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Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant

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Abstract

1. Fencing is one of the most common methods of mitigating human-wildlife conflicts. At the same time, fencing is considered one of the most pressing threats emerging in conservation globally. Although fences act as barriers and can cause population isolation and fragmentation over time, it is difficult to quantitatively predict the consequences fences have for wildlife.
2. Here, we model how fencing designed to mitigate human-elephant conflict (HEC) on the Borderlands between Kenya and Tanzania will affect functional connectivity and movement corridors for African elephants. Specifically, we (a) model functional landscape connectivity integrating natural and anthropogenic factors; (b) predict seasonal movement corridors used by elephants in non-protected areas; and (c) evaluate whether fencing in one area can potentially intensify human-wildlife conflicts elsewhere.
3. We used GPS movement and remote sensing data to develop monthly step-selection functions to model functional connectivity. For future scenarios, we used an ongoing fencing project designed for HEC mitigation within the study area. We modelled movement corridors using least-cost path and circuit theory methods, evaluated their predictive power and quantified connectivity changes resulting from the planned fencing.
4. Our results suggest that fencing will not cause landscape fragmentation and will not change functional landscape connectivity dramatically. However, fencing will lead to a loss of connectivity locally and will increase the potential for HEC in new areas. We estimate that wetlands, important for movement corridors, will be more intensively used by the elephants, which may also cause problems of overgrazing. Seasonal analysis highlights an increasing usage of non-protected lands in the dry season and equal importance of the pinch point wetlands for preserving overall function connectivity.

5. *Synthesis and applications*. Fencing is a solution to small-scale human-elephant conflict problems but will not solve the issue at a broader scale. Moreover, our results highlight that it may intensify the conflicts and overuse of habitat patches in other areas, thereby negating conservation benefits. If fencing is employed on a broader scale, then it is imperative that corridors are integrated within protected area networks to ensure local connectivity of affected species.

KEYWORDS
African elephant, circuitscape, conservation planning, fences, human-elephant conflict, landscape connectivity, step-selection function

1 | INTRODUCTION

Fencing has a long history in conservation management and has proven to be an effective tool for alleviating human-wildlife conflict by keeping wildlife out of certain zones, controlling animal movements and disease outbreaks (Durant et al., 2015; Gadd, 2012; Hayward & Kerley, 2009; Kesch, Bauer, & Loveridge, 2015). Conservation fencing involves separating biodiversity from the factors that threaten it, and a common application of fencing is to restrict animal movements to mitigate human-wildlife conflict (Hayward & Kerley, 2009; Kesch et al., 2015; Slotow, 2012). Fencing to relieve human-elephant conflict (HEC) is a specific focus of conservation managers, because of the severity of the conflicts that ultimately lead to retributive persecution by people and death of animals, and because of the difficulties in applying other management schemes (Hoare, 2012, 2015; Western & Waithaka, 2005).

At the same time, fencing raises many concerns regarding its potential effect on wildlife and has recently been listed as one of the main emerging issues for global conservation and biodiversity (Sutherland et al., 2017). Among the possible impacts are constrained access to essential habitats, blocking of migration routes and pathways for escaping natural threats for the species (Kowalczyk, Schmidt, & Jędrzejewski, 2012; Mbaiwa & Mbaiwa, 2006), loss of genetic exchange (Kowalczyk et al., 2012), and overgrazing and habitat degradation in fenced enclosures (Boone & Hobbs, 2004). Simultaneously, fences can have negative impacts for humans by excluding local people from historically used areas, interrupting the seasonal movements of pastoralism and causing spatial division of communities (Lindsey, Masterson, Beck, & Romañach, 2012).

Strategic planning for fences may reduce negative effects on species, but currently the only country in Africa that requires environmental impact assessment (EIA) for fencing is South Africa (Lindsey et al., 2012). EIA is a legal decision-making instrument recognized by international law designed at mitigating and assessing how human activities affect the environment (Morgan, 2012). Although fencing has a direct impact on the environment and may cause mass mortality events (Gadd, 2012), very often it is not regulated and commonly in many countries across the world. Recent political trends of broad-scale border fencing between countries bring new concerns how these changes will be affecting human and wildlife well-being (Linnell et al., 2016; Sutherland et al., 2017).

Given the impact of fencing on blocking of animal movements, mitigation measures should anticipate the effects of fences and should ideally consider species-specific landscape connectivity. One way to model landscape connectivity is to build a functional connectivity model that represents an animal's ability to traverse a variable and varying landscape (Cushman, McKelvey, & Schwartz, 2009). Functional connectivity modelling is a suitable approach to assess impacts of fencing and it can be applied using a variety of different datasets and methods, including GPS movement data (Keeley, Beier, & Gagnon, 2016; Milanesi et al., 2017; Thurfjell, Ciuti, & Boyce, 2014; Zeller, McGarigal, & Whiteley, 2012). One of the many advantages of using continuous telemetry datasets is that it accounts for variable connectivity in different areas or across time (Hebblewhite & Haydon, 2010; Pape & Löffler, 2015). Various factors, including seasonality in resources distribution, may affect species mobility and need to be reflected in connectivity models (Mateo-Sánchez et al., 2016; Mui, Caverhill, Johnson, Fortin, & He, 2017).

Elephants are bulk grazers and some families can use the same movement routes over decades (Moss, Croze, & Lee, 2011). Movement corridors are essential for elephant population viability and genetic exchange (Douglas-Hamilton, Krink, & Vollrath, 2005; Kioko & Seno, 2011; Naidoo et al., 2018). Numerous studies on African elephants have focused on resistance-based landscape connectivity and corridor modelling using a variety of available methods and datasets (Cushman, Chase, & Griffin, 2010; Epps, Wasser, Keim, Mutayoba, & Brashares, 2013; Pittiglio, Skidmore, van Gils, & Prins, 2012; Roever, van Aarde, & Leggett, 2013). Although the effect of fencing on elephant seasonal movements, vital corridors, and landscape connectivity is a long-term concern for local conservation, we are unaware of any studies that have predicted the influence of fences on elephant movement corridors and connectivity.

Here, we chose the Borderland area between Kenya and Tanzania (Greater Amboseli Ecosystem, GAE) as a case study for predicting the potential impacts of fencing on elephant-specific landscape connectivity. The Amboseli Ecosystem has a history of HEC spanning 50 years (Kioko, Kiringe, & Omondi, 2006; Western & Waithaka, 2005) and the area has experienced rapid agricultural expansion—with the percentage of agricultural areas increasing from 925 km^2 (11.9% of the ecosystem) in the 1970s to 3,025 km^2 in the 2010s (38.9% of the ecosystem) (from Amboseli Conservation Programme long-term aerial monitoring). At the same time, the elephant population has grown steadily since the 1970s (Moss et al., 2011) leading to increasing conflict with farmers (Kioko et al., 2006; Ngene et al., 2013; Okello, 2005; Western & Waithaka, 2005). The severity of the conflict is intensified by the loss in biomass available to elephants in the area due to competing livestock grazing pressure (Western, Mose, Worden, & Maitumo, 2015).

Fencing for HEC mitigation has been applied in GAE since 1997, when two electrified fences were erected around agriculture fields at Kimana and Namelok (Okello & D'amour, 2008). Because of rising HEC in the last few years, local NGOs and government organisations started constructing a new electrified fence on the upper slopes of Kilimanjaro (Big Life Foundation Report, 2017).

