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Analyzing land use change to identify migration corridors of African elephants (*Loxodonta africana*) in the Kenyan-Tanzanian borderlands

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Abstract

Context: East African ecosystems are characterized by the migrations of large herbivores that are highly vulnerable to the recent development of anthropogenic land use change.

Objectives: We analyzed land cover changes in the Kenyan-Tanzanian borderlands of the greater Amboseli ecosystem to evaluate landscape connectivity using African elephants as an indicator species.

Methods: We used multi-temporal Landsat imagery and a post classification approach to monitor land cover changes over a 43-year period. GIS based methods were accompanied by a literature review for spatial data on land cover changes and elephant migrations.

*Results:*Land cover changed considerably between 1975 and 2017. Wood- and bushlands declined by 16.3% while open grasslands increased throughout the study region (+10.3%). Agricultural expansion was observed (+12.2%) occupying important wildlife habitats and narrowing migration corridors. This development has led to the isolation of Nairobi National Park which was previously part of a large contiguous ecosystem. Eight migration corridors were identified of which only one is formally protected. Two others are almost completely blocked by agriculture and three are expected to become endangered under continuing land use changes.

Conclusions: Landscape connectivity is still viable for this ecosystem (except for Nairobi National Park). However, the current situation is very fragile as anthropogenic land use changes are threatening most of the identified large mammal migration corridors.
Sustainable land use planning with regard to important wildlife habitats and connecting corridors is a crucial task for further conservation work to safeguard a viable future for wildlife populations in the Kenyan-Tanzanian borderlands.

Keywords:
Landscape connectivity, land cover change, Amboseli National Park, Arusha National Park, Nairobi National Park, migration corridors

Introduction

East African savanna ecosystems are characterized by seasonal migrations of large herbivores such as elephants (*Loxodonta africana*), wildebeest (*Connochaetes taurinus*) or zebra (*Equus bruchelli*), representing a vital driver of ecosystem heterogeneity by distributing resources over a vast landscape (Sinclair et al. 2007; Harris et al. 2009). Predominantly accelerated by human activities, i.e., agricultural expansion and fencing, wildlife migrations are becoming progressively blocked, leading to population declines and the loss of population connectivity (Harris et al. 2009; Rudnick et al. 2012).

Protected areas throughout sub-Saharan Africa therefore tend to become isolated islands within an anthropogenic altered landscape (Newmark 2008; Wegmann et al. 2014). For example, Tarangire National Park (NP) in northern Tanzania acts as the dry season retreat for a variety of wildlife. Migratory species historically used nine different routes towards their wet season dispersal areas in the surroundings of the national park (Lamprey 1964). Within the last few decades, several routes have been blocked by cultivation leaving only few viable migration corridors (Msoffe et al. 2011; Morrison et al. 2016). Most wildlife populations have dropped (Bolger et al. 2008; Morrison et al. 2016) and the majority of elephants is now confined to Tarangire NP itself (Gereta et al. 2004; Galanti et al. 2006). The connectivity of elephant populations has been driven by landscape features (e.g., slopes), whereas the recent expansion of anthropogenic land use changes restricts individual movements, disrupts connectivity and prohibits genetic exchange between different populations (Epps et al. 2013).

To prevent or counteract these developments, modern conservation planning requires strategies to maintain or restore landscape connectivity and to allow species migrations (e.g., Rudnick et al. 2012). This can be achieved by identifying important migration corridors and subsequently the protection of these areas by excluding anthropogenic land use changes (Rudnick et al. 2012; Riggio and Caro 2016).

In this study we aim to identify bottlenecks for population connectivity of migratory elephants (used as indicator species) in the Kenyan-Tanzanian borderlands and to define the location of important migration corridors. We therefore combine an extensive dataset on remotely sensed land cover changes with a literature review on elephant populations and migrations over the last four decades.

Material and methods

Study region

The greater Amboseli ecosystem in southern Kenya encompasses about 10.000 km² (fig. 1) of winter dry savanna characterized by wooded grasslands, bush thickets and woodlands (Pratt et al. 1966; Western 1973; Kottek et al. 2006). Rainfall is inter-annually highly variable (132 to 757 mm) and droughts are a relatively common phenomenon (Altmann et al. 2002; Ntiati 2002). The rainy season from November to May is bi-modal and rain is almost absent in the dry season from June to October. The area has a low potential for rain-fed agriculture but is favorable for pastoralism, the traditional livelihood of the resident Maasai communities (Pratt et al. 1966; Grandin 1991). Over the last few decades many Maasai have started cultivating and the wetter areas of the ecosystem are being progressively converted into agriculture (Campbell et al. 2000; Okello and Kioko 2011). Amboseli NP (fig. 1) offers valuable year round surface water supply (swamps and seasonal lakes) but is surrounded by arid to semi-arid landscapes with only marginal access to water in the dry season (Pratt et al. 1966; Western 1982). During dry seasons, wildlife concentrates in the small protected area of Amboseli NP (Western 1975). With the onset of the rainy season, vegetation starts to regenerate and migratory species such as elephants, wildebeest and zebra disperse into the unprotected areas, marking the boundaries of Amboseli ecosystem by their migratory oscillations (Western 1975).

