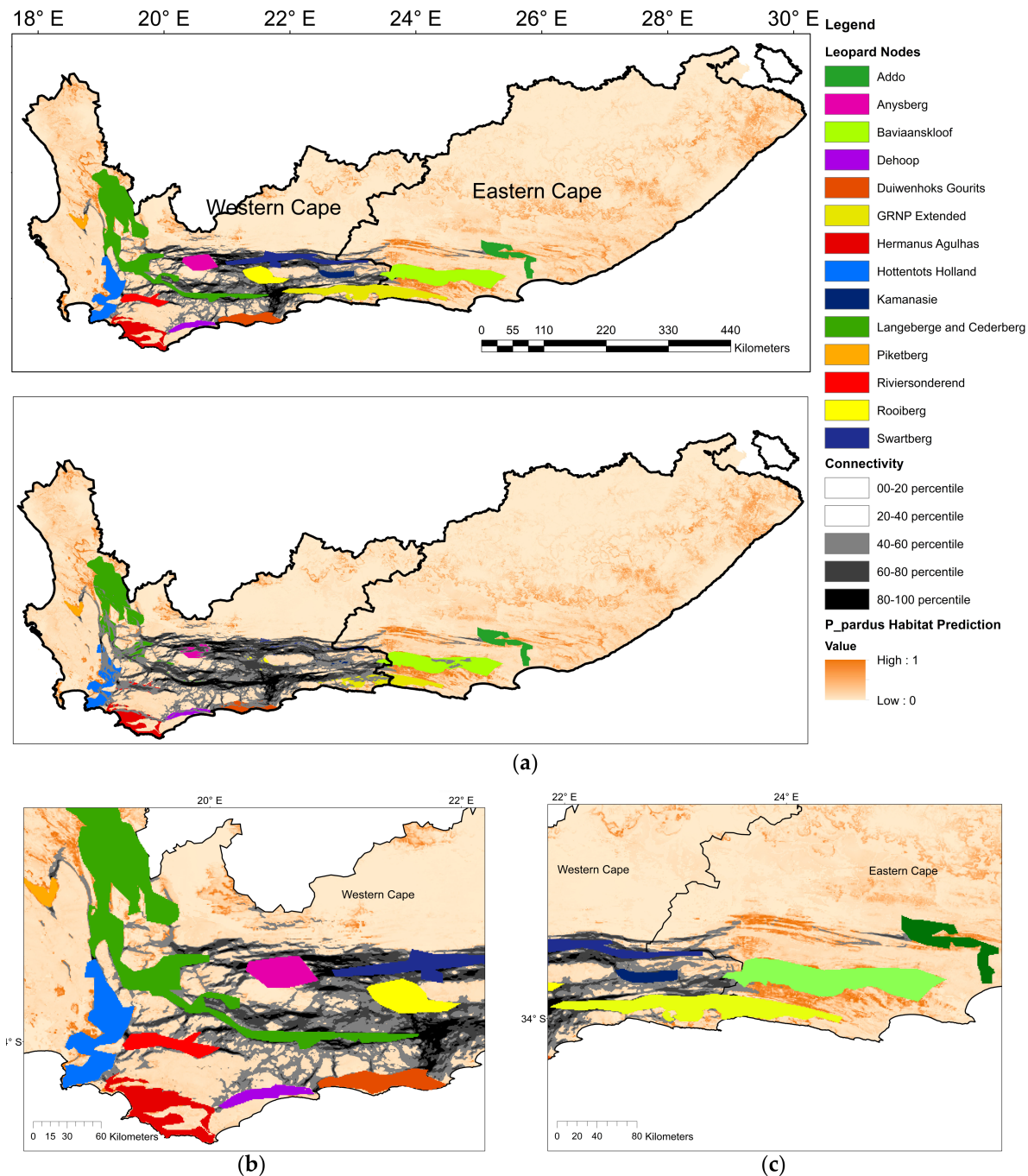

Figure 5. (**a**) The figure above indicates 14 nodes known to host leopard populations, connected by connectivity categories. Connectivity categories were based on natural breaks in the data (Jenks method). We display categories indicating potential permeability (40–60 percentile), moderate permeability (60–80 percentile and high permeability (80–100 percentile) overlaying predicted leopard habitat for reference. The figure below depicts connectivity categories overlaying nodes. (**b**,**c**) provides a finer scale focus on the Western Cape and Eastern Cape, respectively.

