



Land-cover change and human population trends in the greater Serengeti ecosystem from 1984–2003

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ABSTRACT

The growth of human populations around protected areas accelerates land conversion and isolation, negatively impacting biodiversity and ecosystem function, and can be exacerbated by immigration. It is often assumed that immigration around protected areas is driven by attraction in the form of economic benefits, but in many cases, people may be pushed from their areas of origin toward protected areas. Mitigating the effects of immigration around protected areas necessitates understanding the actual mechanisms causing it, which can be aided by analysis of patterns of land-cover change. Our goal was to identify the reasons for human population growth and land-cover change around the protected areas in the greater Serengeti ecosystem (henceforth “the park”), and to relate agricultural conversion from 1984–2003 to trends in human demography. We found that conversion of natural habitats to agriculture was greatest closer to the park (up to 2.3% per year), coinciding with the highest rates of human population growth (3.5% per year). Agricultural conversion and population growth were greatest where there was less existing agriculture, and population density was lowest. Lack of unfarmed land farther from the park, coupled with greater poverty near the park, suggest that movement away from areas with high population densities and land scarcity was likely driving immigration near the park, where arable land was available. Our results are essential for conservation planning for one of Africa’s hallmark ecosystems, and should encourage further examination of population growth and land-cover trends near protected areas throughout the developing world.

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1. Introduction

Effective conservation of even the largest protected areas is impacted by what takes place outside their boundaries (Cantú-Salazar and Gaston, 2010; Hansen and DeFries, 2007). As human populations in rural areas continue to grow, especially in the developing world, protected areas become isolated by surrounding land-cover change (DeFries et al., 2005). Effecting conservation thus requires a better understanding of human interactions with natural resource bases both inside and outside protected areas. A recent study reported a global pattern of higher human population growth surrounding protected areas on a broad scale (Wittemyer et al., 2008), but the potential causes for such a pattern are a source of debate (Joppa et al., 2010; Scholte and de Groot, 2010).

The causes of immigration around protected areas can be grouped into push and pull factors. Push factors cause people to

leave their areas of origin and include lack of access to land and natural resources, declining soil productivity, and high population pressure. Pull factors drawing people into new areas can be availability of natural resources, including land, employment, and access to markets and social services, and reunification with family (Oglethorpe et al., 2007). These mechanisms have similarly been referred to as frontier engulfment (i.e., when agriculture expands and “bumps into” a protected area boundary) and attraction (pull factors) (Scholte and de Groot, 2010). Prior studies interpreted elevated immigration rates near protected areas as a result of perceived benefits associated with the protected areas themselves (Wittemyer et al., 2008), but empirical evidence for this assumption is sparse (Scholte and de Groot, 2010), and a better understanding of the importance of pull- versus push-factors is important given the strong conservation implications of human population growth surrounding protected areas.

Population growth near protected areas is of conservation concern because both biodiversity and ecosystem function within protected areas are affected by the broader landscape context in

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which they are situated. For example, while tropical forest cover in protected areas fairs well relative to adjacent unprotected lands, the protected areas' ability to preserve species richness and ecological processes is negatively affected by forest loss in surrounding areas, a process which is accentuated in smaller reserves (DeFries et al., 2005, 2010). Likewise, elevated housing growth rates around protected areas in North America threaten their ability to conserve species by increasing isolation and decreasing effective size (Radeloff et al., 2010). In Ghana, human density surrounding protected areas is a major predictor of local species extinctions, particularly of ungulates and carnivores, and extinction risk for these animals inside the protected areas was greater closer to the border with the human settlements (Brashares et al., 2001), likely because conflict between people and far-ranging carnivores is a major cause of mortality near protected area boundaries (Woodroffe, 1998), and bushmeat hunting is strongly correlated with distance from human settlements (Hofer et al., 2000). Similarly, large mammal extinctions in 13 national parks in the western United States are significantly correlated with human density around the parks, although not with park size (Parks and Harcourt, 2002). Human activities and density also facilitate the invasion of exotic species into protected areas (McKinney, 2002) and domestic animal populations can increase the transmission of disease to wildlife (Cleaveland et al., 2000).

Mapping the spread of agriculture can elucidate an important mechanism behind population growth (Scholte and de Groot, 2010; Joppa et al., 2010). Currently, about 75% of the poor in developing countries live in rural areas and depend on subsistence agriculture (The World Bank, 2007). Growing human populations, surging food demand, and an increasing reliance on bioenergy will exert tremendous pressure to convert natural fertile lands to agriculture and to intensify low-intensity production systems (Beringer et al., 2011; Kiers et al., 2008; Tilman et al., 2001). Latin America and sub-Saharan Africa, because of the distribution of remaining available land, are predicted to bear the brunt of this expansion, which could lead to the loss of one-third of remaining savannas, grasslands and tropical and temperate forests (Alexandros, 1999; Pereira et al., 2010). Under such scenarios, there is little doubt that protected areas will continue to be engulfed by advancing agricultural frontiers, as people are forced to leave their areas of origin to access arable land (Scholte and de Groot, 2010). If protected areas are to persist as havens of biodiversity, early detection and analysis of the factors contributing to encroachment, such as agricultural expansion, will be necessary to try to mitigate the worst of these impacts by enacting land use plans in buffer areas.