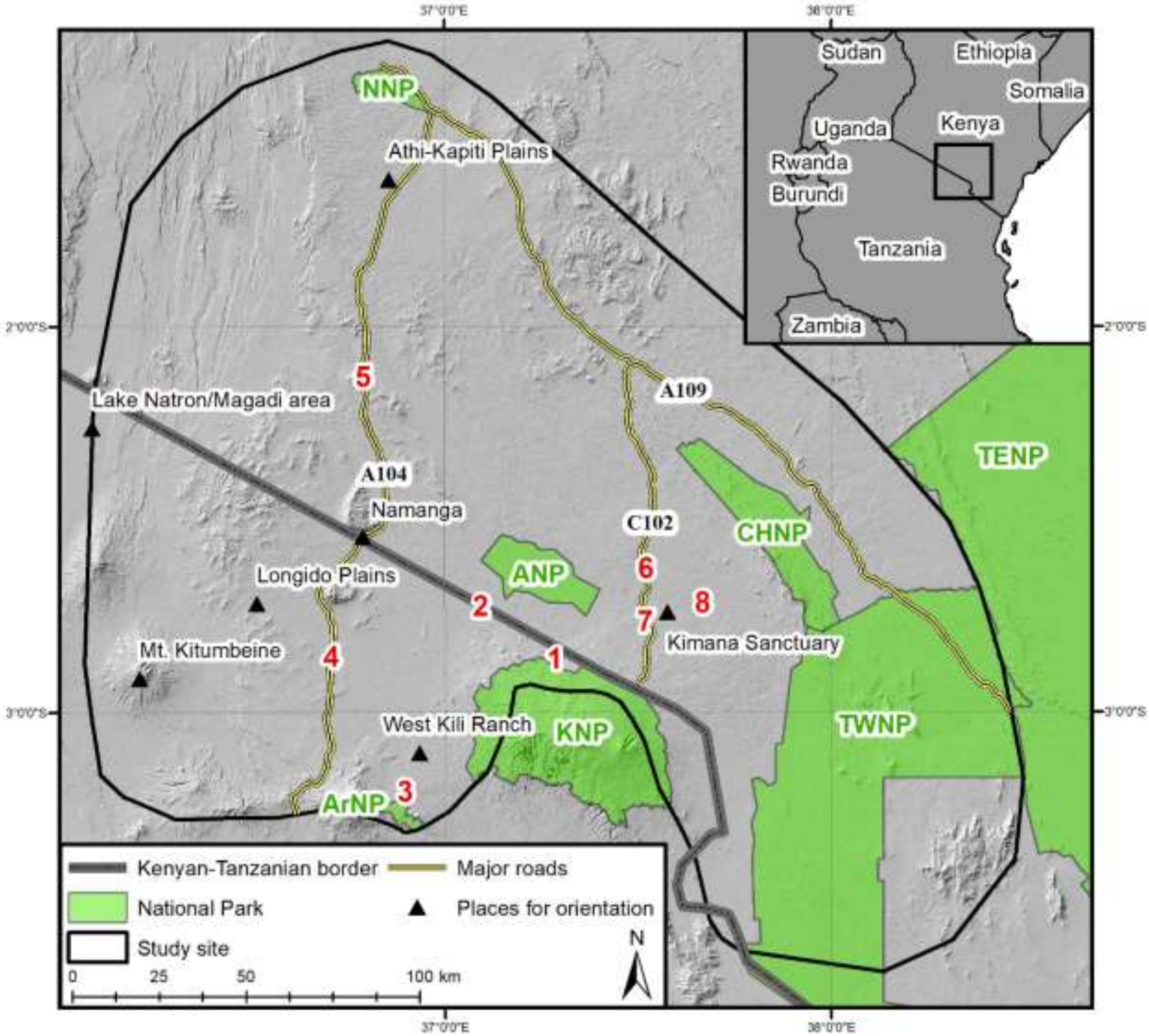

Figure 1: Overview of the study site as digital elevation model (NASA and METI 2011) with locations of migration corridors: 1 = Kitendeni, 2 = Transborder, 3 = Kisimiri, 4 = Kikoti's crossing, 5 = Bissil, 6 = Mbirikani, 7 = Kimana, 8 = Lenkati/Lolterish. Abbreviations: ANP = Amboseli National Park, KNP = Kilimanjaro NP, TWNP = Tsavo West NP, TENP = Tsavo East NP, CHNP = Chyulu Hills NP, ArNP = Arusha NP, NNP = Nairobi NP.

The greater Amboseli ecosystems stretches from the northern slopes of Mt. Kilimanjaro in Tanzania north to the Chyulu Hills of Kenya. The eastern boundary is a transitional area shared with wildlife populations from Tsavo West NP, whereas the western boundary is more fluid since distinct populations of migratory species are some hundred kilometers away (Western 1975; Western and Lindsay 1984). The Amboseli basin occupies about 8,750 km² and is defined by the year-round home range of the elephants from Amboseli NP (Croze and Lindsay 2011). The entire study region, with the linkages between Amboseli NP and neighboring ecosystems, covers approximately 45,865 km² and spans north towards the Athi-Kapiti plains and ultimately Nairobi NP. There are no elephants present in this area, but migratory movements of wildebeest and eland (*Taurotragus oryx*) were known to occur between Nairobi NP and the Amboseli basin (Hillman and Hillman 1977; Estes and East 2009). The western boundary of the study region is defined by the occurrence of a distinct elephant population at the Nguruman escarpment

(Western and Lindsay 1984, Lake Natron/Magadi area in fig. 1).

Elephants as indicator species

Elephants in savanna ecosystems act as a keystone and umbrella species (Laws 1970; Western 1989; Hoare and Du Toit 1999) and are therefore ideal to monitor landscape connectivity and to identify important migration corridors (Roever 2013).

In 1973, elephants numbered about 600 individuals in the core population of Amboseli NP (Western and Lindsay 1984; Moss 2001). The population has progressively increased in size to 1658 individuals recognized by Amboseli Elephants Research Project (AERP, Moss and Lee 2017) and some 300 individuals are additionally distributed over the study region (Kenana et al. 2013a,b). In the 1970s, the Amboseli elephants migrated north towards the Nairobi/Mombasa road (north of Chyulu Hills NP), south into the forested slopes of Mt. Kilimanjaro, east towards Kimana swamp and westwards to Ol Donyo Orok hill at Namanga village (Western and Lindsay 1984, fig. 1). South of the Tanzanian border elephants were reported from Arusha, Tarangire and Lake Manyara NPs (Lamprey 1964; Vesey-FitzGerald 1974), although Lamprey (1964) did not mention migrations of elephants towards the Kenyan border. Anecdotal accounts report sightings of roaming elephants between the Momella lakes of Arusha NP and the Longido Plains (Vesey-Fitzgerald 1968; fig. 1).

Today, there are several distinct elephant populations present in the study region: in Amboseli NP (~1800 elephants), Tsavo West NP (~12,000 including Tsavo East), Mt. Kilimanjaro NP (~100 elephants), Arusha NP (~200 elephants) and between Lake Natron and Lake Magadi (Kenana et al. 2013a,b; TAWIRI 2015; Ngene et al. 2017a,b).

Review of ancillary spatial data

We conducted a structured literature search with key terms, synonyms and combinations of terms using Web of Science and Google Scholar search engines to gather information on two topics: land use change and elephant distributions. First we used key terms on land use and land cover change, habitat characterization and vegetation mapping. Secondly, the search was expanded to elephant sightings, distributions and migratory movements. Key terms and synonyms were always combined with a geographical area (e.g., Amboseli, Kilimanjaro, Lake Natron, Nairobi NP, Tsavo etc.) to focus on research relating to this site.