3.3. Functional Corridor Assessments

In total, the 294 cameras were placed along the five corridors and run for 99,268 camera trap nights, detecting a total of 38 wildlife mammalian species along 124 km of rivers (Table 3). In total, two leopard captures were detected along two of the five surveyed corridors (Table 3). The captures occurred at 11.0 km and 14.7 km (Euclidean distance) from the closest known leopard habitat patch to the Breede, and Duiwenhoks corridors, respectively (Figure 3). Total operational camera trap days between the two surveys (Breede-1 and Duiwenhoks) reached 37,795 days (Table 3) with Breede-1 reaching 12,821 camera trap days before a leopard was captured, and the Duiwenhoks corridor reaching 3351 camera trap days before the leopard was captured. The remaining three corridors did not record any leopard activity (Table 3).

4. Discussion

Wide-ranging mammals depend on large enough habitat patches and habitat connectivity to persist in fragmented landscapes [25,29]. We combined species data and environmental variables to predict leopard habitat distribution and delineate landscape connectivity. We found that leopard habitat in the Eastern Cape and Western Cape was strongly correlated to moderate slopes and areas of natural land-cover such as forests, shrublands as well as forest plantations. Modified landscapes, such as cultivated land, and highly human populated areas appeared to obstruct leopard presence. As a result, high-quality leopard habitat appeared to be continuous along the east and west direction of the prominent mountain ranges expanding across the two provinces and continued in a north and south directions along the Cederberg Mountain chain in the west (Figure 5). Mountainous, rugged areas offer important habitat for leopard and other large carnivores [39,62–64]. However, leopards occupy non-mountainous areas in regions such as Kwa-Zulu Natal, South Africa, and elsewhere in Africa [65,66]. Therefore, it is likely that mountainous areas are strongly selected because these areas offer refugia from human activity [15,39]. The distributional range estimated in this study appeared to correspond well with that described by Swanepoel et al. [39].

The connectivity model using Circuitscape is a useful addition to habitat prediction in delineating potential functional corridors linking habitat patches across complex landscapes. This allowed the identification of leopard nodes that may be in risk of isolation due to low predicted connectivity. The easternmost leopard node (Addo) appeared to have severed connectivity to neighbouring leopard habitat patches. The nearest node to Addo was the Baviaanskloof node, where potential barriers such as cultivated areas and human population density may contribute to the apparent connectivity impediment. Connectivity was also restricted between Addo and habitat in the northwest direction where connectivity to the Swartberg node also appeared to be severed, likely due to a combination of transformed landscapes and limited slopes being present in this area. The Hermanus-Agulhas and De Hoop (HA and DH) nodes showed limited connectivity potential to leopard populations along the Langeberg–Cederberg and Riviersonderend nodes.

The genetic population structure of leopards in the Eastern Cape and Western Cape is reportedly represented by three sub-structured populations [4]. One of these populations occupies the HA and DH node, where gene flow to the other two genetic populations to the north and northeast was reported to be very low [4]. This provides support of our findings of limited leopard habitat and connectivity between the HA and DH nodes to the northern nodes [4]. Human-associated landscape features are known to fragment natural landscapes and restrict mammalian connectivity [4,15,25,27]. The vast cultivated landscapes between the Langeberg–Cederberg node and the HA and DH nodes appear to fragment habitat and restrict connectivity in the region.

