Conservation Biology

Conservation Methods

Characterizing the landscape of movement to identify critical wildlife habitat and corridors

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Abstract: Landscape planning that ensures the ecological integrity of ecosystems is critical in the face of rapid human-driven habitat conversion and development pressure. Wildlife tracking data provide unique and valuable information on animal distribution and location-specific behaviors that can serve to increase the efficacy of such planning. Given the spatiotemporal complexity inherent to animal movements, the interaction between movement behavior and a location is often oversimplified in commonly applied analyses of tracking data. We analyzed GPS-tracking-derived metrics of intensity of use, structural properties (based on network theory), and properties of the movement path (speed and directionality) with machine learning to define homogeneous spatial movement types. We applied our approach to a long-term tracking data set of over 130 African elephants (*Loxodonta africana*) in an area under pressure from infrastructure development. We identified 5 unique location-specific movement categories displayed by elephants, generally defined as high, medium, and low use intensity, and 2 types of connectivity corridors associated with fast and slow movements. High-use and slow-movement corridors were associated with similar landscape characteristics associated with productive areas near water, whereas low-use and fast corridors were characterized by areas of low productivity farther from water. By combining information on intensity of use, properties of movement paths, and structural aspects of movement across the landscape, our approach provides an explicit definition of the functional role of areas for movement across the landscape that we term the *movescape*. This combined, high-resolution information regarding wildlife space use offers mechanistic information that can improve landscape planning.

Keywords: animal movement, connectivity, clustering, GPS radio telemetry, graph theory, landscape planning, movement corridor, network theory, space use

Caracterización del Paisaje de Movimiento para Identificar Hábitats y Corredores de Fauna Importantes

Resumen: La planeación de paisajes que asegura la integridad ecológica de los ecosistemas es muy importante de cara a la rápida conversión de hábitats llevada por la acción humana y la presión del desarrollo. Los datos de rastreo de fauna proporcionan información única y valiosa sobre la distribución animal y el comportamiento específico por localidad que puede servir para incrementar la eficiencia de dicha planeación. Dada la complejidad espaciotemporal inherente al movimiento animal, la interacción entre la conducta de movimiento y la ubicación con frecuencia se ve sobre simplificada en los análisis de información de rastreos aplicados comúnmente. Analizamos las medidas derivadas de rastreos por GPS de la intensidad de uso, las propiedades estructurales (basadas en la teoría de redes) y las propiedades de la vía de movimiento (velocidad y direccionalidad) con aprendizaje automatizado para definir los tipos de movimiento espacial homogéneo. Aplicamos nuestra estrategia a un conjunto de datos de rastreo a largo plazo de más de 130 elefantes africanos (*Loxodonta africana*) en un área bajo presión ocasionada por el desarrollo de infraestructura. Identificamos cinco categorías de movimiento específico por localidad exhibidas por los elefantes, definidas en términos generales como intensidad de uso alta, media y baja. También identificamos dos tipos de corredores de conectividad asociados con movimientos rápidos y lentos. Los corredores de intensidad de uso alta y movimiento lento estuvieron asociados con las características similares de paisaje asociadas a las áreas productivas cercanas a cuerpos de agua, mientras que los corredores de intensidad

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baja y movimiento rápido estuvieron caracterizados por áreas de baja productividad alejadas de los cuerpos de agua. Con la combinación de la información sobre la intensidad de uso, las propiedades de las vías de movimiento y los aspectos estructurales del movimiento a lo largo del paisaje, nuestra estrategia proporciona una definición explícita del papel funcional que tienen las áreas de movimiento en el paisaje, la cual denominamos *paisaje de movimiento* (*movescape*). Esta información combinada y de alta resolución con respecto al uso espacial por la fauna ofrece información mecánica que puede mejorar la planeación del paisaje.

Palabras Clave: concentración, conectividad, corredor de movimiento, movimiento animal, planeación del paisaje, telemetría por radio GPS, teoría de gráficos, teoría de redes, uso del espacio

摘要: 在人类驱动的栖息地快速转换和发展压力之下, 确保生态系统生态完整性的景观规划十分重要。野生动物追踪数据可以提供关于动物分布和特定位置行为的独特且有价值的信息, 有助于提高此类规划的有效性。考虑到动物运动固有的时空复杂性, 常用的追踪数据分析方法通常会过度简化运动行为和位置之间的相互作用。我们利用机器学习, 分析了基于 GPS 追踪数据的几个指标, 包括使用强度、结构特性 (基于网络理论) 和运动路径特性 (速度和方向), 以定义同质空间的运动类型。我们将该方法应用于一个长期追踪数据集, 该数据集来自一个受到基础设施建设压力地区的 130 多只非洲草原象 (*Loxodonta africana*) 。我们确定了大象展示出的五种独特的特定位置运动类型, 并定义为高、中、低使用强度, 还确定了快速、慢速运动的两种连接廊道。高使用强度和慢速运动的廊道有相似的景观特征, 与靠近水源、生产力高的区域相联系, 而低使用强度和快速运动的廊道则以远离水源、生产力低的区域为特征。我们的方法结合了使用强度、运动路径特征和跨景观运动的结构特征, 为跨景观运动区域的功能提供了明确的定义, 我们称之为 *“movescape”* 。以上这些关于野生动物空间利用的高分辨率综合信息为改进景观规划提供了机理信息。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 动物运动, 连接度, 聚类, GPS 无线电遥测, 景观规划, 运动廊道, 网络理论, 图论, 空间利用

Introduction

Land conversion driven by agriculture expansion, resource extraction, and related infrastructure development is accelerating globally (Tilman et al. 2011) and is recognized among the most prevalent drivers of wildlife population decline and a key risk factor for species persistence (Brook et al. 2008). Human-driven landscape changes interfere with the movement and behavior of animals and affect multiple processes at individual, population, and community levels that can have adverse effects on animal fitness and ecosystem functions (Allen & Singh 2016). Preserving and maintaining areas critical to wildlife populations is a primary step for the mitigation of the increasing impacts of human footprint expansion on natural systems. As such, application of effective approaches to identify locations key to wildlife is crucial to conservation efforts.

