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RESEARCH ARTICLE

Moving through the mosaic: identifying critical linkage zones for large herbivores across a multiple-use African landscape

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Abstract
Context Reduced connectivity across grassland ecosystems can impair their functional heterogeneity and negatively impact large herbivore populations. Maintaining landscape connectivity across human-dominated rangelands is therefore a key conservation priority.
Objective Integrate data on large herbivore occurrence and species richness with analyses of functional landscape connectivity to identify important areas for maintaining or restoring connectivity for large herbivores.
Methods The study was conducted on a landscape with a mosaic of multiple land uses in Laikipia County, Kenya. We used occupancy estimates for four herbivore species [African elephant (*Loxodonta africana*), reticulated giraffe (*Giraffa reticulata*), plains zebra (*Equus quagga*), and Grevy's zebra (*Equus grevyi*)] and species richness estimates derived from aerial surveys to create resistance surfaces to movement for single species and a multi-species

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assemblage, respectively. We validated single-species resistance surfaces using telemetry data. We used circuit theory and least cost-path analyses to model linkage zones across the landscape and prioritize areas for connectivity restoration.
Results Resistance layers approximated the movements of our focal species. Results for single-species and multi-species connectivity models were highly correlated ($r_p > 0.9$), indicating similar spatial patterns of functional connectivity between individual species and the larger herbivore assemblage. We identified critical linkage zones that may improve permeability to large-herbivore movements.
Conclusion Our analysis highlights the utility of aerial surveys in modeling landscape connectivity and informing conservation management when animal movement data are scarce. Our results can guide management decisions, providing valuable information to evaluate the trade-offs between improving landscape connectivity and safeguarding livelihoods with electrified fences across rangelands.

Keywords Aerial surveys · Barrier mapper · Circuit theory · Conservation planning · Functional connectivity · Least-cost path

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Introduction

Maintaining functional connectivity in grassland ecosystems is critical for conserving large herbivores. This is especially true for species that track dynamic spatio-temporal gradients in resources availability, while minimizing predation risk and human interference (Frank et al. 1998; Owen-Smith 2004; Hobbs et al. 2008; Harris et al. 2009; Fynn et al. 2016). Given their vast home ranges, most large herbivores often occur in, or seasonally disperse to, lands that are outside officially designated protected areas (Ceballos et al. 2005; Western et al. 2009; Ogutu et al. 2016). In these mixed-use landscapes, anthropogenic landscape transformations increasingly restrict large herbivore movements (Harris et al. 2009; Linnell et al. 2016; Tucker et al. 2018), limiting their ability to disperse, migrate, or access areas with preferred resources (Boone and Hobbs 2004; Fryxell et al. 2005; Newmark 2008; Hobbs et al. 2008; Seidler et al. 2015; Linnell et al. 2016). The reduced movements can result in widespread population declines, disrupt wildlife community structure and gene flow, and alter ecosystem functions (Western and Maitumo 2004; Bolger et al. 2008; Hayward and Kerley 2009; Ripple et al. 2015; Ogutu et al. 2016; Said et al. 2016; Veldhuis et al. 2019).

In increasingly fragmented rangelands, landscape conservation planning strategies should aim to balance people's needs for producing food and supporting livelihoods with a connected landscape that favors movement of entire assemblages of wild herbivores (Rudnick et al. 2012; Donaldson et al. 2017). Connectivity—'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993)—is, however, often species- and process-specific (Kindlmann and Burel 2008; McClure et al. 2016), constraining cross-species inference from connectivity studies. This may be especially true for migratory herbivores that have specific habitat requirements and display high fidelity to migratory routes, such that a corridor for one species does not necessarily support the movement of other species (e.g., Sawyer et al. 2018). For animal dispersal and non-determined seasonal movements, known as linkage zones (Graves et al. 2007), multi-species connectivity analysis may provide more effective solutions (Brodie et al. 2015; Krosby et al. 2015). Such approaches to connectivity analysis can be valuable for prioritizing functional conservation strategies that permit entire herbivore communities to follow changing vegetation productivity through annual cycles (Fynn and Bonyongo 2010).

A devolved ‘conservancy’ model of conservation has emerged over the last two decades in some African countries as a potential solution to the acknowledged lack of space in officially recognized state parks and reserves to protect wildlife (Lindsey et al. 2009; KWCA 2016). This conservancy model allows individual or communal landowners to designate their private property for the ‘purposes of wildlife conservation and other compatible land uses’ (KWCA 2016), offering the opportunity to have rights over wildlife conservation and management, rather than solely the state, as has traditionally been the case (Nelson 2012). In Kenya, for instance, conservancies have increased by 11% in the last 20 years the amount of land that offers protection to wildlife outside the traditional model of government managed protected areas (KWCA 2016; Tyrrell et al. 2019). However, individual conservancies do not necessarily create connected or adequate habitats for wildlife. This is mainly due to the use of fences (Evans and Adams 2016; Løvschal et al. 2017; Weldemichel and Lein 2019) to demarcate land ownership, exclude trespassers, manage human-wildlife conflict (namely to prevent subsistence crops from being eaten or damaged by wildlife, particularly African elephants (*Loxodonta Africana*)) (Hayward and Kerley 2009) and to manage and protect endangered species, such as black (*Diceris bicornis*) and white (*Ceratotherium simum*) rhinoceroses (Hoare 1992).

Conservancies often cover only part of the annual range of many species. Large herbivore species, such as elephants (Douglas-Hamilton et al. 2005), Grevy’s zebra (*Equus grevyi*; Levikov 2014), plains zebra (*Equus quagga*) and Thomson’s gazelles (*Eudorcas thomsonii*; Harris et al. 2009) move or historically moved across large areas in central Kenya. Seasonal movements between higher-quality wet season areas (generally represented by livestock grazing properties) and dry season areas of lower quality but more abundant vegetation and water (generally represented by conservancies) are also important for maintaining population stability of large herbivores across rangelands (Fynn et al. 2016; Russell et al. 2018). Therefore, maintaining landscape connectivity is crucial for the long-term survival of wildlife populations. Because fences are one of the main structures limiting the movement of large herbivores (Boone and Hobbs 2004; Newmark 2008; Hobbs et al. 2008; Fynn and Bonyongo 2010; Seidler et al. 2015; Linnell et al. 2016; Løvschal et al. 2017), methodologies that rapidly and accurately identify vital areas for connectivity are critical for guiding regional conservation planning. Approaches that benefit entire animal communities should thus be prioritized, balancing the need to maintain landscape connectivity and protect wildlife with the wildlife-related costs that people living next to conservancies incur.