Identifying and promoting movement along corridors can offset the negative effects of habitat fragmentation by connecting isolated populations [24,59,67]. We identified narrow, linear corridors running through the highly transformed area between the Langeberg habitat to the coastal Duiwenhoks habitat. These areas were also identified as suitable

habitat based on our prediction modelling, and were characterised by large river courses (Breede, Duiwenhoks, Goukou and Gourits), moderate slopes with some remnant riparian vegetation, surrounded by large areas of transformed, cultivated lands. In some places, these corridors become extremely narrow (<20 m) between the river and the transformed agricultural surrounds. These narrow areas caused breaks in habitat prediction, since the model evaluates suitability based on the average conditions at approximately a 1 km^2 scale, but these were identified as potential corridors in the Circuitscape modelling. These corridors may play a critical role in the region, as these sites represent the last potential habitat corridors linking disjunct leopard populations in the region.

While incorporating target specific occurrence data to derive species habitat distribution improves the identification of functional corridors [21], validating corridors using independent data contributes to confirming targeted conservation management efforts [68]. Using camera traps, we detected leopard on two of the river corridors delineated by Maxent and Circuitscape, indicating their use by leopards to some degree. The low leopard detection rates along the river corridors may be expected, as gene flow from source populations in the area is reported to be low [4] and could further be compounded by the naturally low dispersal rates of leopards [69], as well as narrow strips of natural landscapes offering limited sites to place cameras to optimize leopard detection. The river corridors hosted between 23 and 32 mammalian wildlife species, confirming the high ecological value these corridors have in the region. While leopards might rarely use these corridors, these areas may contribute to the long-term genetic rigor and survival of the species in the region. This has implications for the conservation of river courses and associated riparian vegetation, particularly where the surroundings are highly modified. The existence of reduced genetic heterogeneity found for leopards in the region [4] suggests, however, that these predicted corridors do not significantly overcome the gene flow barriers to ensure populations are adequately genetically connected. Ensuring corridors facilitate the successful movement and gene flow among leopard populations is key to local population persistence. Dispersal rates are driven by complex factors such has population density [69,70]. When populations are near saturation, and no space is available for maturing animals to occupy, dispersal rates increase [69,70]. Therefore, where populations suffer from stressors that depress the population, dispersal rates would be lower [70]. Obtaining data from dispersal or the movements of translocated individuals in the area would contribute to better understanding the likelihood of corridors to contribute to leopard meta-population dynamics in the region [71].

Management Implications

Natural landscapes have diminished substantially over the past century, and the leopard is only found in 25% of its historical distribution [28]. This loss of range can be attributed to both extensive habitat transformation [72], which impacts both leopards and prey species, resulting in a loss of available prey [28,40], and to high levels of human caused mortality, principally via human–wildlife conflict and unsustainable leopard harvesting [15,73]. Protected areas are insufficient to contribute to leopard conservation in South Africa [15,39]. Therefore, species management practices have important implications in conserving meta-population dynamics, and managing the genetic viability of isolated populations may become increasingly necessary as altered habitat expands [74,75].

Connectivity is the most frequently cited recommendation to conserve species and ecosystem functioning [76,77]. Our study identified habitat permeability estimates, which highlight areas requiring focused conservation efforts where connectivity might need to be increased. We raise particular concern regarding the limited evidence of connectivity between the HA and DH populations and their counterparts along the Langeberg and Riviersonderend nodes. This may require active management interventions such as maintaining and expanding riparian zones, particularly in transformed areas. Further research is required to determine the presence of leopard populations beyond Addo to the east to predict connectivity potential eastward. However, our study also highlights the limited

connectivity between Addo and populations to the west. Human-caused mortality is a major threat to leopard survival and reducing human–carnivore conflict in and around protected areas, predicted leopard habitat, and corridors will contribute to leopard conservation [15]. Therefore, we encourage conservationists and governmental institutions to advocate for non-lethal conflict mitigation strategies [78]. This can promote community tolerance and raise awareness of the regulatory-role carnivores play in ecosystems [25–27]. Restoring degraded landscapes through strategic land-use planning adjacent to areas such as protected areas, leopard habitat and corridors, would be a valuable conservation effort. Where connectivity is constrained and cannot be overcome with available habitat connections, and genetic structuring is apparent, and populations densities are low, active local translocations could be prudent to bolster genetic heterogeneity [74,79,80].