We included published articles, gray literature and reports in our analysis. Gray literature was excluded when obvious methodological mistakes or inconsistencies in the data were identified resulting in a total amount of 72 articles, 29 concerning land use and 43 elephant distributions. Published land cover maps from different parts of the study region and various time stages were georeferenced and digitalized to be used for ground truthing (see below). We further extracted spatial data on elephant locations and migratory movements from within the last decade to establish a minimum area of confirmed occurrence. Descriptions of migratory movements were further used as supporting information. Finally, we were able to build up a comprehensive database on landscape development (land cover changes) and migratory behavior of elephants.

Acquisition and pre-processing of Landsat scenes

We acquired Landsat scenes from the USGS archive (http://earthexplorer.usgs.gov/, tab. 1). All scenes are level 1 terrain corrected, georeferenced products (L1T) and no georectification was required. We selected Landsat scenes at four different time stages, 1975/76, 1987, 2002/03 and 2017, respectively (tab. 2, hereafter stages 1975, 1987, 2002, 2017). Cloud cover was less than 10 % per scene and the study area was almost free of clouds, so that no correction or masking for clouds was necessary. Radiometric and solar correction was achieved converting raw digital numbers to at-sensor radiance and subsequently to Top-of-Atmosphere reflectance following a protocol according by Chander et al. (2009). Normalized difference vegetation index layers (NDVI) were calculated for every scene and stacked together with RGB (red/green/blue) and infrared bands to a multi-layer raster data set. All calculations and analyses were conducted in ArcMap (ArcGIS Desktop 10.5, ESRI, Redlands, USA). For a step by step workflow refer to figure 2.

Classification

Pre-processed images were subsequently classified using a supervised maximum likelihood classification algorithm. This was based on manually selected training areas for 7 different land cover classes that were selected according to previous studies in Amboseli (tab. 2). To account for varying soil types and spectral variance in land cover classes (e.g., from pale alluvial clay along rivers to dark volcanic soils on the foothills of Mt. Kilimanjaro (Gachimbi 2002; Githiga et al. 2003)), we defined sub-classes for each of the major land cover classes that were merged after classification into main classes (see supplementary material for number of training samples). Land cover classes were assigned according to visual appearance of areas in the satellite image, utilizing a combination of the near-infrared, the NDVI and the green band from the stack of layers. NDVI values were used when judging between vegetation classes was uncertain. Visual interpretation of Landsat scenes was coupled with georeferenced survey data from our literature review on land use, vegetation or habitat types (see tab. 1). If available, we also consulted Google Earth images that had appreciably higher resolution than Landsat scenes (Olofsson et al. 2014). This offered valuable data for the 2017 classification, whereas a detailed vegetation map of Amboseli NP and its surroundings from 1978 (AERP vegetation map, tab. 1) coupled with other review data was used as a baseline for the classification of the first time stage (1975).

Table 1: Technical details of Landsat scenes acquired from USGS archive and references used for ground truthing.

Time stage	Date	Path	Row	Satellite	Ground truthing data from literature
1975/76	21.06.1975	179	062	Landsat 2	AERP vegetation map, Heriz-Smith (1962), Foster and Coe (1968), Vesey-FitzGerald (1974), Andere (1981), Leuthold (1996), Western (2007), Croze and Lindsay (2011), Muriuki et al. (2011)
	29.07.1975	181	061		
	25.01.1976	181	062		
	24.01.1976	180	062		
	11.02.1976	180	061		
1987	18.02.1987	167	062	Landsat 5	Western (2007), Croze and Lindsay (2011), Gichuhi (2016)
	25.02.1987	168	061		
	25.02.1987	168	062		
2002/03	10.02.2002	168	061	Landsat 7	Leuthold (1996), Hemp (2006), Sarkar (2006), Western (2007), Okello and D'amour (2008), Mukeka (2010), Croze and Lindsay (2011), Muriuki et al. (2011), Gichuhi (2016)
	10.02.2002	168	062		
	11.04.2003	167	062		
2017	11.02.2017	168	061	Landsat 8	Chiyo et al. (2014), Gichuhi (2016)
	11.02.2017	168	062		
	08.03.2017	167	062		

Table 2: Definition of land cover classes used for classification of satellite images.

Land cover class	Description
water	open surface water, e.g. in lakes (Lake Natron) or reservoirs
open vegetation	areas with low occurrence of trees or bushes, dominated by grasses, herbs and bare soils
semi-open vegetation	transition between open and closed vegetation, dominated by a grass/herb/shrub matrix
closed shrubs	dense small-leafed vegetation, predominantly composed of shrubs with herbs and grasses in understory
forest	dense broad-leafed vegetation, characterized by a nearly closed canopy cover of trees or water-influenced vegetation in swamps
agriculture	cultivated areas used for crops, e.g. maize, beans
clouds	area covered by clouds

Appearance of land cover classes was cross-validated between time stages to reduce misidentification between classes and years. We encountered a high ratio of missed pixels from agricultural areas, due to similar spectral signatures of semi-open areas compared to agriculture. To adequately monitor the spread of cultivation, we corrected these areas and digitalized them manually. As shown in figure 3, cultivation are detectable as rectangular shaped vegetation patterns from the Landsat images via visual interpretation.

Landsat scenes per time stage were from different dates of the year, resulting in varying appearance of vegetation. This temporal offset was caused by limited availability of scenes with low cloud coverage and different paths of Landsat satellites to cover the whole study area. Classified rasters were mosaiced into one raster per time stage that was used for further analysis.

Accuracy assessment and change detection

We assessed the quality of the classified land cover maps in three different ways (see fig. 2). First, we visually compared each land cover map with the underlying satellite images to search for large-scale classification errors. In a second step, we used ancillary data from our literature review on land cover and habitat types to identify further misclassifications. When land cover maps showed an acceptable degree of correctness, we calculated user's, producer's and overall accuracy for each time stage according to Olofsson et al. (2014) using 320 randomly distributed sample points throughout the study area (see supplementary material for distribution over land cover classes).

Classified and validated satellite images were then used for change detection in a post classification approach. Change detection was conducted bi-temporal, comparing two time stages at once (e.g., 1975 with 1987, 1987 with 2002, 2002 with 2017).