Understanding the processes that govern movement (Nathan et al. 2008) and how to protect this critical behavior has been the focus of increasing research, driven largely by rapid development in tracking technology and analytical approaches (Kays et al. 2015). These developments have led to a better understanding of the myriad of movement-related patterns, including home-ranging behavior (Fleming et al. 2018), resource selection (Avgar et al. 2016), patterns in intensity of use (Bracis et al. 2018), movement syndromes (e.g., residency to migration continuum) (Bastille-Rousseau et al. 2017), and movement modes or behavioral states (Gurarie et al. 2009; Edelhoff et al. 2016). These methods typically focus on a single attribute of movement behavior (e.g., intensity of use or movement speed), which limits insight into the multiple aspects of space use captured through movement data (Wittemyer et al. 2019).

The spatial context of movements is fundamental to interpreting differences in movement properties and to elucidating drivers of movement patterns. However, spatial context in movement ecology has primarily been investigated in terms of patterns in utilization distribution, resource use, and resource selection. Inferences from these approaches generally focus on population-level global patterns in use, but additional inferences can be gained by investigating variation in patterns of use (Bastille-Rousseau et al. 2010; Benhamou & Riotte-Lambert 2012), individual variation in behavior (Leclerc et al. 2016), or how use is associated with different movement modes (Roever et al. 2013). Determining the relationships between path properties or defined movement states and their landscape context directly provides another approach to determine ecological factors structuring movement behavior (Graves et al. 2007). Critically, the value of an area for animal movement extends beyond its importance as assessed via intensity of use or the context of movement path properties (Wittemyer et al. 2019). Some locations are particularly important for animal behaviors or functions including movement connectivity or other properties of animal space-use patterns that are not easily diagnosed using conventional approaches (Jacoby & Freeman 2016). For example, locations of critical importance for animals can represent hubs (e.g., central foraging areas or repeatedly visited sites) or bottlenecks in their movement network that can be independent of the intensity to which they are being

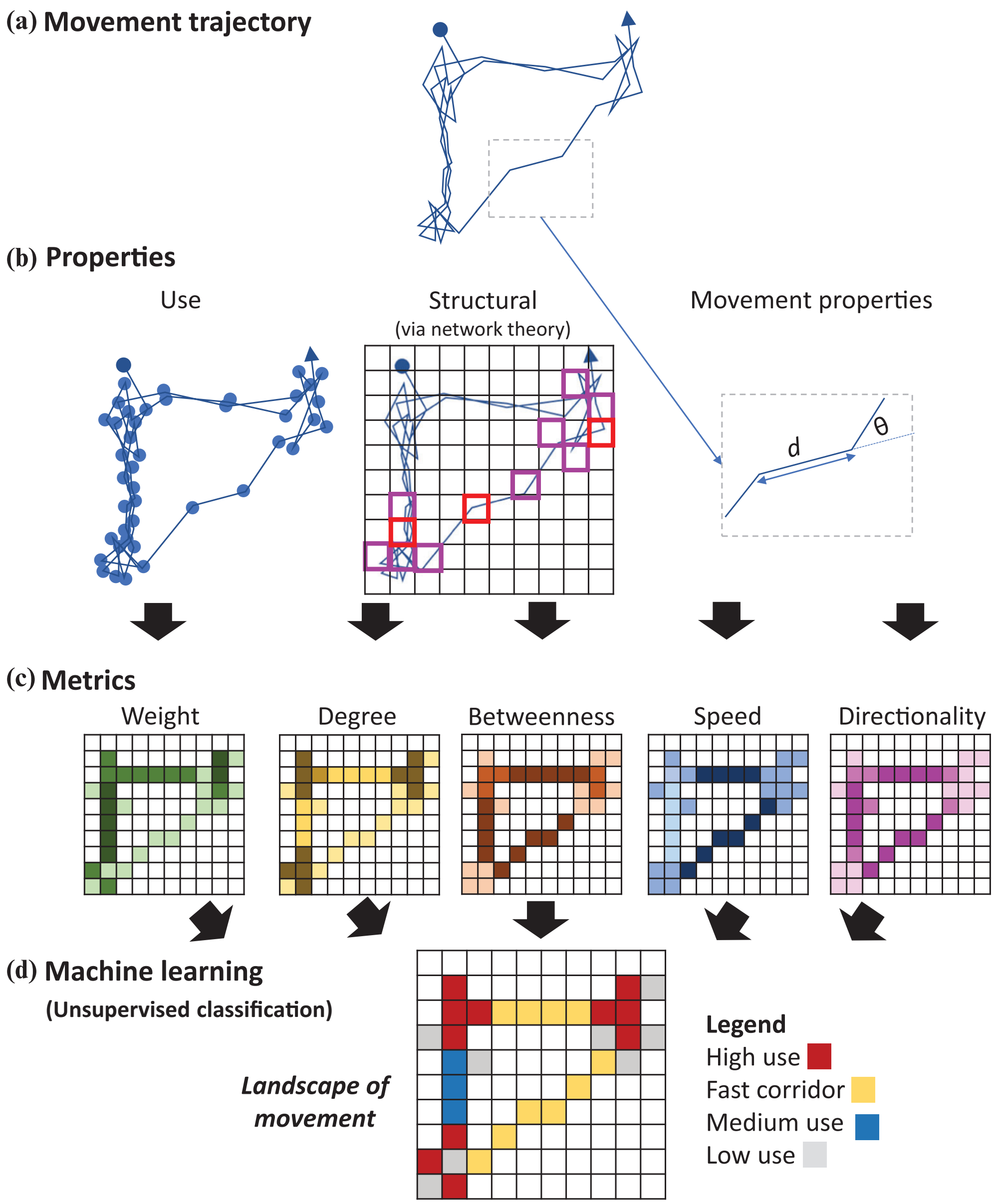

Figure 1. How the functional landscape of movement (i.e., movescape) can be evaluated based on animal movement trajectory: (a) trajectory acquired using telemetry, (b) trajectory used to estimate properties related to intensity of use, landscape structure of movements, or movement path properties (c) metrics of intensity of use estimated by counting the number of locations in an area (i.e., weight), network metrics (degree and betweenness) estimated by evaluating the connection among pixels (e.g. red pixels connected to purple pixels, and metrics of movement path properties estimated using speed and directionality (all metrics derived only for pixels with GPS points), and (d) machine-learning simplification of metrics in [a-c] into a synthetic representation describing the functional role of a location for animal movement.

used. We refer to these additional characteristics of an animal's use of space as structural properties (Wittemyer et al. 2019).