Here, we propose an approach using data from aerial surveys, which are commonly conducted across Africa to monitor large herbivores (Chase et al. 2016; Ogutu et al. 2016; Schlossberg et al. 2018), for modeling connectivity across conservancies and identifying priority areas for restoring connectivity that favors a large herbivore assemblage. Specifically, we integrated occupancy and species richness data derived from aerial surveys to: (i) develop and validate models for identifying areas more suitable for animal movement (i.e., linkage zones) for four large-herbivore species (African elephant, reticulated giraffe (*Giraffa reticulata*), plains zebra, and Grevy’s zebra) using a focal species approach; (ii) model connectivity for an assemblage of 15 large-herbivore species using a multi-species level approach and compare the results with the model outputs for the four focal species; and (iii) identify priority areas for restoring landscape connectivity for large herbivores.

Methods

Study area

The study was conducted in Laikipia County (*c*. 9700 km^2), central Kenya (Fig. 1). Laikipia County is a semi-arid savannah landscape. The main tree species are *Acacia drepanolobium* (syn. *Vachellia drepanolobium*), *A. mellifera*, *A. etbaica* and *A. brevispica*. Grass cover is dominated by *Pennisetum mezianum*, *P. stramineum*, *Brachiaria lachnantha*, *Themeda*

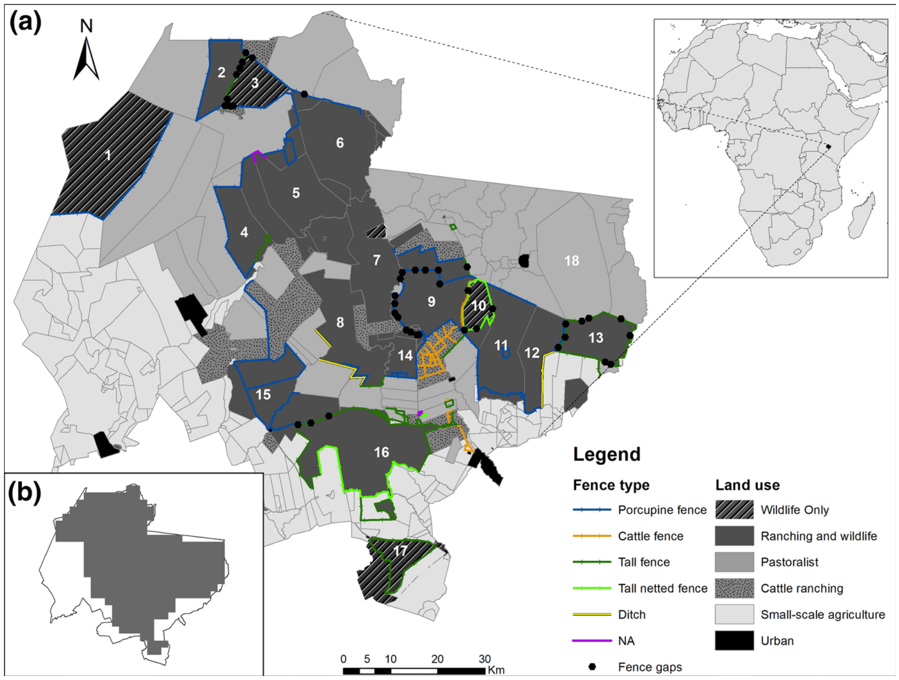

Fig. 1 **a** Map of the Kenya Laikipia County, showing the different property land uses and locations of different types of fences and fence gaps. The numbers indicate the conservancies used as core areas for analysis: (1) Laikipia Nature Conservancy, (2) Mugie-I, (3) Mugie-II, (4) Ol Maisor, (5) Suyian, (6) Loisaba, (7) Mpala, (8) Segera/Mukenya, (9) Ol Jogi, (10) Ol Jogi (Pyramid), (11) Lolldaiga, (12) Ole Naishu, (13) Borana, (14) El Karama, (15) ADC Mutara, (16) Ol Pejeta, 17) Solio, (18) Mukogodo Forest. **b** The dark grey area in the map is the area used to model connectivity and to estimate occupancy and species richness by Crego et al. (2020)

triandra, *Lintonia nutans, Digitaria milanjiana*, *Cynodon dactylon* and *Tetrapogon* (formerly *Chloris*) *roxburghiana* (Butynski and de Jong 2014). Annual rainfall ranges from 1200 mm in the south to 400 mm in the north of Laikipia (Butynski and de Jong 2014). Rainfall is bimodal with a primary peak during the long rains (March–May) and a secondary peak during the short rains (October–December). The short and long rains are separated by a marked short dry season in January–February and a long dry season (June–September; Schmocker et al. 2015).

The Laikipia rangeland system supports an abundant wildlife community, second only to the Greater Mara ecosystem in Kenya (Ogutu et al. 2016). It consists of a mosaic of land tenures, including large private and communal ('group') ranches, state land, private small-holder plots, forest reserves and urban areas (LWF 2012). In addition to wildlife protection and a mix of wildlife and ranching in conservancies, land is used for communal and/or state pastoralist areas that encourage livestock production as the primary economic activity, commercial cattle ranching and small-scale agriculture (Sundaresan and Riginos 2010). Land ownership and use has been contested in Laikipia because of colonial and post-colonial land policies. Maasai pastoralists were evicted from Laikipia in 1911 to make way for the creation of large cattle ranches in the 'white highlands' (Hughes 2006, 2007). After Kenya's independence in 1963, some ranches were subdivided into smallholder plots, while others remained intact. Pastoralists have had seasonal access to grazing on ranches and conservancies, some negotiated with landowners, and some obtained opportunistically. Conflict among pastoral groups, ranchers, and smallholders over grazing and land rights has been significant and is increasing (Fox 2018), with both Samburu and Maasai pastoralists claiming land based on pre-colonial occupation (Cronk 2004; Hughes 2006).