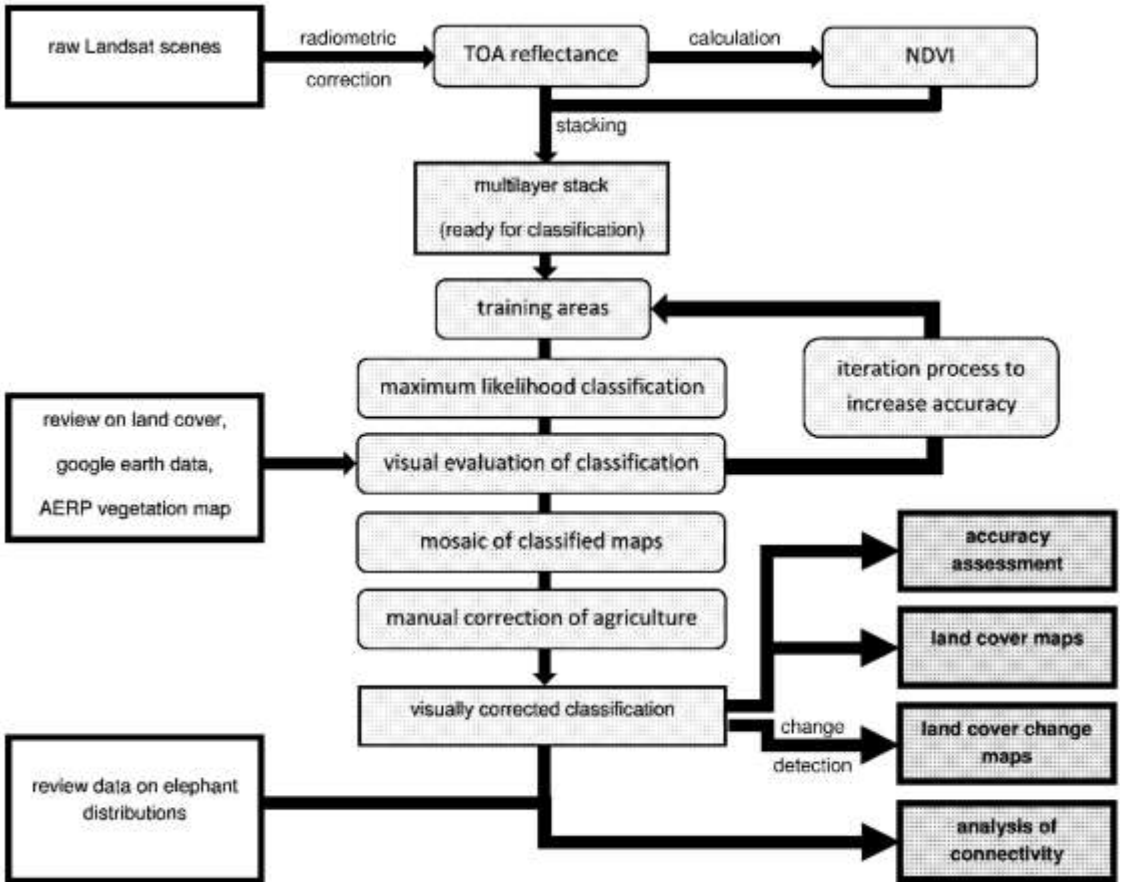

Figure 2: Work flow diagram to illustrate the interactions of different working steps. Data input is in the left column, output data in the lower right and working steps in between.

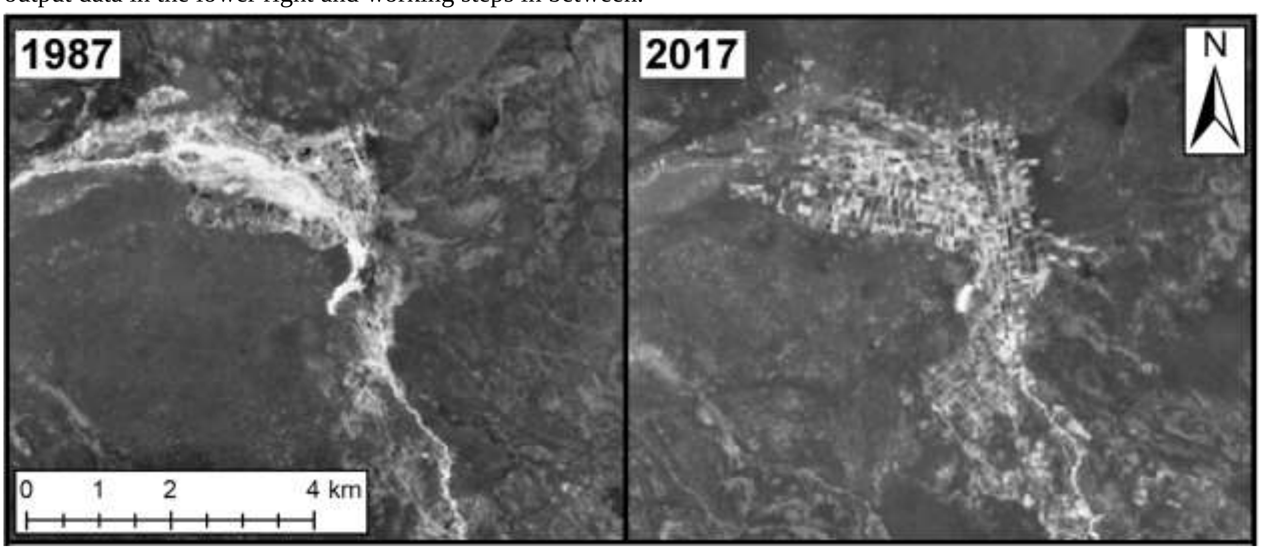

Figure 3: Development of Namelok swamp, 5 km east of Amboseli NP. Light areas are characterized by dense swamp vegetation. In 1987, the core area of the swamp was uncultivated, edges are under limited cultivation. In 2017, the core area is completely transformed into small scale agriculture.

Results

Accuracy assessment

Overall accuracies were 91.2%, 93.2%, 92.8% and 92.5% for the subsequent time stages from 1975 to 2017. User’s and producer’s accuracies by class did not fall below 80.0 % and 87.1 %, respectively (see supplementary material for class level accuracies).

Minor inaccuracy occurred in the overlapping areas of two satellite images from different seasonal stages of the year, especially in the Lake Natron/Magadi area, where water levels vary throughout the year. However, these areas are small in size and therefore have a negligible effect. Cloud cover resulted in a limited amount of areas of missing data, e.g., in the 1975 time stage, where clouds covered a part of the Athi-Kapiti Plains (black patch, fig. 5).