We used a functional connectivity model to predict how the new electrified fence erected for HEC mitigation will affect elephant movement corridors and seasonal functional connectivity. We applied a methodological framework that allows integrating fencing scenarios into a seasonally changing environment for further impact assessments. We demonstrated how the connectivity model predictions could be used to (a) provide insights on potential consequences of the fence for functional connectivity of the elephants, and (b) evaluate whether fencing is an appropriate solution for alleviating human-wildlife conflicts.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located in the borderland between Kenya and Tanzania and part of the GAE. The rainfall in the area is highly variable, and is bimodal with a long rainy season from March–May, and

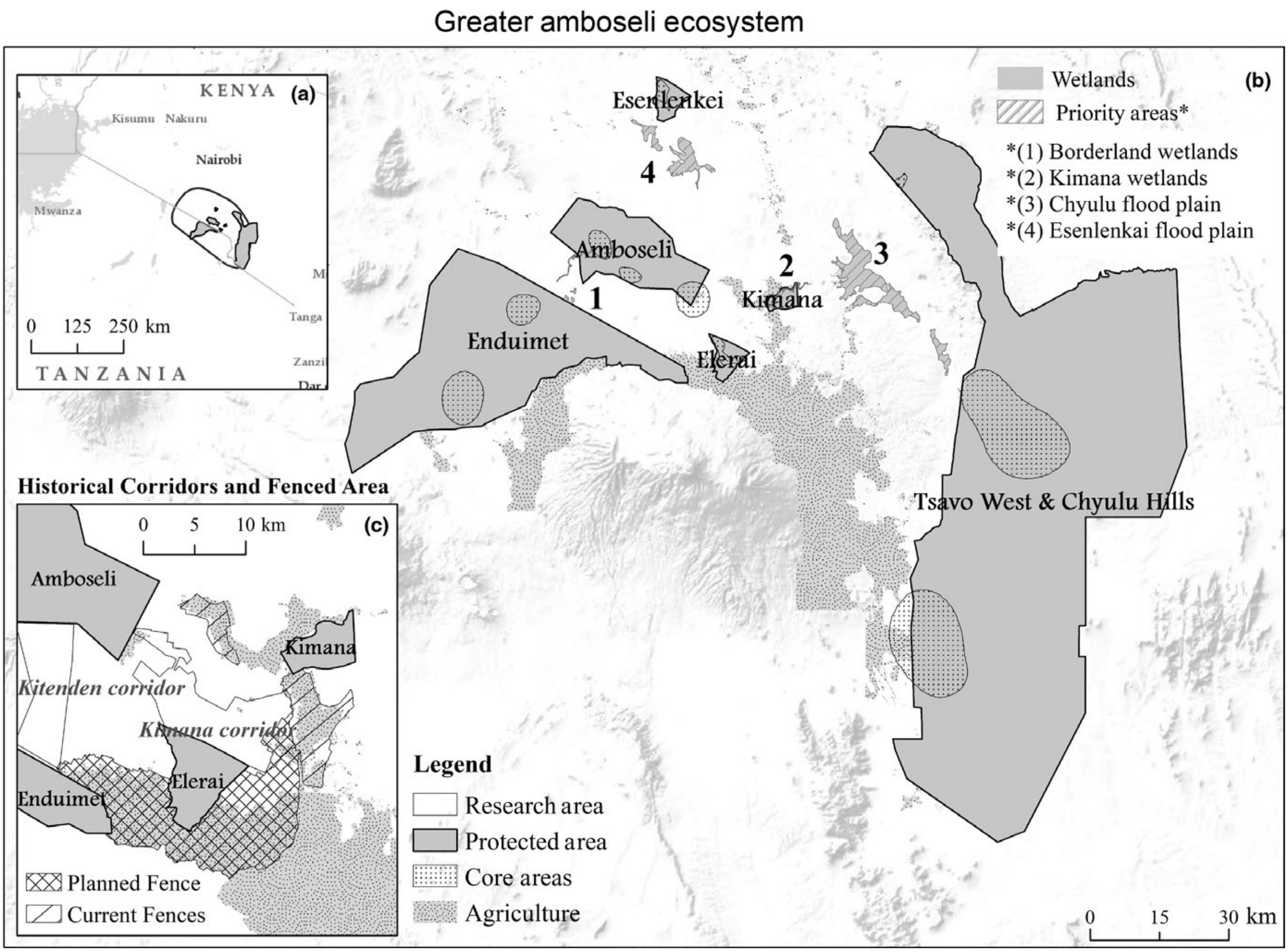

FIGURE 1 (a) Study area in the Borderland between Kenya and Tanzania; (b) Protected lands with the core areas estimated from the elephants' movement data using 50% threshold of kernel densities. Priority wetlands and flood plains defined as the pinch points by the circuit connectivity model; (c) Present and future fencing situation in the study area and protected historical corridors (Kitenden and Kimana corridors)

shorter rains from October–December. The vast majority of the water sources are perennial and concentrated in the seasonal streams and minor rivers (Okello et al., 2016; Western, 1975). The study area includes three large national parks (NPs), three community conservancies and two historically protected corridors: Kitenden and Kimana that are allocated and sustained through leasing programmes by the International Fund for Animal Welfare (IFAW) and African Wildlife Foundation (AWF) (Figure 1).

GAE currently contains two poorly maintained electrified fences erected for HEC mitigation in 1997 around agricultural fields in Kimana and Namelok regions (Figure 1) (Okello & D'amour, 2008). Construction work on a new 28 km electrified fence on the upper slopes of Kilimanjaro started in 2017 (Big Life Foundation Report, 2017; Space for Giants Report, 2015).

2.2 | Telemetry data

GPS telemetry data were derived from twelve elephants immobilized and collared between 2013 and 2014 within the study area (details in Ngene et al., 2014, 2017). Fix rates, sample sizes, and collaring locations are presented in Table S1 of the Supporting Information. We explored individual movement data for spatial and temporal outliers, and excluded paths with irregular non-consistent GPS fixes. These data were resampled to constant 4-hr intervals and the binned trajectories were separated into discrete serial segments, whenever two sequential GPS fixes had a gap longer than 4 hr. The segments that included fewer than 10 consecutive fixes were eliminated from further analysis.

2.3 | Functional landscape connectivity model

We calculated resistance to movement surfaces using a step-selection function (SSF) (Forester, Im, & Rathouz, 2009; Fortin, Morales, & Boyce, 2005). SSF uses a case–control design, where each habitat covariate used during the observed movement steps is contrasted to the habitats available to an animal using conditional logistic regression (Fortin et al., 2005; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Manly, McDonald, Thomas, McDonald, & Erickson, 2007). In this study, we simulated 10 "available" to each "used" step. The step's lengths were simulated from the empirical movement data using Gamma distribution with a maximum likelihood. Turning angles for the available steps were drawn from a uniform distribution between $-\pi$ and π. Besides habitat variables, we integrated step length as a predictor for excluding possible bias caused by a parametric distribution of step length (Forester et al., 2009). We used publicly available GIS datasets and derivatives from remote sensing data for extracting the environmental covariates (Table S1). Land cover classification and post classification analysis were accomplished previously (Osipova et al., 2018a).

We fitted penalized conditional logistic regression with least absolute shrinkage and selection operator (Reid & Tibshirani, 2014). The advantage of this method over simple conditional logistic regression is that it calculates a penalized log-likelihood allowing us to perform parameter estimation and variable selection simultaneously (Reid & Tibshirani, 2014). This approach avoids autocorrelation and biases in predictors, which is a common problem for telemetry data (Beyer et al., 2010; Street et al., 2016). We used the inverse of these movement probabilities to represent landscape resistance values. This is similar to other studies that have used the inverse of habitat suitabilities to reflect resistances, except that our resistances are based on actual movement data (i.e., step-selection), rather than on presence data (i.e., *point-selection*; Zeller et al., 2012).