Private and group ranches have provided core wildlife habitats, and some have transitioned to wildlife conservancies in recent years. Many of these ranches use electrified fences to reduce human-wildlife conflict by limiting the movement of elephants onto smallholder cultivated plots and to aid in rhinoceros's conservation (Dupuis-Désormeaux et al. 2015; Evans and Adams 2016). Ranchers and conservancies have also fenced their properties to demarcate their boundaries and exclude pastoralists from illegally grazing their livestock inside (Evans and Adams 2016), an issue that reached a violent crescendo with widespread conflict in 2017 (Evans and Adams 2018; Fox 2018).

Fence mapping

In November 2018, we mapped fences and fence gaps across Laikipia County. Fence gaps are designed to restrict black and white rhinoceroses from leaving conservancies while permitting all other wildlife species to move freely (Dupuis-Désormeaux et al. 2016). We primarily mapped fences and fence gaps through driving surveys, recording fence lines with a hand-held GPS unit. We augmented these data by also marking and digitizing all fences we encountered along roads and in high resolution imagery from Google Earth in QGIS 3.4 software (QGIS Development Team 2018). We compared our map with published fence maps and added fences we missed in locations we could not access on the ground (Dupuis-Désormeaux et al. 2015; Evans and Adams 2016). Finally, we consulted with knowledgeable conservancy and ranch staff to validate our map. In total, we digitized 971.04 km of fences across Laikipia County (Fig. 1). We classified fences into five categories based on their type and permeability to animal movements: porcupine (454.09 km), tall netted (85.01 km), tall (286.04 km), ditch (34.60 km), and cattle (103.08 km) fence. Eight kilometers of fences could not be classified (Supplementary Table A1 describes and provides a photo of each fence type). We did not include in the analysis fences encompassing individual plots (occasionally old and broken fences) in areas where small-scale farming is practiced or stone walls. Stone walls are generally broken and highly permeable. Instead, we used broader areas of small-holder agriculture and settlement to account for their effects on animal movements. We mapped 42 fence gaps, located mostly along the borders of four conservancies that have rhinoceroses (Fig. 1, Supplementary Fig. A1).

Functional landscape connectivity

We assessed connectivity across Laikipia County using circuit theory and cost distance functions, two methods commonly used to model landscape connectivity for single species (McRae et al. 2016) and species assemblages (Koen et al. 2014). In circuit theory, all possible pairwise connections of animal movement between areas of interest are modelled by linking random walk theory with electricity theory (Doyle and Snell 1984; McRae et al. 2008, 2016). Animal-specific movement is modeled across the landscape by mimicking the flow of electricity over a conductance surface with resistors, the resistance surface. The resulting map of current density represents the probability of use by a random walker (Doyle and Snell 1984) and can be interpreted as landscape connectivity (McRae et al. 2008, 2016). In cost distance or least-cost path models, the shortest cumulative cost-weighted distance between areas of interest is calculated across a resistance surface (Adriaensen et al. 2003). This model assumes that the shortest cost path offers the best solution for animals moving between two places (McClure et al. 2016).

Resistance is often defined as the inverse of habitat suitability (Chetkiewicz and Boyce 2009). We calculated the resistance to movement from 1 (low resistance to movement) to 100 (high resistance) by integrating data on species occupancy probability (only for individual species models), species richness (only for the multi-species model), human settlements, small-holder farms and fences (Table 1). Data on individual species occupancy and species richness used to create the resistance surfaces across Laikipia were obtained from Crego et al. (2020). To estimate occupancy probability and species richness of an assemblage of 15 herbivore species, Crego et al. (2020) used data from aerial surveys conducted by Kenya's Directorate of Resource Surveys and Remote Sensing (DRSRS) at the end of the short dry season (February to March) of 2001, 2004, 2006, 2008, 2010, 2012, 2015 and 2016. The 15 species included the African buffalo (*Syncerus caffer*), African elephant, Beisa oryx (*Oryx beisa*), common warthog (*Phacochoerus africanus*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), eland (*Taurotragus oryx*), gerenuk (*Litocranius walleri*), Grant's gazelle (*Nanger granti*), Grevy's zebra, hartebeest (*Alcelaphus buselaphus lelwel*), impala (*Aepyceros melampus*), ostrich

Table 1 Resistance values for the different barriers

	Anthropogenic areas	Porcupine fence	Tall fence	Tall netted fence	Ditch	Cattle fence	Fences bordering ranches that exclude wildlife
Elephant	95	60	Infinite	Infinite	72	50	Infinite
Reticulated giraffe	95	65	Infinite	Infinite	82	61	Infinite
Plains zebra	95	40	Infinite	Infinite	53	50	Infinite
Grevy's zebra	95	40	Infinite	Infinite	53	65	Infinite
Herbivore assemblage	95	39	Infinite	Infinite	62	42	Infinite

Infinite means that in the models we assume that animals cannot cross the fence

(*Struthio camelus*), plains zebra, reticulated giraffe, and Thomson's gazelle. In the aerial surveys, parallel transects regularly spaced 2.5 km apart were flown. Transects were subdivided into sampling units at 5-km intervals. Occupancy probabilities were estimated at a spatial resolution of 5 × 5 km (composed of two 2.5 × 5 km transect sub-units) and as functions of distance to permanent water, vegetation productivity (Normalized Difference Vegetation Index) and livestock abundance. Crego et al. (2020) excluded most of the areas dedicated to small-scale agriculture where wildlife had been extirpated. Because we used the results of this model as the basis for constructing the resistance surfaces, we similarly excluded most small-scale agricultural plots (Fig. 1). Crego et al. (2020) provide additional details of the aerial survey data and methods.