The greater Serengeti ecosystem in eastern Africa, comprised of the national park and adjacent reserves and controlled areas (and henceforth referred to as “the park” for simplicity), is a prime example highlighting that conservation efforts, even in the largest protected areas in Africa, are affected by human activities in adjacent unprotected lands. For example, wildebeest (*Connochaetes taurinus*) rely on areas outside of the park during critical dry season parts of their migration (Thirgood et al., 2004), human-wildlife conflicts create antagonism between local people and the conservation objectives of the park (Walpole et al., 2004), local communities rely heavily on bushmeat from the park (Campbell and Hofer, 1995; Mfunda and Roskaft, 2010; Mduma et al., 1998; Ogutu et al., 2009; Sinclair et al., 2007), and domestic dog populations act as reservoirs of diseases that spread to wild carnivores (Cleaveland et al., 2000). These interactions between the park and surrounding communities underscore the need for protected area managers and community planners to understand both patterns of human population growth and the forces that cause population growth in adjacent lands.

Our goal was to discover why and how human populations and land cover around Serengeti are changing. Our specific objectives

were to (a) quantify trends in human population growth and density that might be related to the presence of the park, (b) map land-cover change around the park, and (c) examine relationships between the observed trends in land-cover and human population change.

2. Methods

2.1. Study area

The 14,763 km² Serengeti National Park comprises the core of the greater Serengeti ecosystem. Parts of the park have been protected since 1929, and present day boundaries were largely set in 1959 (Sinclair, 1995). Serengeti National Park is bordered in Tanzania by game reserves, game controlled areas, wildlife management areas and the Ngorongoro Conservation Area, and the Maasai Mara National Reserve and surrounding Maasai areas in the Narok region in Kenya, all of which together make up the greater Serengeti ecosystem. In addition to the park, game reserves and the Maasai Mara exclude human habitation, while game controlled areas, parts of the wildlife management area, and village lands allow for habitation, farming and livestock husbandry. Hunting occurs in game reserves, the game controlled area and wildlife management areas. The Ngorongoro Conservation Area permits habitation and livestock, but seeks to limit farming, although some farming occurs. The complex of game reserves and the park, which exclude habitation, will henceforth be referred to as “the park.”

Rainfall is highly variable in the greater Serengeti ecosystem, but typically peaks in December, and March–May. Rainfall is generally lower in the south and east (500 mm/yr) of the ecosystem than in the north and west (950–1150 mm/yr; Sinclair, 1995). Vegetation cover in Serengeti National Park is influenced mainly by soil type and rainfall and can be broadly classed into the eastern grass plains, central *Acacia* woodlands, and northern broadleaf forests (Sinclair, 1995).

Due in part to the rainfall patterns, areas north-east, east and south-east of the park are occupied by the primarily pastoral Maasai, whereas agriculturalists and agro-pastoralists populate the areas north-west, west and south-west of the park, where climate is more conducive to agriculture. Agriculture is dominated by smallholder farmers with average farm sizes from 0.9 to 3 ha, the majority of which are cultivated by hand hoe (70% nationwide) or ox plough (20%) (www.tanzania.go.tz/agriculture). The highest human densities in the region occur near Lake Victoria, with an average population growth rate of ~3.1% between 1988 and 2002 (Polasky et al., 2008).

2.2. Demographic data

We analyzed ward-level demographic data for Tanzania created by the International Livestock Research Institute (ILRI) in Nairobi and the 2002 Tanzania National Census. Wards are collections of villages, and their size is inversely correlated with human densities. Because human densities in the pastoralist-dominated areas east of the park are very low, the wards are much larger, making east–west comparisons difficult (Fig. 1). We therefore used only the wards in the agro-pastoral areas west of the park to look at rates of land-cover change and human demographic parameters at increasing distances from the park. Rates of population change by ward were calculated using the 1988 and 2002 census data. We separated the wards into the following zones for this analysis: wards with borders adjacent to the park (listed as 0 km distance in following results), and those with centroids (the geographical center of the ward) within 20, 40, 60 and 80 km of the park (Fig. 1). Land-cover change was analyzed according to these same zones