On the basis of resistance surfaces, we modelled potential connectivity using circuit theory and least-cost path (LCP) methods. LCP allows for the estimation of cost-effective distances between the priority habitat patches, while circuit-theoretic connectivity estimates the current flows reflecting the likelihood of random walks and provides metrics that can be directly interpreted in terms of landscape connectivity (Adriaensen et al., 2003; Carroll, McRae, & Brookes, 2012; McRae, Dickson, Keitt, & Shah, 2008; Shah & McRae, 2008). Both methods require an input layer with the core areas—the areas of high importance for the species (protected lands or major resources patches). The connectivity paths were calculated between these areas and their placement strongly affects the final connectivity maps (McRae & Kavanagh, 2011). Here, we defined the core areas as the 50% threshold of the kernel density estimates calculated from the elephants' GPS fixes within the NPs and community conservancies. This approach helps to define the core area used by the elephants in protected lands and to avoid an effect of the artificial boundaries of the protected areas (Koen, Garroway, Wilson, & Bowman, 2010). The analysis was performed in Linkage Mapper (ArcGIS 10.5.1) (McRae & Kavanagh, 2011) and RASTER package in R (Hijmans et al., 2016).

2.4 | Accounting for seasonality

We used monthly rainfall data obtained from the Tropical Rainfall Measuring Mission (TRMM; TMPA/3B43 dataset) to define wet and dry seasons. Months with rainfall less than 30 mm/month were assigned to the dry season (Figure S1 in the Supporting Information). We used a continuous time series of monthly normalized difference vegetation index (NDVI) derived from MODIS (SRTM) modelling forage availability fluctuation. We binned the 2 years of continuous movement data (2014–2015) into monthly subsets and used the corresponding NDVI layers for fitting SSF and modelling resistance surfaces. Finally, we modelled LCP and circuit-based movement corridors connecting large protected areas for each consecutive month (24 surfaces overall).

We calculated mean current densities for each month and plotted the values as a time series for the whole study area, for protected and non-protected lands and for the priority wetlands within the movement corridors. A time-series statistic was applied (i.e., Granger causality test; Granger, 1988) to test if seasonal changes in monthly average rainfall and NDVI can explain changes of monthly connectivity values.

TABLE 1 Results of the *t*-test (*p* values) for predicted resistance and current density values within 1,337 m buffers at GPS locations versus random points

	Resistance		Current density	
	2014	2015	2014	2015
Jan	<0.001	<0.001	<0.001	<0.001
Feb	<0.001	<0.001	<0.001	<0.001
Mar	<0.001	<0.001	<0.001	<0.01
Apr	<0.001	<0.001	<0.001	<0.001
May	<0.001	<0.001	<0.001	<0.001
Jun	<0.01	<0.001	<0.001	<0.001
Jul	<0.01	<0.001	<0.001	<0.001
Aug	n.s.*	<0.01	<0.001	<0.001
Sep	<0.001	n.s.*	<0.001	<0.01
Oct	n.s.*	<0.01	<0.001	<0.001
Nov	<0.001	n.s.*	<0.001	<0.001
Dec	<0.05	<0.001	<0.001	<0.001

Note. **p* value was not significant.

2.5 | Model validations

To evaluate model performance, we retained 10% of the GPS fixes from the empirical data for each month. We buffered each GPS fix with a radius equal to an average step length of an elephant estimated from GPS data (1,337 m), and recorded resistance and current flow values within the buffers for each resistance surface and cumulative current flows map, respectively. We repeated the same procedure with simulated random points and compared the final resistance and current density values using a *t*-test (Koen, Bowman, Sadowski, & Walpole, 2014). If our monthly predictions of elephant movement have high predictive power, then the resistance values should be significantly smaller and the current flow values significantly larger at actual movement points compared to random points.

2.6 | Assessing fencing effects

To reflect existing fencing conditions, we assigned resistance values of 1 (very high relative resistance value) to areas falling within Namelok and Kimana fences (Figure 1). Since the resistance values range from 0 to 1, this step makes the fenced area highly resistant to movement, but still permeable as these fences are partly broken and occasionally raided by elephants (Okello & D'amour, 2008). As for the future fencing scenario, we increased a resistance value to 100 in the area within the Kilimanjaro fence (future fencing scenario), as it is expected to be well maintained and completely impermeable. This approach was recommended by (McRae & Kavanagh, 2011) for delineating the impermeable areas in Linkage Mapper (ArcGIS 10.5.1).

To highlight the areas most affected by fencing, we calculated the difference between existing and future connectivity values for each month. We subtracted the future from the existing connectivity raster modelled using LCP and circuit-theory. All cells of the resulting differences surfaces were standardized using *z*-scores, and we reclassified them to range between −1 and 1 (lowest to highest values), and summed all rasters. With this procedure, the lowest negative values high-light areas with the largest connectivity losses caused by the fence, while the highest positive values reflect areas with largest connectivity gains. To evaluate temporal connectivity changes, we computed a spatial correlation coefficient (Tjostheim's coefficient; Hubert, Golledge, Costanzo, & Gale, 1985) that summarizes the association between two spatial variables with values ranging from 0 (no spatial correlation) to 1 (perfect spatial correlation). We calculated the correlation coefficient for the whole study area and for the areas of high management priority (i.e., wetlands, historical corridors, and potential human-conflict areas). In addition, we compared changes in the ranks of the corridors and protected areas by estimating monthly highest centrality scores for the existing and future scenarios.

3 | RESULTS

3.1 | Model results and validation

We modelled 24 resistances and connectivity maps (monthly sequence from January 2014 until December 2015) reflecting sequential seasonal changes for the study area. Most resistance ($N = 20$) and all cumulative current flow ($N = 24$) (Media S1 of the Supporting Information) models revealed high potential for predicting movements (Table 1). Compared to predictions from random movements, empirically derived movement predictions showed significantly lower resistance values (0.28 ± 0.005 and 0.46 ± 0.007 for GPS fixes and random points, respectively; *t*-test, $p < 0.05$), and significantly higher cumulative current flows (0.12 ± 0.003 and 0.02 ± 0.001; *t*-test, $p < 0.05$).

3.2 | Seasonal patterns

Potential landscape connectivity has a seasonal character of gradually increasing in the wet months and decreasing in the dry months with the highest cumulative current flow values in the wettest months (March 2014 and May 2015; $\mu = 0.19 \pm 0.091$ and $\mu = 0.19 \pm 0.133$ accordingly); and lowest values in the first rainy months after the dry season (October 2014 and November 2015; $\mu = 0.087 \pm 0.053$ and $\mu = 0.092 \pm 0.049$) (Figure 2). However, this pattern is reversed when protected areas are excluded from the analysis (Figure 3a,b). The difference in connectivity contribution of the non-protected wetlands and seasonal flood plains in wet and dry season revealed that they change their relative input simultaneously (Figure 3a). The synchronous time series indicates that the elephants do not rely on specific wetlands and all of them are similarly important for maintaining connectivity during the dry season. While Kimana and Borderland wetlands are natural sources of water, Esenlenkai and Chyulu Hills flood plains attracts elephants during the dry seasons because of the good protection and artificial water sources provided by the conservancy.