Single-species connectivity models

We assessed individual functional connectivity for four species (African elephant, reticulated giraffe, plains zebra and Grevy's zebra) for which we had empirical GPS movement data for model validation. We derived the resistance surface to model connectivity from the average occupancy probability over the eight years of data. The use of species occupancy information assumes that species move more across areas of more suitable habitat (i.e., where they are more likely to occur; Zeller et al. 2012) and the averaged occupancy across years approximates the areas more consistently suitable for movement during the monitored period. For each species, we resampled the 5 × 5 km raster to 100 × 100 m to incorporate fences, rasterized at 100 m spatial resolution, into the resistance surface. We inverted occupancy probability values to convert occupancy to resistance, scaled between 1 and 100 (i.e., minimum to maximum resistance). We estimated values of resistance to different fence types and for each species, by asking 21 experienced local managers, conservancy staff and researchers, whether they believed a species could cross particular fences (e.g., jump, walk over or walk under wires). We then calculated resistance as the inverse of the percentage of positive responses (i.e., permeability; Table 1; Supplementary Fig. A2). We assigned infinite values, therefore assuming complete impermeability to animals, to all electrified tall fences and fences bordering properties where ranchers actively exclude wildlife (Table 1). These resistance values are intended to be general approximations of resistance to movement. While we assumed that tall electrified fences are impenetrable to all animals, we recognize that certain elephant bulls can learn to break through these sophisticated fences (Evans and Adams 2018). Fence gaps were exaggerated (~ 200 m) to incorporate them in the 100 m resolution resistance layers.

To account for human settlements and small-scale farms that commonly erect small fences, we incorporated anthropogenic areas. Based on Jacobson et al. (2015), we mapped small farms and human settlements to a 100 m spatial resolution. We assigned a high resistance value (95) to those areas, based on the assumption that animals avoid areas which have greater human populations and infrastructure, including fences (Seidler et al. 2015). For each pixel across the landscape, we used the maximum value of resistance identified across each of these data layers. All computations were conducted using R (R Development Core Team 2016).

We modeled connectivity between conservancies using Circuitscape software 4.0 (McRae et al. 2016). In Circuitscape, one ampere of current is given to each core area to run across the resistance surface and a cumulative current density map is produced as the combination of all possible pairwise connections (McRae et al. 2008). We ran models using the pairwise method and eight neighboring cells. Additionally, we identified the least-cost path network that connects conservancies using Linkage Mapper v. 2.0.0. (McRae and Kavanagh 2011), a GIS toolbox developed for connectivity analysis that is based on cost-distance surfaces. We calculated least-cost paths utilizing the cost-weighted method and pruned the network to a maximum of three connected nearest neighbors to avoid cluttering the network with connections between distant conservancies. After mapping the linkage zones among conservancies, we used the Centrality tools from the Linkage Mapper toolbox, which calculates current flow centrality across the network, providing an estimate of the importance of each link between conservancies for animal movement within the defined network (McRae and Kavanagh 2011). We compared the mean least-cost path and centrality scores among species using analysis of variance.

These methods require core areas to calculate connectivity and least-cost paths, the placement of which can highly affect final outputs (McRae and Kavanagh 2011). We focused on assessing landscape connectivity among Laikipia conservancies and one forest reserve. To incorporate the effect of fences that border many of these properties in the analysis, we used the centroids (750 m radius) of 17 conservancies and one forest reserve as core areas (Fig. 2). We used all conservancies larger than 100 km^2 with the exception of Pyramid Conservancy (50 km^2), which we incorporated to account for the effect of the tall fence designed to contain rhinoceros. We divided Mugie Conservancy in two to incorporate the effect of the tall fence that intersects the property.

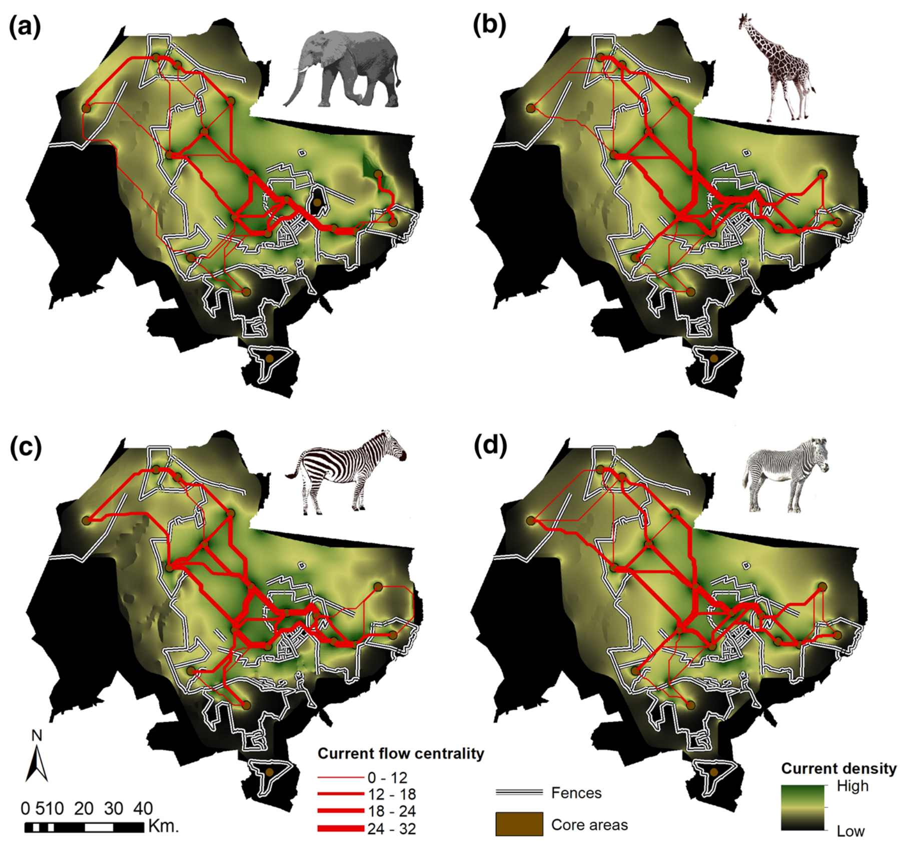

Fig. 2 Cumulative current map, least-cost path and current flow centrality results for **a** elephant, **b** reticulated giraffe, **c** plains zebra and **d** Grevy's zebra across the Kenya Laikipia County. Core areas are the centroids of the 18 conservancies used to model connectivity

Multi-species connectivity model

We used a similar approach to model connectivity at the multi-species level. Instead of using occupancy probability, we averaged species richness from the eight years of aerial survey data estimated from the multi-species occupancy model (Crego et al. 2020). We assumed areas that support a higher diversity of wild herbivores across time provide more suitable habitats that facilitate movement of most species. Consistent with the single-species analyses, we resampled the 5 × 5 km raster to 100 m, inverted the raster values, and scaled species richness from 1 (minimum resistance) to 100 (maximum resistance). We incorporated the resistance values of fence type (based on expert opinion) as the mean resistance for all the 15 species included in the model (Table 1, Supplementary Fig. A2). We also assigned infinite values to tall electrified fences that impede movement of all large animals or fences bordering properties that actively exclude wildlife. Finally, we incorporated settlements and small-scale farms, assigning a resistance value of 95 to these cells. We ran Circuitscape using the same model specifications described for the single-species models. We compared the output of the multi-species model for each raster with corresponding values generated by each of the single-species models using the Pearson's correlation coefficient.