Table 3: Percentages of land cover classes and land cover changes over the last 4 decades.

Land cover class	1975	change	1987	change	2002	change	2017	overall
forest	3.0%	- 0.5%	2.5%	+ 0.5%	3.0%	- 0.6%	2.5%	- 0.5%
closed shrub	25.5%	- 0.6%	24.9%	- 7.5%	17.4%	- 8.2%	9.2%	- 16.3%
semi-open	43.1%	- 0.6%	42.5%	- 1.6%	40.9%	- 2.7%	38.2%	- 4.9%
open	18.8%	- 3.1%	15.7%	+ 6.5%	22.2%	+ 6.9%	29.1%	+ 10.3%
agriculture	8.4%	+ 5.7%	14.1%	+ 2.0%	16.1%	+ 4.5%	20.6%	+ 12.2%

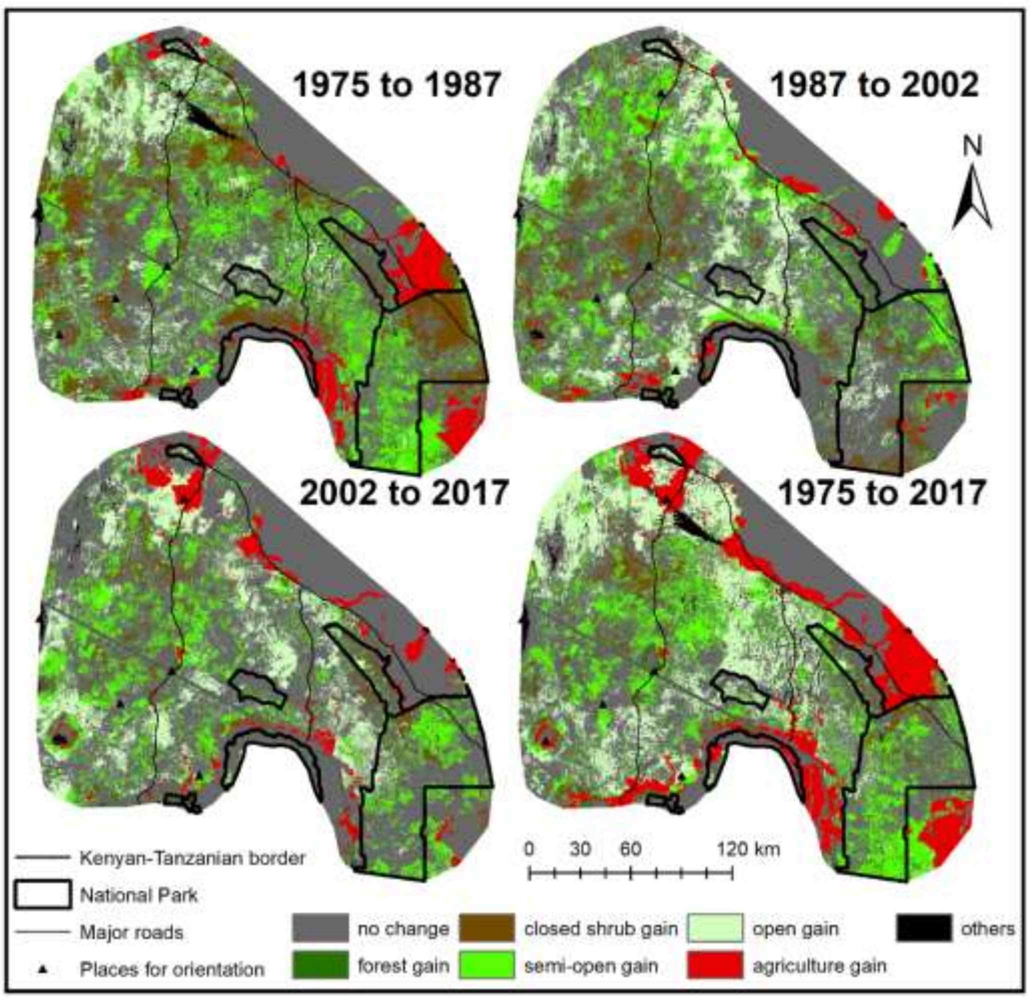

Figure 4: Change maps depicting bi-temporal gain of land cover classes.

Land cover changes

Amboseli ecosystem and the surrounding landscapes are characterized by a mosaic of open grass and herb dominated areas, dense shrub thickets and transition zones of these two land cover types with varying proportions of woody to non-woody plants. Dense broad-leafed forests only occur at higher elevations, e.g., the Chyulu Hills NP, Mt. Kilimanjaro and other mountains. The permanent swamps of the Amboseli basin are represented by the same class as the mountainous forest, due to their high NDVI values.

Mountainous forests were relatively stable in extent (tab. 3). A major decline occurred at the eastern flank of Mt. Kilimanjaro between 1975 and 1987, when forests were extensively converted into agriculture and agroforestry (fig. 4 and 5). The swamps of the Amboseli basin (except Amboseli NP), have undergone an almost complete conversion into small-scale agriculture (fig. 3 and 5). Moreover, land use shifts to agriculture have occurred especially at the margins of the study region, expanding down the slopes of Mt. Kilimanjaro and Mt. Meru over the whole period. Within the last 15 years, cultivation has significantly expanded in the Athi-Kapiti Plains, south of Nairobi NP. During the same period, first land conversions to agriculture have occurred along the road C102 towards Amboseli NP and on the slopes of Namanga and Longido hills (letter one south of Namanga, fig. 4 and 5). Half way between Amboseli NP and the Athi-Kapiti Plains, there has also been a notable increase of small-scale cultivation along the Selengei dry river.

A significant loss of vegetation density throughout the study region was observed. Closed shrub vegetation was thinned out to the semi-open transition stage, whereas this class itself has lost a large proportion of its area to grass dominated, open vegetation types (tab. 3 and fig. 4 and 5). The shrub thickets on the elevated areas between Amboseli NP and Lake Natron/Magadi decreased significantly during the study period. Accordingly, Amboseli basin has become a more open landscape by the reduction of former tree and shrub cover (fig. 4, gain of open vegetation class). Similar developments were observed for the area west of Mt Kilimanjaro towards Mt. Kitumbeine and in the Athi-Kapiti Plains resulting in an overall loss of woody vegetation (tab. 3).