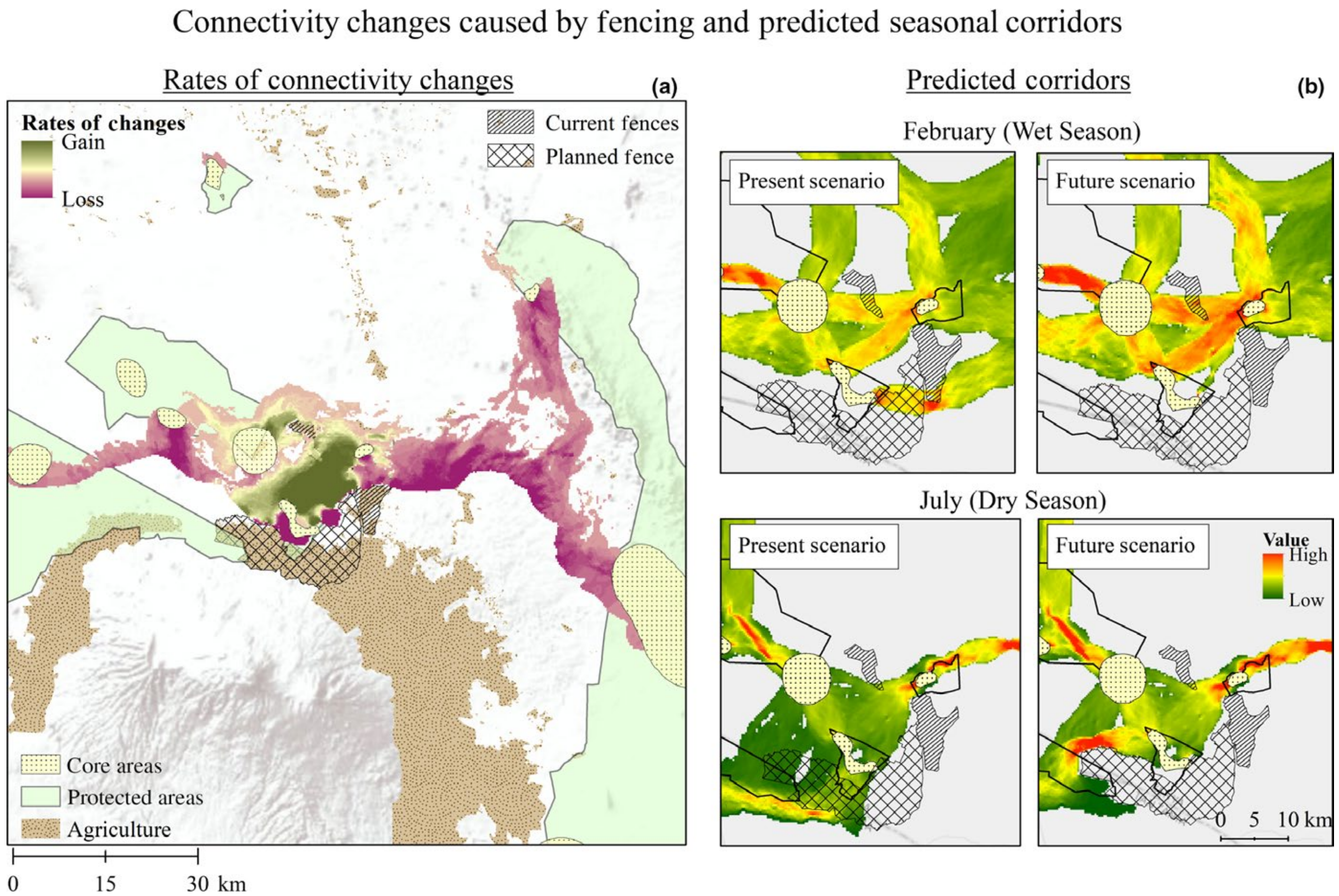

FIGURE 2 (a) Predicted rates of connectivity changes caused by the fencing using least-cost path and circuit theory. Connectivity *loss/gain* are the areas that predicted to be less/more intensively used by the elephants after building the fence; (b) Illustration of the seasonal corridors for wet and dry months predicted for current and future fencing situation

The results of Granger causality tests show that seasonal changes of the cumulative resistance values can be predicted to some degree by changes in the mean monthly rainfall, and especially by NDVI values (Granger causality test; $p = 0.08$ for monthly mean rainfall, $p = 0.04$ for monthly mean NDVI) (Figure 4; Figure S1).

3.3 | Fencing effect

Spatial correlation analysis of the current flows for existing and future scenarios revealed that fencing will not cause significant changes in overall connectivity. Correlation coefficients between current and future current flow surfaces were higher than 0.5 for all months. Generally, correlation coefficients were slightly higher for the wet season (Figure 4).

The number of corridors predicted for the future scenario is not significantly different from the existing scenario (14.37 ± 2.45 and 14.12 ± 2.35 for existing and future scenarios). The centrality score assessment showed that the three corridors with the highest centrality scores stay equally important for the existing and future scenarios (corridors connecting Amboseli with Enduimet, Elerai, and Kimana conservancies (22, 13, and 7 times ranked as 1st, 2nd, and 3rd).

Major connectivity losses were predicted for the future fencing scenario around the corridors connecting Kimana and Elerai conservancies to Tsavo West NP and the corridors between Kenya and Tanzania. Conversely, non-protected lands among Kimana, Elerai, and Amboseli NP will increase the cumulative current density values (Figure 2). Therefore, fencing is not predicted to cause connectivity losses, because new restrictions to movement increase usage of other corridors.

3.4 | High management priority and potential conflict area

The strongest input for maintaining overall connectivity in non-protected areas occurs in the corridors between eastern Amboseli and the Elerai Conservancy (21 of 24 times ranked as 1st); Amboseli and Enduimet (12 times ranked as 2nd); Amboseli and Kimana Conservancy (seven times ranked as 3rd). Amboseli NP, Kimana, and Elerai Conservancies had the highest centrality scores for most models (23, 12, and 8 models of 24 scored these areas as 1st, 2nd, and 3rd in ranking) (Table 2).

We identified four wetlands and flood plains most commonly highlighted by the model as pinch points within the corridors