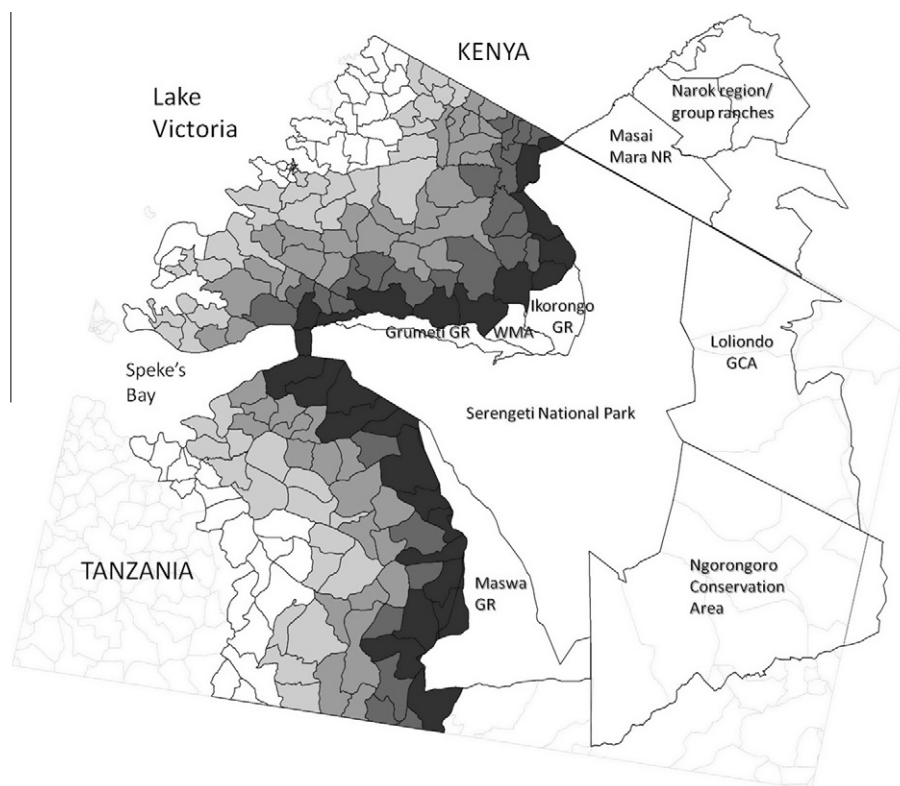


Fig. 1. Serengeti National Park and surrounding protected areas, with wards zones used in the analysis in western Serengeti. Wards adjacent to the park are indicated in dark gray, and those with centroids falling within 20, 40, 60 and 80 km from the park become successively lighter. Larger wards east of the park are shown in very light gray. GR = game reserve, WMA = wildlife management area, GCA = game controlled area, NR = National Reserve.

to examine relationships between human population density, growth rate, and agricultural expansion relative to proximity to the park. Urban wards (1 ward in the 40 km zone and 11 in the 80 km zone) in the 2002 census were excluded.

2.3. Land cover change mapping

We mapped land-cover change in the greater Serengeti ecosystem using 30-m resolution Landsat TM and ETM+ imagery from the USGS archive (www.glovis.usgs.gov). The greater Serengeti ecosystem falls at the intersection of four Landsat footprints (path/row 169/061, 169/062, 170/061 and 170/062). We acquired at least four images from different seasons for each of the time-periods 1984–1987 and 2002–2003 (dates were partially determined by image availability). The use of multiple images per time period allowed us to include images representing different phenological states, which was important for differentiating between cropland and natural areas (Kuemmerle et al., 2008). Changes were mapped by classifying all images jointly into six classes: stable agriculture (unchanged between 1984 and 2003), stable savanna (including grassland, savanna and woodland), stable forest, savanna and forest that converted to agriculture during the study period (henceforth referred to as “agricultural conversion”), water, and cloud. We performed classifications using support vector machines (SVM) implemented in the software ImageSVM (Janz et al., 2007). SVM are non-parametric classifiers capable of handling complex, non-linear class boundaries that are common for change detection problems and frequently outperform traditional statistical classifiers. A detailed technical description of SVM is found in Huang et al. (2002).

We parameterized the classifications by digitizing training areas using high resolution imagery in Google Earth (Kuemmerle

et al., 2010) (the images were from GeoEye and Digital Globe, and mostly captured from 2002 to 2004, with several images from 2001, 2005, and 2009, and we assumed that once converted, agriculture did not revert back to natural areas) with expert knowledge of the area, and for the earlier time periods, by visually interpreting the Landsat images. The number of training areas per class varied from ~50 to close to 400, depending on the areal cover of the classes. We randomly sampled 500 points from within the training polygons for each class and used them to parameterize the SVM. To control for differences in phenology and atmospheric conditions among footprints, we classified each footprint independently. To address clouded areas, we first ran classifications on the full multi-temporal stack of images. We then removed images with clouds from the image stack, reran the classification, and filled areas classified as cloud in the full classification with the classified areas from the cloud-free stacks.

To validate the classification, we assigned 100 random points to each of the land-based classes, with a minimum distance of 500 m between all points within the same class. We evaluated these points against high-resolution imagery and all Landsat images in the multi-temporal stacks, and assigned true land cover classes to those that had been misclassified. We used the classified and true land cover class assignments to create a standard contingency/confusion matrix to calculate the overall accuracy of the classification and the user’s and producer’s accuracy of each class (Congalton, 1991).

