The Space Between

A geospatial analysis of connectivity between lion populations in East Africa

by

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Abstract

Lion (*Panthera leo)* populations and habitat range are in steep decline. Lions are increasingly isolated in protected areas and other pockets of habitat. Habitat fragmentation lowers effective population size and increases vulnerability to threats such as inbreeding depression and localized catastrophes. Conserving connecting habitat between lion populations is critical for mitigating effects from fragmentation. With approximately half of all remaining lions and a rich network of protected areas, the East African Community presents vital opportunities to preserve connectivity. I collected 69,068 lion presence locations from field researchers and overlaid these locations with a suite of environmental variables. Due to strong biases in the presence data, I used an intuitive approach of creating a habitat envelope from observed presence data, and then identified combinations of environmental conditions that are conducive to lion presence. By determining the distribution of these environmental conditions, I predict areas with habitat through which lions can disperse, though may not be resident. I then identify contiguous patches of connecting habitat that link protected areas with documented lion populations. I find that while many protected areas remain connected, Uganda's lion populations in Murchison Falls and Queen Elizabeth National Parks are critically isolated. Furthermore, my analysis suggests several bottlenecks and gaps that constitute high priority areas for conserving or restoring connectivity.

Contents

Introduction

Lion (*Panthera leo*) populations have declined precipitously in both size and extent, with losses more severe than for other African carnivores (Patterson et al. 2004, Bauer et al. 2005, IUCN 2006). Losses will continue (Riggio et al. 2013). Recent estimates suggest that approximately 35,000 lions remain in Africa, but that lions currently occupy only 25% of their former range (Riggio et al. 2013). In contrast to the current population, as many as 500,000 lions may have existed in 1950 (Myers 1975). As lions' range shrinks, they face severe threats including loss of prey, habitat disturbance, and conflict with humans (Nowell & Jackson 1996, Ray et al. 2005, IUCN 2006, Bauer 2008, Linnell et al. 2008). People are the ultimate source of these threats. Furthermore, populations in protected areas frequently suffer losses through edge effects when lions on the periphery of protected areas come into conflict with adjacent human populations (Woodroffe & Ginsburg 1998). Several studies find that human presence is a driving factor of lion decline and extinction. A rough estimate of twenty-five people per km^2 is the maximum human population density that resident lions can tolerate (Woodroffe 2000, Loveridge & Canney 2009, Riggio et al. 2013). Protection of only a small portion of lions' range (Nowell & Jackson 1996, Crooks 2011) exacerbates threats to lions. Without concerted conservation efforts, lions will go extinct or become extremely rare (Loveridge & Canney 2009).

Lions are a valuable species and a useful tool for the conservation of ecological communities. They perform ecological functions that may benefit human communities (Ripple et al. 2014). As an apex predator (Vanak et al 2013), lions play a critical ecological role (IUCN 2006, Sergio et al. 2008, Ripple 2014), and their decline may result in trophic cascades that fundamentally alter communities and reduce biodiversity (Crooks & Soule 1999, Ripple et al. 2014). One of the famed "Big Five" African mammals, lions are a primary attraction of the tourism industry (Nowell & Jackson 1996, Ray et al. 2005, IUCN 2006, Naidoo et al. 2011) and bring significant financial benefits to countries and some local communities (Packer et al. 2009, Lindsey et al. 2007). Lions contribute to the conservation of wild habitat that might otherwise be converted for human use (Lindsey et al. 2012). As a habitat generalist (Nowell & Jackson 1996, Bauer et al. 2005), lions are an effective conservation umbrella species (Carroll et al. 2001, Ray et al. 2005, Caro 2010, Caro & Riggio 2013); their conservation benefits a host of other wildlife populations (Branton & Richardson 2010). Carnivores are also good indicator species for studying habitat disturbance and for conservation planning (Soule & Terborgh 1999, Morrison Et al. 2007). Thus lion declines have significant repercussions for both ecological and human communities.

As a result of population losses and anthropogenic threats, lions are becoming rare outside of protected reserves and other fragments of suitable habitat (Woodroffe 2001, Ogada et al. 2003, Patterson et al. 2004, Packer et al. 2005, Loveridge & Canney 2009, Mesochina 2010, Bauer et al 2012). The loss of habitat, both spatially and qualitatively, is the foremost threat to carnivores (Crooks et al. 2011), and rapid human population growth and economic development in Africa lead to higher anthropogenic pressure across lions' range (Loveridge & Canney 2009). As a result, despite the continent's rich community of carnivores, connectivity for these populations is lower than in other geographic regions (Crooks et al. 2011). Carnivores are more vulnerable to fragmentation than other taxa, primarily because they live at lower densities than their prey species (Noss et al. 1996, Woodroffe & Ginsberg 1998, Ceballos & Ehrlich 2002, Kissui 2008, Ripple et al. 2014). Carnivores such as lions that are classified as Vulnerable to extinction (IUCN 2013) suffer significantly higher rates of fragmentation than species of Least Concern (Crooks et al 2011), strong evidence that connectivity is directly linked to lion conservation.

The area of a habitat patch and the severity of its isolation are primary factors affecting the abundance of its carnivore populations (Crooks 2002). Furthermore, the habitat area needed to sustain a particular abundance of a carnivore is related to the size of that carnivore (Crooks 2002). Thus lions require larger habitat patches than some other African carnivores and are particularly at risk from fragmentation (Crooks 2002). Local threats are not the only concern, as species with fragmented ranges are more vulnerable to climate change and other range-wide transformations (Heller & Zavalenta 2009).

Isolated lion populations pose serious conservation challenges. The smallest populations are most vulnerable (Nowell & Jackson 1996). Isolation causes inbreeding depression and can reduce fertility (Nowell & Jackson 1996, Frankham 2005), as occurred with lions in Ngorongoro Crater (Packer et al. 1991, Ray et al. 2005). Fragmentation reduces lion abundance and effective population size, and increases vulnerability to extinction (Nowell & Jackson 1996, Frankham 2005, Hilty et al. 2006). Isolation may cause genetic drift (Soule & Mills 1998). In addition, marginal populations may depend on immigrants from more productive source populations to maintain stable numbers (Hanby et al. 1995). Without immigrants, these populations may not persist.

Genetic variation in lions shows that historically, populations were connected throughout Eastern and Southern Africa (Dubach et al. 2013). Male lions always disperse from their natal prides and female dispersal is a primary factor in population expansion (Dolrenry et al. 2014).

Bjorklund (2003) found that lion populations require at least 50 prides to avoid inbreeding depression, but that 100 prides are preferable. Inbreeding decreases survival and lowers fecundity. The number of lions and the area necessary to sustain a minimal viable population changes in response to wide variation in pride size (VanderWaal et al. 2009) and territory size (Bjorklund 2003). In terms of genetic stability, however, large prides are not a substitute for the space needed to sustain 50 exclusive pride territories. Few reserves and national parks are sufficiently large to sustain minimum viable populations (Nowell & Jackson 1996, Bjorklund 2003). In addition, lions often depend on areas adjacent to reserves for additional resources (Kissui 2008). Africa suffers high birth rates, rapid economic development, and extensive land conversion (Balmford et al. 2001, Doos 2002). As a result, habitat on the periphery of protected areas is dwindling rapidly or has already disappeared. Thus, when populations containing 50 prides are not feasible, it is imperative that lions immigrate from other populations. Furthermore, Bjorklund (2003) found that a lack of dispersal from natal prides leads to inbreeding, and so it is important for lions to emigrate out of populations in addition to immigrating into them.

One method for mitigating habitat fragmentation for lions is to conserve connectivity between populations (Brown & Kodric-Brown 1977, Hilty et al. 2006). Ecological connectivity is "the movement of organisms or ecological processes across landscapes" (Crooks et al. 2011). A corridor is a geographic area of habitat "in a dissimilar matrix, that connects two or more larger blocks of habitat and that is proposed for conservation on the grounds that it will enhance or maintain the viability of specific wildlife populations in the habitat blocks" (Beier & Noss 1998). It is critical that a corridor provide a functional link between habitat patches, as opposed to just a theoretical link (Crooks et al. 2012). Well-designed studies consistently find that corridors can reduce the impacts of fragmentation (Brown & Kodric-Brown 1977, Beier & Noss 1998). More specifically, Norton et al. (2010) found that naturally occurring corridors are more effective than human-created alternatives and that designated corridors can increase movement between patches by 50%. Well-connected landscapes can also influence meta-population dynamics through mechanisms such as a rescue effect, whereby immigrants contribute demographically and genetically to a population (Brown & Kodric-Brown 1977, Packer et al. 1991). The rescue effect increases population resiliency (Loveridge & Canney 2009) and decreases the risk of a population going extinct (Nowell & Jackson 1996).

Connectivity is essential for lion conservation (Dubach et al. 2013). Dolrenry et al. (2014) modelled the effects of connectivity between several lion populations in East Africa and found that male lions can disperse at large distances while females exhibit shorter dispersal, but are requisite for recolonizing habitat patches. Connectivity has enabled lions to recolonize areas (Dolrenry et al. 2014) and subsidize marginal populations (Hanby et al. 1995). However, while numerous studies have geographically mapped the resident range of lions, thus far no one has mapped, at a regional scale, the distribution of habitat that may not sustain resident lion populations but can act as corridors linking populations. Mesochina et al. (2013) found that lions use a significant portion of their range through Tanzania only temporarily, which confirms lions' movement through non-resident areas. Large carnivores have also demonstrated an ability to tolerate high human population density under certain conditions (Athrey et al. 2013, Linnell et al. 2001). Ascertaining those conditions is critical to distinguishing between resident habitat and dispersal habitat.

Lions are well-studied, but research has been biased towards populations in protected areas (Bauer et al. 2005, Loveridge & Canney 2009). Our knowledge of lion distribution and behavior outside reserves, particularly in areas with high human impacts, is deficient (Chardonnet 2002, Van Dyck & Baguette 2005, IUCN 2006, Dolrenry 2013). Yet one-third of lions live outside of reserves (Riggio et al. 2013). In order to develop conservation strategies for maintaining connectivity, it is critical that we improve our understanding of dispersal habitat that may function as corridors (Dubach et al. 2013). Vanak et al. (2013) found that dispersing lions broaden their diet from the species' main prey base, and that prey availability is a factor in lion movement. That study also found that lions demonstrate a preference for thick riverine vegetation during the dry season and that they tended to avoid woodland and open scrub. Several studies found that lions in pastoral lands were less active during daylight than lions in neighboring reserves with similar habitat, and that lions in human-dominated landscapes alter their feeding behavior (Maddox 2003, Mogensen 2011). Similarly, Mogensen et al. (2011) found that lions in pastoral lands acted more like reserve lions during periods of high vegetation growth. These findings suggest that dispersing lions adapt to their circumstances. Assumptions about lion foraging from resident populations may not apply to dispersing individuals.

Research on other large carnivores corroborates the notion that lions dispersing outside of protected areas may act differently than lions in ideal habitat. Dickson et al. (2005) tracked cougars and found that they moved through riparian vegetation more than grassland, woodland, or desert habitat. The cougars moved rapidly through human-dominated areas. In India, a population of leopards exists in areas with 300 people per km^2 by adapting their diet; other carnivores also inhabit the same landscape matrix of agricultural lands and wild habitat (Athreya et al. 2013).

Atypical populations such as these leopards provide a compelling argument for approaching conservation at the landscape level rather than managing protected areas in isolation (Athreya et al. 2013). In the absence of persistent and ubiquitous persecution, carnivores are very adaptable and can survive in situations previously thought intolerable.

Management practices further complicate strategies for conserving carnivore habitat and connectivity. Linnell et al. (2001) found that North American carnivore density can increase in areas of growing human population if land use policies are well-designed. Their research found no direct correlation between carnivore and human abundance. Their findings suggest that population density thresholds are not absolute, but depend on other factors such as how humans use the landscape.

It is clear from this body of literature that lions and other carnivores demonstrate tendencies in their movement patterns and some of these tendencies relate to combinations of factors, rather than individual variables. For example, estimates of human density thresholds that preclude resident lion populations are useful for management, but do not necessarily account for individuals moving rapidly through an area. Other factors likely influence the relationship between lions and human population density (Loveridge & Canney 2009).

Lion connectivity studies are further limited by insufficient data to determine maximum dispersal distances for individuals, though males can likely emigrate to populations more than 300 km distant from the source (Dolrenry et al. 2014). However, even 300 km may not be their maximum dispersal distance. Tigers can emigrate up to 650 km (Joshi et al. 2013).

Connectivity Modelling

Numerous studies have sought to model connectivity for large carnivores and other taxa. Conventional models have two components: habitat suitability modelling and corridor modelling. Studies typically estimate habitat suitability from statistical models or from expert opinion (Rabinowitz & Zeller 2010, Kertson et al. 2011, Poor et al. 2012). The second step predicts which areas in the landscape function as corridors based on paths through suitable habitat. Many analyses depend on models that identify corridors based on routes of minimum cost-distance or routes predicted based on electrical circuit theory (Poor et al. 2012). However, these models are poor predictors of actual animal movement (LaPoint et al. 2013). Customized stochastic movement models, an alternative approach, incorporate variation and individual decision-making in dispersing animals (Gardner & Gustafson 2004). But they require prodigious data to parameterize correctly, which are particularly difficult to obtain for rare carnivores.

Probability models of suitable habitat assume that dispersing animals act according to conditions where the species is most abundant. Dispersal habitat is not the same as resident habitat, but connectivity models derived from species distribution models do not recognize the distinction (Carroll et al. 2011). Connectivity analyses based on distribution models are therefore likely to under-predict movement potential, especially in landscapes where conditions outside of protected areas may be widely different from conditions in protected areas. This issue is especially relevant to my research, which incorporates presence-only data primarily from clusters of unrepresentative research areas. Few statistical models are suitable for the presence-only data I collected. Many statistical models also assume linearity in relationships between predictor and response variables. However, linearity rarely represents ecological reality (Loveridge & Canney 2009).

Constraints in the data further limit my analysis. With a large study area and a fairly coarse grain size for connectivity modelling, the environmental datasets used for this analysis contain error and may not represent fine-scale patterns in lion movement. Statistical models also assume unbiased input data. However, the presence data I collected exhibit clear biases. There were no consistent sampling protocols and research areas reflect sites of ongoing lion research, namely in areas where lions are most common. The data are clustered in the areas where researchers work and, therefore, are spatially autocorrelated. Without consistent data on dates of samples, I was unable to account for temporal autocorrelation in the data as well.

With a primary interest in the behavior of lions away from lion population centers and aware of the constraints of the presence data, I eschewed statistical approaches in favor of a model that identifies all ecological conditions in which lion presence is recorded, rather than the most probable conditions. By identifying where similar ecological conditions occur across the landscape, I can predict all areas where we would expect lions to occur, even if only temporarily. This focus on all habitats that lions use, as opposed to habitats where lions are most abundant, is a fundamental advantage in predicting dispersal habitat.

Annuli – concentric, exclusive distance classes – present an intuitive method for parsing the landscape and examining environmental conditions in which lions occur. Many ecological analyses incorporate distance classes, such as tests of autocorrelation (Diniz-Filho et al. 2003), and annuli have been used to spatially compare occurrence rates of ecological phenomena (Nakamura et al. 1997, Santos & Tabarelli 2002, Joppa et al 2008, van Noordwijk 2011).

The most important constraints to my analysis are sampling biases in the lion presence data and error in interpolated (rainfall), remotely sensed (vegetation indices, elevation), and modelled (population density) datasets. Distance classes, whether geographic or distributional, control for this error and accurately represent the precision of my analysis. Given the presence-only nature of the lion occurrence data, distance classes create clear, understandable buffers around observed occurrence that can capture some areas of false-absence in the occurrence dataset and imprecision in environmental datasets.

Previous Studies

This paper builds off a foundation of research that explores habitat distribution and connectivity for lions, and connectivity more broadly in East Africa. Most recently, Dolrenry et al. (2014) used incidence function models to predict the dispersal of lions between major populations. They analyzed how dispersal affects population demographics, but did not spatially predict where lions move through the landscape that separates resident habitat patches. Instead, the authors used data collected from dispersing lions to predict average and maximum dispersal distances for male and female lions. Their models further constrain connectivity based on patch size and spatially explicit human density data. Their research reveals significant differences between male and female dispersal: male lions disperse further and “rescue” populations regularly, whereas female lions disperse shorter distances but have a greater colonizing effect than males. Crucially, the authors note the importance of lion survival during dispersion and that even large populations still require dispersal to remain viable.

Jones et al. (2009) took a different approach to connectivity by evaluating individual wildlife corridors throughout Tanzania. They gathered expert knowledge to classify corridors’ status and estimate the scope and severity of threats to each corridor. The paper describes 31 separate corridors that link protected areas. The authors concluded that Tanzania’s wildlife corridors are critically threatened, with most likely to disappear by the end of this year. The principle threats to connectivity, the study finds, are land conversion, the bushmeat trade, and extractive industries.

Other studies take a broader view, modelling the distribution of lions throughout Africa. Loveridge and Canney (2009) mapped the distribution of lions using two methods to estimate the extent of lions’ range and their density across that range. The first method predicts lion density in response to data on prey density and its correlates, rainfall and soil nutrients. The second model applies statistical hurdle models that predict presence or absence and estimate population density, and then combine the two outputs to estimate abundance. Both parts of the hurdle model regress lion data against a suite of environmental variables. The authors conclude that in some areas, their models over-predict lion abundance, but in others, such as the Selous-Niassa ecosystem, the models are highly representative.

Similarly, Celesia et al. (2009) modelled lion distribution and density throughout Africa in relation to climactic factors, biotic variables, and landscape features. Like Loveridge and Canney, they used regressions to relate lion data to environmental variables, but they acquired all of their lion data from just 21 protected populations. The authors applied hierarchical partitioning to determine the individual importance of each predictor variable independently. They found that climactic factors explain most of the variation in lion distribution and density, while landscape features explain approximately another third.

The latter two studies are critical to our knowledge of where lions occur and what conditions constitute resident habitat, but they are less effective at predicting dispersal habitat. The former two studies inform our understanding of the role connectivity plays in lion population dynamics and where wildlife corridors occur in a large portion of the study area. However, neither explicitly identifies dispersal habitat specifically for lions that links resident populations. This paper applies a regional analysis that bridges the gap in scale between the continental distribution models and the national and transnational connectivity studies. It also seeks to link the mapping component of the Tanzanian wildlife corridors with the meta-population dynamics that Dolrenry et al. describe.

These goals reflect the work of Rabinowitz and Zeller (2010) to map corridors for jaguars throughout their range in the Americas. Their research was founded on similar principles as this study: fragmented populations, high vulnerability to isolation, a need for connectivity to mitigate these threats, and a desire to inform regional conservation strategies. However, Rabinowitz and Zeller base their analysis on expert opinion rather than biological data, and rely on simplistic least-cost paths to predict habitat. This paper, on the other hand, takes an approach rooted in biological data. It improves on statistical models because it does not emphasize resident habitat over dispersal habitat.

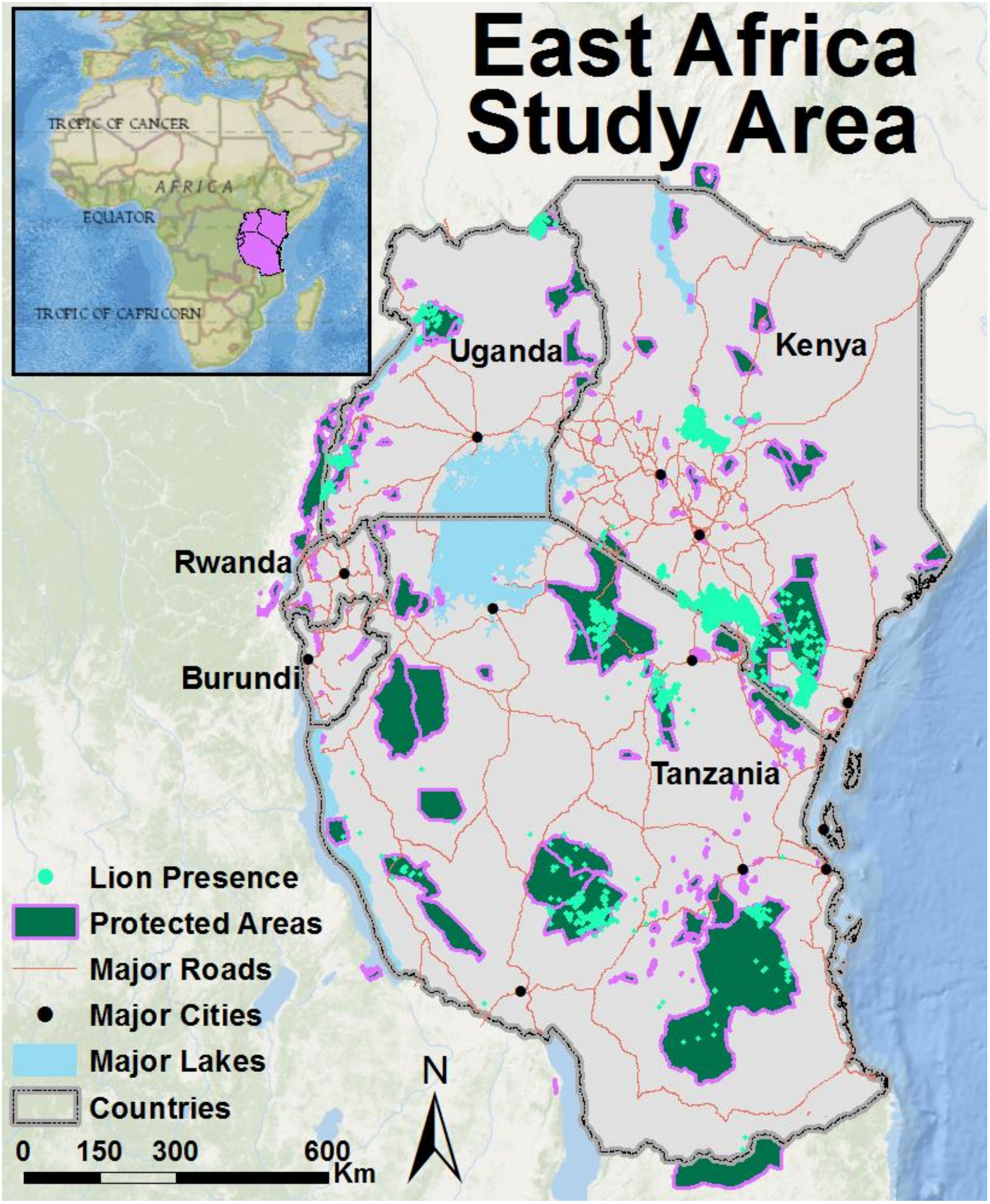

Figure 1: Map of the East African Community study area and recorded lion occurrence.