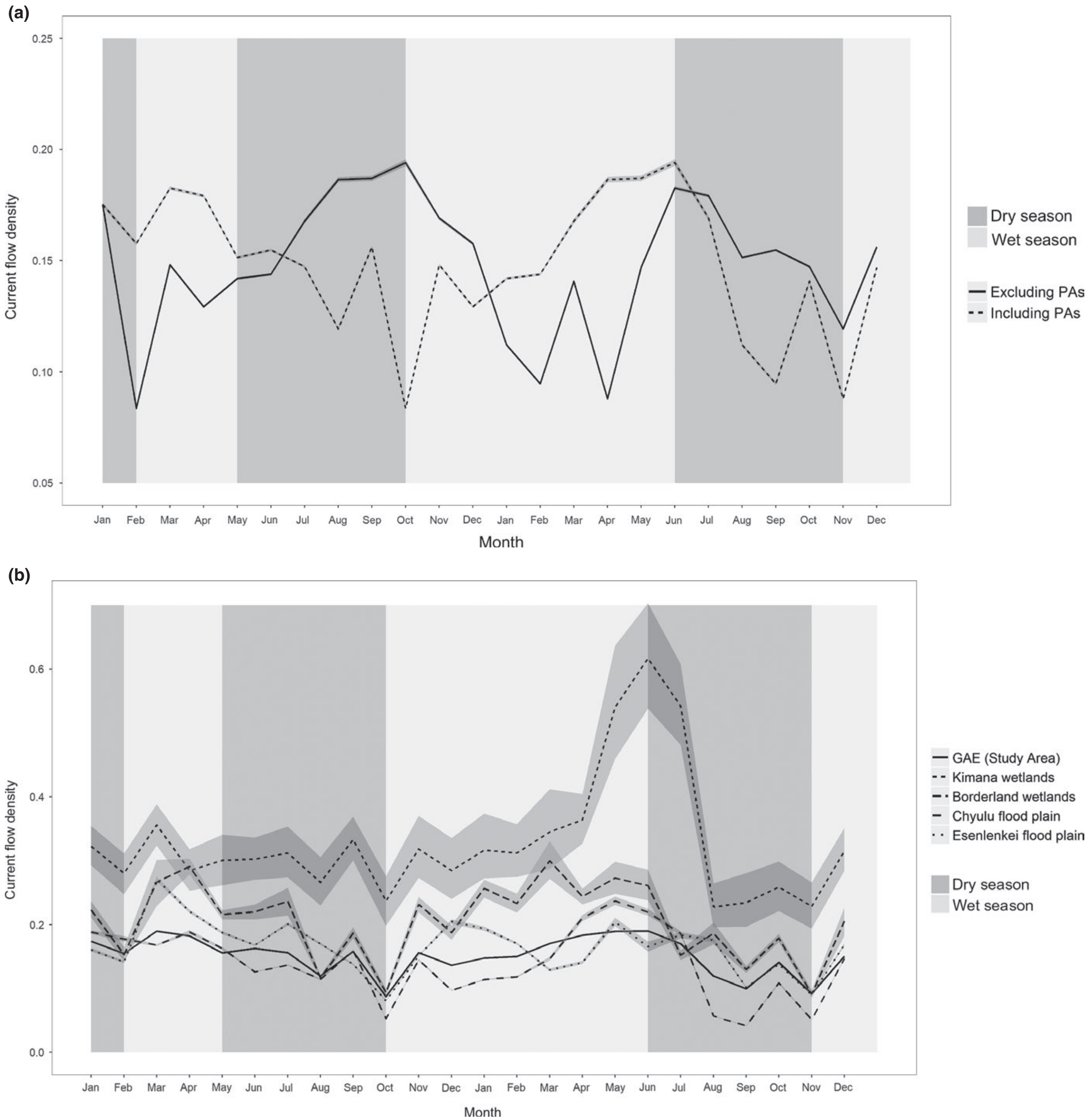

FIGURE 3 Mean current flow density values estimated and plotted for each month (2014–2015). (a) Mean current density for the entire area and for the wetlands selected as pinch points; (b) Mean current density plotted for the entire research area and excluding protected areas (PAs)

(Figures 1b and 3a). Current flow analysis for these areas revealed that flow densities in Kimana and Borderland wetlands are constantly higher than the average current flows for the whole area, while Esenlenkai and Chyulu flood areas experience fewer currents. Cumulative flow of Kimana wetlands has the highest values compared to others and the magnitude increases in the dry months. All these areas tend to increase conductivity values in rainy months, and decrease them in dry months (Figure 3a).

Only Kimana wetland and nearby Kimana historical corridor will be significantly affected by fencing (mean conductance values are 0.3 ± 0.18 versus 0.4 ± 0.18 for current and future scenarios; monthly spatial correlation values are less than 0.5, Figure 4), while the Kitenden corridor did not change in current flow (0.2 ± 0.08 for current and future scenarios; monthly spatial correlation values are higher than 0.5). The same increase in conductance was detected for an agriculture field adjacent to Kimana wetland (Figure 4). Another

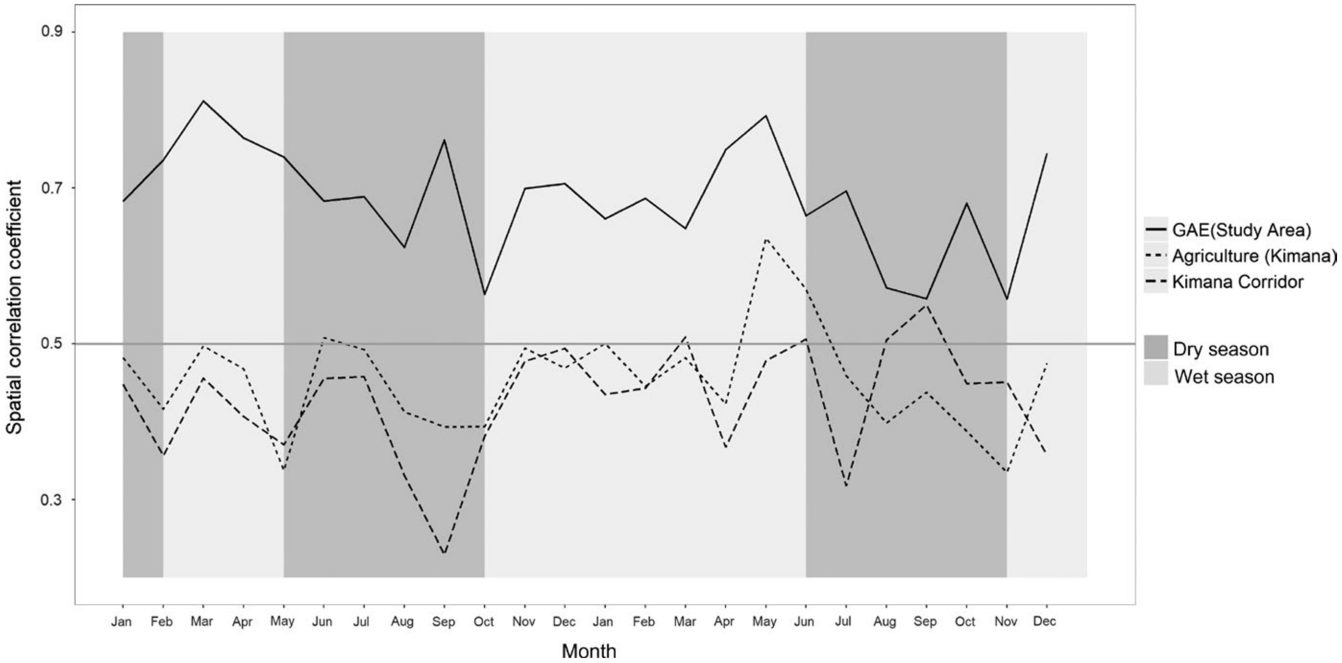

FIGURE 4 Spatial correlation coefficients (Tjostheim's coefficient) calculated for monthly circuit connectivity surfaces modelled for current and future fencing scenarios. The plot includes values for the entire study area, for Kimana historical corridor and the adjacent agriculture area

agriculture patch lying on the pinch point of the corridor connecting Kimana conservancy and Tsavo West NP did not reveal any significant changes in conductance potential (0.2 ± 0.12 and 0.2 ± 0.11; monthly spatial correlation values are higher than 0.5).

4 | DISCUSSION

Crop raiding is the most prevalent type of HEC in Africa and Asia, and is increasing sharply with the spread of farms into elephant range areas such as Amboseli (Graham, Notter, Adams, Lee, & Ochieng, 2010; Pozo, Coulson, McCulloch, Stronza, & Songhurst, 2017). This conflict has led to an increase in human and elephant fatalities across much of Africa (Gadd, 2005; Lindsey et al., 2012; Okello, 2005; Western & Waithaka, 2005). There is debate surrounding possible management schemes to mitigate this conflict, but fencing is still the most common tool as it gives an immediate, although not necessarily most effective, resolution to conflicts (Hayward & Kerley, 2009; Sitati & Walpole, 2006). Despite a broad application of fencing in HEC mitigation, it rarely has been a part of a preliminary EIA (Hayward & Kerley, 2009). Our study illustrates how empirical movement data can be combined with connectivity modelling to predict the consequences of planned fencing on elephant movements across the landscape.