Over the last three decades, connectivity projects were employed at state level in the USA [81], national level in Bhutan [82] and continental scale in Europe (Natura 2000, EU Habitat Directive). However, no regional connectivity maps exist for carnivore conservation in South Africa. Coordinated planning between municipalities, provinces, and national regions with inputs from private, non-governmental and government conservation agencies should be adopted in South Africa to reduce and perhaps reverse the negative effects of habitat loss. Our models provide the first interprovincial connectivity map for leopard in South Africa. Our results can assist environmental managers in identifying sensitive and important biodiversity corridors to ensure species persistence. We recommend species management plans address the connectivity of leopard populations at provincial, national and even pan-African scales. This should be considered in transport and large development projects in South Africa to promote species conservation (e.g., Trans-Canada Highway, Banff National Park [83].

Appendix A. Predicting Leopard Prey Distribution

Between 2011 and 2021 five large scale camera trap surveys (258 camera trap stations) were deployed as part of a broader leopard ecology study (Devens et al., 2018; 2021; Tshabalala et al., 2020). From this survey, we detected prey species expected to contribute to leopard diet [38–40] at 244 camera stations (Figure A1). We included species that are considered free roaming, occurring both in- and outside of protected areas (Table A1). We created a single predictive layer incorporating all potential prey species, as leopards are not restricted by a specific species as prey, and these species were often captured on the same camera traps.

Habitat covariates considered to influence potential prey distribution included environmental variables: land-cover, elevation, slope and human population density, distance to roads and distance to rivers (Table A2). This model indicated an excellent fit with the AUC of 0.915 (Figure A2) and the predicted distribution (Figure A3) was used in the leopard habitat suitability modelling.
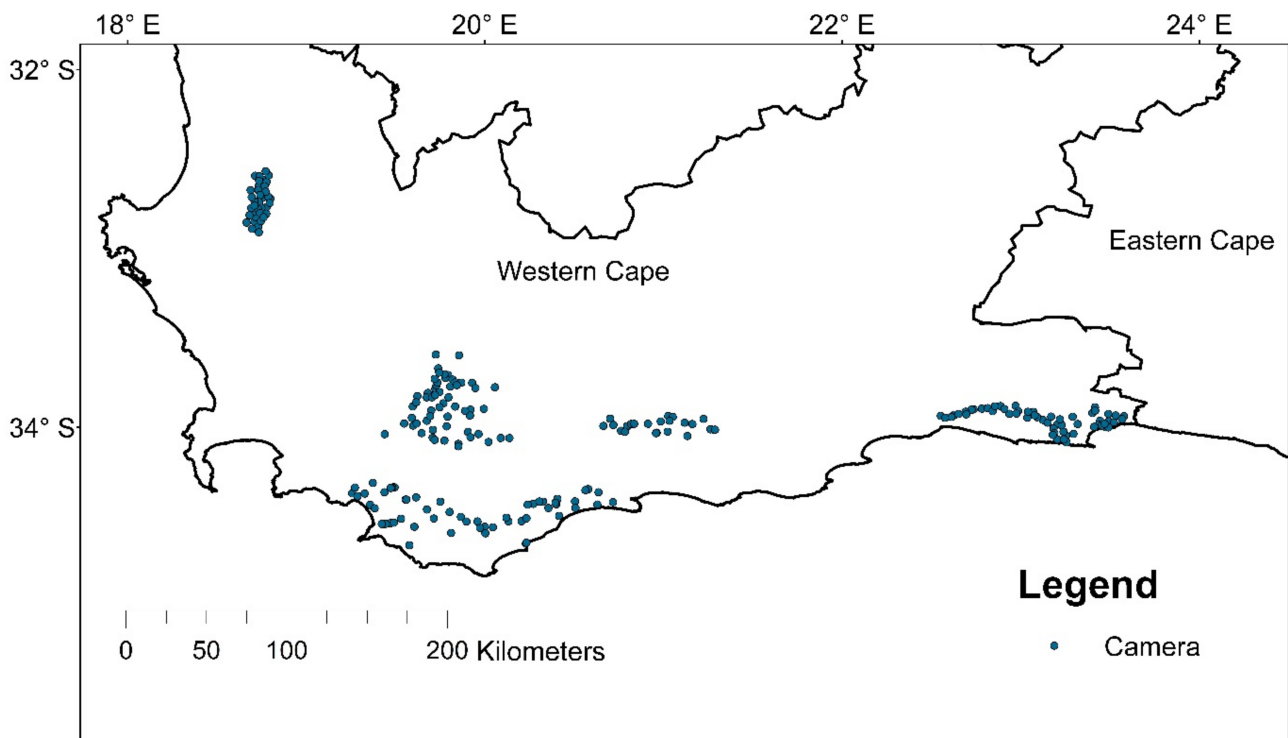