Combining information on intensity of use, movement path properties, and structural aspects of locations across the broader movement network can offer more general insight on the functional role of a location as defined by animal movement behavior (Fig. 1). A synthetic representation of these analytical products allows the characterization of a functional landscape of movement or movescape, which integrates the spatial representation based on intensity of use, temporal representation based on movement trajectory properties, and broader spatial context that can be unveiled using network theory (Bastille-Rousseau et al. 2018). Different types of movement can be segregated along these axes (i.e., intensely used, centrally connected areas accessed with slow or fast movements). For example, a spatially explicit definition of movements of high connective value (as defined using a network approach) combined with information on the intensity of use and movement phases occurring at high connective locations can serve to quantitatively demarcate corridors associated with fast directional movement and limited residency time relative to corridors where animals move slowly with longer residency times and, therefore, extend the range of an individual as well as facilitate connectivity (i.e., slow corridor) (Fig. 1). Combining these different streams of movement properties within a single landscape opens new avenues to understanding of movement ecology and animal interactions with the environment. The movescape can serve to define the functional importance of locations for animal movement across the landscape that could be directly integrated into conservation actions.

To exemplify the potential of combining movement path and structural properties with information related to intensity of use, we integrated 5 metrics (Fig. 1) to explore movement of a population of African elephants (*Loxodonta africana*) inhabiting northern Kenya. We applied graph theoretic approaches to the elephant movement data (Bastille-Rousseau et al. 2018) to derive a metric of intensity of use (weight) as well as metrics related to structural properties (degree and betweenness) to characterize locational importance for connectivity. We also extracted movement path properties regarding average speed and directionality at these same locations. We used machine learning to detect homogeneous movement types (clusters) within space (defined within pixels) from these 5 streams of information to define movescapes of elephants, including different intensities of use (high-, medium-, and low-use areas), location-specific velocity (slow and fast movements), and importance to connectivity (high and low connectivity values that underpin corridor definition). Of particular interest, the combination of these metrics allowed definition of different types of corridors, which we simplified to those associated with fast and directed movements or slow and meandering movements (i.e., connectivity vs. extended-use corridors [Bennett 1999]). Finally, we evaluated whether the detected movement types were mostly influenced by environmental variables (i.e., productivity, water, and human presence) or social variables (i.e., use by other elephants). Overall, our framework integrates properties related to intensity of use with functional and structural movement patterns to define the movescape.

Methods

Study Area

The Laikipia-Samburu ecosystem in northern Kenya (approximately 0.4°S to 2°N, 36.2°E to 38.3°E) is inhabited by the country's second largest elephant population. The elephant population is of conservation interest, and the study area is a designated site for the Convention on International Trade in Endangered Species Monitoring of Illegal Killing of Elephants program (Wittemyer et al. 2014). Land use in the ecosystem consists of community conservancies, communal land, government managed national reserves and forest reserves, and private lands. The area has a variety of land-cover types, including cool moist highland forests and semiarid savannah. The system generally has 2 wet seasons and 2 dry seasons annually.

Data Collection

We analyzed GPS data collected from 2001 to 2019 from 138 elephants (69 females and 69 males) as part of a long-term research project. All animal handling procedures were approved by Colorado State University (IACUC protocol 18-7741A). Most collars acquired locations on the hour, but a minority of collars acquired locations at 30-minute intervals or every 2 hours. Erroneous locations were filtered by using a speed filter of 9 km/hour, and all trajectories were resampled every 2 hours to accommodate the different schedules of collars. After resampling, elephant tracking data sets from the 138 individuals averaged 11,794 locations (range 53–58,031), and the total sample was 1,627,598 locations. Individual movement networks were composed of 7,507 pixels (range 40–25,293) of 100 m^2.

Estimation of Movement Metrics

Our analytical approach entailed several steps as illustrated in Fig. 1 and Supporting Information. We used movement data to evaluate several movement metrics (step 1, Fig. 1) and machine learning to assign a location to a specific movement class (steps 2 and 3, Supporting Information); compiled location-specific environmental variables (step 4), and performed a regression evaluating the impact of these variables on the probability of detecting a specific movement class (step 5). Finally, we integrated the functions developed in this analysis to the R package moveNT (https://github.com/BastilleRousseau/moveNT) (vignette provided in Supporting Information to assist reader).

We evaluated the movement network of each tracked individual (step 1, Supporting Information) with the approach presented in Bastille-Rousseau et al. (2018). This package calculates network metrics from a movement path by laying a grid over the trajectory in which each pixel of the grid that contains GPS locations represents a network node. The trajectory is used to identify connections (edges) among the 100-m^2 pixels (nodes), and connections are tallied into an adjacency matrix. For each pixel, we calculated the weight (number of locations within a pixel), degree (number of other pixels a given pixel is connected to), and betweenness (importance of a pixel to access the rest of the network). We also extracted the average speed of movements within this pixel (based on all movement steps initiated within a pixel) and the mean cosine (dot product) of the turning angles of steps within a pixel (Wall et al. 2013), an indication of how directional movement is within a pixel.

Clustering of Movement Functions Within Pixels

Gaussian mixture models were used to cluster pixels based on the 5 variables (weight, degree, betweenness, speed, and dot product). Clustering was applied independently to each individual data set (step 2, Supporting Information) by defining the optimal number of clusters in 1–8 clusters with the Bayesian information criterion (BIC) (Fraley & Raftery 2002). We limited the number of cluster to 8 because we expected a maximum of 8 functionally meaningful clusters (low use, medium use, high use, and movement corridor, each associated with a meandering or directed movement phase reflecting high speed and high dot product).