The Borderland elephants in GAE provide an example of how fencing may bring immediate, localized relief to HEC. Erecting the 28-km long fence around the agriculture fields on the upper slopes of Kilimanjaro is an example, where construction of an electrified fence was considered the best and most urgent option by the local community (Space for Giants Report, 2015). A number of challenges remain, including the maintenance responsibility and costs, but rapid installation of the fence has seen a large reduction in farm losses

TABLE 2 Top ranking protected areas and movement corridors based on centrality score values for present and future fencing scenarios

	Present	Future
Protected areas		
Rank 1	Amboseli (upper core) (23)	Amboseli (upper core) (22)
Centrality score	17.5 ± 1.87	17.7 ± 1.74
Rank 2	Kimana (12)	Kimana (14)
Centrality score	14.5 ± 1.60	14.8 ± 1.65
Rank 3	Elerai (8)	Amboseli (lower core) (9)
Centrality score	13.5 ± 1.33	13.5 ± 1.42
Corridors		
Rank 1	Amboseli-Elerai (21)	Amboseli-Elerai (22)
Centrality score	8.4 ± 1.23	8.2 ± 1.03
Rank 2	Amboseli-Enduimet (16)	Amboseli-Enduimet (13)
Centrality score	6.5 ± 0.85	6.5 ± 0.91
Rank 3	Amboseli-Kimana (7)	Amboseli-Kimana (7)
Centrality score	5.2 ± 0.10	5.4 ± 0.83

Note. Corridors/protected areas were included in the table only when they were top ranked maximum number of times (the number of selected models is provided in parenthesis).

as well as human and elephant deaths (Big Life Foundation Report, 2017).

The results of our study show that even though relatively large areas of elephant habitat will be isolated by the fence, it is unlikely to severely affect functional connectivity for the species across broad scales. The planned fence was intended to block areas between Enduimet and Elerai conservancies, yet the major connectivity routes occur in a north-south direction and pass through western Kilimanjaro's slopes (Enduimet Wildlife Management Area), and those in the east-west direction connecting Amboseli with Tsavo West NP through Kimana Wildlife Sanctuary (Ojwang et al., 2017). The deterrence of elephants from the farming areas will likely lead to increased use of the northern areas of the Amboseli ecosystem where rainfall is too low to support farming (Western & Lindsay, 1984).

Although fencing will not cause an overall decrease in landscape connectivity, it will create additional pressure on areas where conflict does not currently exist. Kimana wetland showed the highest conductance potential compared to other wetlands and flood plains, and, at the same time, it will be most affected by fencing. Increases in conductance are also significant in the Kimana historical corridor and in the agriculture fields nearby. These results suggest that building the fence on the upper slopes of Kilimanjaro for HEC mitigation will increase the probability of HEC elsewhere in the area. At the same time, an increasing presence of elephants in the protected historical corridor may come with harmful side effect such as fast habitat degradation caused by population concentration in safe protected areas (Western, 1989).

In a highly seasonal environment where biodiversity depends on the amount of rainfall, time-series analysis provides important information to conservation decision-making. Adding a seasonal component to our analysis helped to prioritize seasonal corridors, identify commonly used routes and to confirm the time of the year where elephant movements may cause HEC. As the importance of non-protected lands increased in the dry season and HEC occurs more often in the driest periods (King, Lala, Nzumu, Mwambingu, & Douglas-Hamilton, 2017; Kioko et al., 2006), we suggest that the movement corridors with the highest ranks predicted for the dry period should receive special attention in local management planning and be considered for more formal protection within conservation estates.

Fence construction for human-wildlife conflict mitigation has two major disadvantages: they are expensive to maintain over the long term and may have unpredicted negative consequences for wildlife at larger spatial scales (Hayward & Kerley, 2009). There are extensive discussions on alternative management schemes that could be applied to mitigate HEC, including bee hives, capsicum-based products, or buffer crops (Hoare, 2012; King et al., 2017; Osborn, 2002). Another tactic would be to change elephant behaviour in non-intrusive ways, for example, via surface water manipulation (Chamaillé-Jammes, Valeix, & Fritz, 2007). These methods are often less costly but still effective alternatives to fencing as they decrease the severity of the HEC, but keep the outfenced area partly permeable (Slotow, 2012). Another advantage of these methods is direct involvement of the rural communities, which can change their attitude towards wildlife (Osborn & Parker, 2002). However, there are many uncertainties related to these approaches, and some of the long-term maintenance-related costs are comparable with those of electric fences (Grant et al., 2008).

While our results are specific to the Borderland elephants in GAE, the shifting of conflicts due to local mitigation measures is likely a general challenge for the management of human-wildlife conflicts. We therefore suggest managers to conduct an EIA before implementing actions to reduce human-wildlife conflicts, and to consider not only local but also broad-scale impacts. Assessing the costs and benefits of different mitigation measures is essential for finding optimal solutions (Lindsey et al., 2012; Ringma, Wintle, Fuller, Fisher, & Bode, 2017) and our study provides a framework for modelling and assessing connectivity for EIAs. Considering connectivity is crucial, because some local measures (e.g. fencing) might lead to immediate local successes, but shift the problem elsewhere by changing wildlife movement routes. This is essentially a "cost" incurred by the measure which needs to be compared to its predicted benefits. While other mitigation measures (e.g. management of water resources) might show less pronounced reductions in local conflicts compared to fences, they might also not simply shift the problem to other sensitive areas, thus causing smaller costs at the landscape scale.

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AUTHORS' CONTRIBUTIONS

L.O., N.B., and D.W. conceived the ideas and designed methodology; M.M.O., S.J.N. and S.N. collected the data; L.O. analysed the data; N.B. and M.W.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n1804pf (Osipova et al., 2018b).

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REFERENCES

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, *64*(4), 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use–availability designs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1550), 2245–2254. https://doi.org/10.1098/rstb.2010.0083

Big Life Foundation Report. (2017). Amboseli HEC Mitigation Fence Phase I Update.

Boone, R. B., & Hobbs, N. T. (2004). Lines around fragments: Effects of fencing on large herbivores. *African Journal of Range & Forage Science*, *21*(3), 147–158. https://doi.org/10.2989/10220110409485847

Carroll, C., McRae, B. H., & Brookes, A. (2012). Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. *Conservation Biology*, *26*(1), 78–87. https://doi.org/10.1111/j.1523-1739.2011.01753.x

Chamaillé-Jammes, S., Valeix, M., & Fritz, H. (2007). Managing heterogeneity in elephant distribution: Interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, *44*(3), 625–633. https://doi.org/10.1111/j.1365-2664.2007.01300.x

Cushman, S. A., Chase, M., & Griffin, C. (2010). Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. *Spatial complexity, informatics, and wildlife conservation* (pp. 349–367). Retrieved from http://link.springer.com/chapter/10.1007/978-4-431-87771-4_19 https://doi.org/10.1007/978-4-431-87771-4

Cushman, S. A., McKelvey, K. S., & Schwartz, M. K. (2009). Use of empirically derived source-destination models to map regional conservation corridors. *Conservation Biology*, *23*(2), 368–376. https://doi.org/10.1111/j.1523-1739.2008.01111.x