Figure A1. Location of 258 camera traps used to predict potential prey species distribution model.

Table A1. Number of prey species used to predict prey distribution and the number of locations each species was captured.

Species	Number of Stations Captured
Bushbuck (*Tragelaphus scriptus*)	102
Cape Grysbok (*Raphicerus melanotis*)	147
Duiker–Common (*Sylvicapra grimmia*)	113
Grey Rhebok (*Pelea capreolus*)	24
Klipspringer (*Oreotragus oreotragus*)	32
Steenbok (*Raphicerus campestris*)	13
Rock Hyrax (*Procavia capensis*)	24
Porcupine (*Hystrix africaeaustralis*)	194
Red Rock Rabbit (*Pronolagus rupestris*)	6
Scrub Hare (*Lepus saxatilis*)	93

Table A2. The relative contributions of the environmental variables to the Maxent model in predicting prey distribution.

Variable	Percent Contribution	Permutation Importance
Elevation	42.8	73.9
Land-cover	29.2	5.2
Slope	20.8	17.6
Roads	5.6	2
Human Population	1	1
Rivers	0.7	0.2
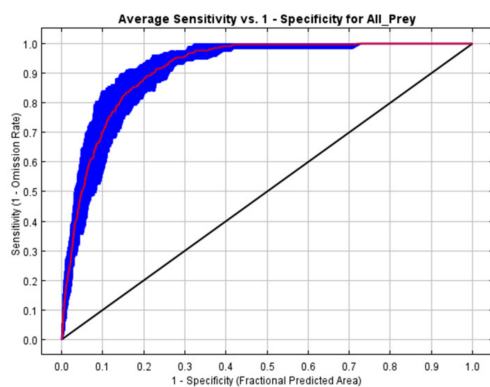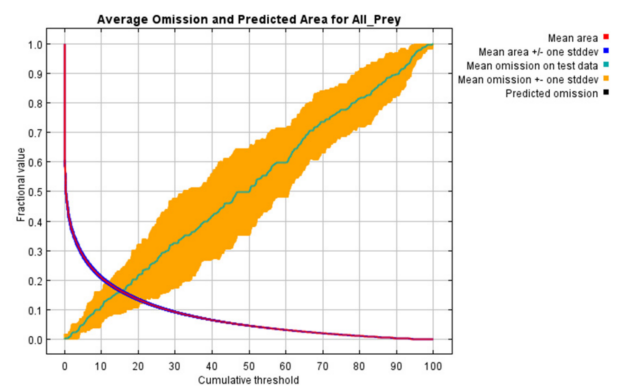
(A) **(B)**