Landscape connectivity restoration

To identify priority areas of connectivity restoration, we used the Barrier Mapper tool from Linkage Mapper v. 2.0.0. (McRae and Kavanagh 2011) for the multi-species analysis. This tool identifies areas in which reducing resistance to movement (e.g., through fences removal) will restore landscape connectivity (McRae et al. 2012). Barrier Mapper works by applying a moving window around each pixel so that the resistance is reduced to a value of 1 and then quantifies the reduction in cost-weighted distance compared to the analysis with the original resistance surface (McRae et al. 2012). Higher reductions in cost-weighted distance (i.e., increase in connectivity) indicate areas of higher restoration potential. We applied a minimum moving window assessment, ranging from 1 to 51 km, with 2-km increments. This range accounts for the barrier effect of fences at short distances, but also across large properties with barriers given low habitat quality. For each pixel we calculated the sum of connectivity improvement scores between all core areas and all scales, highlighting areas that impede movement between multiple pairs of conservancies (McRae et al. 2012).

Single-species model validation

The quality of connectivity models is heavily influenced by the resistance layers on which the models are based (McClure et al. 2016). Therefore, it is important to ensure that the resistance layers accurately represent areas of animal movement for each species. One of the most common approaches used to validate resistance layers involves comparing them with telemetry data (McClure et al. 2016; Osipova et al. 2018). We incorporated telemetry data from ten elephants, three reticulated giraffes, six plains zebras and five Grevy's zebras, all representing adult individuals from different animal groups (Supplementary Table A2). For each animal, we subset the GPS tracking data to dry periods (1 December to 31 March) to match the dataset used to model species occupancy (Crego et al. 2020). Tracking data also overlapped the years used to map species occupancy (2001–2016), except for the reticulated giraffe dataset, which was collected during 2017–2018. Further details on the dataset used for validation are provided in the Supplementary Table A2.

There is no standard methodology for testing how well telemetry data aligns to resistance surfaces. Here, we used two commonly implemented approaches. First, we investigated whether animal fixes for the four focal species occurred in areas with lower resistance to movement than a random sample across the study area. This approach assumes that the resistance surface is a good representation of animal movement if resistance values at the actual movement locations are significantly lower than random locations (McClure et al. 2016; Osipova et al. 2018). To evaluate potential differences, we buffered each GPS fix with a radius equal to the mean hourly step length of the species calculated from the data (elephant = 464 m [SD = 697]; reticulated giraffe = 266 m [SD = 249]; plains zebra = 366 m [SD = 445]; and Grevy's zebra = 374 m [SD = 464]) and extracted the mean resistance value at these locations. To reduce spatial autocorrelation, we rarefied the dataset to a single fix per day (06:00 local time when animals tend to be more active). For each animal (or movement burst for animals with data during multiple dry periods), we also simulated an equal number of random points as GPS fixes. We buffered and extracted mean resistance values at each random point. We tested whether animals moved across areas of low resistance values in a similar fashion to random points using a generalized linear mixed model (GLMM) with a logit link function, in which GPS locations were treated as the response variable, resistance values as the fixed effect and individuals (or bursts) as a random effect to account for the lack of independence among individuals (or bursts from different years). For giraffe, we used a generalized linear fixed-effects model (GLM) given the lack of enough individuals to fit a random effect. We fit the model using the *lme4* package in R (R Development Core Team 2016) and assessed statistical significance at alpha = 0.01.

Second, we asked whether observed animal paths occurred in areas with lower resistance to movement than random paths generated across the study area. We hypothesized that the resistance surface is a good representation of animal movement if resistance values at the actual movement paths are significantly lower than random paths (McClure et al. 2016). We generated ten correlated random walks per animal (or movement bursts) within the study area, each time starting and ending at different random locations, using the *adehabitatLT* package in R (R Development Core Team 2016). Turning angles and hourly distances between points were randomly sampled from each animal trajectory. We retained one fix per day from each animal trajectory (actual and simulated) and extracted resistance values using a buffer with a radius equal to the mean hourly step length. We contrasted both datasets using the logistic GLMM (GLM for giraffe) as previously described.

Results

Landscape functional connectivity

Resistance layers in general accurately represented actual movement by the individuals of our four focal species. Mean resistance values at observed animal locations for elephant, reticulated giraffe, plains zebra and Grevy's zebra were significantly lower than corresponding means at random locations ($p < 0.01$; Table 2). Likewise, the mean resistance values along the observed paths were significantly lower than the corresponding values for random paths for all focal species except plains zebra ($p < 0.01$; Table 2).

The cumulative current density maps for elephant, reticulated giraffe, plains zebra and Grevy's zebra (Fig. 2) resembled the map derived from the multi-species analysis (Fig. 3), identifying nearly identical areas of high connectivity. The cumulative current density estimated by the multi-species model was highly correlated with the cumulative current density for elephant ($r_p = 0.87$), reticulated giraffe ($r_p = 0.98$), plains zebra ($r_p = 0.96$) and Grevy's zebra ($r_p = 0.96$; Fig. 4). Similarly, mean least-cost path length did not differ among the four species or the multi-species model ($F_{4,155} = 0.474$, $p = 0.75$) and centrality scores were also similar among the four species and the multi-species model ($F_{4,155} = 0.357$, $p = 0.84$). Fences and fence gaps affected the network of least-cost paths, with paths tending to be selected across fence gaps and hence avoiding crossing over fences with high resistances to movement (Figs. 2 and 3).