In addition, we used Landsat images from 1989/1990, 1994/1995 and 1999/2000 to examine rates of change in ~5-year time intervals. We assigned 218 random points (200 points stratified by the amount of converted land in each zone, with additional points added to get a minimum of 20 points in the outermost zones) in western Serengeti and checked in which period conver-

sion had occurred. Conversion rates based on the percent of the land area in the ward zone were calculated for each ward zone, and normalized by the number of years in each time period to yield annual conversion rates by time period and zone.

3. Results

3.1. Human population trends

Human populations surrounding Serengeti changed rapidly in recent decades. In the agricultural areas west of Serengeti, population growth rates were highest where densities were lowest ($R^2 = 0.75$), and varied dramatically with distance from the park. Wards closest to the park had the lowest human densities (98 people/km²) and the highest rates of human population growth (3.5% per year) over the study period from 1988 to 2002, while those farthest from the park and closest to Lake Victoria had the highest densities (160 people/km²) and lowest growth rates (2.5% per year) (Fig. 2).

3.2. Land cover classification

The land cover change analysis of the greater Serengeti ecosystem highlighted the stark contrast between protected and unprotected areas along the western boundary of the ecosystem (Fig. 3a), and regional and national differences in land use that reflect differences in culture, livelihood strategies and land tenure policy. Areas east of the park are primarily pastoralist, and although agriculture is increasing in these areas (at least in Loliondo if not Ngorongoro), by 2003 agriculture was still minimal and found close to human settlements. In contrast, agriculture was by far the dominant land cover west of the park (Fig. 3b). The overall classification accuracy of the land cover map was 83% ($\kappa = 0.79$), with the agricultural conversion change class proving the most difficult to classify (producer's accuracy = 73.5%), perhaps partly because the lack of high resolution imagery in the earlier time periods necessitated visual interpretation of the coarser Landsat imagery, and agricultural classes appear fairly similar in those images. The stable classes of agriculture, forest and savanna yielded producer's accuracies between 92% and 94% (Table 1). Our classifications showed that agriculture and savanna were the most dominant land covers (Fig. 3a and b), the latter being found primarily within the protected areas and parts of the adjacent Kenyan and Tanzanian Maasailand. In these eastern areas, the park was still linked to its surroundings in both Kenya and Tanzania, whereas in large parts of the west, a sharp edge had developed between the park and adjacent agricultural lands. In Kenya, most of the conversion was of isolated forest patches and parts of the Nar-

ok region near the large wheat cropping schemes (Fig. 3a). Overall, agricultural conversion and forest accounted for less than 10% of the entire study region, but conversion increased in dominance when only considering western Serengeti, where the majority of the conversion took place (Fig. 3b).

3.3. Land-cover change

In the western Serengeti, agricultural conversion was greatest close to park boundaries where there was the most remaining arable land, dwindling to almost nothing in the zones farthest from the park where there was the greatest amount of stable agriculture and almost no remaining arable land (Fig. 4). Over the full study period from 1984–2003, zones closest to the park exhibited conversion rates between 1.6% and 2.0% of the land area in the zone per year, while the zones farthest from the park showed steadily decreasing annual conversion rates from ~1.0% to 0.1% per year (Fig. 5a). The high rates of conversion in the zones closest to the park drove the overall trends in conversion for all of western Serengeti, discussed below (Fig. 5b). In fact, these rates would likely be even higher if they reflected the true amount of remaining arable land. Some lands on steeper and rocky slopes cannot be converted but were included in the overall calculations because it was not possible to accurately predict the occurrence of non-arable land.

3.3.1. Change rates by period

The majority of the agricultural conversion occurred during the first decade of the study period, with 41.7% occurring between 1984 and 1990, 30.7% between 1990 and 1995, 12.4% between 1995 and 2000, and 15.1% between 2000 and 2003. Annual conversion rates for the entire western Serengeti study area mirrored this trend, with the greatest annual change rates occurring in the earliest time period (1.02% per year), and tailing off in more recent time periods (Fig. 5b). A slight uptick between 2000 and 2003 appeared to be driven by conversion in the 20-km zone where conversion rates reached 2.3% of the zone per year, the highest observed rate for all zones and time periods (Fig. 5a and b).

3.3.2. Change rates by distance from the park

The zone closest to Lake Victoria, and farthest from the park (80-km zone) experienced by far the lowest rates of conversion in all time periods, and steadily decreasing rates (from 0.14% to 0.03% per year) from the beginning to the end of the study period. Rates of conversion in the 60-km zone similarly showed a decreasing trend with time, except for an increase in the most recent period. In fact, all zones, except for the 80-km zone, showed an increase in annual conversion rates in the most recent time period, relative to the period before it. Zones adjacent to the park and in the 40-km zone had the highest annual conversion rates in 1990–1995, with rates between 1984 and 1990 a close second. The 20-km zone had greater annual rates of conversion than any other zone, and these were in the most recent and earliest time periods (2.3% and 1.9% per year, respectively), with wards adjacent to the park showing the next highest rates (~1.5% per year) in the first two time periods.