Figure A2. (**A**) Receiver operating characteristic (ROC) curve averaged over the ten replicate runs. The average test AUC for the replicate runs is 0.915, and the standard deviation is 0.0022. (**B**) The test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs.
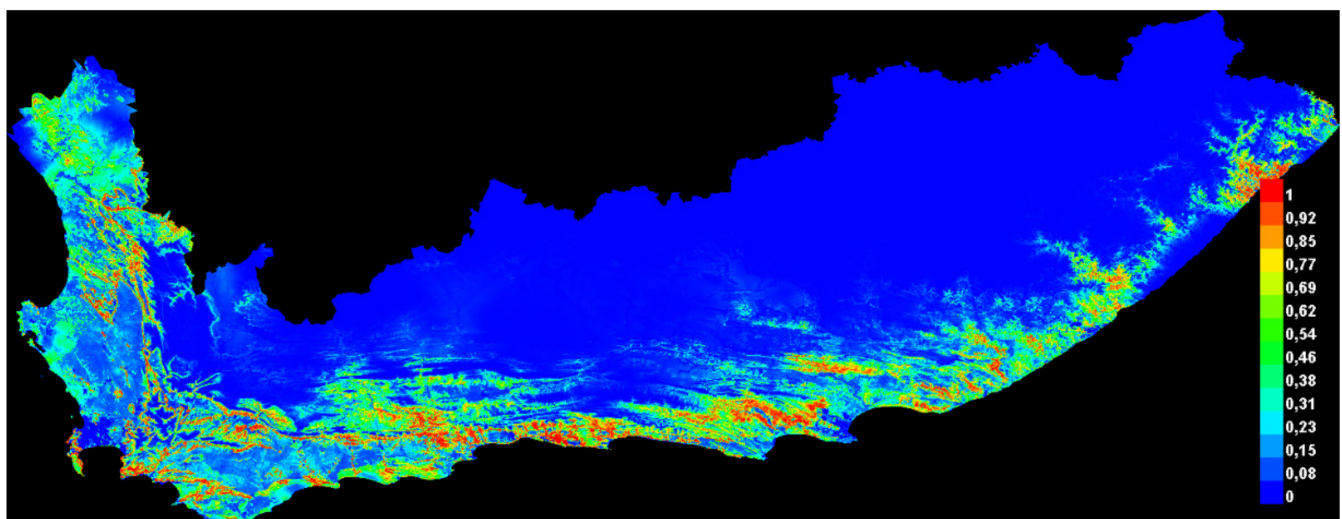

Figure A3. Predicted distribution of potential prey species for leopard from low presence (0) to high presence (1).

Appendix B. Camera Trap Placements along Corridors

The study was conducted along five potential corridors, identified based on (1) Circuitscape outputs where current-flow values predicted high permeability for leopard, and

(2) the presence of remnant natural vegetation linking known leopard habitat patches at either end, that (3) host genetically disjunct leopard populations at low densities [4,29]. Cameras were deployed between 2015 and 2021 (Figure 3; Table 3 In text). Four of the five corridors were linear rivers and the fifth was a stepping-stone between two known leopard populations (Figure 3). The four rivers discussed below, flow in a North-South direction through the Agulhas plains between the Langeberg and Riviersonderend Mountains and the coast toward the Indian Ocean (Figure 3).

Camera Setup

Cameras used in this study consisted of CuddeBack™ E2, E3, G, and AttackIR models (Table A3). Cameras were set to detect target species leopard and small mammals at a height of 50–60 cm. Camera deployment locations differed between corridors due to the width and breadth of the corridors and are described individually below and can be seen in Figure 3.

All cameras were set for a three-minute interval between triggers. Cameras were visited on a four to six-month interval to change batteries, download memory cards and perform general site maintenance.

Klein Swartberg (Stepping-Stone)

The Klein Swartberg extends approximately 124.62 km^2 and acts as a potential stepping stone between two known leopard habitat patches to the North (Riviersonderend Mountains) and the Hottentot Holland and the Hermanus Agulhas nodes (Figure 5). Due to the shape of the site, we set 18 camera trap stations (36 camera traps) in a grid fashion at ~2.2 km apart. A camera trap station consisted of two cameras facing each other in order to capture both flanks of the passing animals in attempts to identify individuals [28]. The cameras were operational for 7576 camera trap days, captured 13,861 images, detected 22 wildlife species, and no leopard were detected (Table 3).