In general, conservancies located in the center of Laikipia County (e.g., Mpala, Ol Jogi, Loisaba, Elkarama, Suyian, Segera, Loldaiga) were critical in maintaining connectivity across the study area. Both, the single-species models and the multi-species

Table 2 Validation results for species resistance layers across the Kenya Laikipia County

	Resistance (mean ± SD)				
	Animal locations	Random	p value	Correlated random walk	p value
Elephant	43.02 (14.57)	51.87 (20.10)	< 0.001	55.07 (19.96)	< 0.001
Reticulated giraffe	46.18 (5.3)	62.82 (12.91)	< 0.001	58.63 (10.82)	< 0.001
Plains zebra	25.14 (6.91)	28.77 (18.38)	0.009	26.06 (8.43)	0.118
Grevy's zebra	62.95 (2.70)	78.34 (9.45)	< 0.001	67.83 (8.52)	< 0.001

For each species, the mean (± SD) resistance values for actual GPS locations, random locations, and locations from correlated random walks are presented. P-value < 0.01 are significant.

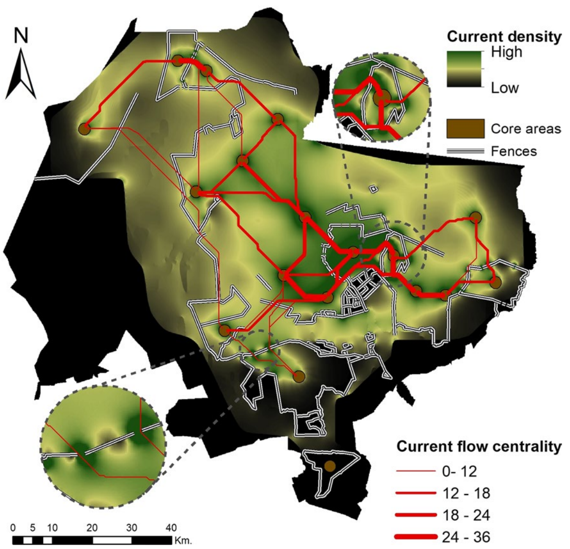

Fig. 3 Cumulative current map, least-cost path and current flow centrality results for an assemblage of 15 large herbivores across the Kenya Laikipia County. Core areas are the centroids of the 18 conservancies used to model connectivity. The zoom-in circles show the details of current density across different fence gaps

model, showed higher cumulative current density and centrality scores for the central conservancies than for the peripheral ones (Figs. 2 and 3, Supplementary Materials B). In the extreme south of the County, one conservancy (Solio) is isolated from the other conservancies by a tall electrified fence that impedes large herbivores from crossing into the surrounding farmland. Ol Pejeta, a conservancy also in the south of the County, is solely connected by three fence gaps in the north that facilitate movement through the electrified fence. In the west, Laikipia Nature Conservancy is disconnected from the center of the landscape, with current density being high towards the northern regions (Mugie Conservancy) but only for elephant and plains zebra and for the multi-species model. The east and center of Laikipia are currently connected by a single corridor that concentrates current density through a fence gap (Figs. 2 and 3).

Landscape connectivity restoration

The Barrier Mapper analysis identified four important areas for restoring connectivity for the herbivore assemblage across the landscape (Fig. 5). One area in the center of Laikipia corresponds to the presence of a cattle ranching property (Area A in Fig. 5) that had low species richness, hence high resistance to movement (Supplementary Fig. A3). Another area is a bottleneck created by the presence of fences and cattle ranching properties connecting the east and the center of Laikipia (Area B in Fig. 5). The other two areas in the north and south (Areas C and D in Fig. 5) correspond to a combination of pastoralist group ranches and high fence density.

Discussion

Private and communal lands are crucial for the future of wildlife conservation outside parks and reserves (Nelson 2008; Drescher and Brenner 2018; Tyrrell et al. 2019). Across Kenya, where over 65% of all wildlife are found on private and communal lands, conservancies play a major role in protecting wildlife outside formally protected areas (Ogutu et al. 2016; Tyrrell et al. 2019). However, effective conservation on private and communal lands relies largely on balancing a trade-off between the need to maintain landscape connectivity for animals that follow dynamic spatiotemporal trends in vegetation productivity and water availability (Fynn and Bonyongo 2010) with that of protecting endangered species and mitigating the costs that wildlife can impose on people's livelihoods. The lack of this balance can have dramatic adverse impacts on wildlife populations as exemplified by the recent catastrophic collapse of the once spectacular Athi-Kaputiei Ecosystem in Kenya due to uncontrolled densification of fences and other land use developments (Said et al. 2016).

We used aerial surveys and fence maps to investigate functional landscape connectivity for large herbivores and to prioritize areas for connectivity restoration. Our results demonstrate that the resistance layers for four focal species successfully approximated actual animal movement. The high correlations between the cumulative current density models for the focal species with that of the large herbivore assemblage, indicates that data of varying quality can be used to effectively represent functional connectivity when movement data from GPS tracking devices is scarce or unavailable. Based on our models, we identified critical linkage areas that can potentially improve landscape connectivity. Our approach will guide managers to plan management strategies that