To estimate general population-level clusters in the movement properties, we applied a second clustering approach to the center (mean) value of each cluster derived for individuals (step 3, Supporting Information). At the population level, we tested for 2–8 clusters with BIC to select the optimal numbers. Two-step clustering ensured that equal weight was given to each individual in the clustering procedure (Supporting Information). These population clusters were associated qualitatively with different potential types of movement (fast corridor, slow corridor and high-, medium-, and low-use areas) based on the center of each cluster. Population-level maps illustrating movement categories over the landscape were created by overlaying individual-level classification, meaning that a pixel could be associated with different categories. We also created additional maps of movement corridors based on linear interpolation of the movement steps in Supporting Information. The R package mclust (Scrucca et al. 2016) was used for this part of the analysis.

Environmental Variables

A series of spatial covariates were compiled to relate to elephant landscape of movement (step 4, Supporting Information). These covariates included a 30-m Landsat land-cover classification reclassified into 4 land-cover types (forest, wooded savannah, open savannah, and other types) and land ownership (national and forest reserves, community conservancies, private conservancies, private lands, and communal lands). Euclidean distance to roads and water were also used where water sources where characterized as permanent and seasonal sources. Human footprint in the area was characterized by manually digitizing human features across the area based on imagery available through Google Earth. We used this information to generate a layer of distance to villages and towns and a layer of spatial density of dwellings (bomas), which were extracted across a 500-m radius moving window. Elevation data at a 30-m resolution were obtained from the Shuttle Radar Topography Mission and were used to generate slope and terrain ruggedness index (TRI) layers. Normalized difference vegetation index (NDVI) was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation product (Justice et al. 1998). The MODIS vegetation indices, which span the years 2000–2018, are provided at 250-m resolution every 16 days. We extracted average NDVI and mean interannual variability as the SD in NDVI for each pixel as a measure of vegetation predictability (Bastille-Rousseau et al. 2017).

Statistical Analyses

We extracted all environmental covariates for each pixel of an individual movement network grid. For each of these pixels, we extracted how other individuals were using the areas as defined by the assigned movement types. We used mixed-effects logistic regression with individual elephants as a random factor and with various contrasts (Table 1) to evaluate the impacts of environmental and social (other elephants' space use) variables on the different types of use (step 5, Supporting Information). For these regressions, we kept only pixels that had >95% classification certainties for the use type (assuming pixels with uncertainty in the use category were not important). Given some pixels were used by >1 individual, the same pixels could be present more than once in the same regression (either as the variable coded as one or zero). Due to the large data set and more conservative outputs of BIC (Aho et al. 2014), we performed model selection with BIC in a 3-step process, first choosing the more parsimonious subset of environmental variables, then the subset of social variables (female and male use), then testing whether environmental, social, or both sets of variables provided a better fit. Each model included a spatial autocovariate to account for spatial autocorrelation (i.e., autologistic model) based on an inverse weighting scheme, a neighborhood radius of 5000 pixels (i.e., 500 km), and a symmetric neighborhood matrix (Bardos et al. 2015). Models were also tested for multicollinearity with the variance inflation factor (no variables had a factor value >10) (Dormann et al. 2012). Given

Table 1. Contrasts used as the response variables in logistic regressions testing the impacts of covariates on animal movement types.

Variable coded as 1[*]	*Variables coded as 0*[*]	*Variables excluded*[a]	*Results in*
High use	medium use, low use	corridor	Table 3
Corridor (fast)	high use, medium use, low use	corridor (slow)	Table 3
Corridor (slow)	high use, medium use, low use	corridor (fast)	Table 3
Medium use	low use	high use, corridor	Supporting Information
Corridor (fast)	corridor (slow)	high use, medium use, low use	Supporting Information
Low use (fast)	low use (slow)	high use, medium use, corridor	Supporting Information

[*]Variables included (and their coding in the logistic regression).

Table 2. Summary of the unsupervised classification applied to various metrics of movement of 138 African elephants inhabiting northern Kenya.

	Cluster 1	*Cluster 2*	*Cluster 3*	*Cluster 4*	*Cluster 5*	*Cluster 6*	*Cluster 7*	*Cluster 8*
Weight[a]	−0.337	0.625	1.604	1.203	2.915	0.394	−0.383	−0.380
Degree[a]	−0.357	0.718	1.580	1.393	2.603	0.510	−0.411	−0.412
Betweenness[a]	1.602	1.353	0.817	0.009	0.550	0.019	−0.112	−0.266
Speed[a]	0.531	0.144	0.374	−0.364	−0.548	−0.223	0.765	−0.230
Dot product[a]	0.006	0.094	−0.337	−0.059	−0.143	−0.021	0.605	−0.258
Proportion of pixels[b]	0.090	0.068	0.007	0.047	0.049	0.122	0.140	0.478
Proportion of individuals[c]	0.804	0.616	0.196	0.572	0.993	0.551	0.725	0.775
Movement type	fast corridor	slow corridor	high-use (fast)	high-use	highest-use	medium-use	low-use (fast)	low-use (slow)

[a]*Average (center) of the cluster, where positive values indicate a higher mean and negative values indicate lower mean of that movement property in the designated cluster than in other clusters.*
[b]*Spatial proportion of each cluster based on the percentage of an individual's range in pixels assigned to a given cluster. See also Supporting Information for individual variation in the proportion of pixels.*
[c]*Proportion of studied individuals in the cluster.*

documented differences in movement behavior of males and females (Bastille-Rousseau & Wittemyer 2019), analyses were performed separately for males and females. We used the area under the curve (AUC) of the receiver operating characteristic curve to evaluate performance of the logistic regression. We used the R packages AICcmodavg (Mazerolle 2017), MuMIn (Barton 2018), and spdep (Bivand & Piras 2015) for this part of the analysis. We conducted an additional analysis to evaluate the association in movement types among individuals (see Supporting Information).