Study Area

The five countries of the East African Community (henceforth East Africa) cover more than 1.7 million km^2 of land (28.86° – 41.89° E, 11.75° S – 4.63° N) from the Great Lakes region of central Africa to the continent's east coast (Figure 1). The five countries have a combined human population of 154.3 million people ranging from 10 million in Burundi to 46.6 million in Tanzania. The region is characterized by high population growth rates ranging from 2.1% – 3.3%, and a total population density of approximately 90 people per km^2 (CIA 2014). However, while several large population centers (e.g. Nairobi, Dar Es Salaam, Kampala, Lake Victoria) are spread across the region, much of the landscape has minimal human presence. Human population is dense in the smaller countries in the west and around Lake Victoria, and less dense in Kenya and Tanzania, particularly in areas of low rainfall, such as northern Kenya and rain shadows west of mountain ranges.

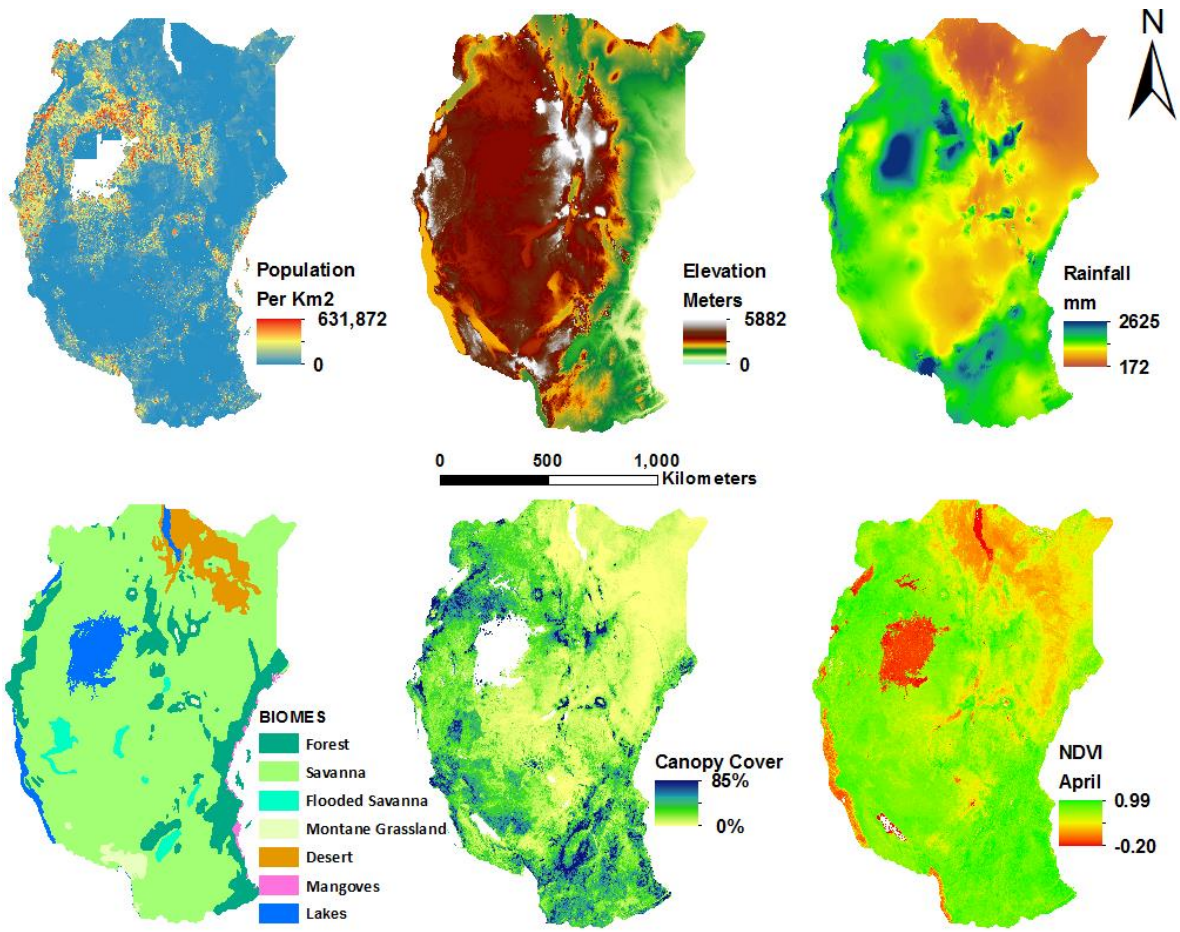

Figure 2: Environmental characteristics of East Africa.

The landscape ranges in elevation from sea level along the coast to 5882 m at the top of Mt. Kilimanjaro (Jarvis et al. 2008, Figure 2). The vast majority of the region lies above 500 m. Annual total rainfall (172 – 2625 mm) is lowest in the arid Somali region of the northeast and greatest around Lake Victoria and on the mountains of northern Tanzania and Kenya (Hijmans et al. 2005). The region experiences bimodal rainfall (Bradfield & DeWitt 2012), with most precipitation occurring in October – December and March – May (Gelorini & Verschuren 2013). However, rainfall patterns vary widely both regionally and temporally based on climate systems such as the Intertropical Convergence Zone and the el Nino-Southern Oscillation (Gelorini & Verschuren 2013). Recent years suggest significant declines in rainfall during the March – May period (Bradfield & DeWitt 2012), which creates uncertainty about the effects of climate change on the region.

East Africa includes seven biomes, but is particularly renowned for three. It consists primarily of Tropical and Subtropical Grasslands, Savannas, and Shrublands (Olson et al. 2004). Arid savannas occur in areas with less than 820 mm of annual rainfall and moist savanna occurs in areas with at least 1000 mm annually (East 1984). In a transition zone in central Tanzania, the savanna gives way to miombo woodland landscapes that dominate southern Tanzania. While most of the landscape has less than 20% canopy cover, patches of ecologically diverse montane rainforest occur across East African mountain ranges. The eastern arc mountains stretching from southeastern Kenya to east-central Tanzania exhibit the world's highest rates of endemic plants and vertebrates per unit area (Myers et al. 2000).

East Africa hosts numerous protected areas ranging in size from the 48,000 km^2 Selous Game Reserve to many smaller national parks, wildlife reserves, forest reserves, and community reserves (IUCN & UNEP 2009, Figure 3, Appendix A). Several ecosystems, all with contiguous networks of national parks and reserves, host lion populations with more than 500 individuals, in particular the greater Serengeti, Selous, Ruaha, and Tsavo ecosystems (Bauer & Van Der Merwe 2004, Riggio et al. 2013).

Historically, lions have been widespread across East Africa (Bauer and Van Der Merwe 2004). Largely as a result of the population centers in its large protected areas, East Africa holds approximately half of all lions (Mesochina 2010, Riggio et al. 2013), with estimates of total lion populations ranging from 7,199 – 22,335 individuals (Buaer et al. 2005, Appendix B). Bauer & Van Der Merwe (2004) inventoried known populations and estimated 11,000 individuals. East African populations exhibit the least genetic distance of all regional populations (Dubach et al. 2013), which suggests that its populations have been well-connected. Research from Kenya and Tanzania, however, shows that lion dispersal is currently limited (Dolrenry et al. 2014). Jones et al. (2009) found that a majority of corridors in Tanzania were critically threatened and unlikely to persist after five years because of habitat loss. Thus, the historical links between populations are in dire jeopardy.

I designated the spatial extent of the study area by including the entire administrative areas of the five countries and excluding regions classified as lake ecoregions (Olson et al. 2004). I did not include islands in the Indian Ocean or lakes in any analyses.

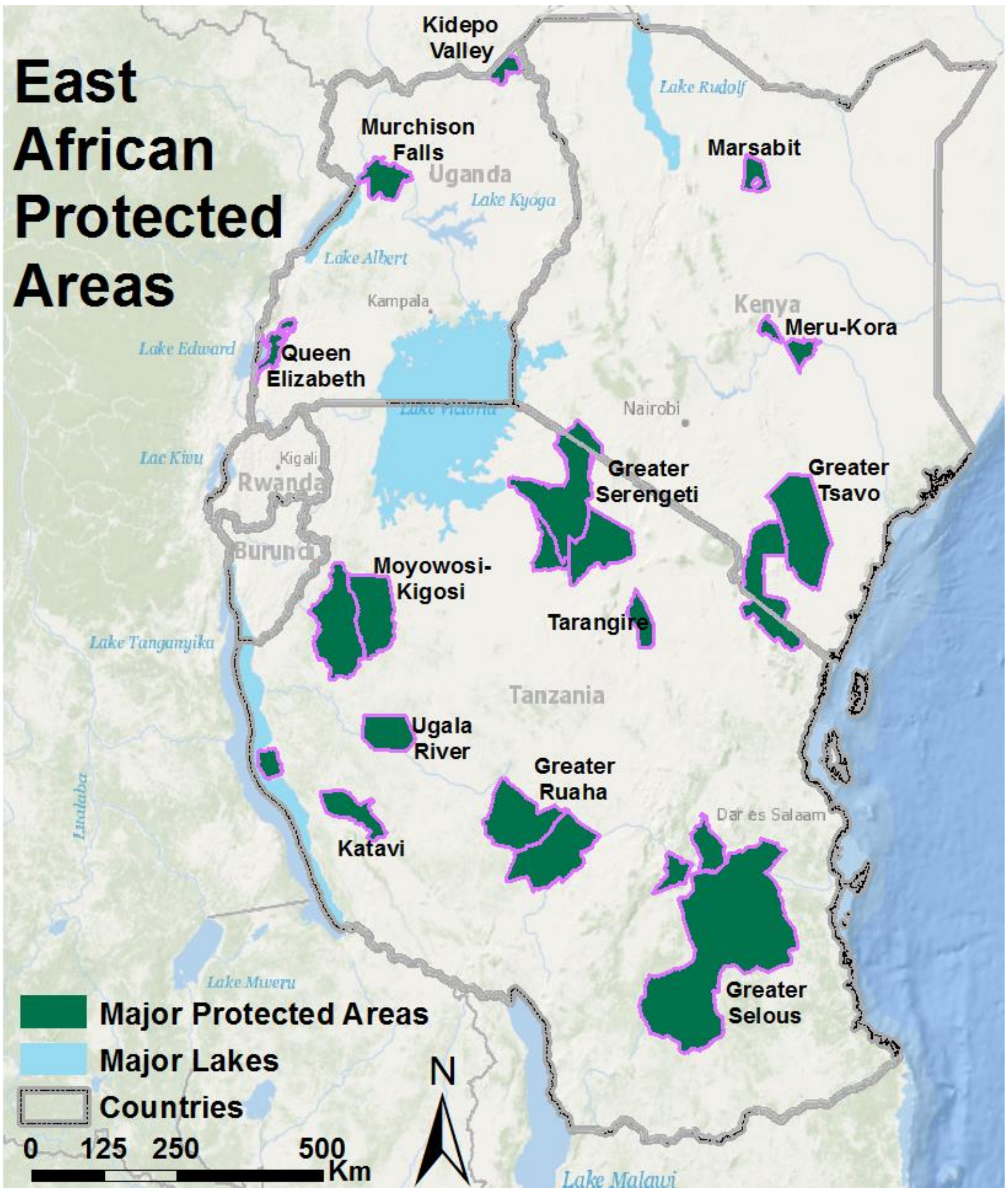

Figure 3: Major protected areas of East Africa

Objectives

With approximately 50% of all lions (Mesochina 2010), extensive lion research (Bauer et al. 2005, Dolrenry et al. 2014), a rich network of protected areas, and high variation in ecological conditions and human impacts, the five countries of the East African community—Burundi, Kenya, Rwanda, Tanzania, and Uganda—present many of the best and most pressing opportunities for conserving connections between populations. Their shared political institutions and cultural history are conducive to transnational conservation projects.

This paper is concerned specifically with the movement of individual lions and their genes across their range. This research is intended to guide conservation planning and help researchers prioritize areas of concern. I aim to accomplish three objectives that will enable conservation of dispersal habitat, and thus preserve lion connectivity, across East Africa: 1) identify geographic areas that are suitable for lion dispersal, 2) identify priority areas for connectivity, and 3) identify populations that have the highest risk of isolation.

To accomplish these objectives I analyze 69,068 lion presence points that I acquired from 16 field research teams and relate lion presence to a suite of environmental variables. My analysis focuses on where lions are capable of occurring (i.e. habitat conducive to dispersal) rather than areas where lions are resident or most common. I use an intuitive approach of creating a habitat envelope and then use annuli to examine the interactions of variables to predict conditions that are compatible with lion dispersal, even if they are not compatible with permanent habitation. Within the broader context of my objectives, I seek to answer the following research questions:

1) Which variables most strongly influence lion presence?
2) What environmental factors influence lion tolerance of human presence?
3) In what combinations of variables do lions occur and where in East Africa do those combinations occur?
4) How do areas with these environmental conditions spatially relate to existing populations of lions, and which patches of dispersal habitat intersect two or more protected areas with lion populations?
5) Which areas of dispersal habitat are most critical to preserving connections between lion populations?
6) Where do gaps occur between patches of dispersal habitat that constitute prime targets for restoring connectivity?

7) Which existing lion populations are most isolated from other populations, and thus most in need of active management to ensure the long-term viability of lions?

Methods

Data

I conducted all data processing using ArcGIS 10.2 (Esri 2013). With the exception of input datasets, I performed all analyses using a 500 m grain size.

Presence Data

I collected 69,085 lion presence data from 17 researchers or research teams working in Kenya, Tanzania, or Uganda (Appendix C). Communication with researchers revealed no contemporary presence data for lions in Burundi or Rwanda.

Researchers' methods for data collection included telemetry data, sightings, spoor counts, and confirmed incidences of lion-human conflict. Some researchers provided occurrence data as GPS coordinates using a variety of coordinate systems, all of which I reprojected into WGS 1984 geographic coordinates. For researchers who listed a distance to sighting, I excluded points with a distance greater than 250 m, one-half of the grain size of my analysis. Other researchers provided grid cells with confirmed lion presence, primarily from telemetry data; this method was used to protect original data. All such grid datasets had a grain of 250 m or smaller. I converted the presence cells to centroids referenced to the WGS 1984 datum. Few researchers provided data on date, time, or number of individuals for their data. Data points were collected from 2004 – 2013.

I then aggregated all 69,085 lion point locations and reprojected them into the WGS 1984 Africa Albers Equal Area Conic coordinate system. I used this coordinate system for all subsequent analyses. I removed 17 locations that were clearly inaccurate, such as a point off the coast of Tanzania, a point in the middle of Lake Turkana, Kenya, and several points just outside national borders, and thus outside the study area. The final dataset of lion presence consisted of 69,068 locations (Figure 1).

I randomly assigned 90% (62,160) of the points as training data and the remaining 10% (6,908) of points as test data to validate the model.

I created a stratified random sample of 10,000 pseudo-absence or background data points to compare environmental conditions across the landscape with conditions at the lion presence locations. I stratified the background points by WWF ecoregion (Olson et al. 2004), weighted by ecoregion area. I selected a stratified random sample in order to ensure that the background points captured the full variation of environmental conditions across the landscape.

Environmental Data

I selected environmental variables based on a review of the literature and publicly available datasets for the study area. Such studies form a consensus around including both ecological and anthropogenic predictor variables. Rabinowitz & Zeller (2010), considered vegetation cover, human population density, elevation, distance to roads, and distance from settlements in their study of Jaguar connectivity throughout the Americas. Loveridge and Canney (2009), modelled the distribution of lions across Africa in relation to precipitation, vegetation cover (NDVI), soils, livestock density, a human footprint dataset, temperature, protected areas, and human population density, and found that mean NDVI is a good predictor of lion residency. Kissui et al. (2010) found that cub production is higher near rivers and in thick vegetation, but that distance from roads has no impact. Similarly, Joshi et al. (2013) studied connectivity for tigers and found that human settlements and road density impact movement, but distance to roads does not.

For this report, I considered 15 variables (Table 1): human population density at three scales, distance to dense human populations, distance to rivers, distance to lakes, distance to major roads, distance to protected areas, April NDVI, August NDVI, percent canopy cover, total annual rainfall, dry-season (June – October) rainfall, elevation, and slope. I did not include land use data because national data sets are incompatible and because conventional global land use and land cover datasets are poor predictors of mixed savanna and agricultural landscapes (Riggio et al. 2013).

All environmental datasets were reprojected into the WGS 1984 Africa Albers Equal Area Conic coordinate system. Whenever possible, I collected data for an area that extended to a 20 km buffer around the study area to account for influence of environmental factors along the borders of East Africa. All input datasets were processed at 500 m resolution using a snap raster such that grids for each variable aligned.

Vegetation

A review of the literature suggests that vegetation quantity and structure affects large carnivore behavior and movement (East 1984, Hayward et al. 2007, Loveridge & Canney 2009, Rabinowitz & Zeller 2010, Joshi et al. 2013, Loarie et al. 2013).

The Normalized Difference Vegetation Index (Rouse et al. 1973) is a measure of vegetation abundance derived from remote sensing data. NDVI relates to a wide range of ecological processes

(Pettorelli et al. 2005), including wildlife distribution and behavior (Pettorelli et al. 2011). Above-ground vegetation correlates with herbivore abundance in Africa (Coe et al 1976), which represents prey availability for lions (Loveridge & Canney 2009). Prey abundance, in turn, is the primary factor in a habitat's carrying capacity for carnivores, explaining approximately 60% of the variation (Hayward et al. 2007). Vegetation also influences hunting behavior, with males typically hunting in areas with shorter line-of-sight than where they rest (Loarie et al. 2013). Several studies include NDVI as a predictor variable when modelling distribution of lions (Loveridge & Canney 2009), or connectivity for other large carnivores (Joshi et al. 2013).

NDVI data were collected from NASA's MODIS MOD13Q1 16-day composite global dataset of vegetation indices, with a resolution of 230 m (Huete et al. 2002). I acquired scenes during the rainy season sampled April 22 – May 7 and during the dry season, sampled August 12 – August 27. For each season, I mosaicked seven scenes that covered the entire study area for each of the last five years for which data were available, 2008 – 2012. The MOD13Q1 dataset includes a pixel reliability layer. I masked out pixels classified as No Data, Snow/Ice, and Cloudy. I calculated 2008 – 2012 average NDVI for each sampling period, including only values of suitable reliability.

Vegetation Continuous Fields, also known as percent canopy cover, is available from NASA's MODIS MOD44B annual dataset at 230 m resolution (Hansen et al. 2002), with sampling beginning and ending in March. The most recent available datasets are for 2010 – 2011, and so I mosaicked the seven scenes covering the study area for each year with the sampling period beginning in 2008 – 2010 and calculated average canopy cover from those datasets.

Climate

Studies show that climatic factors correlate with lion distribution (Celesia et al. 2009, Loveridge & Canney 2009). Rainfall also correlates with African herbivore abundance (East 1984). Celesia et al. (2009) found that temperature and precipitation collectively explain 62% of the variation in lion demographics across its global range. This report, however, treats elevation as a substitute for temperature, as temperature does not fluctuate across the study area at the same scale as discussed in Celesia et al. Precipitation is a reliable predictor of habitat for lions, particularly through its correlation with herbivore density (Coe et al. 1976, East 1984). Precipitation explains 28% of the variation in lion demographics across their range (Celesia et al. 2009), and 70% of the variation in prey biomass, which in turn shows a correlation with lion abundance of 0.92 (Loveridge & Canney 2009).

Table 1: Summary of sources and processing steps for environmental datasets.

Variable	Source	Pre-processing
Vegetation Index	MODIS NDVI	Averaged monthly NDVI values (230 m pixels) over five years (2008 - 2013) after removing low-quality pixels from each dataset.
Canopy Cover	MODIS VCF	Averaged annual percent canopy cover (230 m pixels) over the three most recent years for which data are available (2008-2010)
Rainfall	WorldClim	Collected average monthly precipitation under current conditions. I summed all twelve months and resampled to 500 m pixels to estimate total annual rainfall. I also summed the months of June - October and resampled to 500 m to estimate dry season rainfall.
Elevation	SRTM	Collected from USGS at 250 m resolution. I did not perform pre-processing.
Slope	SRTM	I calculated slope from the SRTM elevation dataset.
Lakes	WWF GLWD-3	I selected pixels classified as "lakes" or "reservoirs" and calculated the distance to these areas for each 500 m pixel in the study area.
Rivers	WWF GLWD-3	I collected the GLWD-3 flow accumulation data and manually applied a threshold of at least 1,000 accumulated pixels to designate rivers. I based this threshold on manual comparison of flow accumulation with rivers evident from satellite imagery.
Ecoregion	WWF Ecoregions	I designated ecoregions by the WWF Eco-Number. I excluded the "lakes" ecoregion from the study area.
Roads	Tracks4Africa	I selected primary and tarmac roads from the Tracks4Africa dataset and calculated the distance from roads for each 500 m pixel in the study area.
Protected Areas	WDPA	I selected all protected areas within 20 km of East Africa with an IUCN classification. I also included the Ngorongoro Conservation Area.
Human Density	AfriPop	I calculated people per km^2 at spatial scales of 1 ha, 1 km focal radius, and 5 km focal radius.
Distance to Human Population	AfriPop	I set 228 people per km^2 as the maximum tolerated human density and the threshold for high population density (Table 3). I calculated the distance to areas of high human population density for each 500 m pixel in the study area.