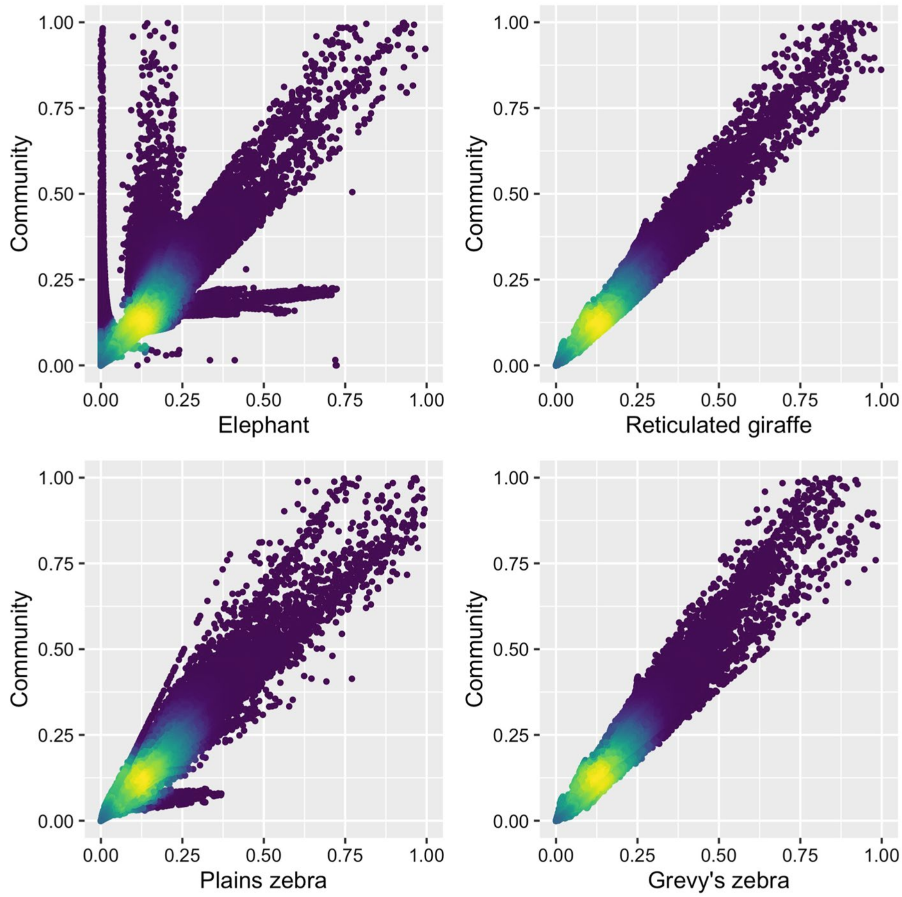

Fig. 4 Correlations between the multi-species and single species (elephant, reticulated giraffe, plains zebra and Grevy's zebra) cumulative current density outputs across the Kenya Laikipia County. Colors indicate point density from low (purple) to high (yellow)

can balance the trade-off between promoting connectivity in the most important linkage zones and minimizing the risk of human-wildlife conflict with local communities.

Landscape functional connectivity

Model validation results using telemetry data illustrate that resistance layers were consistent with the observed movements of collared elephant, reticulated giraffe and Grevy's zebra. For these species, random locations and simulated correlated random walks had higher mean resistances and standard deviations than empirical observations, suggesting that animals consistently moved across areas with lower resistance than expected by random movements. However, resistance values for plains zebra were similar for the empirical and simulated data, likely due to the wide distribution of this species across the landscape. The high occupancy probability across Laikipia resulted in low resistance to movement in most areas (Supplementary Fig. A3), and hence in no significant difference between the empirical and simulated data.

The cumulative current density models for the four species were similar to, and highly correlated with, the cumulative current density for the multi-species model. Only elephants had more marked differences because they are excluded from certain conservancies and also had higher cumulative current densities across the northern pastoralist lands than predicted by the multi-species model (Fig. 2). These results, however, show that connectivity models were a good representation of landscape functional connectivity of the larger species assemblage, supporting previous findings that single-species models can be used to model connectivity that represents a similar group of species (Brodie et al. 2015).

The use of habitat suitability models for constructing resistance layers to model connectivity has, however, been criticized (Scharf et al. 2018). One

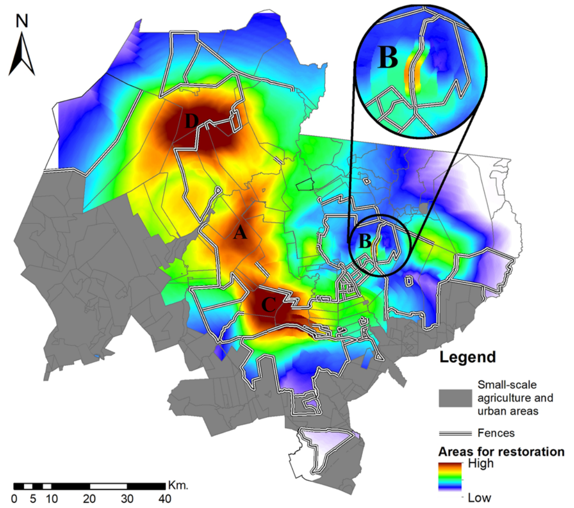

Fig. 5 Barrier analysis for the Kenya Laikipia County, based on the resistance surface of an assemblage of 15 large herbivore species. The greatest values of connectivity restoration potential were detected in four areas: **a** at the center of Laikipia where ranching properties exist; **b** in a bottleneck produced by the presence of fences and ranching properties connecting the east and the center of Laikipia; **c** and **d** in the south and north where a combination of pastoralist lands and high fence density exist

important reason is that animal migration or dispersal can occur outside the habitat areas generally used by some species (Vasudev et al. 2015). As a result, movement data are often preferred for modeling connectivity (Scharf et al. 2018). This may be especially important for mapping corridors intended to protect migratory routes. However, animal tracking devices designed for large terrestrial mammals are expensive (i.e., over USD 1500 per unit plus the cost of fitting and downloading data) and require complex capture/collaring operations. The expense and logistics are thus often beyond the scope of many projects and frequently limit sample sizes as well as the diversity of species that can be collectively monitored. Another reason is that resistance surface values rarely account for the variation in habitat suitability models. However, current density results are robust to relative changes in cost values if the rank order of costs is accurate (Bowman et al. 2020). Thus, Circuitscape models are robust to the inherent variation of habitat suitability models. Our results demonstrate how habitat suitability models can be harnessed for identifying important areas for maintaining habitat connectivity. This may be especially important for ecosystems that are increasingly threatened by linear infrastructure development, such as fences, roads and railways (Osipova et al. 2018; Zeller et al. 2020).

While contemporaneous GPS tracking of multiple species is relatively rare across African savannahs, aerial monitoring of wildlife populations is widespread. Our research highlights how these data can be operationalized to better assess functional connectivity across these vast landscapes. This integration of aerial surveys, occupancy modeling, and connectivity analysis may provide critical information for supporting important management decisions for highly diverse and globally important wildlife communities. One drawback of using aerial survey data to model connectivity is that they are generally conducted during the dry seasons, when clear weather conditions and reduced foliage increase visibility of animals on the ground (e.g., Chase et al. 2016; Ogutu et al. 2016). During the rainy season, increased availability of forage and surface water may reduce livestock-wildlife competition (Odadi et al. 2011a, b), two of the main variables restricting wild herbivore distribution (Ogutu et al. 2010, 2014b; Tyrrell et al. 2017; Crego et al. 2020), and expand suitable habitats for wild herbivores. Our results using aerial surveys conducted during the dry season, highlight the linkage zones that animals are most likely to use to move among conservancies when conditions are harshest. Conservation of these zones is critical for allowing animals to track resources (e.g., vegetation and water) during dry periods. Future studies that incorporate information on animal distribution during the wet season will be important to ensure the necessary landscape connectivity for animals to access essential resources year-round.

