The Impact of Fire and Large Mammals on the Ecology of Queen Elizabeth National Park

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2010

i. Financial support

Financial support was provided for this work from several sources. A grant to Woods Hole Research Center (WHRC) as part of the NASA Protected Area Watch (PAWAR) project has funded an analysis of fire frequency in Queen Elizabeth National Park and Virunga Park and also funded the time of several of the Wildlife Conservation Society staff to undertake the modeling approach described here. The John D. and Catherine T. MacArthur Foundation provided support for some of the basic data collection and mapping that was made by WCS, and USAID and USFWS grants contributed to the aerial surveys of wildlife in 2006 and the aerial photo mapping of the park in 2006. Both WCS and WHRC are grateful for their continued support.

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Introduction

Understanding the impact of fire and large mammals on African Savannas is essential for ecologically sustainable management. Fire impacts both vegetation and wildlife directly by killing species in both categories but it is the longer term effects on vegetation which are the more important to understand as this ultimately affects the species composition of wildlife over the longer term. Similarly large mammals, particularly elephants and hippopotamuses can affect vegetation through their grazing and browsing and ultimately determine the composition of other species in the savanna. The factors that determine where large mammals are abundant determine where their impacts are greatest.

Factors determining large mammal abundances

The ecological factors that determine animal densities in any particular area are many and varied. In general they can be grouped under the following categories:

a. Edaphic factors: soil, geology, water availability, fire etc
b. Food supply: availability of vegetation for herbivores and prey for carnivores
c. Disease: disease can play an important role in regulating populations
d. Human impacts: impacts of hunting or poisoning by man

There have been studies of large mammal abundances in several savanna protected areas in Africa over the years and their impacts on the vegetation coupled with the impacts of fire. However, not many savanna ecosystems have been studied in great detail to assess the factors that determine large mammal abundances. The main parks that have been studied at this level of detail are Serengeti National Park in Tanzania and the Kruger National Park in South Africa.

Extensive work in the Serengeti National Park in Tanzania has assessed the factors that drive the wildebeest migration and the migration of other antelopes species (Sinclair and Norton Griffiths, 1979; Sinclair and Arcese, 1995). This research over the years showed that rainfall and food availability, specifically mineral availability (particularly phosphorus) for reproduction were the main drivers of the migration. Research in Kruger National Park (Du Toit, Rogers and Biggs, 2003) showed that food availability, which was primarily affected by rainfall and fire were the main factors determining abundances of large ungulates although disease, particularly anthrax, also regulated population numbers.

Food availability therefore seems to be important at both these sites and in African Savannas this is often related to rainfall, which can affect large mammal biomass (Coe, Cumming and Phillipson, 1976).

Impacts of fire and large mammals on African Savannas

Fire and elephants together are known to affect savanna ecosystems extensively but there is still debate over the importance of each factor. Elephants push over trees and are thought to encourage the expansion of grassland which also increases the fuel load for fire, allowing a site to burn more regularly and more intensively (Dublin, Sinclair and McGlade, 1990). However heavy grazing of the grassland created by other ungulates can remove the fuel load, creating grazing lawns that continue to be maintained by the grazers (Archibald *et al.* 2005). Long term monitoring of woodlands in Botswana showed different impacts of fire and elephants depending on the type of woodland. Those dominated by *Colophospermum mopane* were heavily affected by elephants while those dominated by *Baikiaea plurijuga* were heavily affected by fires. The structure of *Acacia erioloba* woodlands did not appear to be affected by either fire or elephants greatly (Ben-Shahar, 1998). In Amboseli National Park, Western and Maitumo (2004) showed that elephants are the most likely cause of woodland loss in the park since the 1960s.

An assessment of fires across southern Africa showed that rainfall over the previous 18 months was a strong predictor of fire extent in protected areas but not outside where people most likely control the extent of fires (Archibald *et al.* 2010).

Queen Elizabeth National Park

Queen Elizabeth National Park is located in the western (or Albertine) Rift Valley, southwest Uganda near the Rwenzori Mountains. It covers a total area of 1,978 km^2 of hills, plains, forest, and swamp, and abuts the border of the Democratic Republic of Congo (DRC). The Queen Elizabeth Conservation Area includes Kigezi Wildlife Reserve (269 km^2) and Kyambura Wildlife Reserve (154 km^2) making a total area of about 2,401 km^2 of managed habitat (Rwetsiba *et al*. 2002). QENP is continuous with Parc National des Virunga in Congo and as such forms one of the largest protected area systems in Eastern Africa, the Greater Virunga Landscape (Plumptre *et al*. 2007a), the most species rich landscape for vertebrates in Africa (figure 1). Together with the Virunga Park these two parks contain more bird species than any other on the continent and the landscape as a whole contains more mammals than anywhere else in Africa (Plumptre *et al*. 2007a). QENP was gazetted in 1952 as one of Uganda's first National Parks. The Park was re-named Rwenzori National Park by Idi Amin in 1972 but the name was dropped following the fall of the regime in 1979.