I collected current monthly rainfall data from Worldclim (Hijmans et al. 2005), a global interpolated dataset, at 30 arc-second (~1 km) resolution. I resampled to 500 m resolution. I summed monthly average to determine annual rainfall, and summed average rainfall for the months of June – October to determine dry-season rainfall.

I collected elevation data from the USGS Shuttle Radar Topography Mission (Jarvis et al. 2008) at 250 m resolution.

Landscape features

I acquired spatial and qualitative data on protected areas from the World Database of Protected Areas (IUCN & UNEP 2009) and subset the database to include only protected areas within East Africa or its 20 km buffer. I calculated distance from protected areas for a 500 m raster dataset.

I derived slope from the SRTM dataset at 250 m resolution.

I derived rivers from the WWF HydroSHEDS dataset (Lehner et al. 2006). The HydroSHEDS stream network is based on flow accumulation, and does not precisely match the location of rivers. I manually compared flow accumulation from the HydroSHEDS stream network to satellite imagery and established a threshold of 1,000 accumulated cells as an indicator of actual stream presence. I subset the stream network to only include features with a flow accumulation above this threshold, and calculated distance from streams across the entire study area for a 500 m raster dataset.

I derived distance from lakes for a 500 m raster dataset from the WWF Global Lakes and Wetlands Database Level 3 dataset (Lehner & Doell 2004), which I subset to include only water bodies designated as lakes or reservoirs.

I derived major roads from the Tracks4Africa Enterprises road dataset (Tracks4Africa 2010), subset to include types 1 – 6 (highways and main roads) and 11 (secondary tar roads).

Human Population

I collected data on human population density from the AfriPop Alpha version 2010 (Linard et al. 2012) estimates of people per 1 ha grid square for each of the five countries in the study area. I multiplied cell values by 100 in order to represent the values in terms of people per km^2. I calculated the mean population density within a 1 km radius and a 5 km radius in order to test the effects of human presence at varying scales, while also retaining the original 1 ha scale. I therefore incorporate three measures of population density into the analysis.

I created a distance to settlement dataset by identifying a threshold for high human population density (see results), and then calculating the distance to areas of high population density for a 500 m raster dataset. I did not use a settlement layer because I did not have a dataset consistent across the study area at the scale of this analysis. Population at the one-hectare scale of the AfriPop dataset, however, provides a fine-scale metric of high-impacted areas that I can relate directly to the occurrence of lions across the landscape.

Other studies have included variables such as livestock density, land use, and land cover. For many variables, I determined that data quality was insufficient (e.g. land cover, Riggio et al. 2013), or datasets were inconsistent or incomplete for the study area (land use).

I considered including density variables for roads and rivers. I decided, however, that these datasets contain too much uncertainty. In particular, I lacked confidence in distinguishing road characteristics such as number of vehicles per day. This factor is potentially critical as some minor roads may facilitate lion movement, while others may hinder it (Zeke Davidson, personal communication, October 9, 2013).

Sampling

I sampled each environmental dataset at each presence location within the training dataset, and at a composite dataset of all training data and background points. In all cases, I performed sampling using bilinear interpolation because the lion presence locations lack precision. Bilinear interpolation samples the eight cells surrounding each point. It assigns a value to each point based on the weighted average of the surrounding cells, with the closest cells having the greatest influence. Bilinear interpolation accounts for the fact that points occurring on the periphery of a cell may represent a lion occurrence that actually was located in an adjacent cell.

Dispersal Habitat Analysis

I analyze habitat conducive to lion dispersal by applying several successive methods that repeatedly refine predictions of suitable habitat (Figure 4). Each step is critical to providing a more restricted study area for subsequent steps. I process suitable habitat in five steps: 1) explore data to identify significant relationships between environmental factors and lion occurrence, 2) create an envelope model to constrain the relevant landscape, 3) analyze paired interactions of environmental annuli, 4) analyze complex annuli interactions between sets of variables, and 5) identify habitat patches that connect lion populations in protected areas.

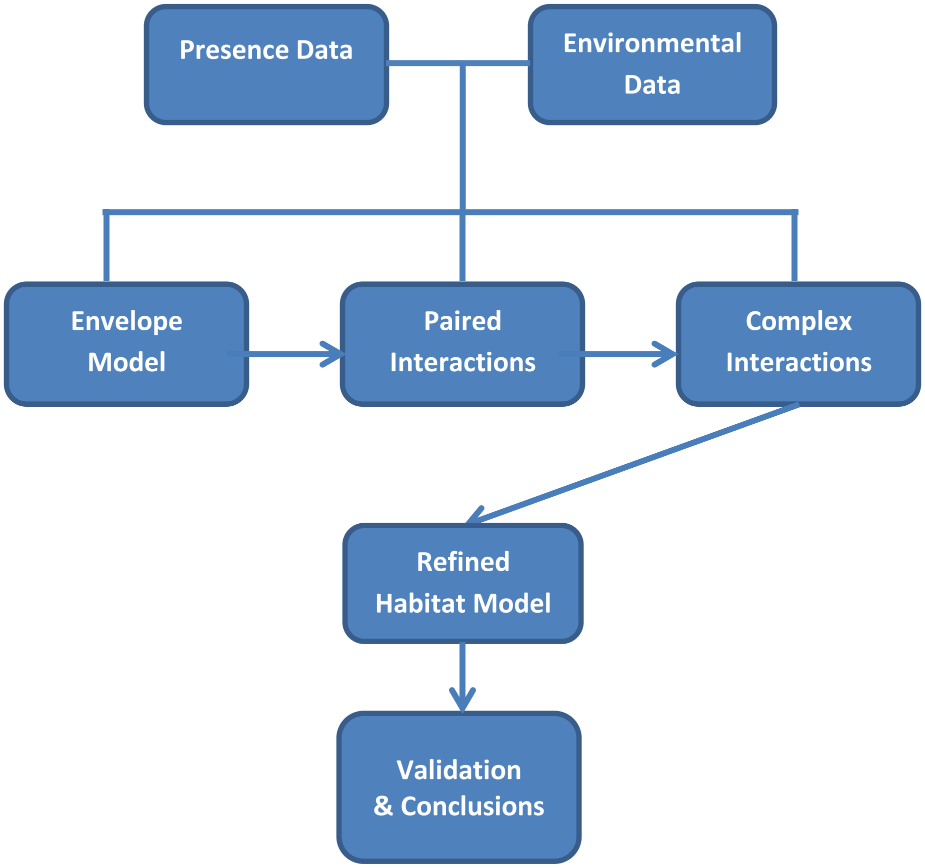

Figure 4: Flowchart of habitat analysis methods.

Annuli Formulation

I separated variables into two categories: localized and non-localized. Localized variables refer to landscape features that are present in certain locations and absent elsewhere. Where the feature is absent, the landscape is classified by the distance of each pixel to the nearest feature. This category includes protected areas, roads, rivers, lakes, and areas of high human density. Non-localized variables refer to variables for which every pixel in the study area has a value that represents a quantity or metric of that variable. Non-localized variables include all vegetation indices, rainfall, elevation, slope, and human population density.

For localized features, I applied annuli at 10 km intervals up to a maximum of 50 km (Joppa et al. 2009), with a final class encompassing all areas beyond 50 km (Figure 5). Thus I had seven classes, 0, 0 – 10, 10 – 20, 20 – 30, 30 – 40, 40 – 50, and greater than 50 km from the nearest feature. For features represented as lines – rivers and roads – a value of 0 represents all areas within 1 km of the nearest feature. A value of 0 – 10 represents areas 1 – 10 km from the nearest feature.

For non-localized variables, I apply annuli in distributional space using intervals of 0.5 standard deviations above and below the mean (Figure 6). Because the variable values are not normally distributed, this interval was necessary to parse data with heavily skewed or leptokurtic distributions.

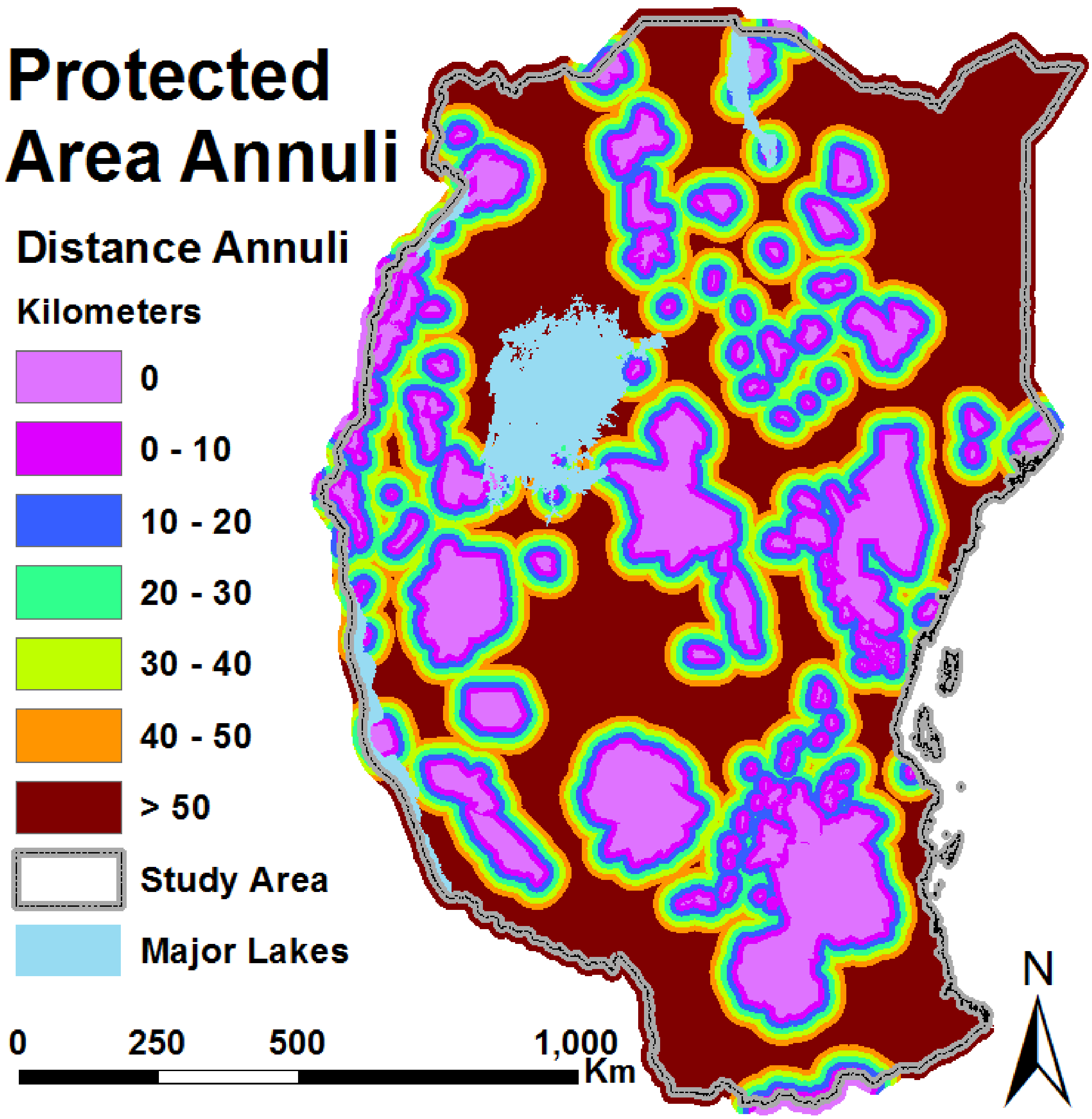

Figure 5: Annuli representing 10 km distance intervals from protected areas in East Africa.

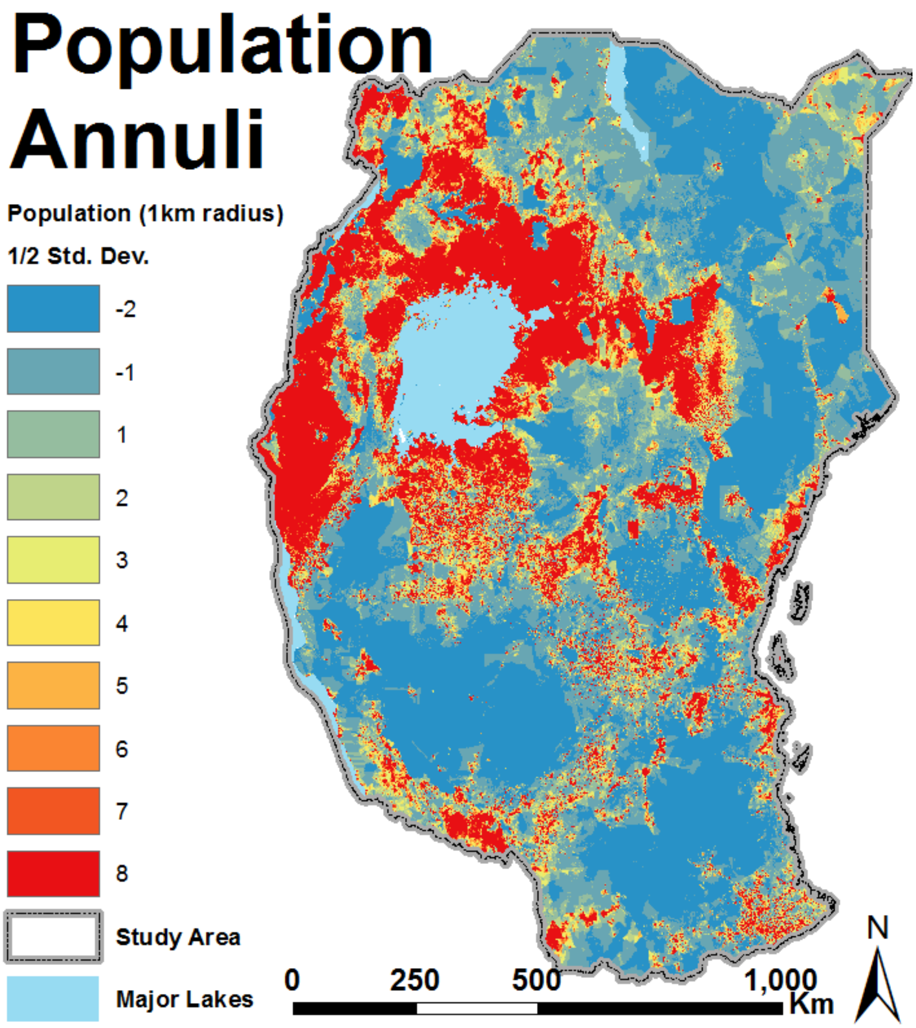

Figure 6: Distributional annuli for mean people per km^2 within a 1 km radius of each 500m cell. Each class represents the number of one-half standard deviations (9 people per km^2) above or below the mean population density (12 people per km^2) at lion occurrence locations. Annulus 8 includes all areas above the 99.9% threshold for tolerable population density.

Ecological relationships between lions and predictor variables change over large geographic scales (Loveridge & Canney 2009) such as my study area. Most of the lion presence locations come from study sites in semi-arid open grasslands of Kenya, rather than the miombo woodland or forest ecosystems of southern Tanzania (where the Selous ecosystem is suspected to harbor the largest single lion population worldwide) and western East Africa. I therefore tested two models. The first model treated the entire study area as a single unit; the second divided the study area into two regions based on classifications from Nangendo et al. (2007, Figure 7): open grassland landscapes (canopy cover less than 10%) and wooded landscapes (canopy cover greater than 10%). I classified each pixel as either above or below the 10% threshold, and then reclassified each cell based on whether the majority of the landscape within an 8.5 km radius was open or wooded. I selected the 227 km^2 focal area as the median home range size observed in East African lion populations

(Celesia et al. 2009). I ran identical analyses for both the unified and divided models to predict dispersal habitat.

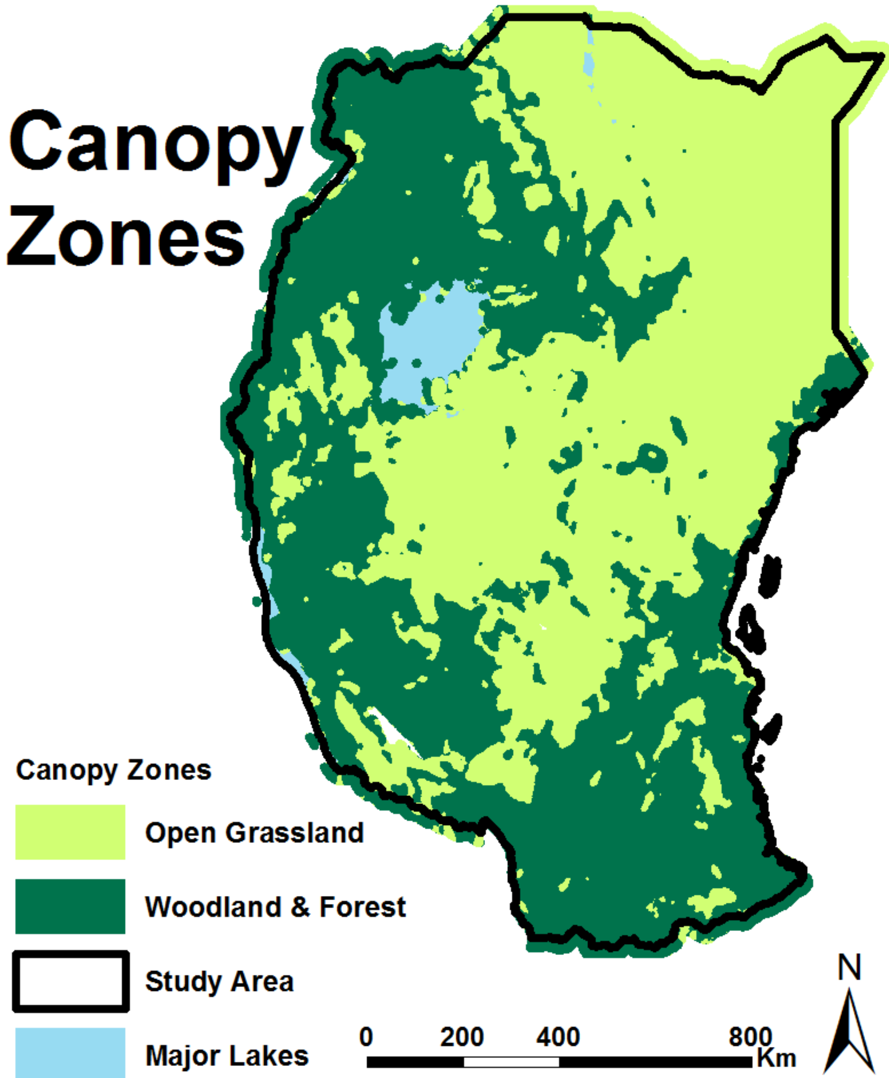

Figure 7: Grassland/Woodland zones for two-part model.

Exploratory Data Analysis

I performed exploratory data analysis in R x64 2.15.2 statistics software (R Core Development Team 2012) using the ecodist package (Goslee & Urban 2007). I tested each environmental dataset for a significant ($\alpha = 0.05$) correlation with presence – pseudo-absence locations and with each other dataset. I set 0.7 as a correlation coefficient threshold above which I would consider environmental variables strongly correlated. However, because I do not apply statistical models, I did not exclude strongly correlated variables from further analysis. The purpose was instead to determine how much variation across the landscape this suite of variables captures.

I qualitatively evaluated each variable in relation to three factors: correlation with presence – pseudo-absence, strong correlations with other variables, importance to lion distribution and behavior in the literature, and potential bias in the dataset. Based on this evaluation, I removed some variables from further consideration.

Habitat Envelope

The habitat envelope serves two purposes. The first is to confine the space for analyzing interactions between variables. Excluding areas outside lions' range reduces the noise in the annuli analysis. The second purpose is to account for outliers. Lions occasionally wander into the suburbs of Nairobi (Dloniak 2012), but that does not mean that Nairobi's suburbs act as corridors for dispersal. Rather, lions occasionally get themselves into bad situations. The envelope excludes some of these extreme circumstances from being classified as dispersal habitat.

To create the envelope, I classified variables based on whether or not they contain outliers. I individually assigned variables to a class based on basic ecological premises (e.g. a difference of 20 m of elevation does not affect lion movement, but a difference of a few hundred people per ha might), rates of change at the extremes of the distribution, and whether thresholds excluded areas with known lion populations. When evaluating the 0.1% extremes of environmental distributions, rapid change between ranked observations indicates likely outliers, while minor change between ranked variables suggests that no outliers are present.

The distribution of percent canopy cover and population density at lion locations illustrates these two classes (Table 2). Whereas the canopy cover decreases only a few percent between the first and twenty-fifth most extreme cases, population density decreases 76%. Lions occurring at human densities of 900 people per km^2 are clearly outliers; lions in 79% canopy cover probably are not.

For variables with outliers, I created an envelope of acceptable habitat for lion presence based on 99.9% of the observed range in lion presence for each variable. For variables with one-sided limits – population density metrics, distance to protected areas – I excluded the most extreme 0.1% of observed values. For two-sided limits – April and August NDVI– I set thresholds for exclusion at 0.05% and 99.95% of the observed range. These thresholds account for the fact that the most extreme conditions (0.1 %) are unlikely to constitute successful conservation areas.

Table 2: The 25 most extreme values of percent canopy cover and human population density (1 ha scale) at lion presence locations.