Landscape connectivity of elephants

Year round elephant meta-populations are reported to occur in the National Parks of Amboseli, Tsavo West, Kilimanjaro, Arusha and in unprotected areas of the Longido Plains, in the region south of Bissil (corridor 5 in fig. 1) and at the Nguruman Escarpment in the Lake Natron/Magadi area. Seasonal movements occur over an extensive area of the study region, especially between Amboseli NP, Chyulu Hills NP and Tsavo West, as well as between Amboseli NP and West Kili Ranch (Wildlife Management Area).

A minimum of eight migration corridors were identified (fig. 1 and tab. 4). Only one is currently formally protected (Kitendeni, fig. 1 and 6A). This corridor decreased in width from 15.4 km in 1975 to 5.3 km when it was protected in 2002. Two corridors are highly threatened by becoming blocked by agriculture (Kisimiri and Kimana, fig. 1 and 6A and C) whereas three corridors are expected to decrease in size under further land use change (Kikoti's crossing, Mbirikani and Lenkati/Lolterish corridor); another corridor is data deficient for its exact location (Bissil corridor, fig. 1). Towards the southern Athi-Kapiti Plains, we could not identify any blockages for migratory movements. However, Nairobi NP and the Kitengela triangle to its south are surrounded by extensive cultivation and conurbations, and therefore disconnected from surrounding ecosystems.

Discussion

Land cover change & anthropogenic influence

On the scale of Amboseli NP, Western (2007) noticed a significant decline in wood- and bushlands, whereas open grasslands and swamps expanded. Our data for 2017 shows a similar tendency for Amboseli NP and its immediate surroundings. The swamps east of Amboseli NP are nowadays almost completely converted into agriculture, although they represent important habitats for several wildlife species that use the wetlands as stepping stones for their migratory movements (pers. com. D. Western, cited in Worden et al. 2003; Sarkar 2006; Okello and Kioko 2011;). Land use change maps suggest (fig. 5) that this development started between 1975 and 1987 while Worden et al. (2003) noted that conversion and subsequent fencing of Namelok swamp has led to the local extirpation of hippos (*Hippopotamus amphibius*), buffaloes and elephants from these areas, significantly decreasing the range for the first two species. Swamps are increasingly under threat from unsustainable use and unplanned expansion of agriculture (Okello and Kioko 2011); our land cover maps indicate (fig. 5) that almost all the swamps of Amboseli basin have been put under cultivation in the last two decades.

Table 4: Corridors of migratory elephants (for location see fig. 1) identified from literature. Status of protection according to land use change (fig. 5 and 6) and literature review.

	Corridor	Width in 2017	Status	Reference for location
1	Kitendeni	5 km	protected	Kikoti 2009, 2016
2	Transborder	12 km	unprotected, but not threatened	Douglas-Hamilton et al. 2005; Kikoti 2009; Okello et al. 2015; Ngene et al. 2017b
3	Kisimiri	0.8 km	highly threatened	Kikoti 2009
4	Kikoti's crossing	3 km	threat expected	Kikoti 2009, 2016
5	Bissil	?	data deficient	Ngene et al. 2017b
6	Mbirikani	3 km	threat expected	Kioko and Seno 2010; Ngene et al. 2017b
7	Kimana	0.4 km	highly threatened	Douglas-Hamilton et al. 2005; Kioko et al. 2006; Kioko and Seno 2011
8	Lolterish/Lenkati	4.5 km	threat expected	Kioko and Seno 2011; Ngene et al. 2017b

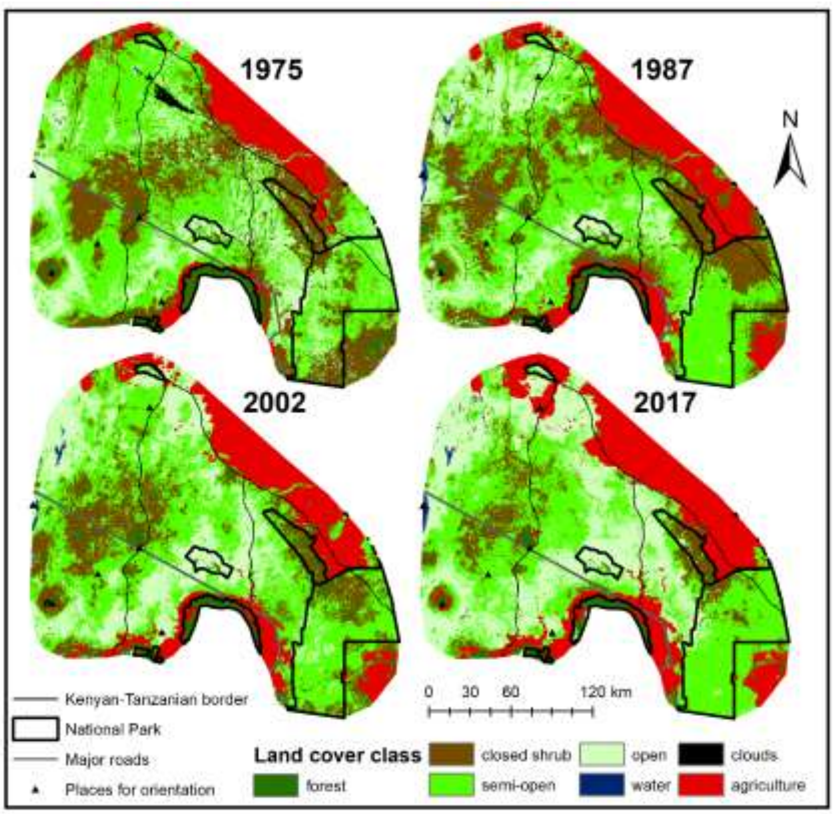

Figure 5: Land cover maps at four different time stages.