Landscape level management implications

Conservancies across Laikipia County are moving towards a more collaborative and ecosystem-level approach to wildlife conservation and management and have collectively created the Laikipia Conservancies Association under the umbrella of the Kenya Wildlife Conservancies Association (LCA 2020). Under this Association, conservancies, despite their differences in land tenure and use, are “aligned through the recognition that a collaborative vision and management approach is critical to the future of conservancies as the core of a broader conservation landscape that supports people and wildlife" (LCA 2020). Maintaining a connected network of conservancies across the landscape is critical for wildlife conservation and connectivity restoration maps essential for guiding management.

However, ensuring a well-connected network of conservancies for large herbivores requires conservancies, government departments and conservation and development NGOs to negotiate two main complex trade-offs. The first trade-off consists in maximizing connectivity while minimizing the cost of human-wildlife conflict incurred by people living along or near conservancy boundaries. For instance, the West Laikipia Fence, that borders the western boundaries of the four main properties and completes a wide trans-Laikipia fence, plays a key role in protecting local communities from elephant incursions (Evans and Adams 2016). Elephant bulls tend to break through electric fences (Evans and Adams 2018) and raid small-holding plots (Supplementary Fig. 4A). Maintaining this electric fence is thus critical for safeguarding local people's livelihoods, but electrified fences built to mitigate human-wildlife conflict should be planned collectively among conservancies at a landscape level, to minimize their length and optimize their placement.

The second trade-off is creating connectivity across conservancies while ensuring the coexistence of wildlife with pastoralists and their livestock (Ogutu et al. 2014a; Evans and Adams 2016; Fynn et al. 2016; Russell et al. 2018). Currently, conservancies in the south (Solio, Ol Pejeta, Mutara) and the west (Laikipia Nature Conservancy) are being disconnected from central and northeast conservancies. For conservancies that are surrounded by farms (e.g., Solio), connectivity restoration may not be possible and only intense management can prevent inbreeding. For the rest of the landscape, our connectivity restoration map (Fig. 4) highlights important areas for which reducing the number of barriers, such as fences or highly degraded properties, can promote connectivity and benefit large herbivore populations. For instance, restoring Eland Downs, the property connecting ADC Mutara and Segera/Mukenya, will be critical to permitting animal movements between the conservancies in the south and center/north of the landscape and avoiding further isolation of the southern conservancies from the rest of the landscape (Area C in Fig. 4). Restoring connectivity might include land purchases, changing land uses to conservancies, restoring degraded habitat, regulating livestock densities or combinations of these interventions. However, for this to happen, it is important to find regional management strategies that not only benefit wildlife, but also protect the livelihoods of pastoralist people, ranchers and other landowners across the landscape.

Despite the need to increase connectivity, the current trajectory of development in Laikipia, if not appropriately adjusted, will likely add more barriers to the landscape. Current plans to expand rhino conservation across the region may increase the number of fences to protect them from poachers. Our results show that fence gaps are important for maintaining landscape connectivity. This is consistent with previous studies demonstrating that animals indeed make use of fence gaps across the Laikipia ecosystem, particularly the species that cannot jump or step over or dig under electric fences (Dupuis-Désormeaux et al. 2016). Well-designed fence gaps will become even more important for reducing the effects of barriers and land fragmentation in a more fragmented future landscape. Additionally, plans to tarmac the main roads across Laikipia County will increase vehicle traffic and potentially add more barriers to movement (LCSA 2019). Kenya is also currently undertaking an ambitious, large-scale infrastructure development project (i.e., the Lamu Port–South Sudan–Ethiopia Transport (LAPSSET) corridor program), that will include roads, railways and pipelines, and connect various rural settlements across the region. It will be important to extend our modeling approach to include the counties neighboring Laikipia in which historical corridors for animal movement existed, complementing current efforts to ensure connected landscapes across Kenya (Ojwang et al. 2017). Moreover, results obtained from aerial surveys have a relatively low spatial resolution. Further analyses using data with higher spatial resolution that can incorporate elevation and slope could be important to gaining a better understanding of connectivity in the hillier areas of north-western Laikipia. Finally, future research should also incorporate the carnivore effects on large-herbivores movement and the potential impact of future climate change scenarios on the landscape heterogeneity and landscape connectivity.

Conclusion

Wildlife conservation is a major challenge in increasingly fragmented landscapes. Critical to resolving this challenge is maintaining connectivity for large herbivores (Fynn and Bonyongo 2010; Beale et al. 2013). We have shown how occupancy and connectivity models can be used to identify important areas for connectivity for a large herbivore species assemblage. Independent tracking data showed that single-species models were consistent with animal movement across the region. In turn, cumulative current density for single-species model outputs were highly correlated with a similar multi-species modeling approach. The multi-species model output was used to assess areas with high potential for connectivity restoration. The future of African wildlife in many countries relies on conservation efforts outside formally protected areas (Tyrrell et al. 2019), which often involve activities that balance the needs of people with those of wildlife (Donaldson et al. 2017). Our modeling framework can help quickly assess functional landscape connectivity and identify critical areas requiring priority conservation efforts that benefit entire animal communities and minimize human-wildlife conflict. Importantly, the use of aerial survey monitoring of large herbivore populations is common across African savannah systems. Incorporating these data to assess habitat connectivity, including historic habitat connectivity where data exist, presents enormous opportunities to make data-driven recommendations about key linkage zones and/or areas that have already been lost to alternative land-uses in the Anthropocene. Given the rapid rate that widespread infrastructural and other land use developments are occurring (Meijer et al. 2018) our approach and findings can benefit decision makers across a variety of ecosystems experiencing similar challenges.

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