Rank	% Canopy Cover	Population Density (people/km^2, 1 ha scale)
1	79	2,236
2	79	1,665
3	79	1,637
4	78	1,412
5	78	1,367
6	78	1,228
7	78	1,154
8	77	1,082
9	77	990
10	77	951
11	77	862
12	77	801
13	76	670
14	76	662
15	76	637
16	75	604
17	75	593
18	75	586
19	74	544
20	74	544
21	74	544
22	74	544
23	74	538
24	73	511
25	73	485

Rainfall provides a clear example of a variable where the 99.9% range excludes significant lion habitat. The 99.95% upper limit of annual rainfall excludes portions of the study area, such as the central and western Selous Game Reserve, where lions occur (Figure 8). This pattern clearly reflects the sampling bias against areas with high rainfall, and is unlikely to accurately reflect the ecological tolerance of dispersing lions. I therefore set the upper limit at the maximum observed occurrence, 1,366 mm of rain annually, rather than the 99.95% threshold of 1,172 mm.

For variables without outliers – rainfall, elevation, percent canopy cover – I set the threshold at 100% of the observed range.

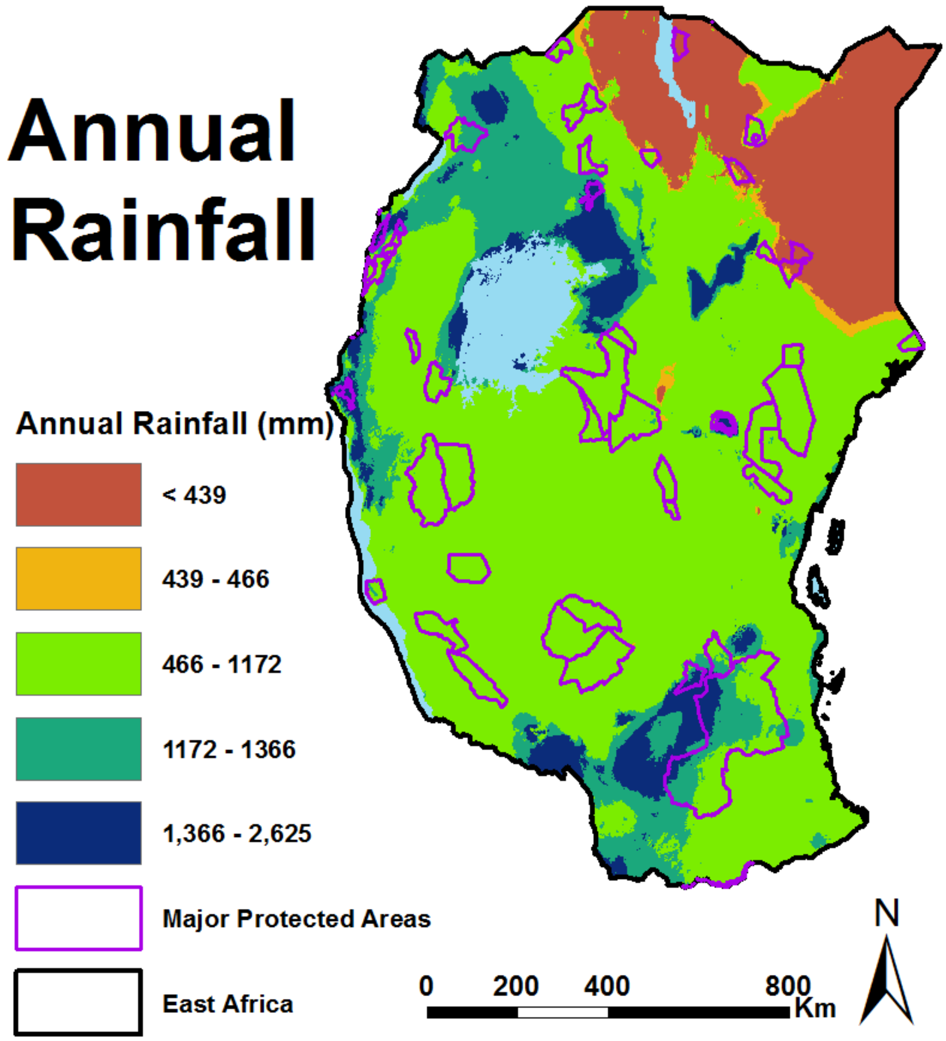

Figure 8: Total annual rainfall in East Africa. 439 mm represents the minimum observed rainfall at a lion presence location. 466 mm represents 0.05% threshold of the range in annual rainfall at observed lion presence locations. 1,172 mm represents the 99.95% threshold. 1,366 mm represents the maximum annual rainfall among lion presence locations. Regions below the minimum and maximum thresholds were excluded from the envelope of habitat suitable for lion dispersal.

Paired Interactions

I examined lion occurrence in relation to pairwise combinations of environmental variables. It is clear from the presence data that lions frequently occur in conditions outside the bounds of typical or preferred habitat. The question this analysis seeks to answer is whether other factors influence lions' ability to tolerate exceptional environmental conditions. For example, the presence training data include thousands of examples of lions occurring beyond the 25 people per km^2 threshold for resident lions. Do other factors facilitate lion movement through these highly populated areas? When we look at the distribution of relative lion occurrence in relation to April NDVI, and compare it to the distribution of only lion occurrence in areas of exceptionally high human density (>50/km^2), a stark contrast is evident (Figure 9).

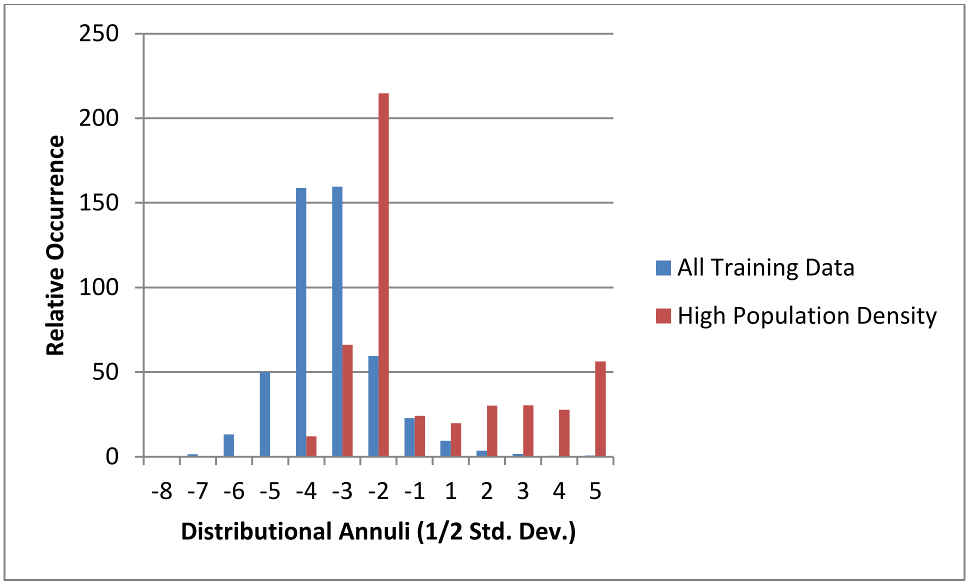

Figure 9: Relative (area-weighted) lion occurrence in relation to April NDVI distributional annuli of ½ standard deviations (0.071) above and below the mean (0.614). All Training Data includes 62,160 lion occurrence points, High Human Population includes 219 lion occurrence locations where mean population density within a 5 km radius is greater than 50 people/km^2.

Clearly, when human population is high, lions use areas with thick vegetation, especially since even annuli 1 – 2 standard deviations below the mean still exhibit relatively high levels of vegetation.

Population and NDVI provide a clear example of how one environmental variable appears to affect the way lions interact with another environmental factor. The paired interactions analysis identifies other similar patterns.

For this part of the analysis, I limited the study area to the environmental envelope. The first step in analyzing a pair of variables is to identify all combinations of their annuli classes in the study area. I then tabulated the number of lion training locations within each unique combination of annuli classes. Finally, I manually evaluated the results by looking for patterns, such as lions only occurring in high population density when NDVI is also high. The risk with the basic annuli approach is that combinations of annuli that do not contain lion presence points may be false absences; failure to detect lions in certain conditions does not necessarily mean they cannot occur under those conditions. Evaluating patterns, as opposed to only considering observed presence/absence, mitigates this risk. For example, if lions occurred in numerous combinations of near-average NDVI and near-average canopy cover, but were absent from a single combination of annuli (e.g. annuli -1, 1 respectively), I did not treat that combination as intolerable habitat. If, however, lions were consistently absent in combinations of high canopy annuli and high NDVI annuli, but occurred in a single combination, I did exclude that combination from acceptable habitat. This subjective process of pattern recognition was necessary to avoid excluding conditions with false absence and to avoid including conditions in which lion presence was a clear outlier, or indicative of local conditions that are not representative of the broader study area.

If no patterns in lion occurrence were evident for a particular pair of variables, or if the selected habitat for a pair of variables excluded large portions of known lion habitat (e.g. protected areas with widespread lion populations), I excluded that pair of environmental variables from consideration.

I overlaid the acceptable habitat conditions for all remaining pairs of variables, and subsequently classified as acceptable habitat portions of the landscape that met the presence conditions for all pairs of variables.

Complex Interactions

While many paired interactions reveal clear patterns in lion occurrence and provide insight into how lions interact with certain environmental factors, collectively they insufficiently differentiate between habitat conducive to lion dispersal and habitat that is intolerable for lions. I therefore tested complex interactions between three or more variables and intersected the combinations of annuli with lion presence training points. I evaluated the complex interactions based on whether patterns in lion occurrence were evident and on how much area from known lion areas each combination of variables excluded. I selected the model that best predicted habitat in these population centers.

Refined Connecting Habitat

Although a patch of habitat may be suitable for lion movement, the patch does not necessarily contribute to connectivity between populations. A single lion might venture into a patch only to turn around and choose a different route. A patch might be disconnected from lion sources, or too small to provide a movement corridor. As the main goal of this research is to determine conservation priorities, it is important to focus on dispersal habitat that is most likely to facilitate movement between populations.

I therefore set a minimum threshold for each unique combination of annuli of 10 lion observations or at least 0.01 lion observations per km^2. This latter threshold was necessary because some combinations of annuli are extremely rare in the landscape, and thus lion occurrence in those annuli is also rare in absolute terms, though may be high in relative terms. 0.01 lion observations per km^2, as a parallel value to density thresholds for resident lion populations (Loveridge &

Canney), is thus a conservative threshold that ensures certain habitat is not excluded purely because of its rarity in the landscape, as opposed to being unsuitable for lion dispersal.

Additionally, I set a threshold of 4 km^2 as the minimum viable patch size for lion movement based on the conclusions on small patches from Crooks et al. (2011). I excluded all pixels surrounded entirely by WWF GLWD-3 lake/reservoir at a 1 km radius. This measure of core lake patches was necessary because East African lakes vary seasonally and annually, and in numerous cases, lion presence points occur on the inner edge of lakes. Using the core lakes avoids excluding the lakeshore habitat.

Finally, I identified contiguous patches that connect two or more known lion populations.

Results

Exploratory data analysis

Exploratory data analysis revealed significant correlations (α=0.05) between presence – pseudo-absence and the entire suite of environmental variables (Table 3). These correlations reflect the availability of data from different regions of the study area as much as they reflect ecological relationships, but they nevertheless provide some insight into which variables capture the most variation in the lion presence dataset.

Table 3: Significant correlations (α = 0.05) between lion presence/pseudo-absence and fifteen environmental variables.

Variable	**R2**
Distance to protected area	-0.26
Distance to major roads	-0.33
Distance to rivers	-0.09
Distance to high human population	-0.14
Elevation	0.34
April NDVI	-0.39
August NDVI	-0.13
Percent canopy cover	-0.40
Population Density (hectare scale)	-0.12
Population Density (1 km^2 scale)	-0.14
Population Density (5 km^2 scale)	-0.20
Annual rainfall	-0.41
Dry-season rainfall	-0.04
Distance to lakes	-0.06
Slope	-0.09

Annual Rainfall, Percent canopy cover, and April NDVI exhibited the strongest correlations. Interestingly, distance to roads revealed a strong (R^2 = -0.33) negative correlation. This relationship suggests that lions are more common closer to roads. I hypothesized that this trend indicates strong sampling bias, with researchers unable to sample habitat far from roads. Furthermore, since roads are a predictor model in the AfriPop dataset, some of the variation in roads is thus captured in other variables. I therefore decided to remove distance to roads from further consideration in the analysis.

One of the most interesting trends is that the correlation between presence and population density strengthens as the scale at which population density is measured also increases. Thus, based on these results, population density within a 5 km radius is a stronger predictor of lion presence than human density within 1 km radius or within 1 ha.

The strong negative correlation between lion presence and percent canopy cover also suggests that the data may be biased against woodland and forest ecosystems. This result was a primary reason for including the separate grassland-woodland models.

Four variables – slope, dry-season rainfall, distance to rivers, and distance to lakes – exhibited correlations that explain less than 10% of the variance in lion presence. In addition, distance to dense human population shows a negative correlation, suggesting lions are more common closer to densely populated areas.

I examined these five variables in greater detail to determine if they demonstrate enough of a relationship with lion presence to justifying including them in the analysis.

Because of the weak correlation between lion presence and distance to lakes, in addition to concerns about inadequate data on seasonal waterholes and wet-season water availability, I removed distance to lakes from further analysis.

To further investigate the other four variables, I created boxplots of the distribution at the lion presence points as opposed to the background dataset (Figure 10). Slope, distance to river, and distance to dense human population all have distributions that are very similar between lion presence locations and pseudo-absence locations. This suggests that those three variables do not have any observable impact on lion habitat use or movement at the scale of this analysis. When we consider uncertainty in the river dataset, and potential bias in the dense population dataset, the argument for excluding these two variables from the analysis becomes stronger. The river dataset, based on flow accumulation, does not account for the amount of available moisture, and thus may not be an accurate representation of rivers in areas with particularly low or high water availability. In the case of distance to dense human populations, lion observations are rare far from human population centers, which may be inaccessible to researchers. Thus the observed relationship between lion presence and distance to high human density may reflect sampling biases more than ecological patterns.

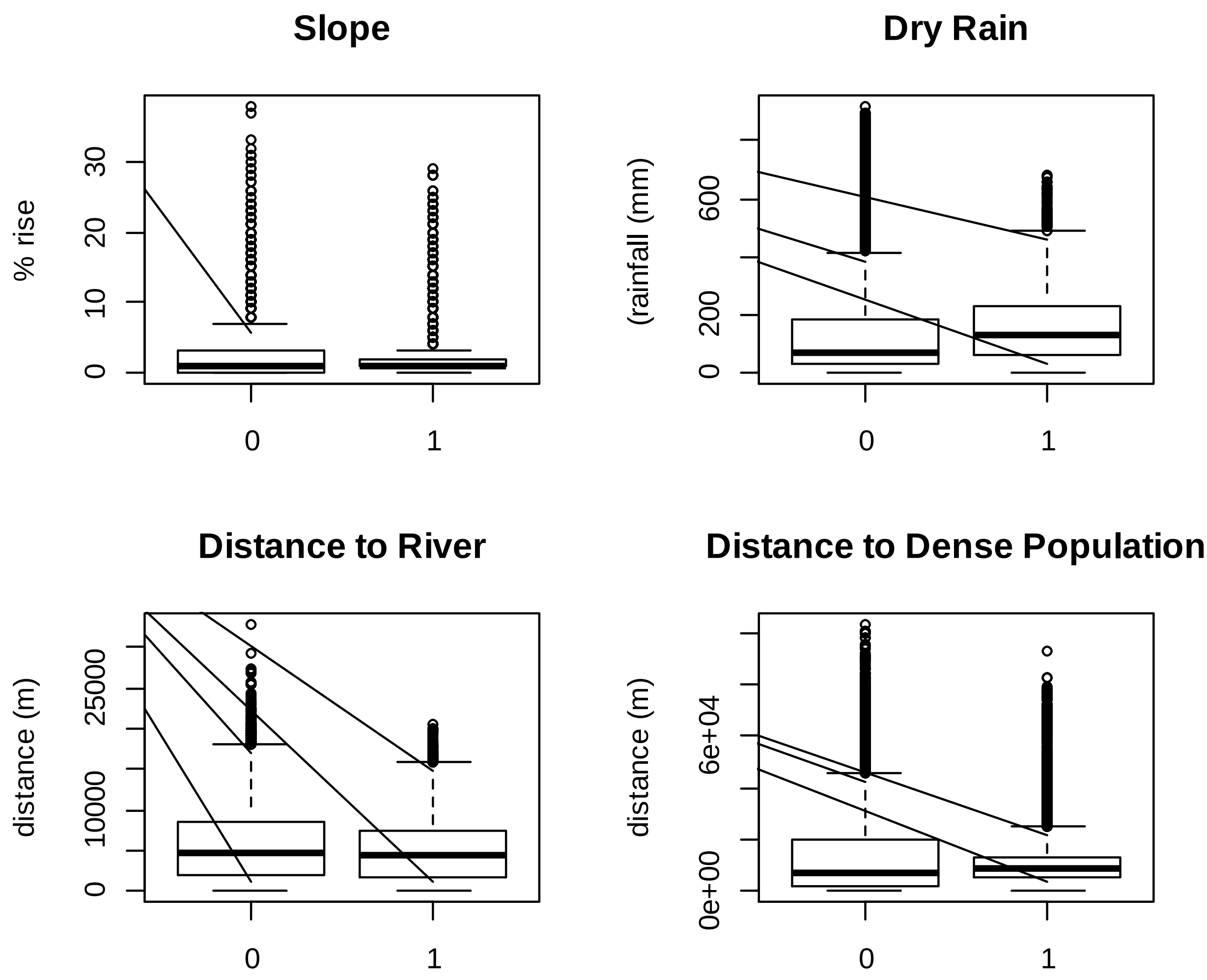

Figure 10: Boxplots of the distribution of lion presence ("1") and pseudo-absence ("0") in relation to four environmental variables. Distance to dense population denotes the distance to the nearest hectare with a population density greater than 228 people per km^2.

The relationship between lion presence and dry-season rainfall is more interesting. Despite the negative correlation between lion presence and dry-season rainfall, and the fact that most lion observations come from semi-arid areas of Kenya and northern Tanzania, mean dry-season rainfall at lion locations is higher than for the landscape as a whole. Furthermore, lions exhibit a greater interquartile range, suggesting that they are more common in areas with high dry-season rainfall than we would expect given a random distribution.

After evaluating the four variables with the weakest correlations to lion presence, I retained dry-season rainfall in the analysis and excluded the other three.

All environmental variables were significantly correlated with each other with the exception of elevation and population density at the hectare and 1 km^2 scales (Appendix D). Most correlations were weak. A few pairs of variables – April NDVI and Percent Canopy Cover, Dry-season Rainfall and August NDVI, the population density variables – exhibited strong correlations (R^2 >0.70). As the variables in each pair are directly related, none of these findings are surprising. Instead, the weak correlations between most pairs of variables suggest that predominantly they represent unique sources of variation in the environment.

A closer examination of conditions where lions occur in highly populated areas reveals other trends. When we look at the 25 lion presence locations with the highest 1 ha population density and the 25 lion locations with the highest 5 km population density, no points occur on both lists (Table 4). Furthermore, when the population density within 5 km is very high, the population density at the exact lion presence point is below 15 people per km^2 more than half the time. In other words, it appears that lions can tolerate dense populations either in a very specific area but not in the surrounding few kilometers, or they can withstand regions of widespread human populations as long as they are in a specific habitat patch without many people.

Woodland Model

The separation of woodland habitat from open grassland habitat provided a means of mitigating the bias in the presence data towards open grassland landscapes. However, the woodland-only model (Appendix E) predicted more suitable habitat with lower accuracy than the unified model. Therefore, this report discusses only the unified model.

Envelope Model

The envelope model incorporated five variables that were delimited to 99.9% of their range, and five variables that contain 100% of their range. Five variables have one-sided limits and five have two-sided limits (Table 5).

Table 4: A comparison of human population density at two spatial scales in lion presence locations with the highest human population densities.

Rank	1 ha	5 km radius	5 km radius	1 ha
1	2236	23	918	0
2	1665	20	439	450
3	1637	136	439	450
4	1412	29	380	450
5	1367	27	335	0
6	1228	29	334	0
7	1154	30	328	14
8	1082	19	292	0
9	990	28	285	450
10	951	28	284	0
11	862	21	257	202
12	801	20	235	49
13	670	28	229	360
14	662	21	198	0
15	637	37	184	0
16	604	21	182	450
17	593	22	179	0
18	586	6	168	7
19	544	10	168	103
20	544	10	161	0
21	544	10	159	8
22	544	10	159	0
23	538	10	159	0
24	511	30	156	0
25	485	29	153	0

Table 5: Ecological and environmental conditions that are conducive to lion dispersal. The acceptable range for each variable is described by either 99.9% or 100% of its observed range at lion presence locations. 99.9% ranges can be either one-sided (threshold at 0.1% or 99.9% most extreme value) or two-sided (thresholds at 0.05% and 99.95% most extreme values).

99.9% Range	Threshold
Population density (5 km radius)	< 93 people/km2
Population density (1 km radius)	< 84 people/km2
Population density (1 ha)	< 228 people/km2
April NDVI	0.15 - 0.83
August NDVI	0.12 - 0.77

100% Range	Range
Annual rainfall	439 mm - 1366 mm
Dry-season rainfall	4 mm – 680 mm
Distance to protected area	< 87.5 km
Canopy cover	< 79%
Elevation	50 m - 2302 m

The envelope of habitat conducive to lion dispersal (Figure 11, Appendix F) does not include very dry areas in northeastern Kenya and the Lake Turkana region. It also excludes very rainy, densely populated areas in Rwanda and Burundi, around Lake Victoria (especially in the northeast), western Uganda, and the southern highlands region in southwestern Tanzania. Portions of the Selous Game Reserve are also excluded, because of high rainfall in the west and areas of extremely dense vegetation in the southeast. A prominent gap in suitable habitat dominates central Tanzania in an area that is far from protected areas. At 90 km from the nearest protected area, a lion would need to travel a minimum of 180 km in order to pass through this area from one protected population to another. Thus, while the habitat in this region may not be intolerable, it would require lions to disperse long distances. Although 180 km is far less than the maximum observed dispersal distance that Dolrenry et al. (2014) found for male lions, it is considerably further than the average male dispersal distance (117 km) and the maximum female dispersal distance (128 km) from that study. While such a feat of dispersal is feasible for males, it should not be considered a conservation priority as it is more worthwhile to focus on maintaining connectivity along shorter routes.