Douglas-Hamilton, I., Krink, T., & Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, *92*(4), 158–163. https://doi.org/10.1007/s00114-004-0606-9

Durant, S. M., Becker, M. S., Creel, S., Bashir, S., Dickman, A. J., Beudels-Jamar, R. C., … Pettorelli, N. (2015). Developing fencing policies for dryland ecosystems. *Journal of Applied Ecology*, *52*(3), 544–551. https://doi.org/10.1111/1365-2664.12415

Epps, C. W., Wasser, S. K., Keim, J. L., Mutayoba, B. M., & Brashares, J. S. (2013). Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. *Molecular Ecology*, *22*(6), 1574–1588. https://doi.org/10.1111/mec.12198

Forester, J. D., Im, H. K., & Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology*, *90*(12), 3554–3565. https://doi.org/10.1890/08-0874.1

Fortin, D., Morales, J. M., & Boyce, M. S. (2005). Elk winter foraging at fine scale in Yellowstone National Park. *Oecologia*, *145*(2), 334–342. https://doi.org/10.1007/s00442-005-0122-4

Gadd, M. E. (2005). Conservation outside of parks: Attitudes of local people in Laikipia. *Kenya. Environmental Conservation*, *1*, 50–63. https://doi.org/10.1017/S0376892905001918

Gadd, M. E. (2012). Barriers, the beef industry and unnatural selection: A review of the impact of veterinary fencing on mammals in Southern Africa. *Fencing for conservation* (pp. 153–186). Springer. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4614-0902-1_9 https://doi.org/10.1007/978-1-4614-0902-1

Graham, M. D., Notter, B., Adams, W. M., Lee, P. C., & Ochieng, T. N. (2010). Patterns of crop-raiding by elephants, Loxodonta africana, in Laikipia, Kenya, and the management of human–elephant conflict. *Systematics and Biodiversity*, *8*(4), 435–445. https://doi.org/10.1080/14772000.2010.533716

Granger, C. W. J. (1988). Some recent development in a concept of causality. *Journal of Econometrics*, *39*(1), 199–211. https://doi.org/10.1016/0304-4076(88)90045-0

Grant, C. C., Bengis, R., Balfour, D., Peel, M., Davies-Mostert, W., Killian, H., … Henley, M. (2008). Controlling the distribution of elephants. *Elephant management: A scientific assessment for South Africa* (pp. 329–369). Johannesburg, South Africa: Wits University Press.

Hayward, M. W., & Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation*, *142*(1), 1–13. https://doi.org/10.1016/j.biocon.2008.09.022

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hijmans, R. J., vanEtten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., … Ghosh, A. (2016). Package 'raster.' R Package. Retrieved from ftp://slartibardfast.gtlib.gatech.edu/pub/CRAN/web/packages/raster/raster.pdf

Hoare, R. (2012). Lessons from 15 years of human–elephant conflict mitigation: Management considerations involving biological, physical and governance issues in Africa. *Pachyderm*, *51*, 60–74.

Hoare, R. (2015). Lessons from 20 years of human-elephant conflict mitigation in Africa. *Human Dimensions of Wildlife*, *20*(4), 289–295. https://doi.org/10.1080/10871209.2015.1005855

Hubert, L. J., Golledge, R. G., Costanzo, C. M., & Gale, N. (1985). Measuring association between spatially defined variables: An alternative procedure. *Geographical Analysis*, *17*(1), 36–46. https://doi.org/10.1111/j.1538-4632.1985.tb00825.x

Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDonald, T. L., & Boyce, M. S. (2006). Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management*, *70*(2), 347–357. https://doi.org/10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2

Keeley, A. T. H., Beier, P., & Gagnon, J. W. (2016). Estimating landscape resistance from habitat suitability: Effects of data source and nonlinearities. *Landscape Ecology*, *31*(9), 2151–2162. https://doi.org/10.1007/s10980-016-0387-5

Kesch, M. K., Bauer, D. T., & Loveridge, A. J. (2015). Break on through to the other side: The effectiveness of game fencing to mitigate human—Wildlife conflict. *African Journal of Wildlife Research*, *45*(1), 76–87. https://doi.org/10.3957/056.045.0109

King, L. E., Lala, F., Nzumu, H., Mwambingu, E., & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conservation Biology*, *31*(4), 743–752. https://doi.org/10.1111/cobi.12898

Kioko, J. M., Kiringe, J., & Omondi, P. (2006). Human-elephant conflict outlook in the Tsavo-Amboseli ecosystem, Kenya. *Pachyderm*, *41*, 53–60.

Kioko, J. M., & Seno, S. O. (2011). Elephant corridor use and threats in the eastern range of Amboseli elephants, Kenya. *Pachyderm*, *49*(1), 70–78.

Koen, E. L., Bowman, J., Sadowski, C., & Walpole, A. A. (2014). Landscape connectivity for wildlife: Development and validation of multispecies linkage maps. *Methods in Ecology and Evolution*, *5*(7), 626–633. https://doi.org/10.1111/2041-210X.12197

Koen, E. L., Garroway, C. J., Wilson, P. J., & Bowman, J. (2010). The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS ONE*, *5*(7), e11785. https://doi.org/10.1371/journal.pone.0011785

Kowalczyk, R., Schmidt, K., & Jędrzejewski, W. (2012). Do fences or humans inhibit the movements of large mammals in Białowieża primeval forest?. In *Fencing for conservation* (pp. 235–243). New York, NY: Springer.

Lindsey, P. A., Masterson, C. L., Beck, A. L., & Romañach, S. (2012). Ecological, social and financial issues related to fencing as a conservation tool in Africa. In *Fencing for conservation* (pp. 215–234). New York, NY: Springer. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4614-0902-1_12

Linnell, J. D., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., … Potocnik, H. (2016). Border security fencing and wildlife: The end of the transboundary paradigm in Eurasia? *PLoS Biology*, *14*(6), e1002483. https://doi.org/10.1371/journal.pbio.1002483

Manly, B. F. L., McDonald, L., Thomas, D., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: Statistical design and analysis for field studies*. Berlin, Germany: Springer Science & Business Media.

Mateo-Sánchez, M. C., Gastón, A., Ciudad, C., García-Viñas, J. I., Cuevas, J., López-Leiva, C., … Saura, S. (2016). Seasonal and temporal changes in species use of the landscape: How do they impact the inferences from multi-scale habitat modeling? *Landscape Ecology*, *31*(6), 1261–1276. https://doi.org/10.1007/s10980-015-0324-z

Mbaiwa, J. E., & Mbaiwa, O. I. (2006). The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. Retrieved from http://www.ubrisa.ub.bw/handle/10311/28

McRae, B., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology and conservation. *Ecology*, *10*, 271–272.

McRae, B. H., & Kavanagh, D. M. (2011). *Linkage mapper connectivity analysis software*. Seattle, WA: The Nature Conservancy.