Results

Individual and Population-Level Clustering

Eight clusters were identified at the population level based on BIC (Table 2), but most individual elephants (77.5% of individuals) were assigned to 5–7 of these clusters, and the remaining individuals were assigned to ≤4 clusters. No elephants displayed each cluster or only 1 cluster. Clusters 5 (high use) and 1 (fast corridors) were assigned to the highest proportion of individuals, but represented limited areas on the landscape (few pixels). Population-level clusters were characterized by different movement types. Clusters 1 and 2 were associated with areas important for connectivity (based on high betweenness values), but the clusters were differentiated with respect to time spent in them (weight) and, relatedly, the speed in which elephants traveled within these pixels. These 2 clusters were descriptively assigned as fast and slow movement corridors. Although relatively common among individuals (assigned to 80% and 62% of individuals respectively [Table 2]), such pixels were relatively rare on the landscape, representing respectively 9% and 7% of the pixels in a given individual's network. Cluster 3, 4, and 5 were associated with high-use areas as indicated by their high weight and degree values. Cluster 5 was characterized by very high use and found in virtually all individuals (99%), despite being assigned to only 5% of pixels in an individual's network (Table 2). Cluster 6 represented medium-use areas, whereas clusters 7 and 8 represented low-use areas that differed in regard to the speed and directionality within a pixel. These low-use clusters were the most common on the landscape; 62% of pixels in individual networks were assigned to these clusters (Table 2 & Supporting Information). However, when combining individual networks into a population-level representation and giving priority to high-use areas when individuals were grouped together (Fig. 2 & Supporting Information), the spatial importance of high-use areas increased. Likewise, many high-use areas were also fast, slow, or both fast and slow movement corridors, especially around the national reserves, where a majority of elephants are tracked leading to high range overlap (Fig. 2). These patterns were also reflected in the spatial-association analysis (Supporting Information).

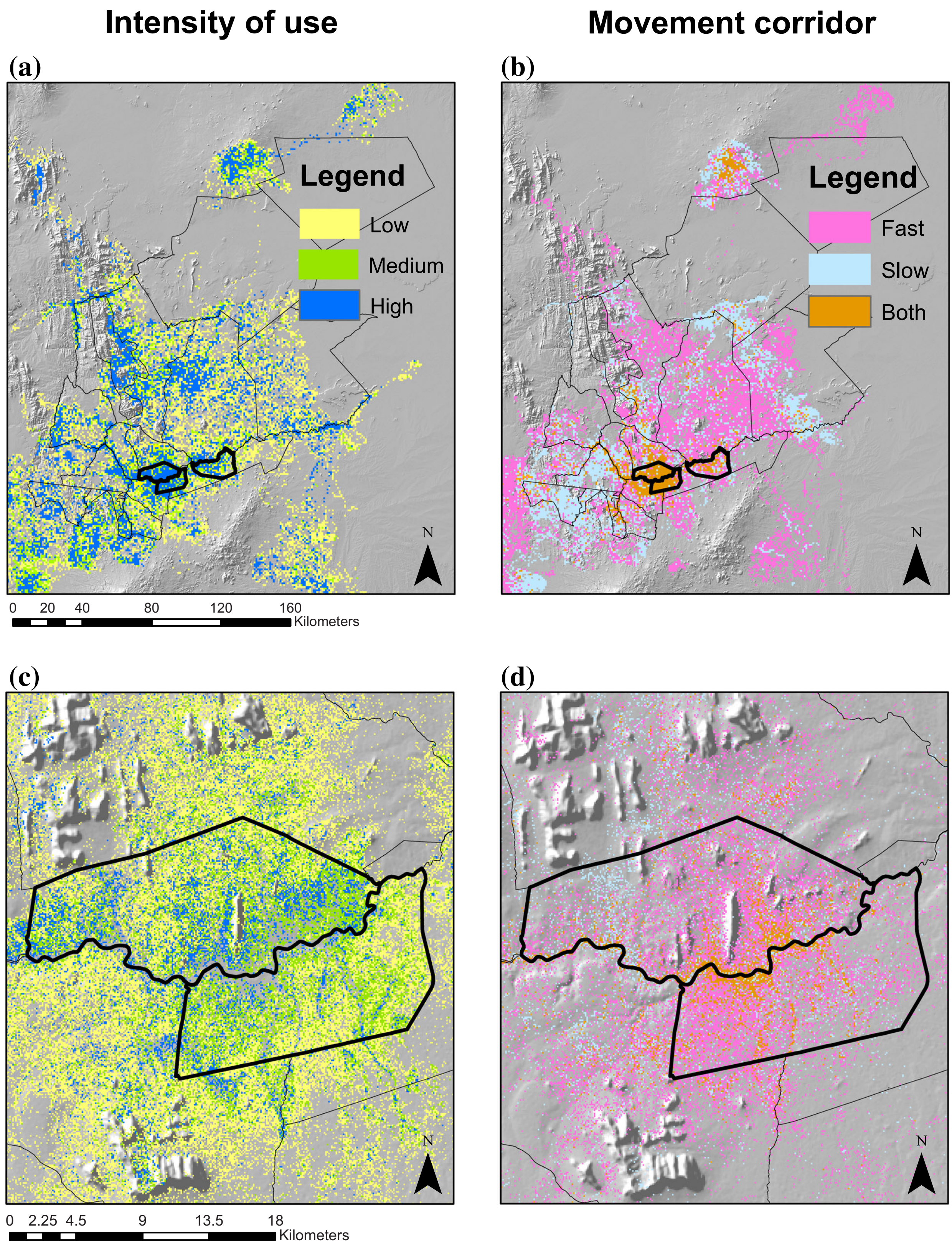

Figure 2. Intensity of use and corridor categorizations of movement properties of 138 elephants in Northern Kenya: (a, b) overall study area with a discretized pixel resolution of 1 km and (c,d) movement based on a pixel size of 100 m centered on the intensively sampled national reserves (bold outlining, national reserves; thin outlining, surrounding community conservancies). When multiple individuals overlap within a pixel, the higher use category is displayed. When the 2 types of corridors are assigned to the same location by different individuals, the both-corridors category is displayed. Additional maps of movement corridors are in Supporting Information.