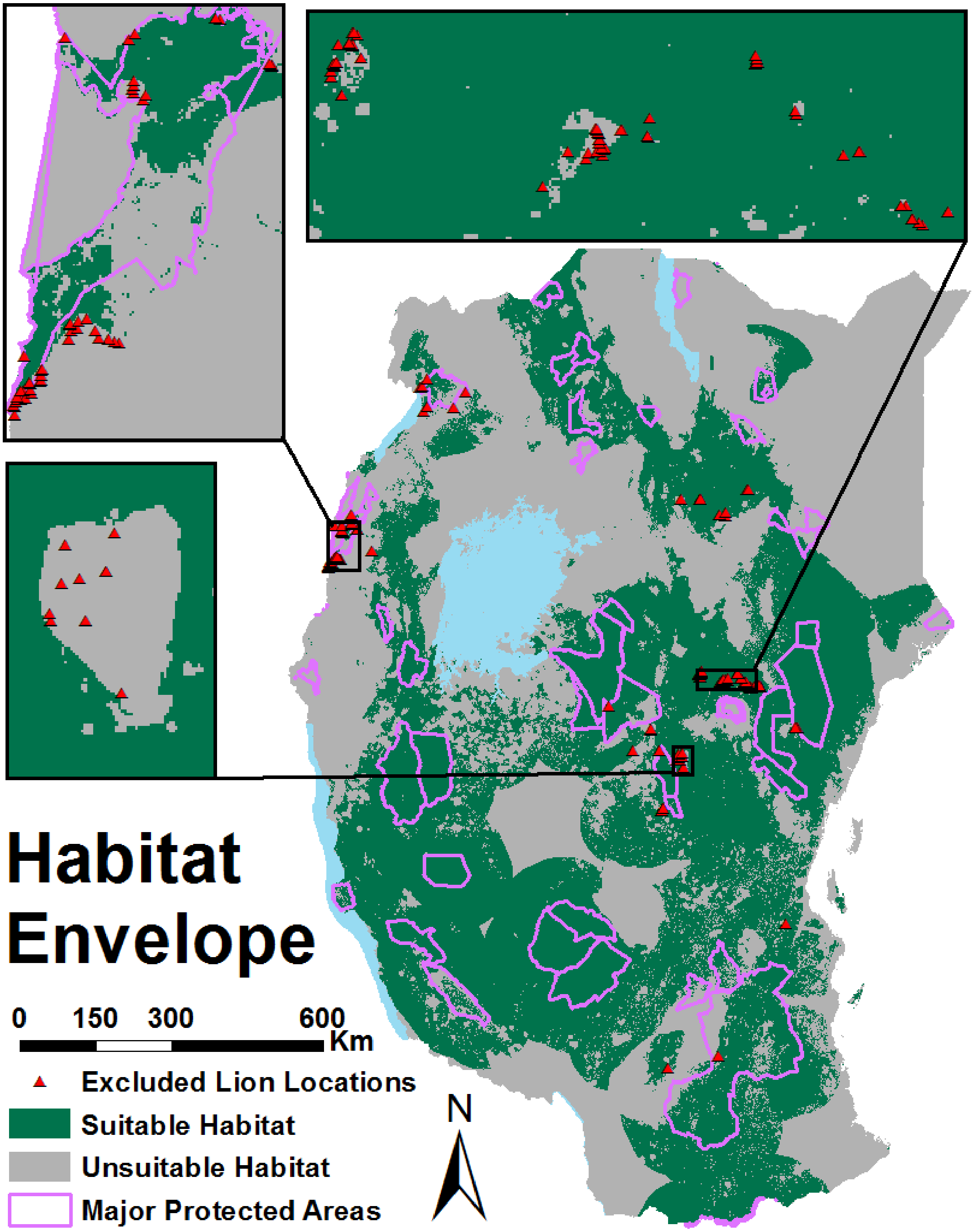

Figure 11: Map of the habitat envelope.

The habitat envelope encompasses 61,963 of the lion points (99.7%) and excludes 197, mostly because of exceptionally high human population density or extreme vegetation levels. The habitat envelope covers 870,000 km^2, or 51% of the study area. A closer look at areas with numerous excluded points (Figure 11) reveals certain local characteristics. In Southern Kenya, to the west of the Tsavo ecosystem, numerous points are excluded in areas with minimal vegetation. However, these areas represent minor pockets of unlikely habitat in a broader region of consistent population. Therefore, these pockets of excluded habitat do not suggest that the area as a whole is not suitable for lion movement.

It is also clear that Queen Elizabeth National Park in southwestern Uganda experiences high human pressure along its southern boundary. In fact, human presence is so strong and so close to the park that areas excluded based on 5 km human density extend well into the park's interior. This pattern suggests the park's southern boundary may act as a population sink as discussed in Woodroffe and Ginsburg (1998).

Finally, numerous points are excluded from an area to the east of Tarangire National Park in northern Tanzania. The excluded patch exhibits a high population density, yet the lion presence records (some of which are less than two years old) suggest that lions do venture into that area. While further analysis is beyond the scope of this paper, Kissui (2008) documented high levels of lion-human conflict in this area.

Paired Interactions

I tested 25 pairwise combinations of variables. Eight combinations incorporating six variables exhibited patterns in lion occupancy (Table 6). The paired-interaction model retains 720,000 km^2 of habitat (42% of the study area), mostly in southeastern and central Kenya, northeast Uganda, and large expanses of Tanzania (Figure 12). It encompasses 99.2% of the lion training locations.

Table 6: Paired interactions of environmental variables exhibiting patterns in relation to lion occurrence.

Variable 1	Variable 2	Pattern
Population 1 ha	Canopy	In areas of high human population density, lions occur in moderately wooded habitat
Population 1 ha	April NDVI	In highly populated areas, lions are rare in open habitat
Population 1 ha	Distance to Protected Area	Lions in densely populated areas are typically near the boundary of a protected area
April NDVI	Canopy	Among areas with exceptionally high vegetation growth, lions are rare in habitat with low canopy cover (i.e. dense bush thickets)
Population 1 km radius	Distance to Protected Area	Lion very far from protected areas are not in areas of exceptionally high population density
Population 1 km radius	April NDVI	In highly populated areas, lions are typically in moderate to dense vegetation
Population 5 km radius	April NDVI	In highly populated areas, lions are typically in moderate to dense vegetation
Population 1 km radius	Population 5 km radius	Lions do not occur in densely populated areas at both the 1 km and 5 km scales

Overall, this map does not drastically differ from the envelope map, although less habitat is present in highly populated areas. At a finer scale, however, a few key modifications to the predicted dispersal habitat become evident. Perhaps the most striking change is the further reduction of habitat around Queen Elizabeth and Murchison Falls national parks in Uganda, further sign of the intense human pressure along the boundaries of those parks. A less apparent change from the envelope model is that the swath of dispersal habitat running from the rangelands of central Kenya to Kidepo Valley National Park in northern Uganda is tenuous along the border between the two countries.

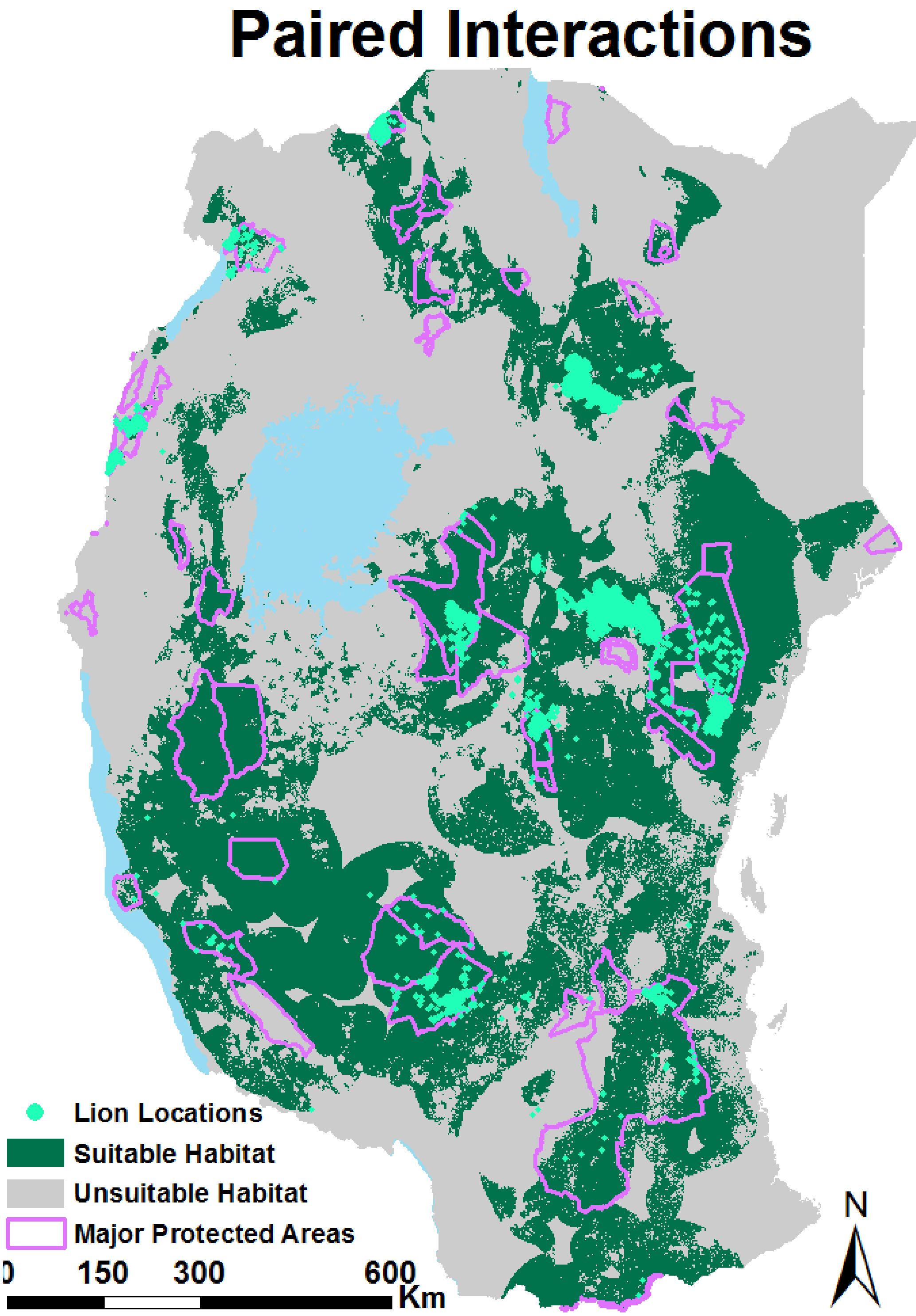

Figure 12: Map of cumulative suitable habitat from eight pairwise combinations of environmental variables.

Given Kidepo Valley's isolation from the other Ugandan parks and the gap separating the central Kenyan rangelands from Meru National Park and the Tsavo ecosystem, the connection between the rangelands and Kidepo Valley populations could be critical to both.

Complex Interactions

The final habitat model includes three variables: population density (5 km radius), April NDVI, and percent canopy cover. This combination of variables demonstrated consistent lion presence only within moderate canopy and NDVI conditions in areas of high population density, and within a much broader range of acceptable vegetation in areas of low human population density. This combination predicts all reserves with major lion populations as dispersal habitat. The final model (Figure 13) covers slightly fewer than 675,000 km^2 and captures 61,662 training points (99.2%). Out of 1,328 unique combinations of the three variables' annuli, 256 (19%) contain at least one lion training occurrence and are retained in the final habitat model.

The final habitat model captures 6,830 (98.9%) of the test locations (Figure 14). Of the 78 test locations that do not coincide with predicted dispersal habitat, the vast majority are either on the edge of predicted habitat patches (e.g. around Queen Elizabeth National Park) or in localized patches of non-habitat in otherwise inhabitable areas (e.g. southern Kenya, central rangelands). Only four locations – one southeast of Ruaha National Park, another south of Murchison Falls National Park, a third west of Selous Game Reserve, and a fourth north of Tarangire National Park on the edge of Lake Manyara National Park – are far from large patches of habitat. Two of them occur within a few kilometers of localized habitat patches.

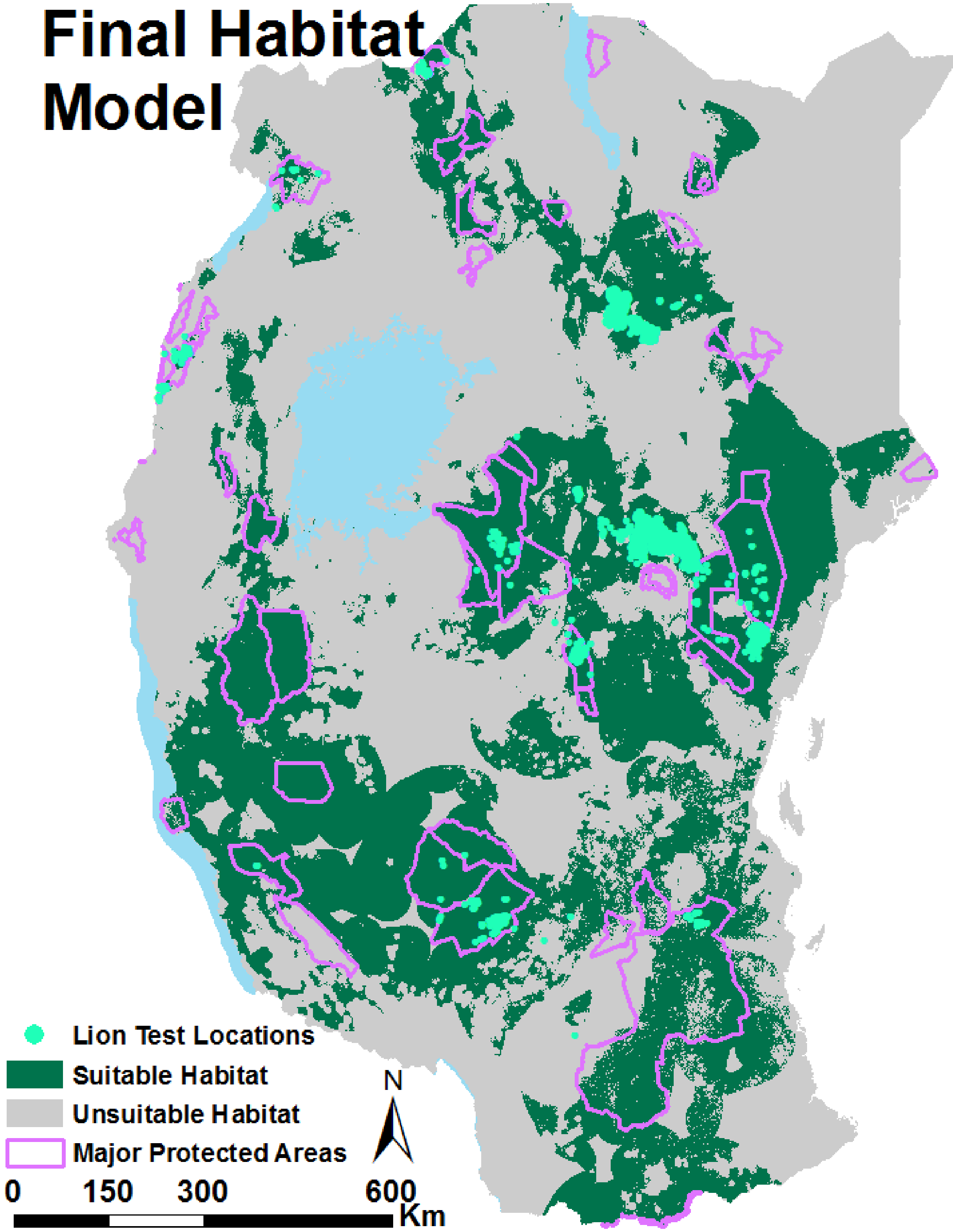

Figure 12: Map of final model of dispersal habitat, overlaid with lion test locations.

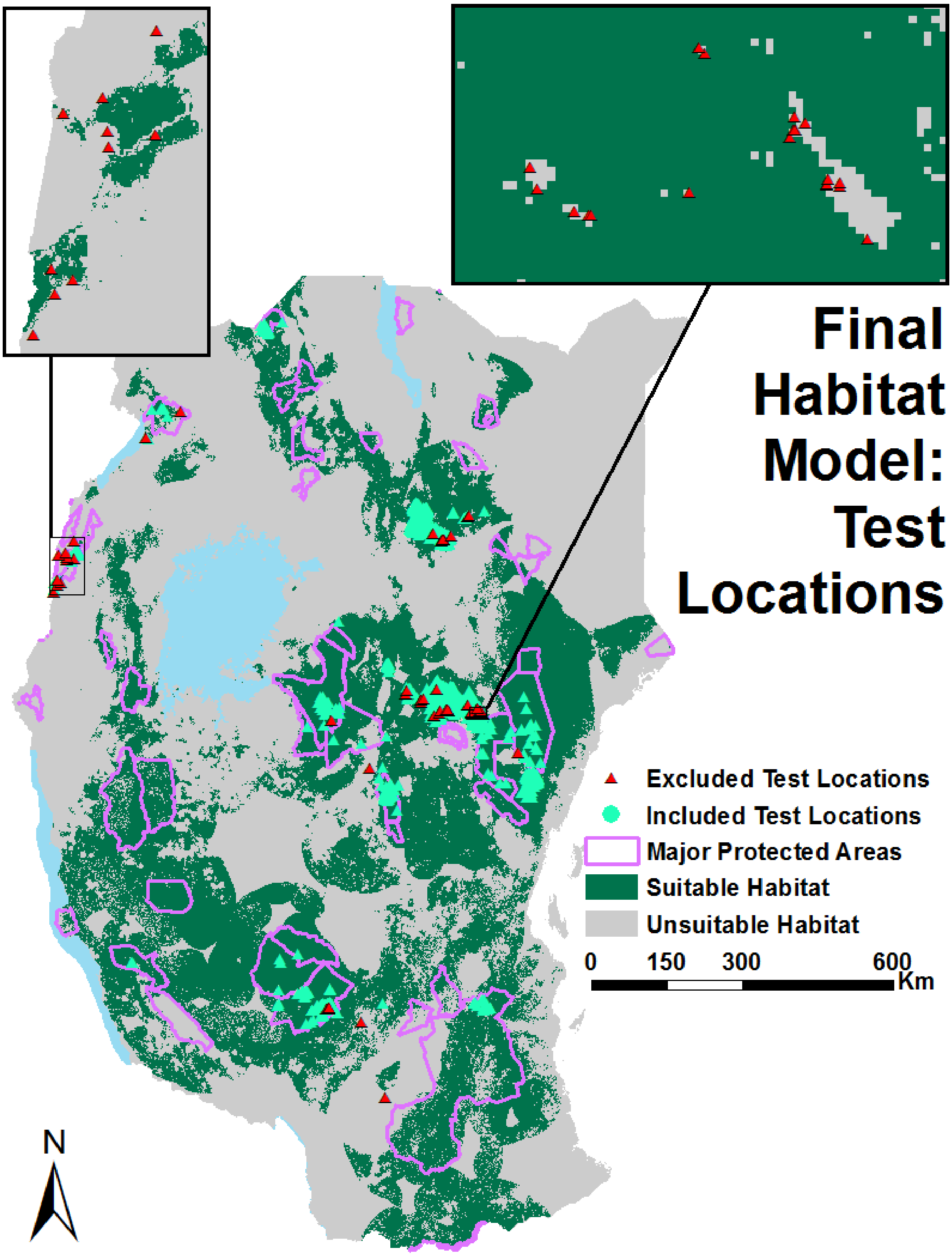

Figure 13: Map of lion test locations excluded from the final habitat model.