Vegetation in African savanna ecosystems is assumed to be non-equilibrium on a large timescale (Gillson 2004; Croze and Lindsay 2011) with factors like fire, herbivory, soil and climate playing key roles in switching between two alternative climax states of vegetation, open grassy or densely wooded savanna (Hobbs 1996; Sankaran et al. 2005; Staver et al. 2011; Fletcher et al. 2014). Our results indicate a large-scale shift from wooded savanna to a rather open grassland stage. Climatic factors may explain this development for Amboseli NP (Western and Van Praet 1973; Croze and Lindsay 2011): increasing precipitation and run-off on Mt. Kilimanjaro has led to a steady raise of the water table and salinity in Amboseli basin, promoting the spread of open areas and the decline of deep rooting trees. High browsing pressure on trees by the elephant population may prevent tree regeneration within Amboseli NP (Western and Maitumo 2004). However, this cannot explain the decline of shrub- and woodlands outside the protected area. Recent aerial surveys (KWS and TAWIRI 2010; Kenana et al. 2013a,b) suggest that only low numbers of elephants are present in the areas between Amboseli NP and Lake Natron/Magadi where woody vegetation has also significantly thinned. This area is under high anthropogenic pressure from wood extraction for charcoal production. Further removal of trees and shrubs by an increasing rural population can be assumed (Ntiati 2002) due to a high demand for natural resources to sustain livelihoods, to build up homesteads (so called bomas) or in search for firewood (personal observation). High densities of livestock (cattle, donkeys, camels, sheep and goats) additionally promote overgrazing and woodland depletion as predicted by Campbell (1986). Between 2010 and 2013, the numbers of livestock (cattle, sheep, goats) has doubled within the study region representing an underestimated driver for vegetation change given that these highly altered areas coincide with areas of human expansion and increasing livestock densities (KWS and TAWIRI 2010, Kenana et al. 2013a,b).

In the Athi-Kapiti Plains, the same trends were observed, but agricultural expansion (greenhouses, plantations) in this area was a striking development since 2002. Furthermore, livestock numbers increased whereas wildlife decreased with wildebeest showing a dramatic collapse (Reid et al. 2008; Ogutu et al. 2013), indicating the obstruction of migration routes (Owen-Smith and Ogutu 2013). High anthropogenic pressure is most likely the main driver in this "peri-urban savanna" (Reid et al. 2008).

Despite the proposed unsuitability for agriculture of the salty soils of ancient Lake Amboseli (Pratt et al. 1966), crop farming is increasingly invading the wetter areas throughout the study region, e.g., down the slopes of the mountains Kilimanjaro, Meru, Ol Donyo Orok (Namanga), Longido, Monduli, Kitumbeine and Gelai, into all swamps of the Amboseli basin and along seasonal rivers (Selengei river). Furthermore, initial areas of cultivation were detected throughout the ecosystem as it is the case along the road C102 (fig. 5). Water has been increasingly made available from dams and bore holes throughout the study region (KWS and TAWIRI 2010) allowing cultivation even in areas where surface water was historically absent during the dry season. These findings are supported by Okello (2012), who observed that human activities (settlements and farming) concentrated along the main roads and water sources leading to a clear-cut (in north-south orientation) and a possible blockage of migration paths. These developments are largely invisible from Landsat satellite imagery (resolution of 30x30 m), but studies from other areas surrounding Amboseli NP confirm the expansion of human activities in clusters along strategic points like roads, bore holes and dams interfering dispersal behavior of wildlife species (Okello 2005; Ellington 2007; Okello 2009; Okello and Kioko 2010).

Apart from expanding cultivation and settlements, human activities are omnipresent throughout the study region (KWS and TAWIRI 2010; Kenana et al. 2013a,b). Displacement of wildlife by various human activities (pastoralism, farming, fencing, charcoal burning etc.) drastically shrinks the available areas for wildlife dispersal. Displacement distances from human activities can range between 100 and 300 m in Amboseli (McNaught 2007; Okello 2009; Okello and Kioko 2010; Okello 2012; Howe et al. 2013), whereas a global compilation of data from GPS-collared mammals revealed, that anthropogenic activities alter the ranging behavior on a much larger temporal and spatial scale than previously expected (Tucker et al. 2018).

Landscape connectivity

Habitat fragmentation and the isolation of protected areas are threatening a variety of African ecosystems

(Newmark 2008; Owen-Smith and Ogutu 2013; Wegmann et al. 2014). The elephants of the Amboseli region are still roaming over a vast area in the Kenyan-Tanzania borderlands (Kenana et al. 2013a,b; Ngene et al. 2017b). However, meta-populations in Kilimanjaro and Arusha NPs as well as in unprotected areas are small, with an estimated number of 100 and 200 individuals in the two National Parks (TAWIRI 2015) and some 300 individuals scattered over the unprotected landscape (Kenana et al. 2013a,b). Meta-populations are localized (Vesey-Fitzgerald 1968; Kikoti 2009; Ngene et al. 2017b) making it a crucial task to maintain their connectivity. For example, elephants from Amboseli NP can reach the forests of Kilimanjaro via the 5 km wide and formally protected Kitendeni corridor (fig. 6). This well used corridor represents the last remaining connection between Kilimanjaro NP and the surrounding rangelands (Kikoti et al. 2010), but whether there is any exchange with "resident" Kilimanjaro elephants is unknown. Seven more corridors were identified that serve as important connections between elephant meta-populations. None of these corridors is protected and agricultural expansion is threatening at least five of them. For example, Arusha NP is connected to West Kili Ranch and the greater ecosystem via the Kisimiri corridor, a narrow strip of land (about 800 m, fig. 6) bordered by dense cultivation and human settlements (Kikoti 2009). Elephant sightings suggest that the corridor is still under sporadic use, but elephants are very cautious and often return before reaching the end of the corridor (Kikoti 2009). To guarantee the security of this migration path, it is essential to counteract the isolation of populations within the small Arusha NP.

East of Amboseli NP are two important corridors (Kimana and Lenkati/Lolterish, fig. 6) that allow connectivity to Kimana sanctuary and further to Tsavo West NP. Kimana Sanctuary is a key area for seasonal overlap and interbreeding of populations from Amboseli and Tsavo West NP (Western and Lindsay 1984). However, Kimana corridor has decreased in width to only 400 m by 2017. Formal protection of this corridor and further monitoring is highly recommended. Lenkati/Lolterish corridor with a width of about 5 km requires further investigation to monitor its use by migrating elephants. Similar exploration of the Bissil corridor is needed as its exact location could not be determined. Mbirikani corridor and Kikoti's crossing are still viable but are expected to decline under further land use changes (Kioko and Seno 2011; Kikoti 2016). Plans should be initiated to guarantee exclusion of agriculture from important areas as long as it is not already too late.