The history of human settlement in the area that is now QENP dates back centuries. On the basis of artefacts collected from the area, it is believed that the Mweya peninsula has been inhabited by man since about 50,000 BC. Mweya's early habitation is thought to be a result of Lake Edward's gently sloping shores, the water's profusion of fish, and animals coming to drink at the shore lines (Spinage 1970). The lack of some large mammal species in the park is thought to be possibly a result of hunting. Other than the hippo, however, large mammals have only recently colonized the park following the decline of the human population in the area towards the end of the nineteenth century (Spinage 1970). It is also thought that some species may have succumbed to disease. For example, Park (1891 cited in Malpas 1978) saw giraffe at the northern end of L. George with the Emin Pasha expedition of 1889 but these subsequently died out most likely as a result of rinderpest. It is also thought that some large mammals have never been there historically. There is for instance no evidence that either of the two rhino species was ever south of the Nile and north of R. Kagera (Kingdon 1974). Until the 1870s, QENP was cattle country ruled over by the Wasongora, a people who became rich and powerful from the Katwe salt deposits. This was the largest salt producing district in central Africa, and Katwe's trade extended both east and west across the continent (Spinage 1982). In about 1871, the 'Waganda warrior hordes of King Mtesa swept the area under the command of the *Katekiro*, the chief of Katwe fled to the small Islands in Katwe Bay but the chief of the Mweya peninsula remained unconquered under the onslaught. The area was re-invaded a few years later by Kabalega of Bunyoro.

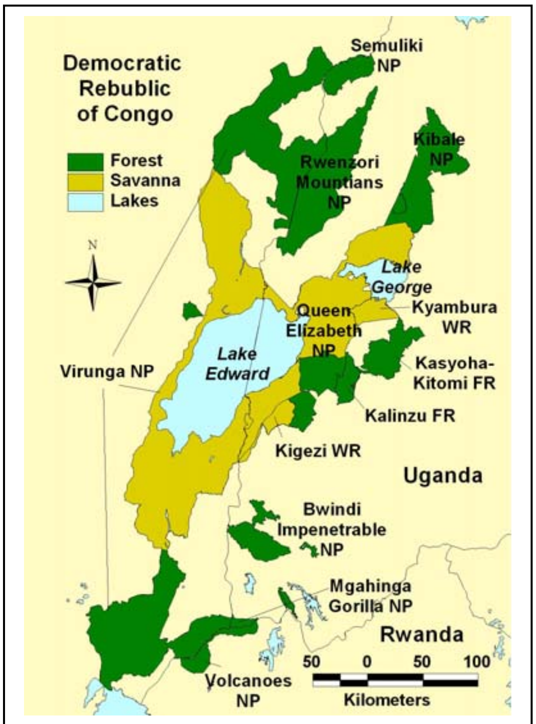


Figure 1. The Greater Virunga Landscape showing the location of Queen Elizabeth Park within the landscape, areas of savanna and forest cover and the international border separating this park from Virunga Park.

Until about 1871, there were herds of cattle in the area, and in June 1889, Mweya peninsula had 81 huts, many goats and sheep, while Katwe was populated by about 2000 people. Rinderpest is believed to have devastated the area in about 1890 (Spinage 1970) and in 1910-12, there was a bad outbreak of trypanosomiasis in the area (Morris 1960 cited in Spinage 1970). As a result, the population was partly evacuated in 1913-14. In May 1921, Kazinga village was re-opened for occupation, cattle grazing, and cultivation. In 1924, there was an increase in trypanosomiasis and the whole area was closed again, a few people were left at Katwe and Katunguru. By 1931, animals had already invaded the depopulated Mweya peninsula. Resettlement occurred in fishing villages, but cultivation was not allowed. Mweya was never re-settled by people except for the park headquarters and associated buildings.