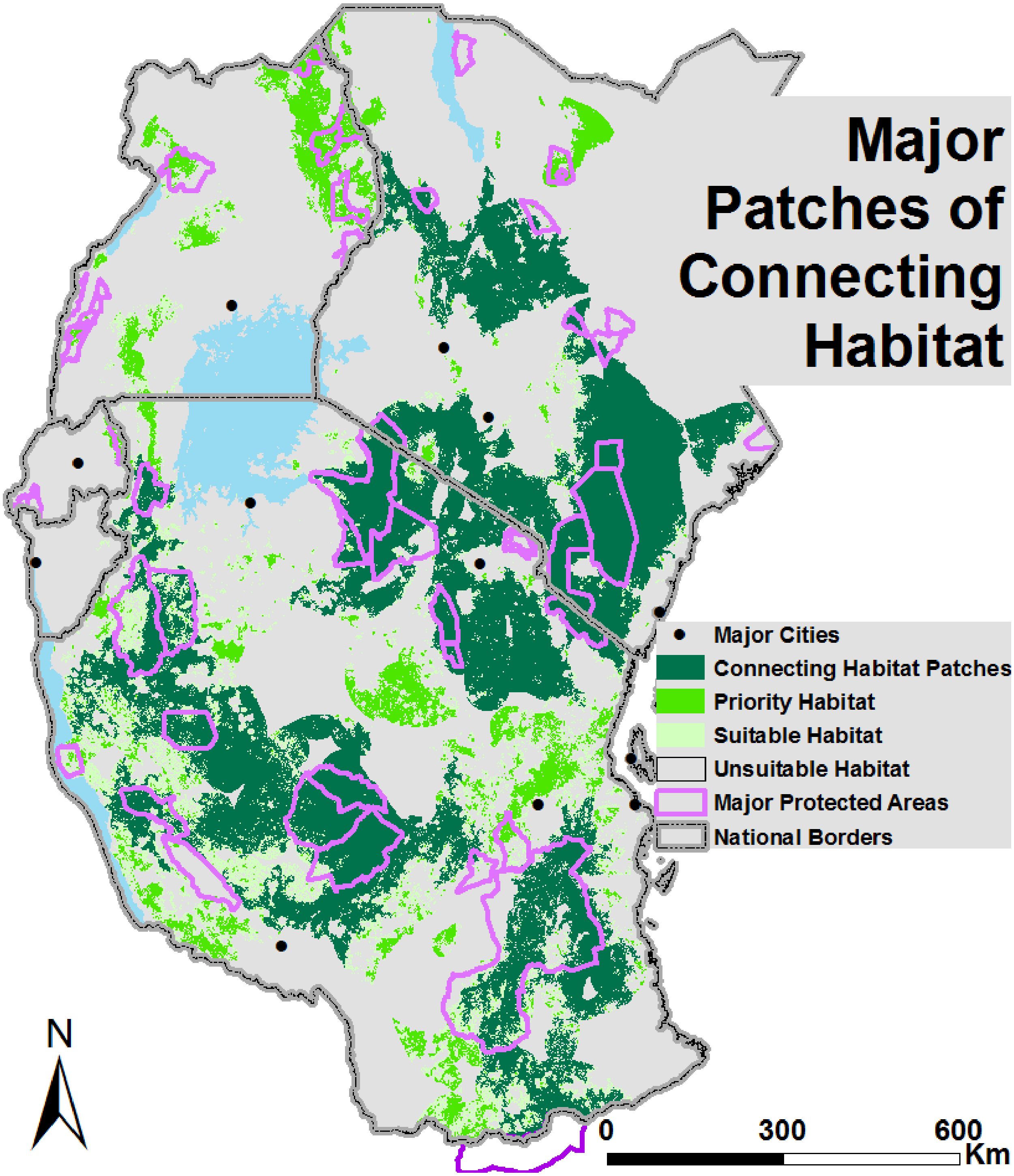

Figure 14: Three classifications of lion dispersal habitat in East Africa: 1) Patches of priority dispersal habitat connecting major protected areas, 2) Other priority dispersal habitat, and 3) suitable, low-priority dispersal habitat. Priority habitat denotes areas with combinations of April NDVI, Canopy Cover, and Population Density annuli that contain at least ten lion occurrences or a relative occurrence of 0.01 lion observations per km^2. Suitable dispersal habitat denotes any areas with combinations of the three variables' annuli that contain one or more lion occurrences.

Refined Model

The refined model prioritizes habitat that is most likely to facilitate lion dispersal. It identifies combinations of annuli from the complex interactions that exhibit repeated lion presence or high presence in relation to the spatial extent of that combination. After applying the thresholds of at least ten lions per annuli combination or 0.01 lions per km^2, the final habitat includes 40,398 individual habitat patches. Fewer than 4% of those patches, however, cover at least 4 km^2 (Figure 15). In terms of dispersal habitat linking populations, a few patches are clearly of greatest importance. The largest contiguous patch of habitat connects the greater Serengeti ecosystem of northern Tanzania with the greater Tsavo ecosystem of southeastern Kenya (Figure 16). It also stretches south to Tarangire National Park. The link between the Serengeti and Tsavo ecosystems is consistent with the population models of Dolrenry et al. (2014). What this analysis shows, however, is that the links are strongest to the north of the Ngorongoro Conservation Area, and even further north in an arc running from Amboseli National Park west to the northern boundary of the Maasai Mara reserve.

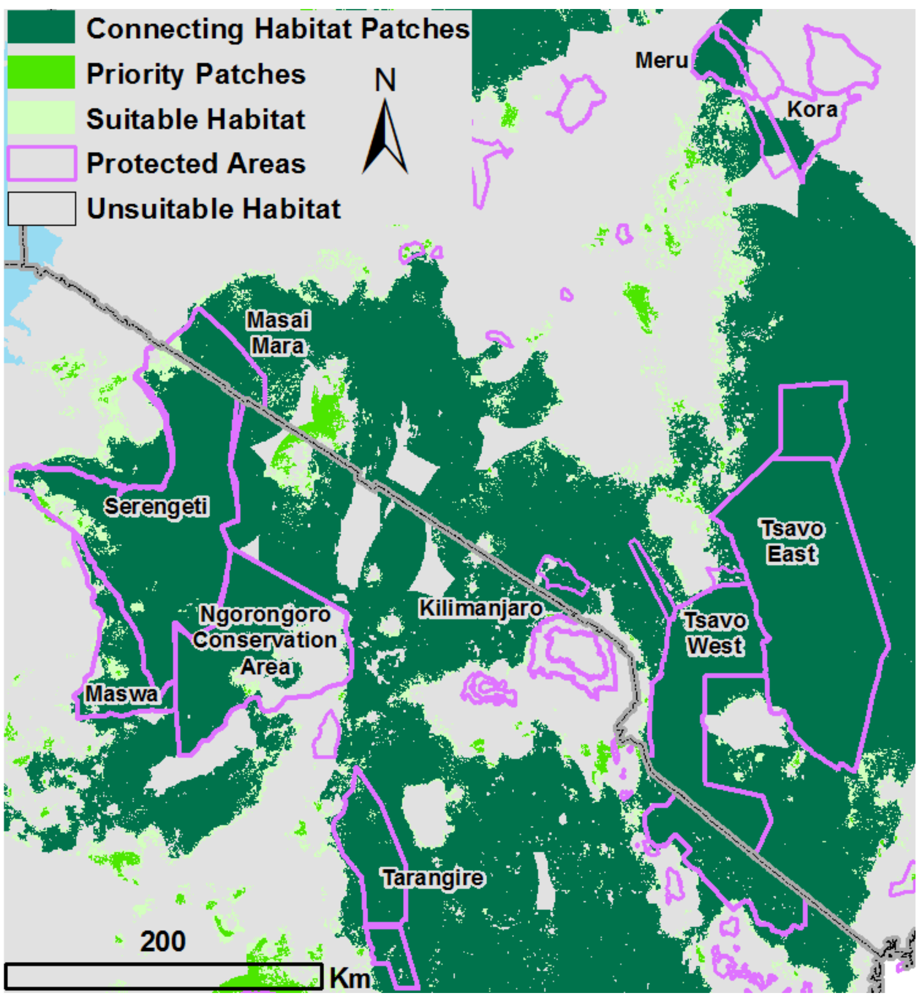

Figure 15: Dispersal habitat between the greater Tsavo and Serengeti ecosystems.

Another major patch of habitat that links protected areas occurs in Western Tanzania (Figure 17). This patch is potentially critical because it links the greater Ruaha ecosystem with Moyowosi and Kigosi game reserves to the northwest. Of greater importance, however, may be the connection between Katavi National Park and the Ruaha ecosystem. Kiffner et al. (2009) estimated 77 – 439 lions in and around Katavi National Park. This estimate suggests the Katavi lion population is on the cusp of, or below, a minimum viable population. It may depend on immigration from Ruaha or other populations to ensure its viability. Kiffner et al. (2009) also found demographic evidence that areas surrounding the park act as lion sinks. The Katavi lion population likely requires continued conservation efforts to ensure that its links to other reserves remain intact.

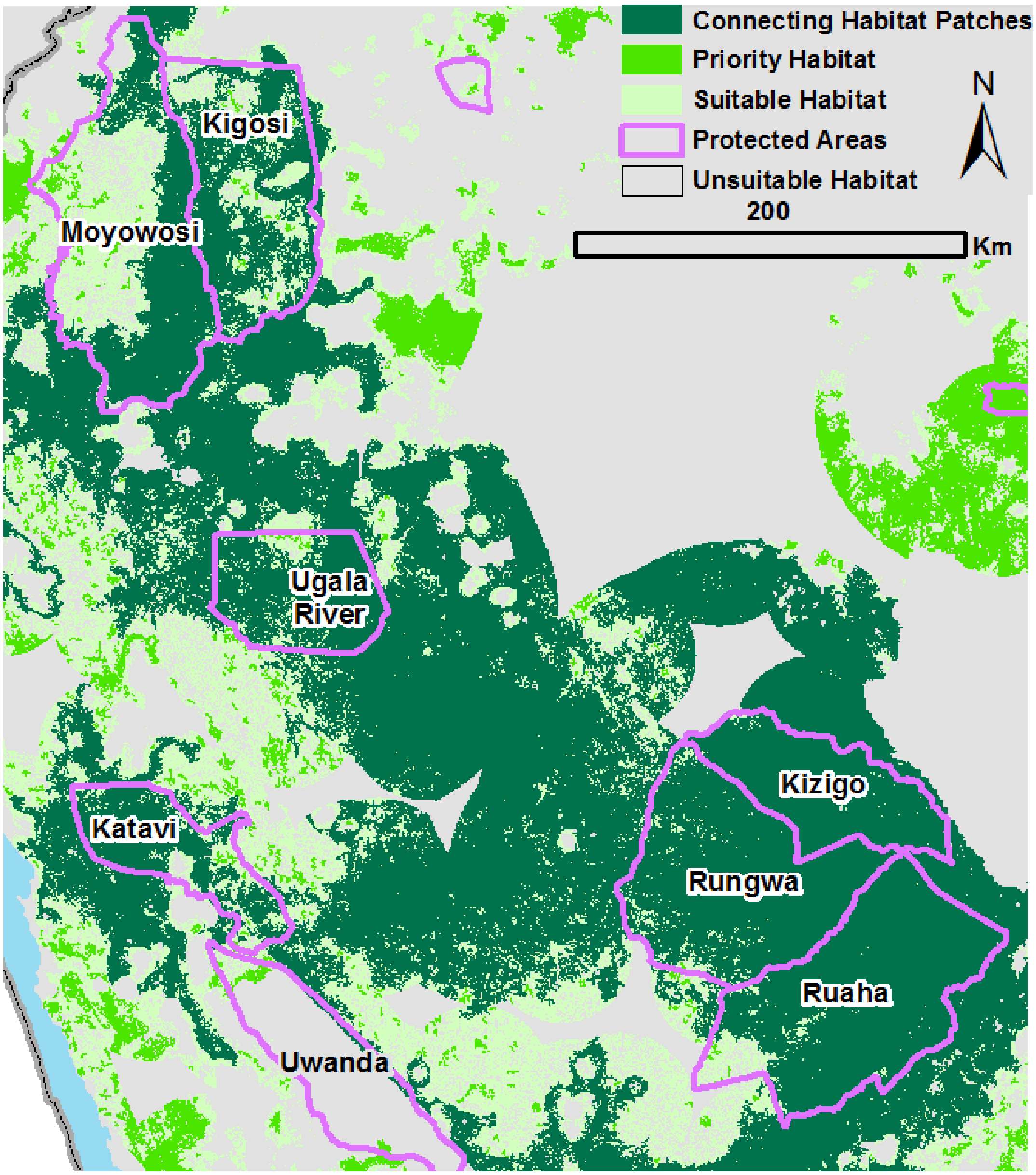

Figure 16: Dispersal habitat between the Ruaha ecosystem, Katavi National Park, and Moyowosi/Kigosi Game Reserves.

The Ruaha-Katavi-Moyowosi/Kigosi patch of dispersal habitat also illustrates the role that small or low-quality protected areas may play in facilitating connectivity. Rungwa Game Reserve and Kigosi Game Reserve, protected areas spanning 9000 km^2 and 7000 km^2 respectively, are approximately 300 km apart. Ugalla game reserve, which is not as well known for its lion population as the other two reserves, sits neatly in the middle and may act as a stepping-stone between the two larger reserves that increases connectivity (Pittiglio et al. 2014). Other reserves, such as Kora National Park in Kenya, may play a similar role.

A third major patch that connects large protected areas is the Selous-Niassa corridor that runs from the southwestern boundary of the Selous Game Reserve to Niassa Game Reserve in northern Mozambique. This corridor has been well documented, particularly with respect to elephant movement (Jones et al. 2009), but it faces numerous threats including mining, human wildlife conflict, and loss of habitat (Jones et al. 2009). This analysis suggests that the corridor remains intact, at least for lions, but its braided nature testifies to the area's land conversion and the vulnerability of the corridor.

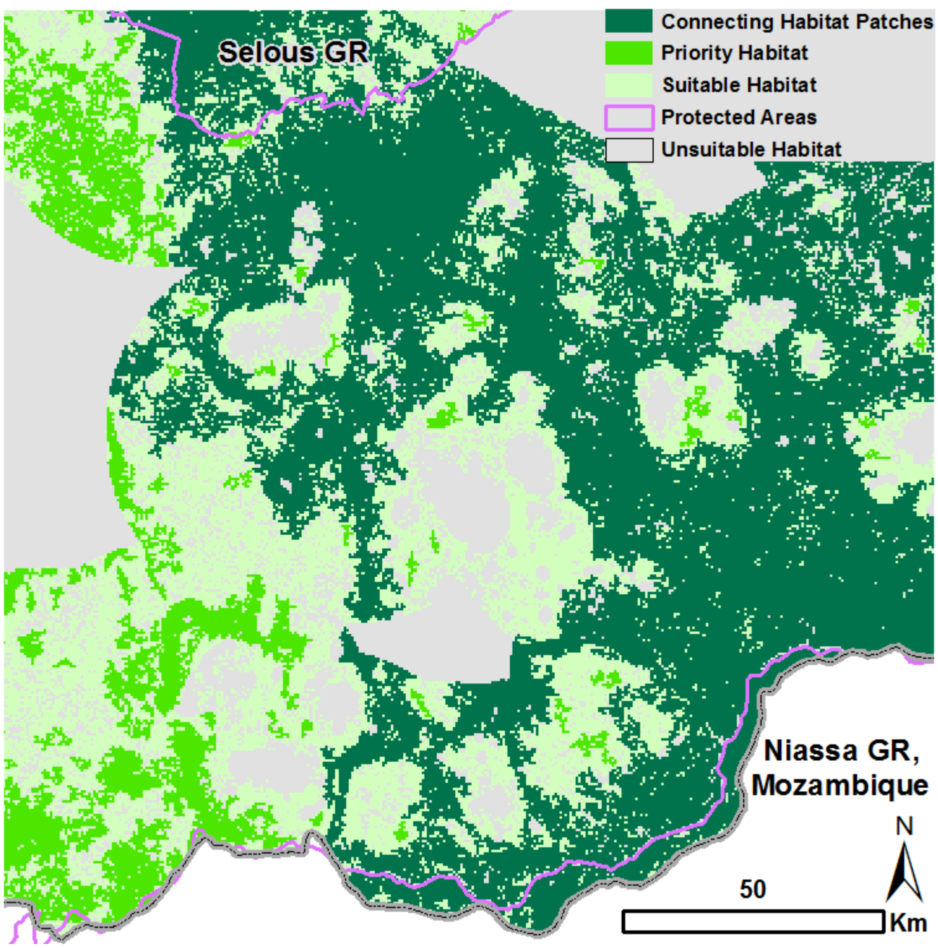

Figure 17: Dispersal habitat between the Selous Game Reserve, Tanzania, and the Niassa Game Reserve, Mozambique.

Several other large contiguous patches of habitat are evident, however, their contribution to functional links between protected areas appears tenuous. In particular, a narrow gap separates two large patches of priority habitat along the Kenya-Uganda border (Figure 19). One patch encompasses the rangelands of central Kenya and runs northwest to the border. The other patch encompasses Kidepo Valley National Park and its lion population, and then runs southeast through a number of reserves until it reaches the border. Along the national boundary, the picture becomes more complex. The two patches are technically disconnected. However, they come within a kilometer of connecting in two places. One is separated by a single 500 m pixel of low-priority habitat. The other is divided by a patch of No Data. Reprojecting the AfriPop human density dataset produces the patch of missing data, which is excluded from the analysis. As a result, a geographic link may exist between the Ugandan and Kenyan patches, even if it is not evident in this study.

Elsewhere, gaps between major patches appear more prominent. To the north of the Selous Game Reserve, for example, a gap exists in Mikumi National Park between the Selous and a patch of dispersal habitat stretching west to Ruaha National Park (Figure 20). Interpreting the results for this area requires an understanding of the surrounding landscape. The Udzungwa Moutains to the southwest contain montane rainforest that is unlikely to allow lion dispersal. Furthermore, between the Selous the Udzungwa Moutains National Park is a valley of dense human population and intense agriculture. In 2009, Jones et al. classified the corridor between the Selous and the Udzungua Mountains as one of the five most threatened corridors in the country. My analysis suggests that the corridor has completely degraded.

The alternative route for lions dispersing out of (or into) the Selous is to pass through Mikumi National Park, cross the A7 highway, and then turn west through forest reserves to reach the patch of contiguous habitat stretching to Ruaha National Park. This analysis finds large portions of the southern Mikumi National Park impassable because of dense vegetation, especially during April rains. It is unclear, therefore, whether the southern portions of the park are actually impassable, or only passable in the dry season, or even whether this is further evidence of bias in the data against lush areas with high rainfall. Mikumi is recognized as hosting lions (TANAPA 2012), which suggests that in this particular area, the model may underrepresent dispersal potential.

Even if dispersing lions pass through Mikumi National Park, however, no obvious corridor connects all the way to Ruaha National Park. The two populations may be entirely fragmented.

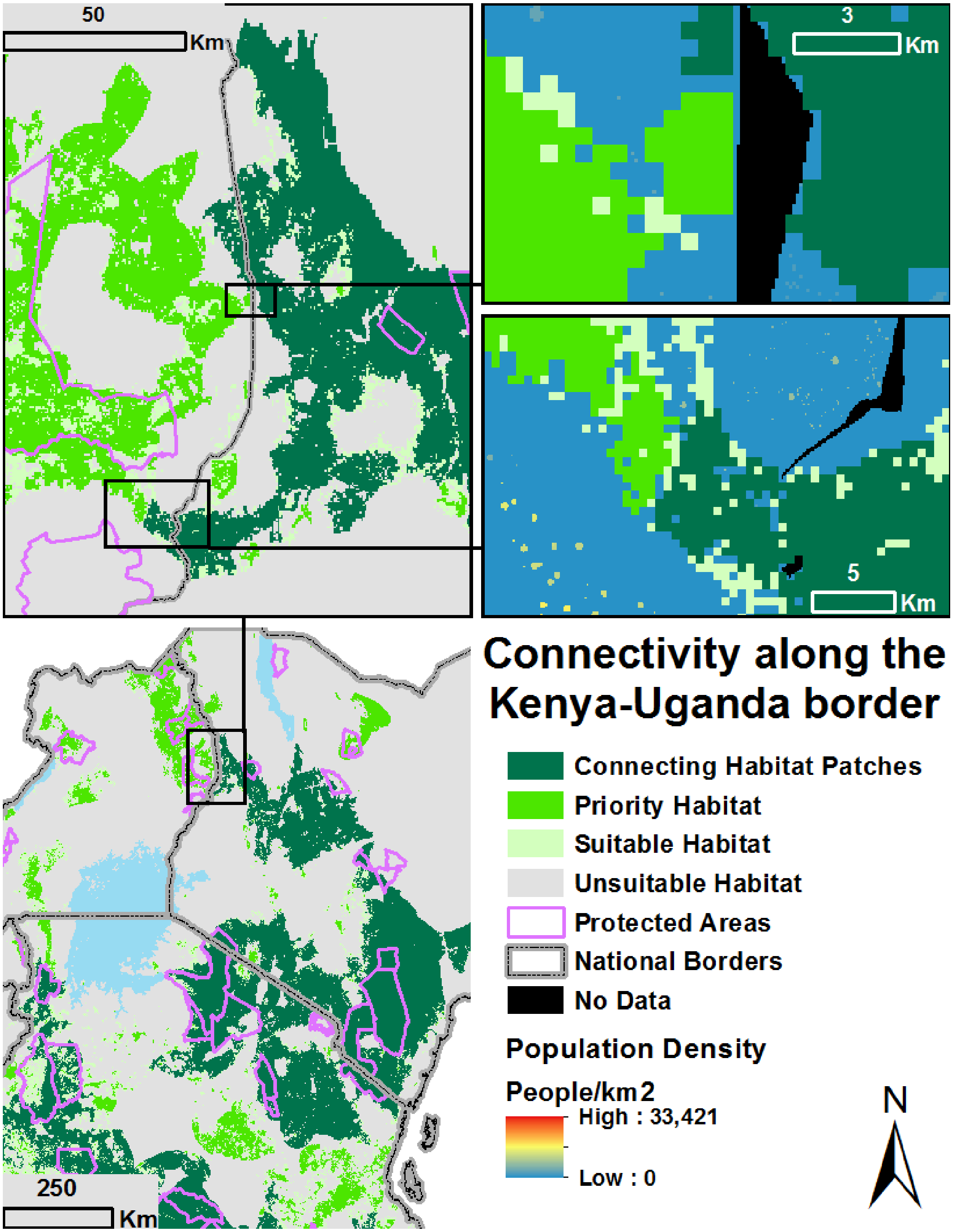

Figure 19: Gaps between priority patches of dispersal habitat along the Kenya-Uganda border.