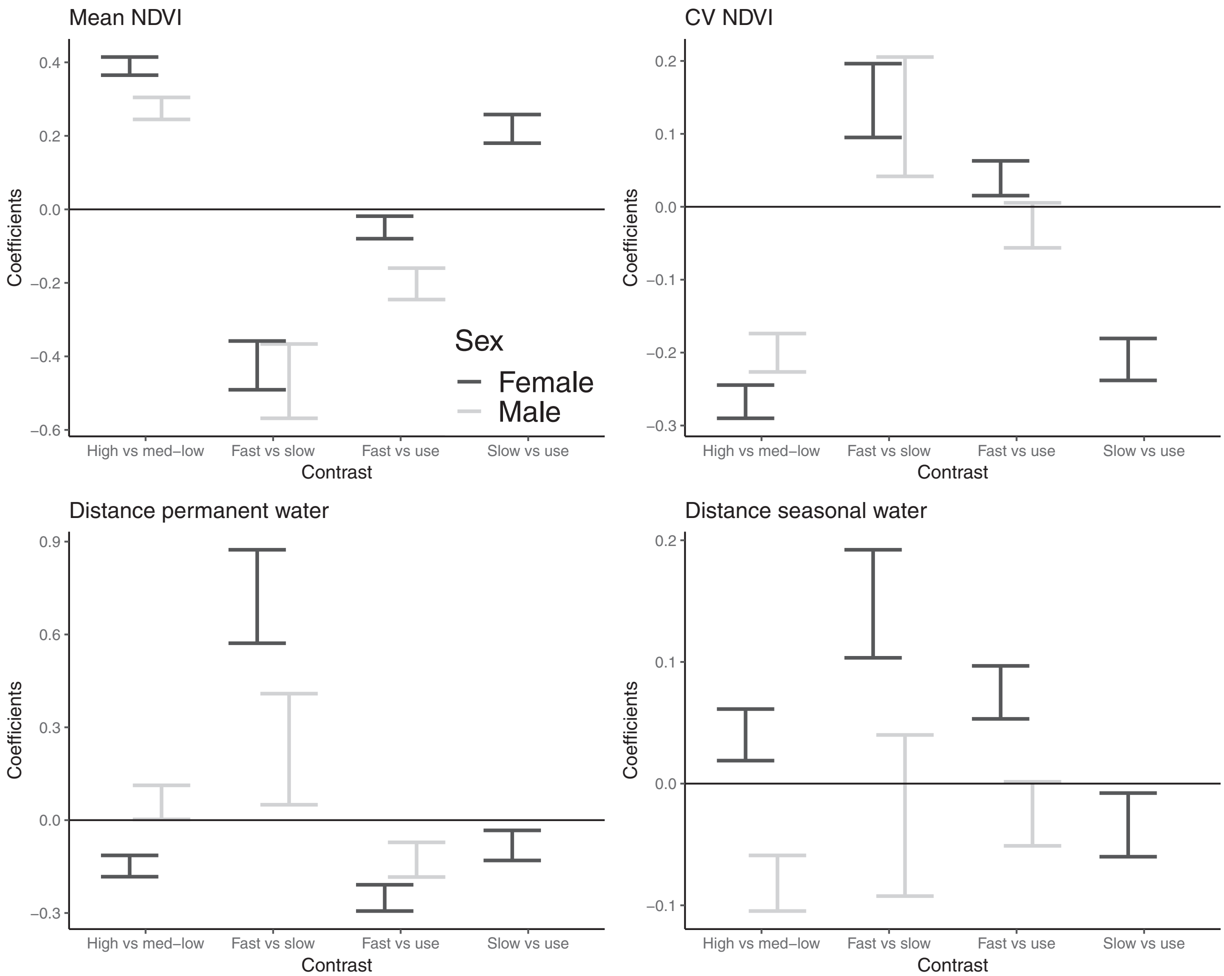

Figure 3. Subset of coefficients and confidence intervals of mixed-effects logistic regressions evaluating the effects of 4 variables (for both sexes: high-use vs. medium- and low-use areas; fast corridor vs. slow corridor; fast corridor vs. high-, medium-, and low-use areas; and slow corridor vs. high-, medium-, and low-use areas) related to productivity and water access on the probability of observing different animal movement types (NDVI, normalized difference vegetation index; CV, coefficient of variation). Complete models are in Table 3 and Supporting Information.

Environmental and Social Influences on Movement Functions

Model selection indicated that both environmental and social variables explained variation among individual movescapes (Supporting Information). Overall, top models of male movescapes were less complex and had similar or slightly higher predictive performance as measured by AUC values than the top models for females (Table 3 & Supporting Information). Likewise, roles of many variables were different between sexes (Fig. 3, Table 3, & Supporting Information) As predicted, vegetation productivity and predictability where the dominant variables related to high-use areas for both males and females, followed by proximity to permanent water (Fig. 3). Human footprint (villages and bomas [traditional cattle corrals]) did not play a strong role in how elephants used space. For females land designation also played a pivotal role in determining high-use areas; private lands and conservancies were preferred relative to communal areas without conservation status. Fast corridors tended to occur in areas with relatively low and less predictable vegetation productivity (Table 3 & Fig. 3), whereas slow corridors were in places of relatively high and more predictable productivity. Relative to slow corridors, fast corridors also appeared to be farther away from water (Supporting Information). For females corridors tended to occur more commonly on community lands, and slow relative to fast corridors differed mostly in response to land designation. Slow corridors occurred in private lands, whereas fast corridors were mostly found in community conservancies and communal areas (Table 3). In terms of variables related to conspecific use, high use was positively influenced by high use by conspecifics. Fast corridors for female were less likely to occur in areas of high use by other elephants (Table 3). Results of contrasts between medium-use and low-use

Table 3. Coefficients (CI) of mixed-effects logistic regressions evaluating the effects of variables related to landscape and conspecifics on the probability of observing different movement types.[a].