3.4. Land cover and human population trends

Taken together, analysis of trends in human populations and land-cover change revealed some striking trends. Zones with the highest growth rates also had the lowest densities, and these were the same zones that exhibited the least amount of existing agriculture at the beginning of the study period, and the greatest conversion to new agriculture by the end of the study period, and were closest to the park. Conversely, both growth and conversion rates

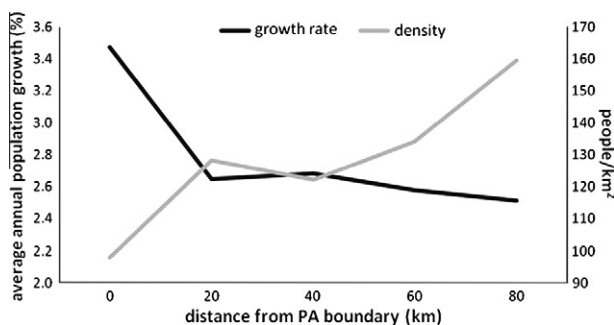


Fig. 2. The average annual rate of human population increase in western Serengeti from 1988–2002 was greatest in wards adjacent to the park boundary, while human density in 2002 remained low in these same areas, and increased with distance from the boundary.

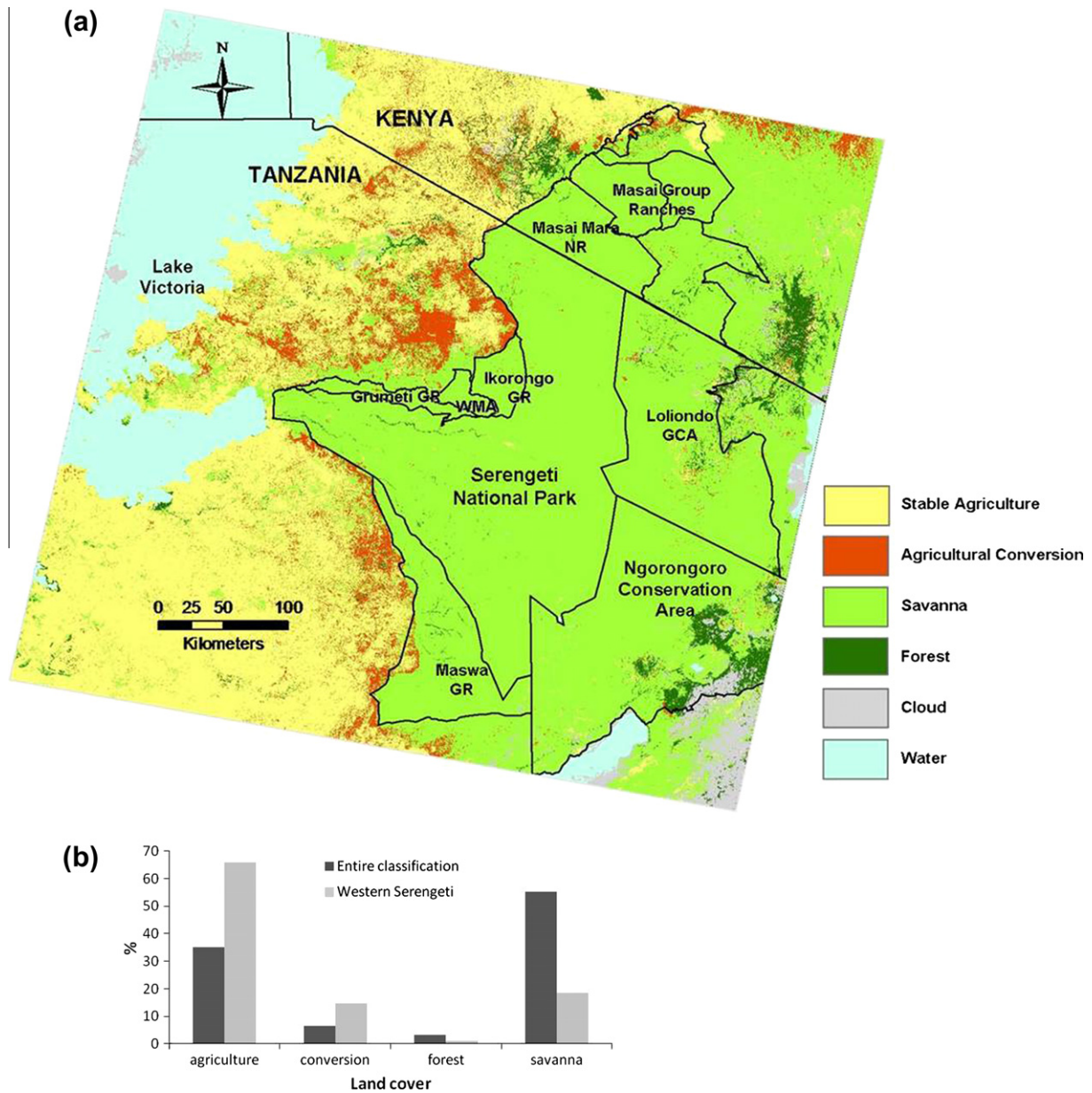


Fig. 3. (a) Land cover in the greater Serengeti ecosystem showing stable savanna, agriculture and forest, and agricultural conversion from 1984–2003. GR = game reserve, WMA = wildlife management area, GCA = game controlled area, NR = National Reserve. (b) Relative class proportions of the entire land cover classification, and the western Serengeti study area defined by wards with centroids within 80 km of the park boundary.