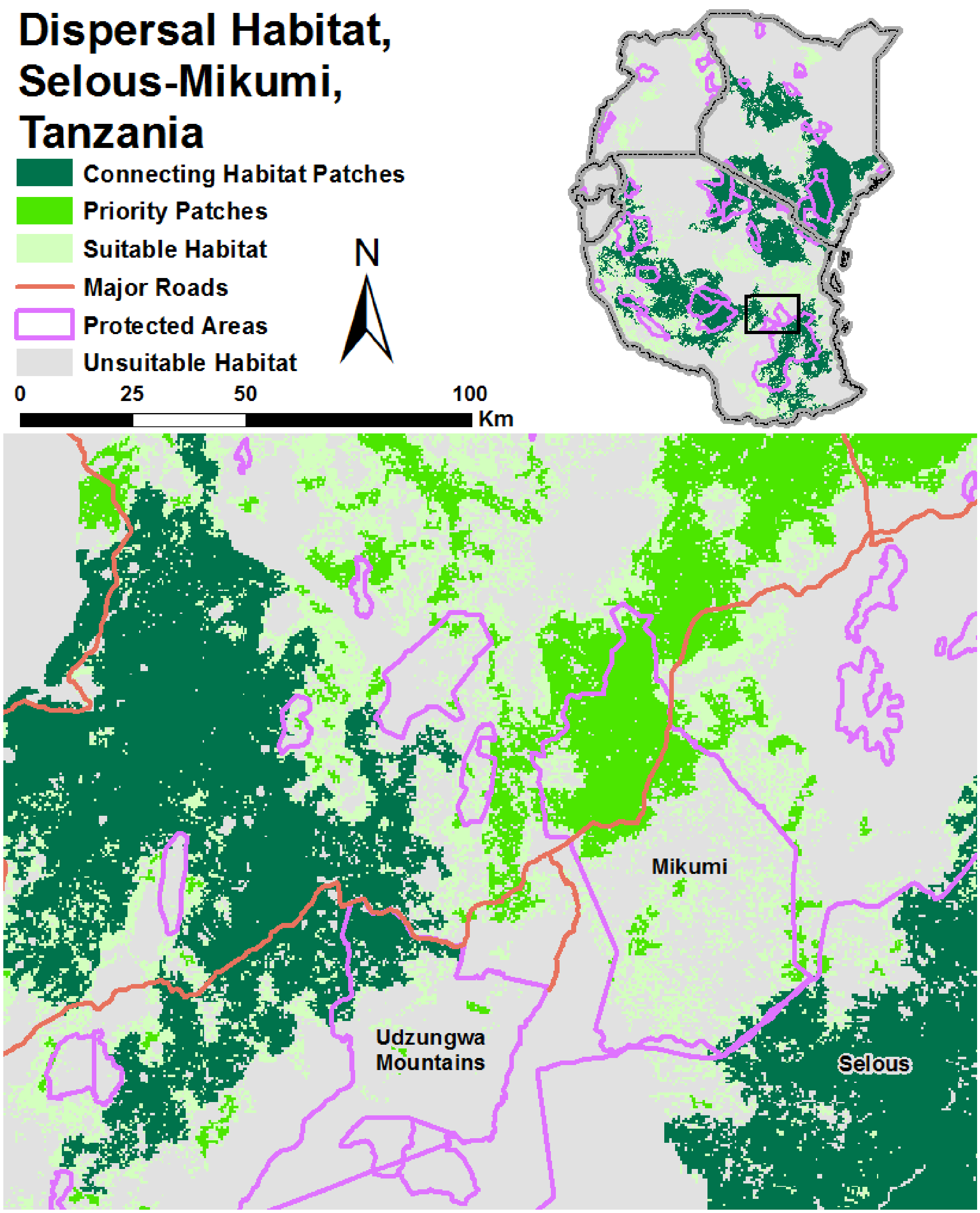

Figure 20: Dispersal habitat around the northern Selous Game Reserve and Mikumi National Park, Tanzania. Unsuitable habitat most results from dense vegetation.

The third and most prominent gap separates Meru National Park from the private and community conservancies of the central Kenyan rangelands (Figure 21). Though only 10 km wide, this gap may be the most difficult to restore because of the towns and dense human population in the area. On the other hand, it presents an opportunity: can we maintain connectivity through landscapes with severe human impacts? As a pastoral area, this landscape may not experience the same rates of land conversion as regions with row crops. Thus, while the gap poses a daunting conservation challenge because of human density, it may be possible to retain considerable habitat.

Perhaps the most striking result of the refined model is not where habitat is but where it is absent. Murchison Falls and Queen Elizabeth are completely isolated; it is unlikely that any functional connectivity exists between either of those parks and any other protected areas in East Africa.

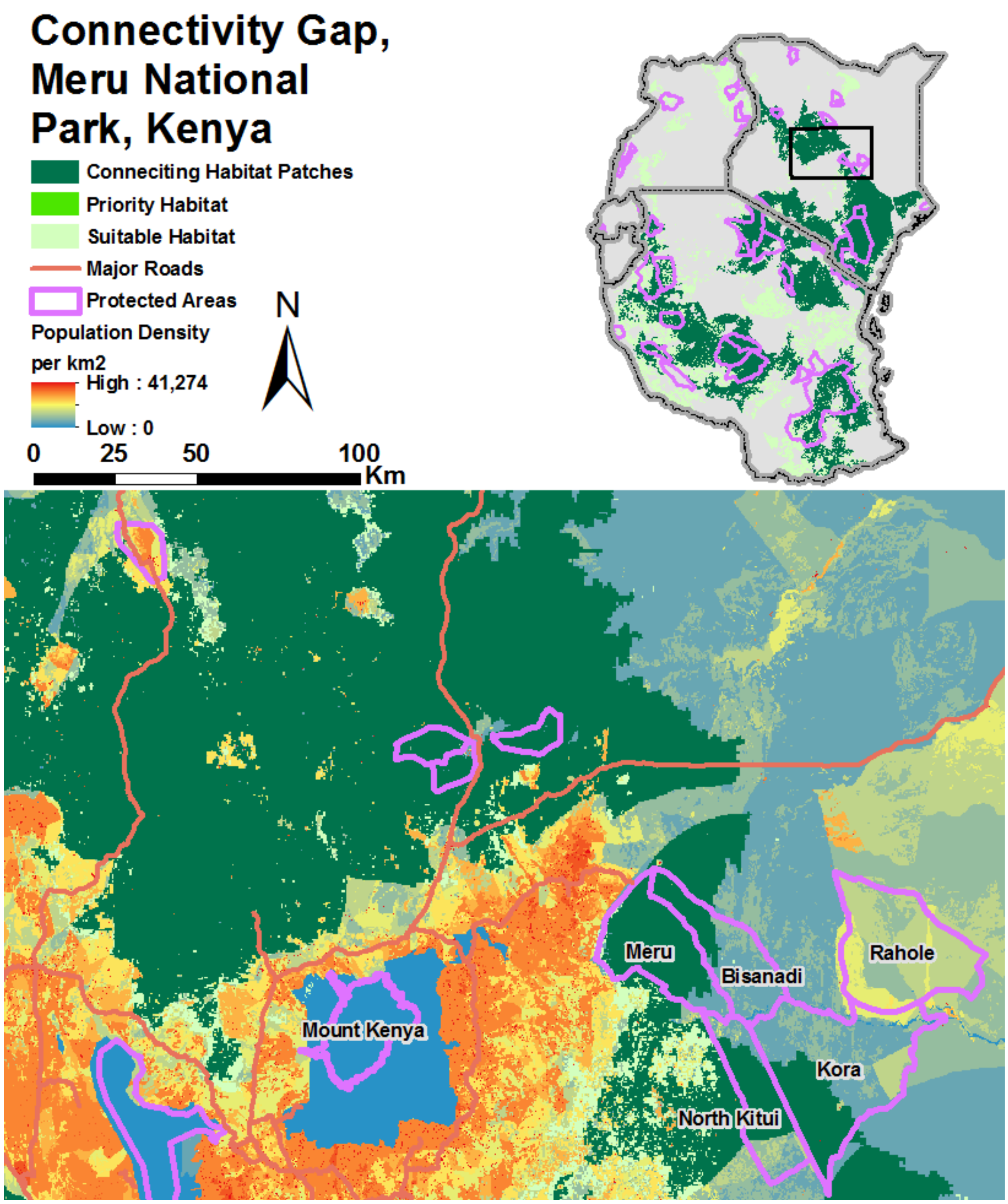

Figure 21: Dispersal habitat and human population density around Meru National Park, Kenya.

Discussion

The multi-stage approach that I employ effectively captured variability in lion presence while addressing considerable error and bias in the input datasets. This analysis finds dispersal habitat is widespread across East Africa and links many of the major protected areas with significant lion populations. It also extends to more marginal reserves, such as Katavi and Tarangire national parks in Tanzania, and Meru and Kora national Parks in Kenya. In Uganda, however, national parks with documented lion populations appear critically isolated.

The final habitat model demonstrated high accuracy levels in predicting dispersal habitat where lion presence points occur. With almost 99% of the presence points withheld to validate the model located in predicted dispersal habitat, it is clear that the results reflect patterns in lion occurrence beyond those specific only to the training dataset. The similarity between accuracy rates in the training lion occurrence dataset and the test lion occurrence dataset testifies to the consistency of the model. However, it also reflects the autocorrelation incorporated into the dataset. Thus, while the accuracy rates are high, they are not comparable to accuracy rates generated from unbiased statistical models.

Although I was unable to statistically describe relationships between environmental variables and lion presence, the results in this paper provide valuable insight for lion conservation and identify numerous target areas for preserving connectivity between lion populations in East Africa. Furthermore, the different stages of the analysis provide clarity on the project's objectives.

Which variables most strongly influence lion presence?

Numerous environmental variables relate to lion occurrence in East Africa, but measures of human population density and vegetation appear to play the strongest roll in dictating habitat conducive to lion movement. Like other studies of lion distribution, climactic factors appear to have strong correlations with lion presence at very broad scales. At the scale of lion movement, however, vegetation indices such as NDVI are superior indicators.

This paper finds clear indications that the scale of variables plays an important role, and this dynamic deserves further research. Lion occurrence data showed clear trends in the relationship between lion presence and human density at increasing scales. The presence data suggest lions can tolerate dense populations at either a fine (1 ha) or broad (80 km^2, or 5 km radius) scale, but not at both. Most likely, the multi-scale relationship indicates lions moving along the edges of human settlements, but data quality and precision in this analysis were insufficient to test this hypothesis. Further research is necessary to determine what scale best captures the relationship between lion presence and human population density.

What environmental factors influence lion tolerance of human presence? In what combinations of variables do lions occur and where in East Africa do those combinations occur?

Vegetation is the main factor facilitating lion occupancy in densely populated areas. Where lions occurred in highly populated areas, they consistently inhabited denser vegetation than in areas with low human density.

As expected in the case of a habitat generalist, this study found that lions inhabit most areas that do not exhibit extreme environmental conditions. Lion occurrence was distributed across broad environmental ranges, particularly for rainfall, NDVI, and canopy cover. Rainy-season and annual environmental variables proved better indicators of lion occurrence and movement than dry-season variables. Furthermore, the dearth of presence data from high-elevation and high-rainfall habitat likely causes this analysis to under-predict lion occurrence in these areas. More fieldwork to identify lion occurrence in areas such as the western Selous, western Tanzania outside of national parks, and additional areas of Queen Elizabeth and Murchison Falls national parks would mitigate this source of bias.

Lion presence was most consistent at moderate levels of ecological variables. Particularly for canopy cover and NDVI, lion presence locations were tightly clustered around the median. In the case of April NDVI and canopy cover, skewed distributions resulted in substantial differences between mean and median values. In many cases, including the vegetation indices, median values are more representative than the mean.

As expected, human population density was the most important limiting factor to lion presence. Population density showed a stronger relationship with lion presence as the scale at which human population was sampled increased.

Habitat conducive to lion occurrence and movement is particularly widespread in western Tanzania, along the Tanzania-Kenya border, and in an arc stretching from Tsavo all the way to Kidepo Valley National Park in northwestern Uganda. While this habitat is not all contiguous, it does provide reason for optimism with respect to preserving connectivity between the most important lion populations in East Africa.

How do areas with these environmental conditions spatially relate to existing populations of lions, and which patches of dispersal habitat intersect two or more protected areas with lion populations?

Contiguous connections of habitat conducive to dispersal are evident between numerous pairs of significant lion populations: Serengeti – Tsavo, Ruaha – Katavi – Moyowosi/Kigosi, and Selous – Niassa. Other populations have considerably more tenuous links to other populations, particularly the rangelands population in central Kenya. Although this analysis found a disconnect between the Kenyan rangelands and a large habitat patch stretching to Kidepo Valley National Park, Uganda, the narrow gap between the two patches and low human population density in that gap suggest lion dispersal through this area is possible.

Which areas of dispersal habitat are most critical to preserving connections between lion populations?

This paper finds that the most prominent bottlenecks for dispersal habitat exist in the Selous-Niassa corridor and between Katavi National Park and the Ruaha ecosystem. With well-documented cases of human-wildlife conflict in both areas (Dickman 2008, Jones et al. 2009, Kiffner et al. 2009), further conservation actions are essential to ensure that dispersal habitat remains accessible to lions. Habitat to the east of the Serengeti ecosystem also requires monitoring to ensure that functional links persist between the northern Serengeti and the Tsavo ecosystems. Similarly, the habitat between Tarangire and its larger neighbors appears more vulnerable than between Serengeti and Tsavo.

In addition, Ugalla Game Reserve may play a critical role as a stepping stone that contributes to connectivity throughout western Tanzania. Field research is necessary to ascertain the amount of lion activity in and around the reserve, and to test potential impacts of the trophy hunting industry on lion dispersal throughout the region. Research elsewhere should also consider the role that small reserves play in facilitating lion movement.

Where do gaps occur between patches of dispersal habitat that constitute prime targets for restoring connectivity?

Three areas exhibit gaps between patches of dispersal habitat connecting to major lion populations: 1) The gap between Meru National Park and the rangelands of central Kenya, 2) the gap along the Kenya – Uganda border between the central rangelands of Kenya and the reserves of northern Uganda, and 3) the gap through Mikumi National Park separating the northern Selous from habitat stretching to Ruaha National Park. The Selous and Ruaha populations are likely self-sustaining, especially considering potential links to Niassa and Moyowosi-Kigosi populations, respectively. Therefore, the lack of functional connectivity between the two ecosystems is not as alarming as the other two gaps. Efforts to restore connectivity should prioritize linking the central Kenyan rangelands with the Tsavo and Uganda protected areas. The connection with northern Ugandan reserves may be misrepresented because of patches along the border for which population data is unavailable. In fact, the Ugandan and Kenyan patches may be contiguous. If that is the case, the area becomes a critical bottleneck that demands conservation, as opposed to a critical gap that requires restoration. Either way, the border region constitutes a prime conservation target and an opportunity to develop transnational conservation plans.

Which existing lion populations are most isolated from other populations, and thus most in need of active management to ensure the long-term viability of lions?

Murchison Falls and Queen Elizabeth national parks are the most severely isolated lion populations in East Africa. Kidepo Valley, on the other hand, is linked with several Ugandan reserves, but may be disconnected from other lion populations in Kenya. The best approach to conserving the Kidepo Valley lion population is to preserve or restore its link with Kenyan populations. In the case of the other two Ugandan national parks, however, wildlife managers should plan for the effects of isolation on their lion populations, and consider other measures such as translocating lions (Dubach et al. 2013). Many of the smaller parks and reserves in Kenya also appear isolated, especially Marsabit National Reserve in the northeast. Surrounded by an arid landscape, this reserve is a rare example of a protected area isolated primarily by climactic factors rather than human impacts. Just as additional input data from high rainfall areas would reduce the bias against wetter landscapes, Marsabit offers the best opportunity in East Africa to test the extent to which arid landscapes limit the dispersal ability of lions.

Improving the Model

This analysis did not identify meaningful relationships between lion presence and geographic features such as roads, rivers, and human settlements. Lions may interact with these features at a finer scale than considered in this paper, or the lack of an observed relationship may simply indicate high error levels in each of these datasets. Additional research on how dispersing lions interact with landscape features could vastly improve the model.

Finally, all the results and conclusions of this paper represent broad approximations of landscape characteristics at a regional scale, and do not always represent local conditions. While this analysis can inform management decisions and identify priority areas, all conservation actions require localized analyses that are beyond the scope of this paper.

Applications

These models and predictions are not a final product, but a first step in establishing functional corridors throughout East Africa for lions. The next step is to conduct additional field work in the areas that this paper identifies as most important for conserving connectivity. It should test whether the predicted habitat patches provide functional links between lion populations, or only theoretical links. Such research would validate the model's predictions and produce additional data to incorporate back into the model, allowing us to refine it further. Connectivity is constantly evolving as landscapes change, and it is essential that we continue to reexamine our predictions and conservation strategies to adjust for ecological changes.

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Appendices

Appendix A: IUCN Classification of East African Protected Areas

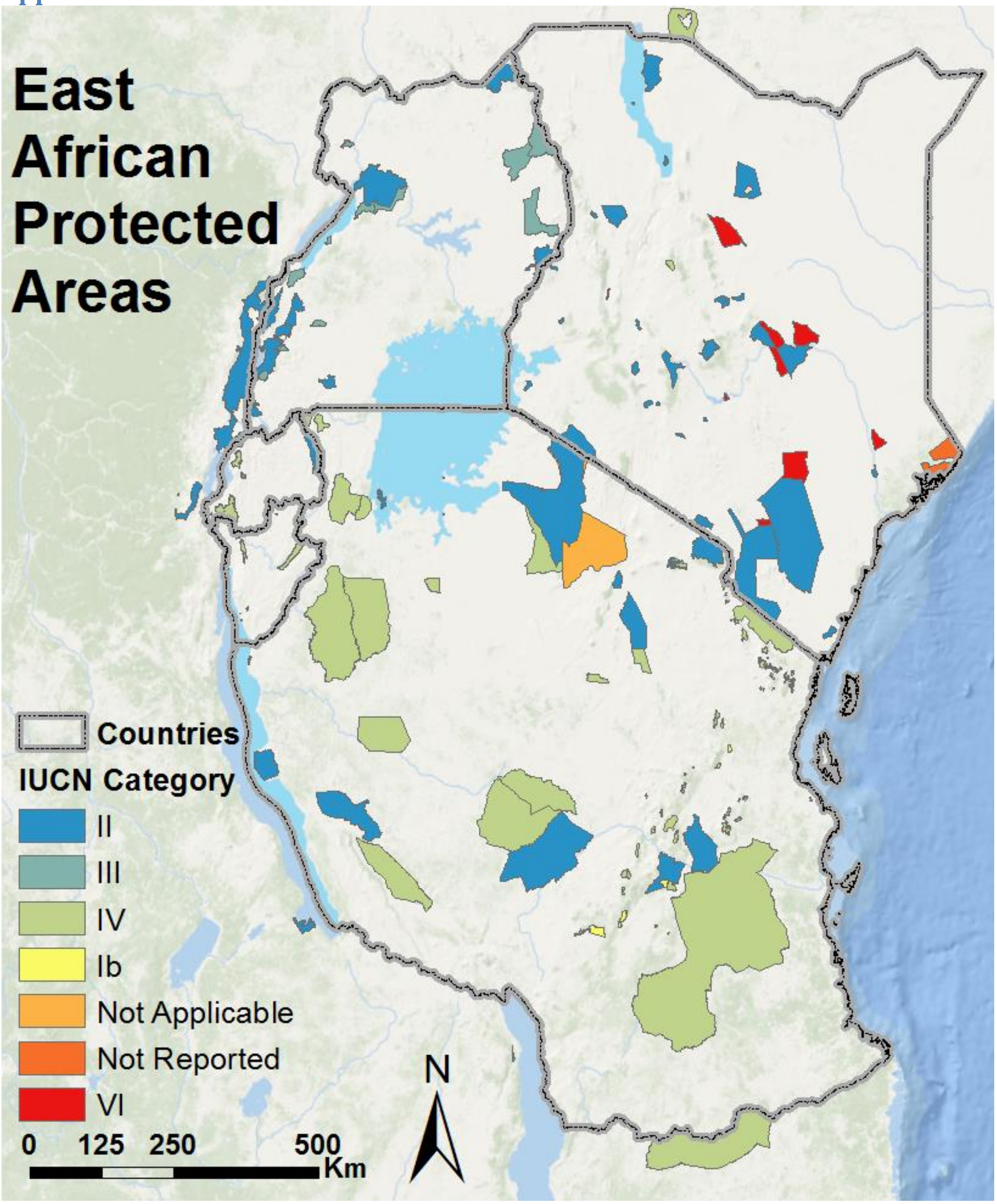

Figure 22: IUCN classification of East African protected areas. II) National Park, III) Natural Monument or Feature, Ib) Wilderness Area, IV) Habitat/Species Management Areas, & VI) Protective area with sustainable use of natural resources.

Appendix B: Lion Population Estimates: East Africa (excerpted from Bauer et al. 2005)

Burundi: No records

Country: Kenya	Chardonnet				Bauer&Merwe			
Area	min	Est	Max	method	min	est	max	method
Aberdares NP	130	162	194	C	5	7	15	6
Amboseli NP	117	130	143	A	20	20	20	4
South, East of Rift Valley					20	20	20	6
North, East of Rift Valley	189	271	353	C	325	650	1300	5
Galana Game Ranch					75	150	225	5
Nairobi NP	20	22	24	A				
Hells Gate & Kedong	7	9	11	B				
Lake Nakuru NP	33	37	41	A				
Laikipia plateau	280	362	444	B	96	120	144	2
Masai Mara NP	492	547	602	A	502	558	614	2
Surrounds of Masai Mara	317	394	487	B/C				
Meru Complex	52	65	78		40	80	120	5
Tsavo NPs	600	750	900	B	338	675	1350	5
Total	2237	2749	3277		1421	2280	3808	

Country: Rwanda	Chardonnet				Bauer&Merwe			
Area	min	est	max	method	min	est	max	method
Akagera NP	32	45	59	C	15	25	35	4
Total	32	45	59		15	25	35	

Country: Tanzania	Chardonnet				Bauer&Merwe			
Area	Min	Est	Max	Method	min	est	max	method
Manyara NP	3412	4437	5222	B	20	20	20	4
Ngorongoro Crater					53	53	53	1
Serengeti & surrounds					1750	2500	3250	3
Tarangire NP								
Selous	3080	4400	5720	C	3000	3750	4500	5
Selous surrounds	378	540	702	C	500	750	100	6
Ruaha Complex	2352	3360	4368	C				
North West	445	637	828	C				
South West	741	1058	1375	C				
Total	10408	14432	18215		5323	7073	7923	

Country: Uganda	Chardonnet				Bauer&Merwe			
Area	Min	est	Max	method	min	Est	max	method
Kidepo Valley NP	18	25	58	C	20	25	30	2
Murchison Falls Complex	255	364	473	C	280	350	420	2
Queen Elizabeth Complex	206	229	253	A	140	200	260	2
Total	479	618	784		440	575	710	

Appendix C: Lion Presence Data Sources and Methods.