	Male			Female		
Coefficients[b]	*high vs. medium and low*	*fast vs. use*	*slow vs. use*	*high vs. medium and low*	*fast vs. use*	*slow vs. use*
Intercept	−2.5 (−3.328 to −1.671)	−3.602 (−4.558 to −2.646)	−5.584 (−6.948 to −4.22)	−4.211 (−4.75 to −3.671)	−4.41 (−5.197 to −3.623)	−8.232 (−9.561 to −6.904)
Mean NDVI	0.275 (0.245 to 0.305)	−0.203 (−0.245 to −0.16)		0.39 (0.365 to 0.414)	−0.049 (−0.08 to −0.019)	0.219 (0.18 to 0.258)
CV NDVI	−0.2 (−0.226 to −0.174)	−0.025 (−0.056 to 0.005)		−0.267 (−0.29 to −0.245)	0.039 (0.015 to 0.063)	−0.209 (−0.238 to −0.181)
Dist water perm	0.057 (0.002 to 0.113)	−0.128 (−0.184 to −0.072)		−0.148 (−0.183 to −0.114)	−0.251 (−0.294 to −0.209)	−0.082 (−0.13 to −0.033)
Dist water seas	−0.082 (−0.105 to −0.059)	−0.025 (−0.051 to 0.002)		0.04 (0.019 to 0.061)	0.075 (0.053 to 0.097)	−0.034 (−0.06 to −0.008)
Elevation				−0.231 (−0.255 to −0.206)	0.039 (0.005 to 0.074)	−0.283 (−0.349 to −0.217)
Slope				0.073 (0.059 to 0.088)	−0.095 (−0.122 to −0.068)	−0.104 (−0.134 to −0.074)
Density boma	−0.02 (−0.042 to 0.003)				−0.036 (−0.059 to −0.014)	−0.036 (−0.06 to −0.012)
Dist Vill	−0.13 (−0.162 to −0.098)				−0.153 (−0.176 to −0.13)	0.138 (0.108 to 0.169)
Dist road	−0.049 (−0.088 to −0.009)				0.085 (0.056 to 0.115)	−0.204 (−0.25 to −0.157)
Community conservation			−0.245 (−0.326 to −0.164)	−0.005 (−0.056 to 0.047)	0.165 (0.107 to 0.223)	0.044 (−0.024 to 0.112)
Forest reserve			−0.484 (−0.664 to −0.303)	−0.735 (−0.846 to −0.624)	0.025 (−0.171 to 0.222)	−0.105 (−0.331 to 0.122)
Communal land			−0.118 (−0.277 to 0.041)	−0.043 (−0.139 to 0.054)	0.147 (0.027 to 0.267)	0.059 (−0.106 to 0.224)
Private land			−0.494 (−0.65 to −0.338)	0.308 (0.194 to 0.423)	−0.44 (−0.617 to −0.264)	1.108 (0.84 to 1.375)

Continued

Table 3. Continued.

Coefficients[b]	Male: *high vs. medium and low*	Male: *fast vs. use*	Male: *slow vs. use*	Female: *high vs. medium and low*	Female: *fast vs. use*	Female: *slow vs. use*
Private conservation			1.274 (0.494 to 2.054)	1.233 (0.866 to 1.6)	−1.287 (−3.248 to 0.675)	
High use male	0.216 (0.201 to 0.231)			0.12 (0.109 to 0.131)		0.069 (0.051 to 0.086)
High use female	0.088 (0.07 to 0.105)			0.187 (0.176 to 0.198)		0.125 (0.108 to 0.143)
High use both					−0.053 (−0.073 to −0.032)	
Corridor male						0.053 (0.034 to 0.073)
Corridor female						0.015 (−0.008 to 0.038)
Corridor both	0.001 (−0.021 to 0.024)			0.008 (−0.008 to 0.023)	0.018 (0.001 to 0.034)	
Autocovariate	10.407 (10.095 to 10.719)	−23.841 (−25.093 to −22.59)	−7.299 (−7.697 to −6.901)	9.108 (8.933 to 9.283)	−13.693 (−14.235 to −13.152)	2.117 (1.837 to 2.398)
AUC	0.852	0.897	0.910	0.866	0.847	0.872
Individual variance	3.382	11.93	22.122	4.3	6.465	22.436
$n = 1$[c]	13,895	7,522	7764	23,355	14,293	10,737
$n = 0$[c]	156,745	188,369	188,369	419,173	46,6148	46,6148

[a]*The 3 contrasts depicted for both sexes are high- versus medium- and low-use areas, fast corridor versus high, medium- and low-use areas, and slow corridor versus high-, medium-, and low-use areas (Table 1). Other contrasts are in Supporting Information. Contrasts among movement types and variable coding are in Table 1; additional contrasts are in Supporting Information.*
[b]*Abbreviations: NDVI, normalized difference vegetation index; CV, coefficient of variation; dist, distance; AUC, area under curve.*
[c]*Number of points coded as 1 or 0 in the logistic regression (1, first term of the column name).*

areas, fast versus slow corridors, and the 2 types of low-use areas are in Supporting Information and confirm trends mentioned above.

Discussion

By combining properties related to intensity of use, structural aspects of animal movement networks, and properties of the movement paths, our framework characterized the functional role of a location for animal movement (i.e., the movescape), the characterization of which can facilitate landscape planning efforts. High, medium, and low intensity of use areas and connectivity corridors associated with fast and slow movements served to identify high-value locations for protection from development or direct connectivity conservation efforts. Such characterization was possible only through the combination of multiple metrics, providing a substantive shift in conservation planning outputs from tracking data that have typically been based on single-movement metrics. The presence and frequency of each type of movement category varied across elephants, highlighting the differentiation in movement strategies in the study population (Bastille-Rousseau & Wittemyer 2019), a trait that may be particularly amplified in elephant behavior. Overall, our framework offers valuable information for conservation planning through the explicit definition of movement types across locations (Fig. 2 & Supporting Information). Our method is straightforward to apply to systems with rich tracking data and allows definition of the movescape that can serve as a foundation to investigation of spatiotemporal behavior.

Improving Conservation Planning with Movement Data

Although delineating corridors has been a key focus of wildlife movement studies for decades, the increasing number and size of tracking data sets is allowing novel approaches to this critical objective. By explicitly quantifying a location's connectivity value in conjunction with its use, our approach characterizes movement corridors based on how these corridors emerge. These corridors are functionally important for dispersal movements in a low-quality matrix (e.g., fast corridor) or can facilitate connectivity while enhancing habitat for other functions (e.g., slow corridors). We found that relative to slow movement corridors (Supporting Information), these fast movement corridors were actually associated with unfavorable landscape features for elephants (i.e., those avoided [Bastille-Rousseau et al. 2020]). Protecting landscape properties associated with slow corridor movement types (e.g., productive areas near water and away from humans), which were similar to properties associated with more highly used areas will be more valuable for elephants. Our results also revealed that these high-use and slow-corridor areas cover a small fraction of the landscape, allowing tractable targeting of key areas for this population. Taken together, these findings illustrate how our approach can directly benefit elephant conservation.