Breede Phase-1

The Breede River was surveyed over two phases. The length of the corridor was approximately 34.9 km (Table 3). During the first phase we placed a trap-line of camera traps to act as a transect. This entailed the set-up of single cameras along the transect line, whereby cameras were placed in a straight line starting as close as possible to the river's edge and leading away from the river in a perpendicular line to transect the natural vegetation to the edge, meeting the surrounding cultivated landscape. Cameras were spaced approximately 20 m apart, placed facing the nearest camera to detect movement along the transect. The trap-lines were located on either side of the river. The number of cameras per trap-line ranged from eight to 22 as a result of the width of the river. Initially six trap-lines were deployed, which was later reduced to five. The cameras were operational for 27,882 camera trap days, captured 44,363 images, detected 23 wildlife species, and one leopard was detected (Table 3).

Breede Phase-2

The trap-line design was modified for a densely clustered, trap-zone setup due to the poor capture rates experienced during the first phase of the Breede river (Figure 3). We focused on relocating the cameras within a 500 m^2 area on either side of the original trap-lines. Cameras were placed on active game trails, farm roads or paths, that would likely be used by a leopard. This resulted in a total of 68 stations distributed among five zones. During this phase the cameras were operational for 21,052 trap nights, captured 62,930 images, detected 27 wildlife species, and no leopards were detected (Table 3).

Duiwenhoks & Goukou

We used the same design to Breede river Phase-2. However, due to the shorter length of these two rivers, we restricted it to two camera trap transect lines, having 12 cameras per transect, divided equally between the two sides of the river. The cameras on the Duiwenhoks were operational for 9913 trap nights, captured 16,354, detected 23 wildlife species and one leopard was detected (Table 3). The Goukou cameras were operational for 15,506 trap nights, captured 23 wildlife species, and no leopards were detected (Table 3).

Gourits

The Gourits river offered challenges to camera placement sites and several cameras had operational failures. The wide riverbed has loose, deep sand that made it difficult to transect areas entirely due to the likelihood of stations being pushed over by cattle or driven over by vehicles. The river course had been dry for six years due to an ongoing drought and made for a good walking route for animals. We placed cameras in the riverbed allowing a more targeted area considered highly suited to leopard movements. There was also a large number of vegetated valleys branching off and large sections of natural vegetation along the river, interspersed among agricultural fields meaning that there were numerous potential routes a leopard could take (Figure 3). Therefore, cameras were more broadly placed along the length of the river, placing cameras in the riverbed as well as in the branching valleys (Figure 3). We lost several the cameras in the riverbed due to the unexpected flooding events. The project started with 55 camera placements, which were moved around as deemed necessary based on flood or theft risk, or landowner activities such as development. We placed a total number of unique camera stations utilized was 72 camera locations (Figure 3). The cameras were operational for 22,979 trap nights, captured 55,509 images of which 32 wildlife species were detected and no leopard activity was detected (Table 3).

Table A3. Collated data regarding the setup periods and setup types, and camera-related information for all the projects. * One trap-line got removed on 15 February 2018. ** This indicates the total number of cameras of each type used and includes when a camera type swapped at a station. *** Lead-acid batteries were 6V 3Ah rechargeable batteries connected to the camera via a cable.

Corridor	Start Date	End Date	Setup Type	Camera Types **	Battery Type	Height	Delay	Picture
Breede Phase 1	29 April 2017	29 August 2018 *	Trap-line	E2 (86), E3 (6)	AA (x8)	50–60 cm	3 min	1
Breede Phase 2	21 August 2018	2O ctober 2019	Trap-zone	E2 (68), E3 (3)	AA (x4)	40–50 cm	3 min	1
Duiwenhoks	27 January 2020	29 March 2021	Trap-zone	E2 (1), E3 (25)	Lead-acid ***	40–50 cm	3 min	1
Goukou	4 February 2020	2 April 2021	Trap-zone	E2 (2), E3 (23)	Lead-acid	40–50 cm	3 min	1
Gourits	25 October 2021	17 March 2021	Widely distributed	E2 (72), E3 (3), A (1)	Lead-acid	40–50 cm	3 min	1
Klein Swartberg	15 May 2015	20 September 2016	Widely distributed	A (18x2)	D-Cell		3 min	1
Piketberg	24 February 2020	On going	Grid	G (70), A (4)	Lead-acid	40–50 cm	3 min	1