Researchers	Region	Number of Data	Data Collection Method	Data Format
Dr. Shivani Bhalla	Northern Rangelands, Kenya	106	Sightings	GPS coordinates
Dr. Henry Brink	Selous GR, Tanzania	309	Sightings	GPS coordinates
Alayne Cotterill	Northern Rangelands, Kenya	31,627	Telemetry	Presence grid cells
Dr. Amy Dickman	Ruaha, Tanzania	2211	Sightings	GPS coordinates
Dr. Stephanie Dolrenry	Southern Kenya, northern Tanzania	29,756	Telemetry	Presence grid cells
Dr. Sarah Durant	Serengeti, Tanzania	45	Sightings	GPS coordinates (Arc1960)
Dr. Phillip Henschel	Tsavo, Kenya	280	Transects	Presence grid cells
Dr. Dennis Ikanda	Selous, Tanzania	62	Sightings, kills	GPS coordinates (WGS1984, Arc1960)
Dr. Roland Kays & Dr. Burce Patterson	Tsavo, Kenya	2193	Telemetry	GPS coordinates
Dr. Christian Kiffner	Katavi NP and Lake Manyara NP, Tanzania	85	Playbacks, sightings, lion tracks	GPS coordinates
Dr. Bernard Kissui	northern Tanzania	1396	Telemetry, sightings	GPS coordinates
Maurus Msuha	Tarangire NP, Tanzania	18	Camera traps	GPS coordinates
Helen O'Neill	Serengeti, Tanzania	264	Sightings	GPS coordinates (Arc1960)
Dr. Alex Piel & Fiona Stewart	Mahale Mtns, Tanzania	4		GPS coordinates
Dr. Paul Schuette	southern Kenya	200	Sightings	GPS coordinates
Alexandra Sutton	Mara, Kenya	7	Sightings	GPS coordinates
The Uganda Wildlife Authority	Uganda	608	Sightings	GPS coordinates

Appendix D: Correlations between environmental variables.

	Protected Areas	Rivers	Elevation	Canopy	Total Rain	Dry-season Rain	Population Density (1km)	Population Density (1ha)	April NDVI	August NDVI	Population Distance	Population Density (5km)	Lakes	Slope	Roads
Protected Areas	1.00	0.02	0.23	-0.03	-0.23	0.31	0.02	0.02	-0.11	0.30	-0.05	0.04	0.11	-0.08	-0.15
Rivers	0.02	1.00	0.21	0.19	0.18	0.24	0.08	0.07	0.08	0.28	-0.06	0.12	-0.12	0.30	0.00
Elevation	0.23	0.21	1.00	0.01	-0.15	0.52	0.00	0.00	-0.16	0.56	-0.26	0.02	-0.46	0.25	-0.46
Canopy	-0.03	0.19	0.01	1.00	0.62	0.17	0.07	0.06	0.70	0.54	0.01	0.11	-0.13	0.37	0.15
Total Rain	-0.23	0.18	-0.15	0.62	1.00	0.21	0.17	0.15	0.59	0.29	-0.12	0.24	-0.12	0.27	0.15
Dry-season Rain	0.31	0.24	0.52	0.17	0.21	1.00	0.10	0.09	0.01	0.76	-0.29	0.16	-0.36	0.14	-0.18
Population Density (1km)	0.02	0.08	0.00	0.07	0.17	0.10	1.00	0.90	0.07	0.08	-0.09	0.86	-0.06	0.06	-0.03
Population Density (1ha)	0.02	0.07	0.00	0.06	0.15	0.09	0.90	1.00	0.07	0.07	-0.08	0.77	-0.05	0.05	-0.02
April NDVI	-0.11	0.08	-0.16	0.70	0.59	0.01	0.07	0.07	1.00	0.41	0.11	0.11	-0.11	0.25	0.27
August NDVI	0.30	0.28	0.56	0.54	0.29	0.76	0.08	0.07	0.41	1.00	-0.18	0.13	-0.41	0.31	-0.10
Population Distance	-0.05	-0.06	-0.26	0.01	-0.12	-0.29	-0.09	-0.08	0.11	-0.18	1.00	-0.13	0.18	-0.16	0.43
Population Density (5km)	0.04	0.12	0.02	0.11	0.24	0.16	0.86	0.77	0.11	0.13	-0.13	1.00	-0.09	0.10	-0.04
Lakes	0.11	-0.12	-0.46	-0.13	-0.12	-0.36	-0.06	-0.05	-0.11	-0.41	0.18	-0.09	1.00	-0.12	0.27
Slope	-0.08	0.30	0.25	0.37	0.27	0.14	0.06	0.05	0.25	0.31	-0.16	0.10	-0.12	1.00	-0.02
Roads	-0.15	0.00	-0.46	0.15	0.15	-0.18	-0.03	-0.02	0.27	-0.10	0.43	-0.04	0.27	-0.02	1.00

Appendix E: Results of Woodland Model.

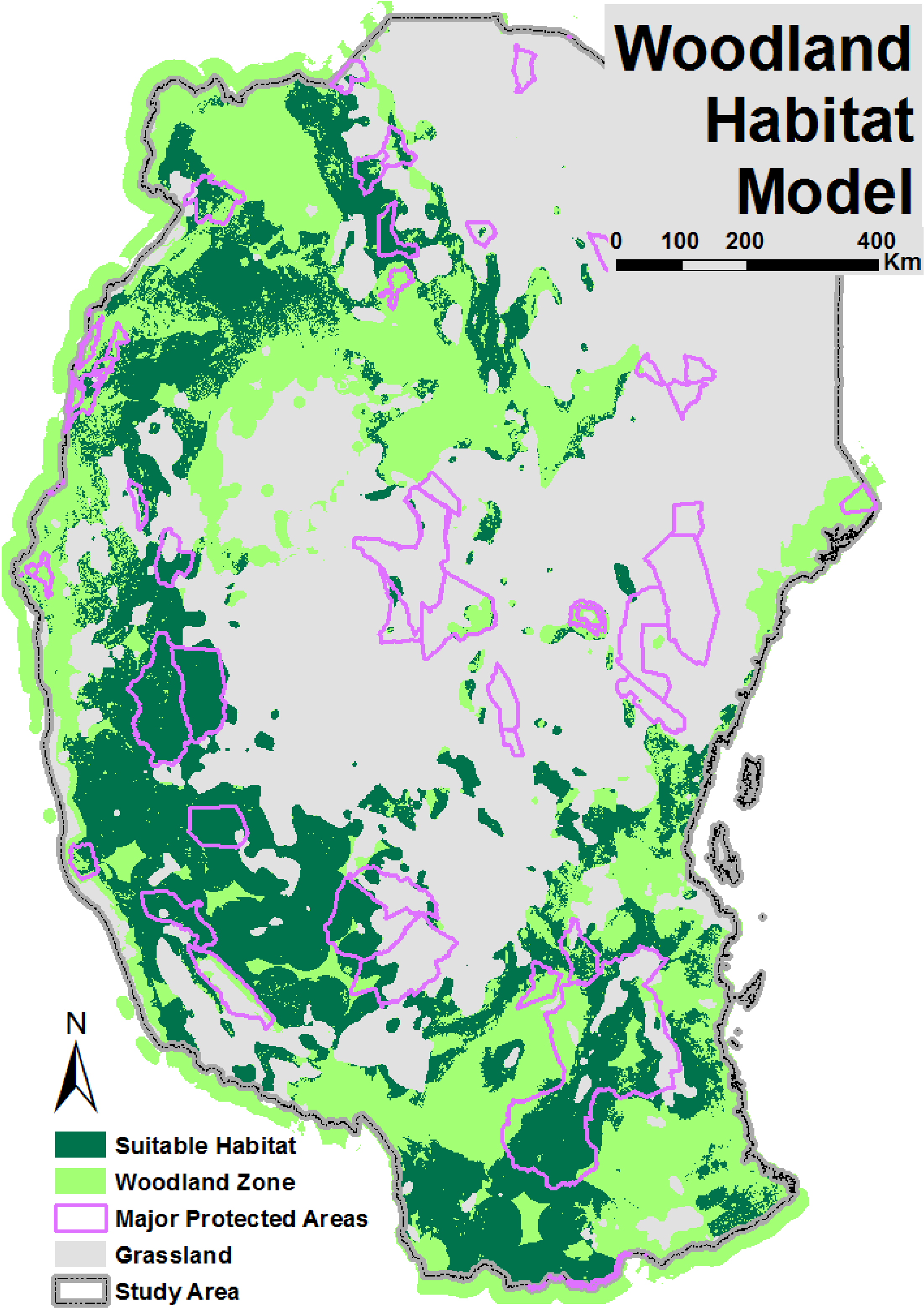

Figure 23: Habitat model for the woodland zone. This model exhibited 97% accuracy for training data points.

Appendix F: Range of each variable in lion dispersal habitat envelope.

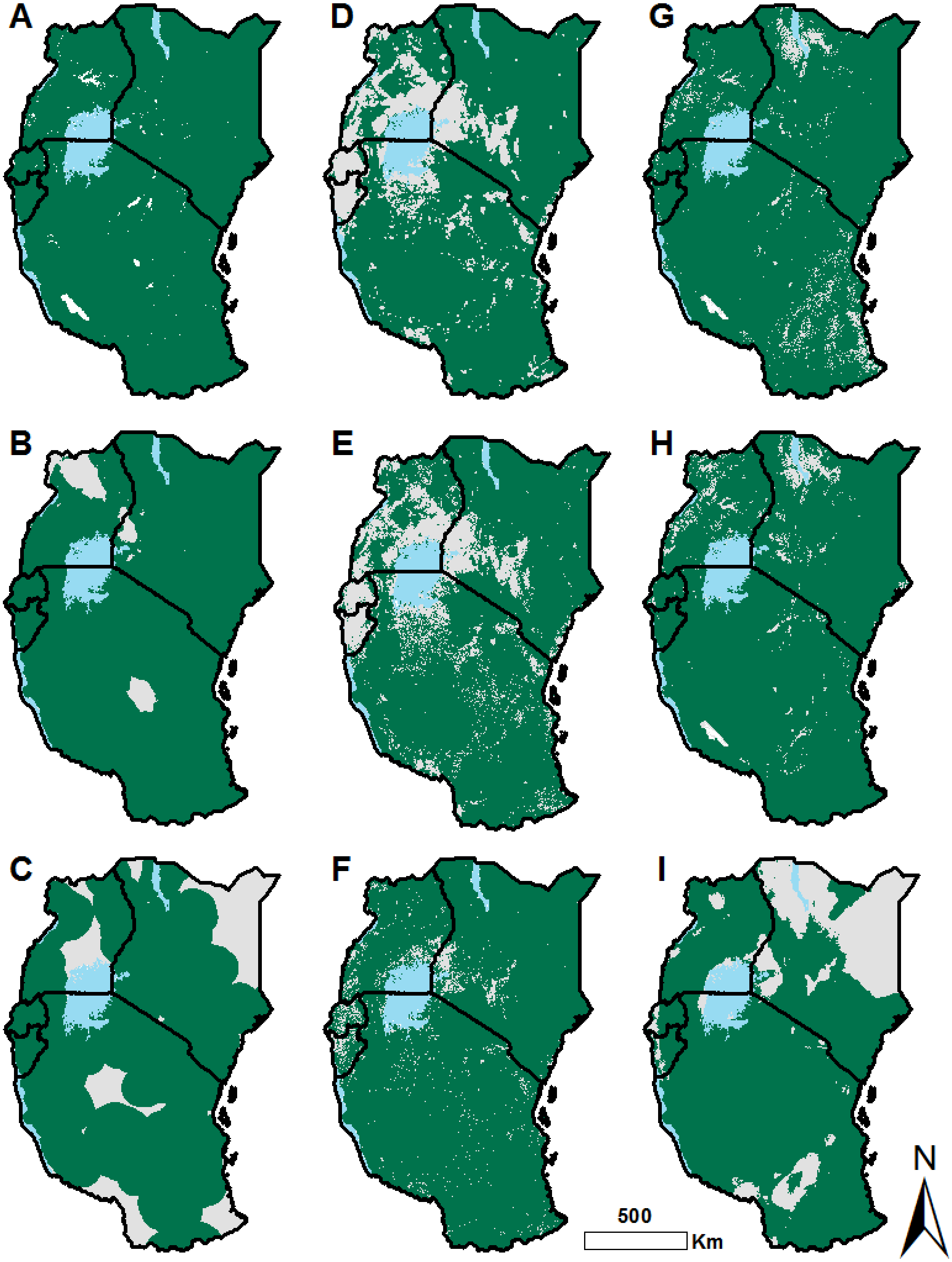

Figure 24: Distribution of habitat within the tolerable range for lion dispersal. Green represents suitable habitat, grey represents unsuitable habitat. A) Percent canopy cover, B) Dry-season rainfall, C) Distance to protected areas, D) Population density (5 km), E) Population density (1 km), F) Population density (1 ha), G) April NDVI, H) August NDVI, & I) Annual Rainfall.

Appendix G: Annuli for each variable within the envelope of suitable dispersal habitat for lions.

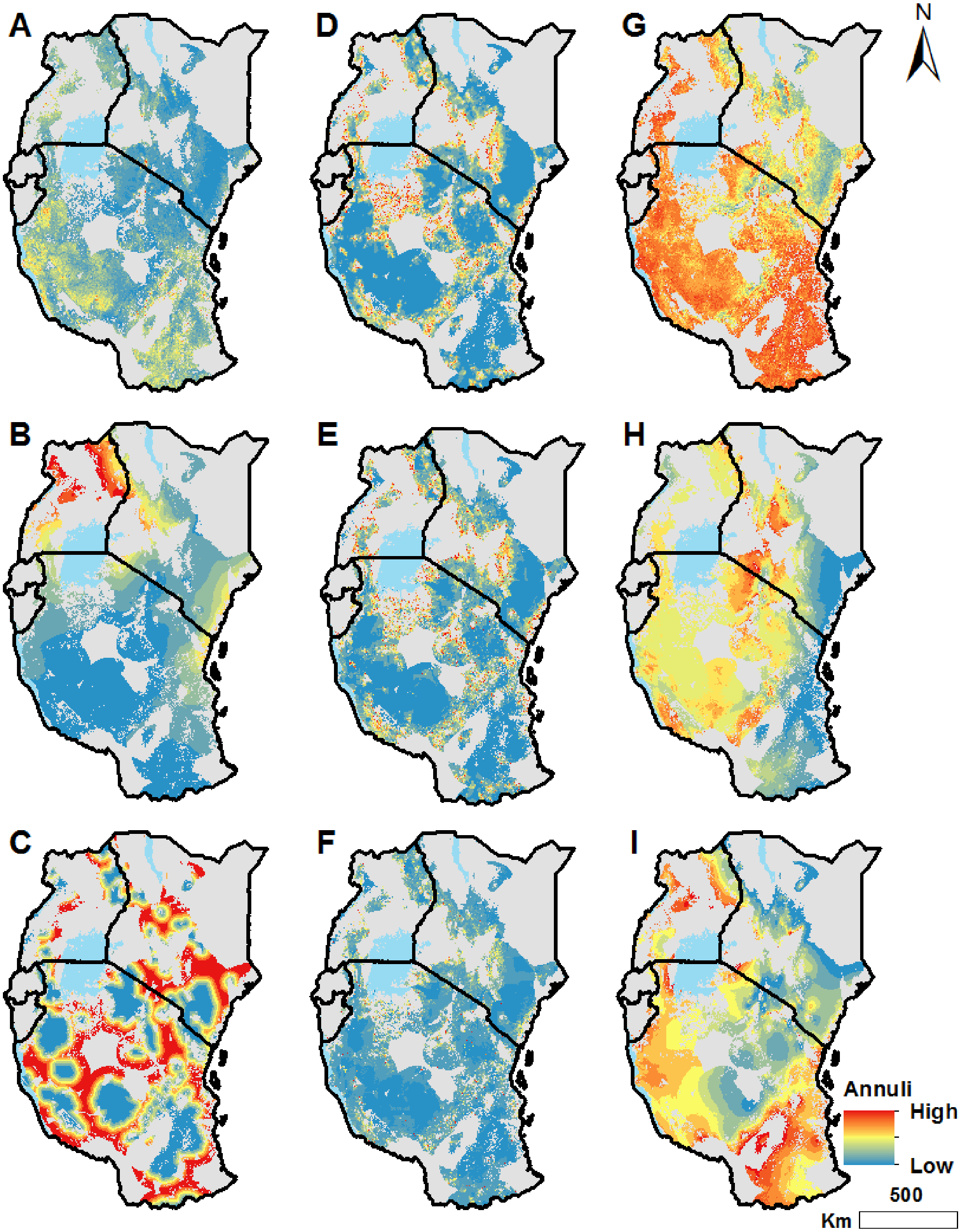

Figure 25: Annuli classes for nine environmental and ecological variables related to lion occurrence. A) Percent canopy cover, B) Dry-season rainfall, C) Distance to protected areas, D) Population density (5 km), E) Population density (1 km), F) Population density (1 ha), G) April NDVI, H) Elevation, & I) Annual Rainfall.

Appendix H: Results of eight paired interactions of environmental variables

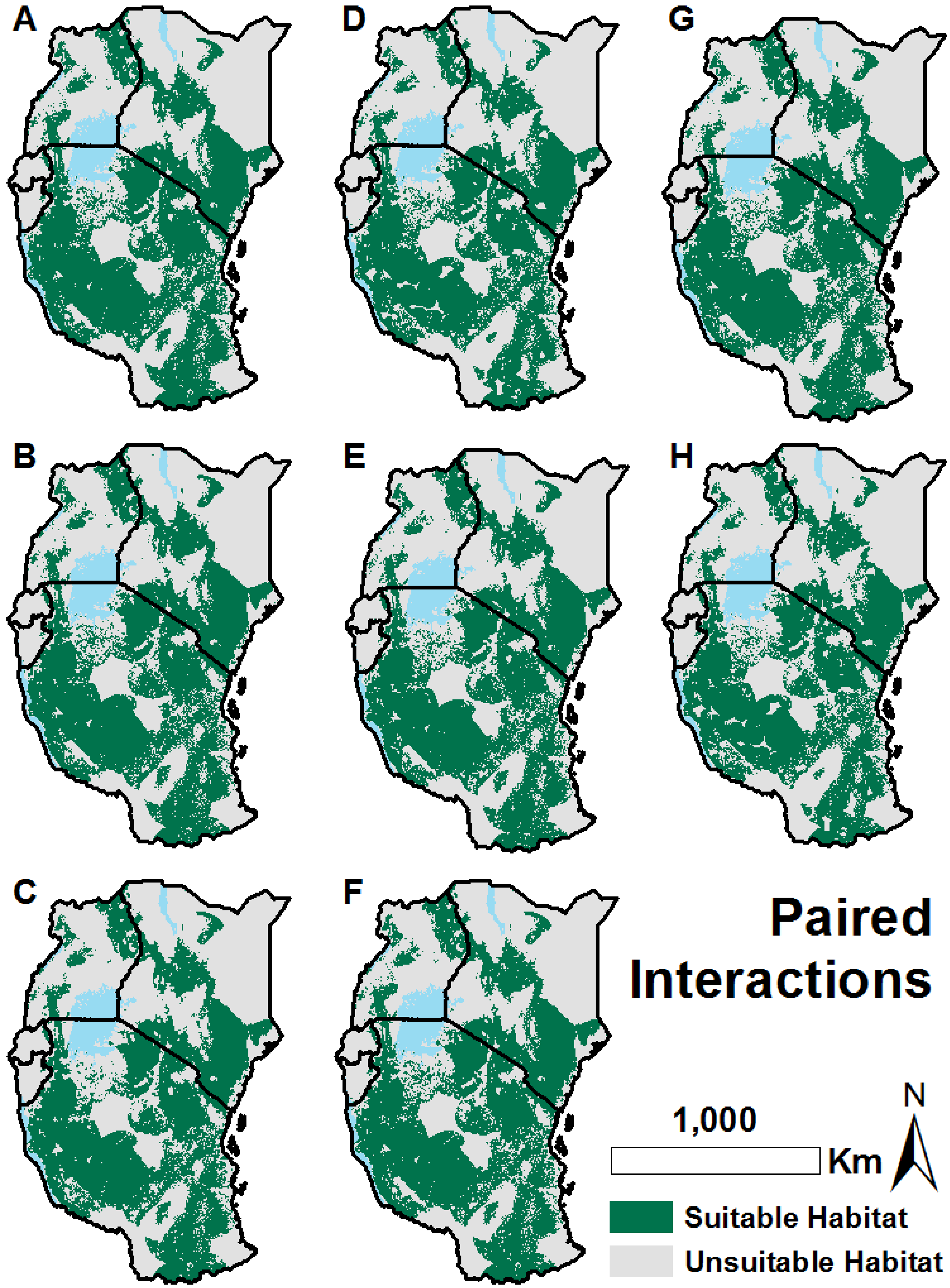

Figure 26: Combinations of annuli for eight pairs of variables that are conducive to lion dispersal: A) Population Density (5 km radius) and April NDVI, B) Population Density (1 km radius) and April NDVI, C) Population Density (1 km) and Population Density (5 km), D) Population Density (1 km) and Distance to Protected Areas, E) Population Density (1 ha) and Percent Canopy Cover), F) Population Density (1 ha) and April NDVI, and H) Population Density (1 ha) and Distance to Protected Areas.