Given the spatial specificity common to directed elephant movements (Polansky et al. 2015), it is unclear whether fast corridors are generally associated with unfavorable landscape characteristics as in other animal systems. Regardless, these results challenge the assumption behind popular approaches to delineate corridors that frequently focus on fast and directional movement as a starting point to build resistance surfaces (Graves et al. 2007; LaPoint et al. 2013; Zeller et al. 2017). Although discussions regarding the role of corridors to augment core habitat have been a part of conservation planning efforts for years (Bennett 1999; Hanski 1999; Pascual-Hortal & Saura 2006), we believe that our approach, by combining multiple movement properties, provides a valuable new tactic for explicitly defining corridor locations for connectivity, as well as their relative value in terms of habitat augmentation.

More broadly, understanding animal movement and the means by which individuals use specific locations on a landscape is critical to conservation planning efforts that require spatially explicit information, such as creating protected areas and mitigating anthropogenic development. By identifying movement properties across a landscape, including the explicit definition of corridors and the level of use in them, our approach provides high-resolution information of the functional role a location plays for animal movement. Identifying critical areas is typically addressed through derivation of population mean behavior, but our approach can also handle more complex space-use strategies within a population and among individuals. For example, we found elephants used the same area differently (e.g., as both fast and slow movement corridors [Fig. 2]). Although this may render landscape planning decision more complicated, it allows managers to understand the fraction of the population affected by specific land-alteration scenarios and to optimize decisions to enhance protection for specific sectors in a population (e.g., females over males).

Toward the Animal Movescape

Although we used 5 movement metrics to capture properties related to 3 aspects of movement (intensity of use, structural, and path properties [Fig. 1]), we recognize there are other ways of capturing characteristics to define the movescape that may reflect other important aspects of movement behavior (e.g., expected displacement [Avgar et al. 2013] or velocity autocorrelation). However, we assert that spatially explicit characterization of movement should be aggregates of the 3 classes of movement properties employed here given that they represent fundamental characterizations of the movement process (Wittemyer et al. 2019). Our framework of integrating these 3 classes directly builds on traditional approaches to derive movement metrics from GPS data. This includes the most commonly used metric of use intensity, broader landscape context through structural metrics, as well as path properties used in the assignment of movement modes related to speed and directionality (Langrock et al. 2012; Edelhoff et al. 2016). Although path properties typically focus on temporal aspects of the trajectory to define behavioral states interpreted as resting, foraging, and displacement, here we projected the path properties used to characterize modes spatially. In doing so, we were able to describe animal movement types that not only incorporate discrete parts of the path trajectory, but also considered how these steps relate to the local intensity of use and the structural importance of a location. A key difference between our approach and the temporal segmentation of modes is that inferences are not made at the step level, but rather on a discrete unit of the landscape (i.e., a pixel). We assert that these functional movement types are not mere expansions of temporal modes but provide a different way to quantify variation in animal movement over time and space (Wittemyer et al., 2019). In particular, incorporating structural properties related to connectivity makes these movement types different from the typical encamped or exploratory (Turchin 1998) or selection or-avoided dichotomies.

Aggregation of multiple movement metrics is fundamental to defining the movescape, but our use of clustering with mixture models could be replaced by other approaches. Multivariate mixed models could be used to integrate multiple metrics and to study covariance among the metrics (Dingemanse & Dochtermann 2013), but such models would be computationally demanding. Clustering the metrics reduces the analyses to a few categories, therefore facilitating interpretation and spatial representation. The advantage of Gaussian mixture models is that uncertainties of the classification are tractable and can be integrated into subsequent analyses. Alternatively, a supervised classification could be used in lieu of the unsupervised classification we employed. A supervised classification would facilitate interpretability of the classification, which can be difficult with an unsupervised approach. However, a supervised classification would require training data that may be hard to acquire, likely necessitating paired observational data from sensors (e.g., camera traps, video, or acoustic monitoring) or direct behavioral monitoring. Finally, it remains that our 2-step clustering, although providing advantages in terms of giving equal weight to all individuals, is convoluted (Supporting Information). A specifically designed algorithm that performs hierarchical (individual and population-level) clustering would prove useful in simplifying this step.

In its essence, an animal's movescape should be largely driven by environmental covariates and variables associated with biotic interactions, similar to how the landscape of fear (Laundré et al. 2001) is a function of interactions between environmental covariates and predator behaviors. Disentangling spatial movement on the landscape and the contribution of environmental and biotic variables on the movescape provide a deeper understanding of the factors structuring animal movement in space. Although we focused on empirical representation of the movescape, our approach is also amenable to covariate based predictive outputs, for example, by creating maps predicting the probability of observing a specific cluster. Such outputs could be used to enhance currently employed approaches. For instance, the probability of movement corridors could be used to parameterize popular connectivity approaches (e.g., circuitscape analyses). This may provide better modeling outputs given our definition of movement corridors is based on multiple movement properties related to actual connectivity.

Mitigating the increasing threats to natural landscapes requires a mechanistic understanding of animal behavior and ecology (Wittemyer et al., 2019). A key step in this process is determining the mechanisms driving animal movement behavior and applying this knowledge to determine wildlife spatial requirements critical to ecologically sensitive land-use planning within a species range. Combining multiple movement properties into a movescape allows a finer mechanistic understanding of the importance of an area for an animal. By characterizing the movescape for species facing threats from habitat loss and change, conservation efforts can focus on key locations, thereby optimizing investment.

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Supporting Information

Supplementary tables and figures (Appendix S1), an additional analysis of association among individuals

(Appendix S2), and a vignette presenting the analytical workflow and introducing the main R functions (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials

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