Table 1
Class accuracies of the land cover classification.^a

	Producer's (%)	User's (%)	Omission (%)	Commission (%)
Stable agriculture	92.0	74.2	8.0	25.8
Agricultural conversion	73.5	94.8	26.5	5.2
Forest	91.9	96.8	8.1	3.2
Savanna	93.9	74.4	6.1	25.6

^a Producer's accuracy is the probability of a reference pixel being correctly classified, a measure of omission error, and user's accuracy is the probability that a pixel classified on the map actually belongs to that class on the ground, which reflects commission error.

were lowest in those areas with the highest human densities and the greatest amount of stable agriculture, which were farthest from the park, and close to Lake Victoria (Figs. 2 and 4).

In contrast, in Loliendo in eastern Serengeti, different patterns of land use and human population trends prevailed, likely driven by different livelihood strategies and environmental conditions.

However, because ward sizes in Loliendo were large, with boundaries of wards adjacent to the park extending 40–50 km from the park (Fig. 1), it was not possible to compare growth rates in Loliendo at different distances from the park, as we were able to in the more densely-settled western Serengeti. On average, though, population growth rates in Loliendo wards were around 2.8%, with

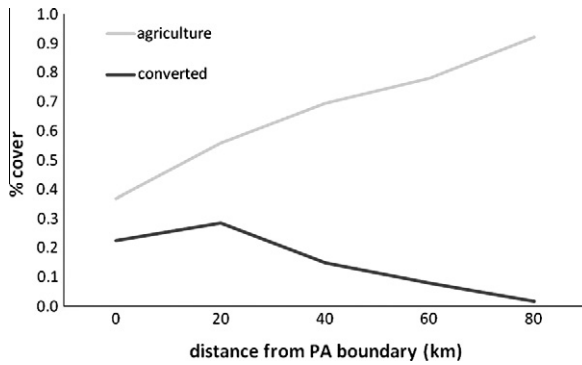


Fig. 4. Percent of each ward zone in western Serengeti under stable or converted agriculture from 1984–2003. Wards closest to the park boundary began with less agriculture, but showed the highest rates of conversion to new agriculture in the study period.

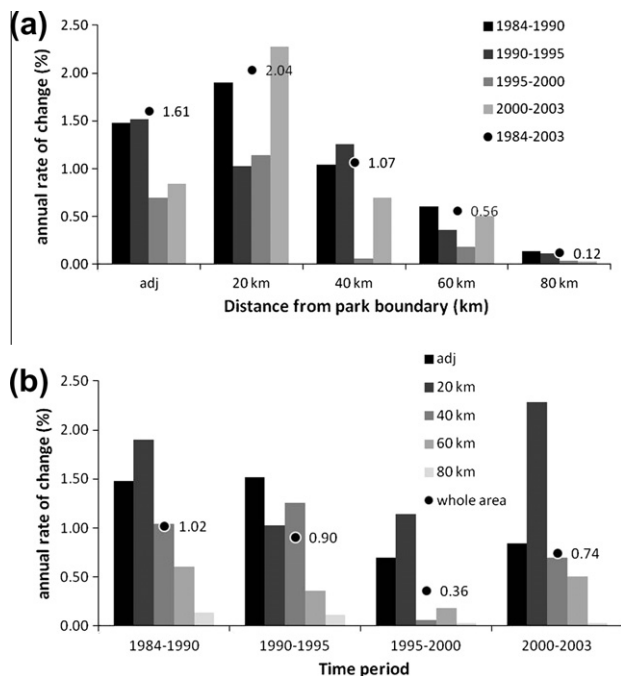


Fig. 5. (a) Annual rates of conversion to cropland for each ward zone, by period of conversion. Dots represent annual rates of conversion within each zone for the entire study period. (b) Annual rates of conversion to cropland for each time period, by ward zone. The dot represents the annual rate of change for each time period estimated for the entire study area, defined by all wards with centroids 80 km or less from the park boundary.

densities ranging from only 4 to 20 (average of 10) people/km². Population growth rates west of the park were similar over the same distance, at around 2.9%, but densities were much higher, from 100 to 135 (average of 117) people/km².