Milanesi, P., Holderegger, R., Caniglia, R., Fabbri, E., Galaverni, M., & Randi, E. (2017). Expert-based versus habitat-suitability models to develop resistance surfaces in landscape genetics. *Oecologia*, *183*(1), 67–79. https://doi.org/10.1007/s00442-016-3751-x

Morgan, R. K. (2012). Environmental impact assessment: The state of the art. *Impact Assessment and Project Appraisal*, *30*(1), 5–14. https://doi.org/10.1080/14615517.2012.661557

Moss, C. J., Croze, H., & Lee, P. C. (2011). *The Amboseli elephants: A long-term perspective on a long-lived mammal*. Chicago, IL: University of Chicago Press. https://doi.org/10.7208/chicago/9780226542263.001.0001

Mui, A. B., Caverhill, B., Johnson, B., Fortin, M.-J., & He, Y. (2017). Using multiple metrics to estimate seasonal landscape connectivity for Blanding's turtles (*Emydoidea blandingii*) in a fragmented landscape. *Landscape Ecology*, *32*, 531–546. https://doi.org/10.1007/s10980-016-0456-9

Naidoo, R., Kilian, J. W., Du Preez, P., Beytell, P., Aschenborn, O., Taylor, R. D., & Stuart-Hill, G. (2018). Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. *Biological Conservation*, *217*, 96–103. https://doi.org/10.1016/j.biocon.2017.10.037

Ngene, S., Njumbi, S., Ngoru, B., Nzisa, M., Bitok, E., Poghon, J., … Gombe, A. (2014). Satellite-linked GPS collars deployed on elephants in Tsavo Ecosystem, Kenya. *Journal of Current Issues in Media & Telecommunications*, *6*(2), 127–157.

Ngene, S., Njumbi, S., Nzisa, M., Kimitei, K., Mukeka, J., Muya, S., … Omondi, P. (2013). Status and trends of the elephant population in the Tsavo–Mkomazi ecosystem. *S Urvival*, *53*, 38–50.

Ngene, S., Okello, M. M., Mukeka, J., Muya, S., Njumbi, S., & Isiche, J. (2017). Home range sizes and space use of African elephants (*Loxodonta africana*) in the Southern Kenya and Northern Tanzania borderland landscape. *International Journal of Biodiversity and Conservation*, *9*(1), 9–26.

Ojwang, O. G., Wargute, P. W., Said, M. Y., Worden, J., Muruthi, P., & Kanga, E. (2017). Mapping wildlife dispersal areas and migratory routes KWS (Technical Report). Government of the Republic of Kenya. Retrieved from http://www.environment.go.ke

Okello, M. M. (2005). Land use changes and human–wildlife conflicts in the Amboseli area, Kenya. *Human Dimensions of Wildlife*, *10*(1), 19–28. https://doi.org/10.1080/10871200590904851

Okello, M. M., & D'amour, D. E. (2008). Agricultural expansion within Kimana electric fences and implications for natural resource conservation around Amboseli National Park, Kenya. *Journal of Arid Environments*, *72*(12), 2179–2192. https://doi.org/10.1016/j.jaridenv.2008.07.008

Okello, M. M., Kenana, L., Maliti, H., Kiringe, J. W., Kanga, E., Warinwa, F., … Mwangi, P. (2016). Population density of elephants and other key large herbivores in the Amboseli ecosystem of Kenya in relation to droughts. *Journal of Arid Environments*, *135*(Suppl C), 64–74. https://doi.org/10.1016/j.jaridenv.2016.08.012

Osborn, F. V. (2002). Capsicum oleoresin as an elephant repellent: Field trials in the communal lands of Zimbabwe. *The Journal of Wildlife Management*, *3*, 674–677.

Osborn, Ferrei. V., & Parker, G. E. (2002). Community-based methods to reduce crop loss to elephants: Experiments in the communal lands of Zimbabwe. *Pachyderm*, *33*(32), e38.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2018a). Using step-selection functions to model landscape connectivity for African elephants: Accounting for variability across individuals and seasons. *Animal Conservation*, https://doi.org/10.1111/acv.12432.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2018b). Data from: Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant (*Loxodonta africana*). *Dryad Digital Repository*, https://doi.org/10.5061/dryad.n1804pf

Pape, R., & Löffler, J. (2015). Seasonality of habitat selection shown to buffer alpine reindeer pastoralism against climate variability. *Ecosphere*, *6*(12), 1–9. https://doi.org/10.1890/ES15-00169.1

Pittiglio, C., Skidmore, A. K., van Gils, H. A. M. J., & Prins, H. H. T. (2012). Identifying transit corridors for elephant using a long time-series. *International Journal of Applied Earth Observation and Geoinformation*, *14*(1), 61–72. https://doi.org/10.1016/j.jag.2011.08.006

Pozo, R. A., Coulson, T., McCulloch, G., Stronza, A. L., & Songhurst, A. C. (2017). Determining baselines for human-elephant conflict: A matter of time. *PLoS ONE*, *12*(6), e0178840. https://doi.org/10.1371/journal.pone.0178840

Reid, S., & Tibshirani, R. (2014). Regularization paths for conditional logistic regression: The clogitL1 package. *Journal of Statistical Software*, *58*(12), 12.

Ringma, J. L., Wintle, B., Fuller, R. A., Fisher, D., & Bode, M. (2017). Minimizing species extinctions through strategic planning for conservation fencing. *Conservation Biology*, *31*(5), 1029–1038. https://doi.org/10.1111/cobi.12922

Roever, C. L., van Aarde, R. J., & Leggett, K. (2013). Functional connectivity within conservation networks: Delineating corridors for African elephants. *Biological Conservation*, *157*, 128–135. https://doi.org/10.1016/j.biocon.2012.06.025

Shah, V. B., & McRae, B. H. (2008). Circuitscape: A tool for landscape ecology. In Proceedings of the 7th Python in Science Conference (Vol. 7, pp. 62–66).

Sitati, N. W., & Walpole, M. J. (2006). Assessing farm-based measures for mitigating human-elephant conflict in Transmara District, Kenya. *Oryx*, *40*(3), 279–286. https://doi.org/10.1017/S0030605306000834

Slotow, R. (2012). Fencing for purpose: A case study of elephants in South Africa. In *Fencing for conservation* (pp. 91–104). New York, NY: Springer.

Space for Giants Report. (2015). *Situation assessment of human-elephant conflict in the Greater Amboseli Ecosystem*. Narobi, Kenya: Big Life Foundation.

Street, G. M., Fieberg, J., Rodgers, A. R., Carstensen, M., Moen, R., Moore, S. A., … Forester, J. D. (2016). Habitat functional response mitigates reduced foraging opportunity: Implications for animal fitness and space use. *Landscape Ecology*, *31*(9), 1939–1953. https://doi.org/10.1007/s10980-016-0372-z

Sutherland, W. J., Barnard, P., Broad, S., Clout, M., Connor, B., Côté, I. M., … Ockendon, N. (2017). A 2017 Horizon Scan of Emerging Issues for Global Conservation and Biological Diversity. *Trends in Ecology & Evolution*, *32*(1), 31–40. https://doi.org/10.1016/j.tree.2016.11.005

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*(1), 4. https://doi.org/10.1186/2051-3933-2-4

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, *13*(3–4), 265–286. https://doi.org/10.1111/j.1365-2028.1975.tb00139.x

Western, D. (1989). The ecological role of elephants in Africa. *Pachyderm*, *12*, 42–46.

Western, D., & Lindsay, W. (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, *22*(4), 229–244. https://doi.org/10.1111/j.1365-2028.1984.tb00699.x

Western, D., Mose, V. N., Worden, J., & Maitumo, D. (2015). Predicting extreme droughts in Savannah Africa: A comparison of proxy and direct measures in detecting biomass fluctuations. Trends and their causes. *PLoS ONE*, *10*(8), e0136516. https://doi.org/10.1371/journal.pone.0136516

Western, D., & Waithaka, J. (2005). Policies for reducing human-wildlife conflict: A Kenya case study. *Conservation Biology Series – Cambridge*, *9*, 357.

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, *27*(6), 777–797. https://doi.org/10.1007/s10980-012-9737-0

SUPPORTING INFORMATION

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