Appendix C. Variance Inflation Factor for Variables Used in Habitat Prediction Models
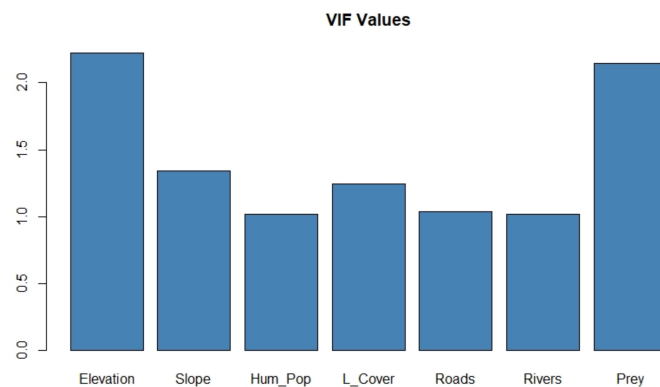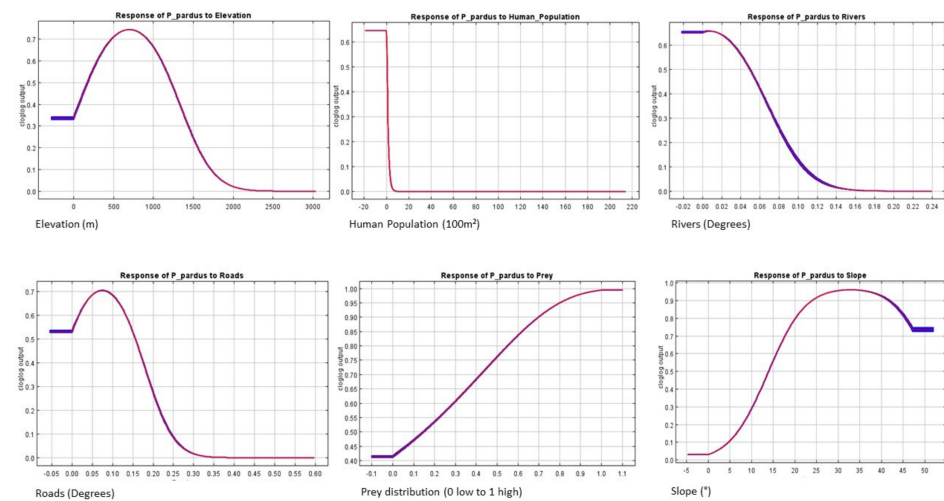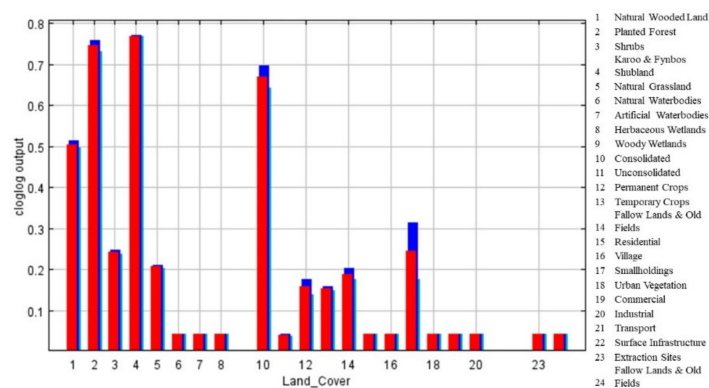

Figure A4. Variance inflation factor (VIF) for variables used in leopard and prey habitat prediction modelling.

Appendix D. Leopard Habitat Prediction Modelling

(**a**)

(**b**)

Figure A5. (**a**) Leopard probability of selection response curves for each environmental covariate used in the full habitat prediction model: elevation (m), human population density (100 m^2), distance to rivers (degrees), distance to roads (degrees), prey distribution (0 low to 1 high), slope (degrees) and (**b**) land-cover categories.

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