4. Discussion

We observed distinct patterns in human population and land-cover change across the greater Serengeti ecosystem. In the agro-pastoralist areas west of the park, population growth rates were highest adjacent to the park, and had a negative relationship with population density. Our analyses also revealed dramatic differences in land cover that can be linked to variations in land use, culture and socio-political conditions. We found the greatest conversion of natural areas to agriculture in the agro-pastoralist

areas along the western border of the park in Tanzania, whereas agricultural conversion in the pastoralist areas east of the park was minimal, and showed no patterns relative to the presence of the park. West of the park, agricultural conversion was inversely related to the amount of stable agriculture. Zones closest to the population centers near Lake Victoria, and farthest from the park, had the most stable agriculture and least conversion to new agriculture, while zones closest to the park had very little agriculture at the beginning of the study period, but showed the greatest conversion to new agriculture.

The patterns that we found are typical of frontier engulfment and an indication of push factors causing human population spread (Oglethorpe et al., 2007; Scholte and de Groot, 2010), and do not support the explanation that populations near the park increased because of economic opportunities provided by the park. Instead, people likely moved away from areas where resources have become scarce (i.e., near the highest population centers near the lake), and to places where resources are still available, which happen to be close to the park. Indeed, surveys in villages adjacent to the park in northwest and southwest Serengeti found that two-thirds to four-fifths, respectively, of the villages' populations are immigrants whose primary reason for moving to these areas was for grazing land or the opportunity to farm (Schmitt, 2010).

In pastoralist-dominated Loliondo, east of Serengeti National Park, conversion of land to agriculture until 2003 was minimal, and mostly limited to areas immediately surrounding human dwellings, consistent with the typical establishment of Maasai farming in this area (McCabe et al., 2010). Almost no agricultural expansion was detected near the park boundary, which may be partly the result of agreements between tour operators and villages in Loliondo that generated income for the villages while also limiting agriculture (Nelson et al., 2009). In villages adjacent to the park in Loliondo, only one-quarter of the residents were immigrants, and their primary reason for immigrating was marriage (Schmitt, 2010), reflecting the lower resource restrictions and human densities in this area, coupled with cultural differences, which led to slower adoption of agriculture.

Our analysis of human population data in western Serengeti corroborated that people were being pushed from densely-settled areas in search of resources. Rural population densities were highest closest to Lake Victoria and farthest from the park, which mirrors the trend in stable agriculture. Annual population growth rates were greatest in the areas with the lowest human densities, and these same areas showed the greatest extent of conversion to agriculture. Visual inspection of the points used to assess conversion rates in different time periods indicated that more recent conversion in areas far from the park was often the result of converting remaining wetlands, highlighting limits to expand agriculture there. Likewise, remaining patches of natural habitat in the more densely-farmed zones typically coincided with hills and rocky outcrops which are often less suitable for farming, indicating that conversion rates of remaining arable lands are actually even higher than reflected here. In contrast, new agriculture in zones closer to the park was typically the result of conversion from savanna, which may previously have been used for grazing land. Taken together, these trends indicate a migration of people away from heavily-farmed, densely-populated areas, and toward low-density areas with available land closer to the park boundary. Similar trends have been observed around a number of other protected areas, including Kafue National Park in Zambia (Joppa et al., 2009).

Our analysis of rates of agricultural conversion throughout the study period further supported the push mechanism behind immigration. In general, annual rates of conversion declined throughout the study period, increasing slightly in the most recent period from 2000–2003. The zone farthest from the park, which had the greatest amount of cultivated land at the beginning of the study period,

exhibited the lowest annual rates of conversion to new agriculture in all time intervals. These rates declined in the earlier half of the study period and remained constant at just 0.03% per year from 1995–2003, whereas conversion in zones closer to the park was occurring at 0.7–2.3% of the land in those zones per year over the same period. This underscores the fact that even at the start of the study period, the zones closer to the population centers around Lake Victoria were limited in the amount of land not yet converted to agriculture, and that any further opportunities to expand agriculture in those areas were exhausted by the end of the study period.

Economic data from village surveys also suggest that pull factors are not the most probable cause for high population growth near the park, where poverty rates were higher. About three-quarters of households in villages directly adjacent to the park in north-west (75.1%) and southwest (71%) Serengeti are below the poverty line (Schmitt, 2010), as compared to 42% and 46%, respectively, of the larger regions in western Serengeti to which these communities belong (Polasky et al., 2008) and 39% of rural populations in Tanzania as a whole (Tanzania National Bureau of Statistics, 2002). Likewise, the majority of people in villages surrounding the park, the same villages in which the majority of people were immigrants, report no benefits from conservation or the park (Schmitt, 2010). The fact that people are moving into very poor areas argues against an economic benefit, both real and perceived, to those living adjacent to the park.

Additionally, areas closer to the park may actually be less desirable to agro-pastoralists, because of high rates of human–wildlife conflict which causes loss of crops and livestock and sometimes human lives, and can substantially impact the livelihoods of subsistence farmers (Naughton-Treves and Treves, 2005; Thirgood et al., 2005). As a result, the newest immigrants to an area typically end up with undesirable plots on the periphery of the human–wildlife interface (Naughton-Treves, 1997), a trend which has also been observed along the western Serengeti park boundary (J. Schmitt, pers. comm.) where human–wildlife conflict is the most severe. In fact, 85% of people in villages adjacent to the park report a cost from wildlife, with 64% reporting the cost to be crop destruction (Schmitt, 2010).