In the northern extent of the study region for example, the isolation of Nairobi NP from the greater Athi-Kapiti Plains has already taken place, as cultivation expanded significantly confining migratory species to the small Kitengela triangle (approx. 190 km²) south of Nairobi NP This development has already led to dramatic population declines and the local extinction of buffaloes and wild dogs (Ogutu et al. 2013). The remaining Nairobi NP/Kitengela ecosystem has a total size of about 300 km². Most large mammal species occur in small population sizes in Nairobi NP (Ogutu et al. 2013), making them vulnerable to climatic extremes and stochastic events like droughts and diseases. For a sustainable management of wildlife populations, a closed-ecosystem management approach should be considered.

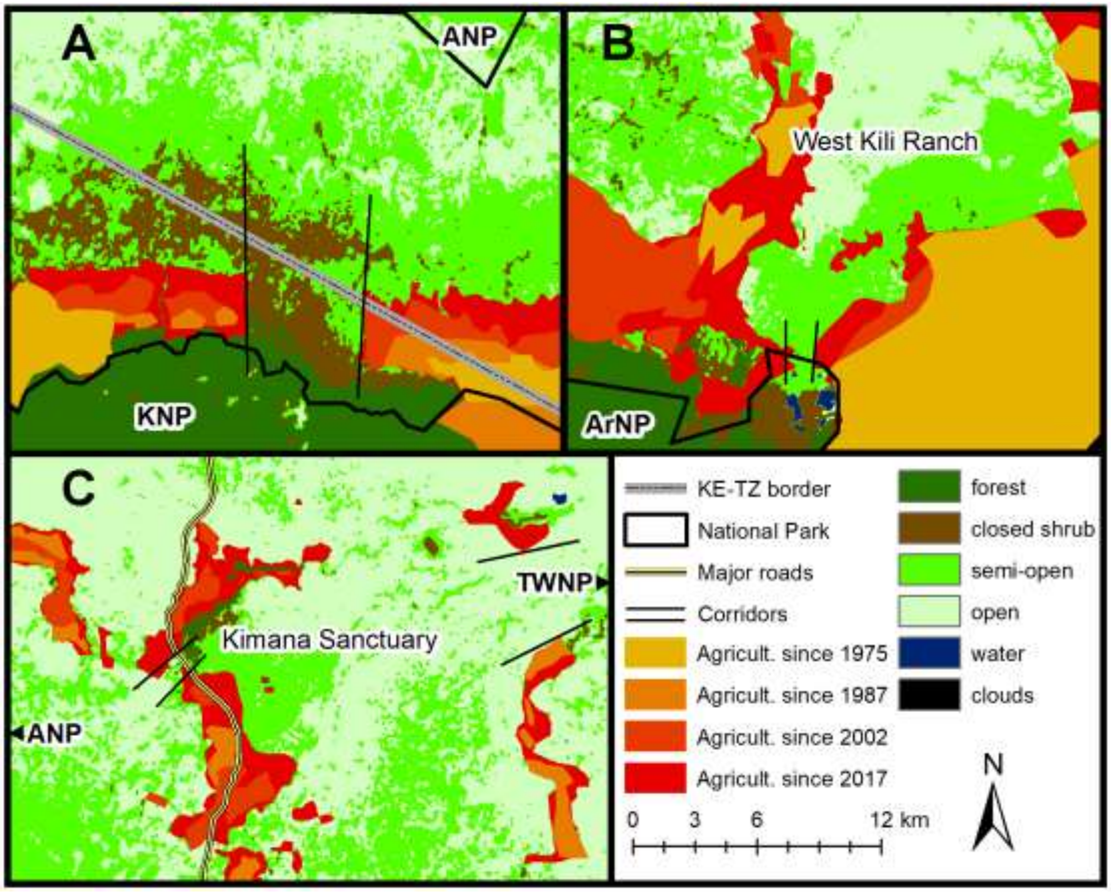

Figure 6: Detailed land cover in 2017 in Kitendeni corridor (A), Kisimiri corridor (B), Kimana corridor (C left) and Lenkati/Lolterish corridor (C right) with expansion of agriculture since 1975. Abbreviations: ANP = Amboseli National Park, KNP = Kilimanjaro NP, ArNP = Arusha NP; TWNP = Tsavo West NP.

Connectivity of elephant meta-populations in our study region is still possible despite notable land cover changes over the last 43 years. Elephant populations still occur in the same areas; although migrations of the Amboseli elephants ceased between 1977 and 1991 due to insecurities, former ranging patterns were resumed afterwards (Koch et al. 1995). Genetic studies on mitochondrial DNA sequences of Kenyan elephants highlight the connectivity of populations across the international border (Okello et al. 2008; Archie et al. 2011). In the eastern extent, elephants from Tsavo West can disperse towards Tsavo East NP and the Tanzanian Mkomazi NP (Ngene et al. 2017a). Further dispersion seems unlikely due to high occurrence of agriculture and lack of surface water supply further east and south of the National Parks (personal observation). Elephants from the Longido Plains and around Lake Natron may connect to the greater Tarangire-Manyara ecosystem, as there is an extensive seasonal migration of wildebeest and zebra from Tarangire and Lake Manyara NP in Tanzania towards the basin of Lake Natron (Morrison and Bolger 2014; Morrison et al. 2016). Further east from the Nguruman Escarpment (Lake Natron/Magadi area, fig. 1), elephants might be connected to the Serengeti-Mara ecosystem as land conversion to agriculture is still low (Kikoti 2009; Estes et al. 2012; personal observation). Migrations further north from Lake Magadi are uncertain as no recent reports could confirm movements of elephants towards the Mau Forest Reserves or Lake Naivasha, although sporadic evidence of movements northwards has been given (Poole et al. 1992). No reports on elephants in Nairobi NP and the Athi-Kapiti Plains are available but dispersal forays may be possible.

Conclusion

The greater Amboseli ecosystem and its surrounding landscapes have passed through distinct land cover changes within the last four decades. While a general tendency of declining wood- and shrublands and increasing open grasslands was observed, cultivation has been expanding into the wetter areas of the region, narrowing migration corridors and blocking dispersal pathways. Wide ranging elephant movements suggest a still viable landscape connectivity throughout the study region (except for the highly fragmented Athi-Kapiti Plains). However, this situation is fragile as increasing human populations, the ubiquitous presence of anthropogenic activities and recent land use changes are threatening most of the identified migration corridors. Sustainable protection of species and conservation of landscape connectivity requires the implementation of target-oriented land use planning and the protection of important wildlife areas and the corridors connecting them.

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