Human–elephant conflict, in particular, has increased in the last decade in villages near Serengeti National Park (Malugu, pers. comm.; Walpole et al., 2004). Farmers greatly fear elephants because they threaten their lives and destroy their crops. Decimated in the 1970s and 1980s, the Serengeti elephant population recovered and expanded its range westward since the international ban on the ivory trade in 1989. Increasing agricultural expansion and human populations adjacent to the park, in conjunction with the westward-expanding elephant population, has created a fertile ground for sometimes intense human–elephant conflicts, leading to human and elephant deaths, crop loss (Walpole et al., 2004), and antagonism towards the protected areas who are seen as the “owners” of the problem animals (Gadd, 2005; Naughton-Treves et al., 2005).

Similarly, the conversion of savanna to agriculture in western Serengeti, accompanied by increasing human populations, impacts the migratory wildebeest (Thirgood et al., 2004), which are at greater risk of hunting when closer to local communities. In fact, in addition to the push factors outlined above, there may be one pull factor of strong conservation concern, and that is the wildlife themselves. Many people in western Serengeti consume bushmeat as a source of protein, and sell it to supplement their income (Mfunda and Roskaft, 2010; Mduma et al., 1998). One of the key predictors of bushmeat hunting is the distance between one's home and the wildlife resource (Hofer et al., 2000). Increasing human populations near the park thus likely resulted in increased bushmeat hunting.

Looking ahead, it is likely that areas close to the park in western Serengeti will continue to experience growth in human population density, and convert remaining natural land to agriculture, unless broad-reaching conservation plans are enacted that also incorporate community engagement and district-level land use planning. As Maasai continue to adopt agriculture (McCabe et al., 2010), we may also expect to see increasing land pressure in Loliondo, and in the Narok region in Kenya.

Although plans for a controversial paved road connecting Lake Victoria to the coast of Tanzania, that would have bisected Serengeti National Park, have been tabled, there are still plans to build paved roads into the communities east and west of the park (written comm. TZ Minister of Natural Resources, 2011). This has the potential to dramatically increase the pace of conversion in Loliondo, and the competition for land. The roads, while likely beneficial to development in some respects (Escobal and Ponce, 2001), also increase access to the area by agriculturalists from outside the region, where there are shortages of arable land. This could lead to a land grab by wealthy farmers from Arusha and other densely-settled areas, unless urgent action is taken to secure land rights in Loliondo. Only weeks after the announcement of the road, there were reports of prospecting for land in Loliondo by wealthy and powerful individuals from Arusha.

The conservation implication of our work is that designing appropriate conservation strategies to preserve protected areas surrounded by increasing human populations and advancing agriculture will necessitate collaboration between biological and social scientists, economists, multi-level governments, protected area managers, NGOs and community organizations. In Serengeti, there are important collaborations being formed to enact a broader view of ecosystem management (see www.serengeticoforum.org). Participatory wildlife management in the form of a quite successful wildlife management area in western Serengeti is contributing income from conservation to local communities, which may help these areas stall the advance of agriculture, as similar collaborations appear to have done in Loliondo. Nevertheless, these efforts can collapse under the strain of land and population pressures, especially with immigration from outside their area of influence, and every effort must be made to try to prevent this from happening. Furthermore, when the assumption is made that immigration around protected areas is benefit-driven, a common response is to suggest the disbursement of benefits farther away from the protected area, to draw people out of the buffer areas (DeFries et al., 2007; Wittemyer et al., 2008). Management plans are sometimes based on this assumption, and suggest building schools and health clinics in communities more removed from the protected areas. However, if immigration is mainly driven by push factors, such an intervention may be ineffective if not coupled with clear livelihood alternatives that are not based on the diminished resource, in this case, arable land. This speaks to the need for management interventions to be multi-faceted, incorporating both land use planning and development of alternative incomes, perhaps in concert with efforts to increase agricultural yields in already developed lands, which can lead to “land sparing” in areas closer to the park (Baudron et al., 2011). Analysis of land-cover change and population trends can inform conservation planners of the spatial scales they should be targeting, and help inform zoning efforts that incorporate both critical species habitat and information about human development (Abbitt et al., 2000).

5. Conclusion

Contrary to the common assumption that elevated population growth near protected areas is the result of pull factors causing immigration, our study suggests that this is not necessarily the

result of attraction to the protected area. Rather, people may be pushed closer to protected areas by advancing agricultural frontiers, as in the case of western Serengeti. Effective, targeted conservation interventions require that we move beyond broad generalizations to correctly identify both the patterns and the drivers of human population trends and their relationship to both land-cover change and protected area effectiveness on a case-by-case basis. In situations in which appropriately-scaled human population data are not available, analysis of land-cover change can act as a good proxy to track population increases while also yielding clues about the drivers of these trends.

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