Large mammal numbers steadily built up as the result of the lower densities of people and by the 1960s QENP had one of the highest large mammal biomass densities recorded on Earth (Petrides and Swank, 1965). The impacts the large herbivores (primarily elephants, buffalo and hippopotamuses) had on the vegetation was great at this time and several studies were made to measure this impact directly in both QENP and Murchison Falls National Park (MFNP).

Civil war in Uganda during the mid to late 1970s and early 1980s and then war in DR Congo from 1996 to 2006 decimated the large mammal populations. However, the transboundary nature of the Greater Virunga Landscape buffered the decline in ungulate numbers by allowing some individuals to see refuge over the international border when poaching was high (Plumptre *et al*. 2007b). As a result the populations in Queen Elizabeth National Park have recovered relatively quickly. Elephant numbers and most large ungulate densities are at levels similar to those estimated in the 1960s because of in migration from DR Congo. As a result of this in-migration it is likely that most ungulate populations are at or near carrying capacity in Queen Elizabeth Park while in Virunga Park they are very low because of rampant poaching by armed groups. In order to assess the factors that might affect population density in these ungulates there is a need to have populations at carrying capacity, otherwise they may not be constrained by any factors.

This study aimed to assess how ungulates respond to habitat types and fire within the Queen Elizabeth National Park and to assess the joint impacts of fire and large mammals on other taxa, notably plant and bird species.

Prior research in Queen Elizabeth National Park, Uganda

Much research was undertaken in Queen Elizabeth National Park in western Uganda in the 1960s and early 1970s. This research focused on the impacts of animals and fire on the vegetation and determined that grazing by elephants coupled with fire tended to open up the habitat and reduce woody vegetation cover (Lock, 1993). Conversely heavy grazing by hippopotamuses tended to reduce grass cover and encourage unpalatable woody shrubs (Lock, 1972). Experiments on the Mweya Peninsula in the late 1960s where the hippopotamus population was culled showed that the recovery of the vegetation allowed an increase in the abundance of other ungulates, particularly buffalos (Eltringham, 1974).

Several autecological studies were undertaken on ungulate species: Waterbuck (Spinage, 1982), elephant (Field, 1971;Malpas, 1978), Hippopotamus (Klingel, 1991; Eltringham, 1999), Uganda Kob (Modha,1971; Balmford, 1992,; Balmford, Albon and Blakeman, 1992; Deutsch, 1994a,194b), buffalo (Grimsdell, 1969), Topi (Yoaciel, 1977; Yoaciel and Van Orsdol, 1981), bushbuck (Waser, 1975; Wronski *et al.*, 2006) and warthogs (Clough, 1969; Clough and Hassan, 1970) and some of these also looked at the impacts of these herbivores on vegetation. Much of the research in Queen Elizabeth National Park was summarized by Olupot *et al.*, (2010) and a summary of the most pertinent information is given here.

Impacts of elephants

Studies of MFNP vegetation showed there have been significant changes due to the extremely high levels of elephant grazing and browsing during the 1950s and 1960s. Before that time, the park had been dominated by woodland, but much of the area had turned to grassland by the 1960s, with a 55-59% reduction in the number of trees over 9 cm diameter at breast height between 1937 and 1956 as a result of elephant damage (Buechner and Dawkins 1961, Laws *et al*. 1975). The greatest impact on the vegetation was south of the river where populations had reached 2 elephants per km^2 by 1968 (Laws 1968). Intense foraging by elephants following fires in the 1960s was largely responsible for preventing the regeneration of trees in this park (Laws *et al*. 1970). Elephant damage suppressed all the 30-40 fire-resistant species except for *Lonchocarpus laxiflorus,* which has root sprouts that can withstand fire (Buechner and Dawkins 1961). The increase in grassland because of the opening up of thickets and damage to trees by browsing elephants led to an increase in the intensity of fires (Smart *et al*. 1985). At the time, elephants caused habitat damage that not only affected the landscape and other animals, but also seemed destined to produce a crash in their own populations. Culling in the late 1960s followed by years of instability and increased poaching eased the pressure on the habitat. Massive reduction in elephant numbers by the early 1980s was followed by the gradual recovery of some of the park's original habitat, with about 75% of the park estimated to be woodland vegetation in 1995, compared to about 18% in 1970 (Mann 1995).

Similarly, surveys in QENP from the mid to late 1980s all suggested a significant influence of the elephant. The dramatic decrease in numbers of elephants between 1970 and the mid to late 1980s, was accompanied by regeneration of *Acacia* trees, and expansion of the *Acacia* woodlands and thicket vegetation in general (Lock 1977a, 1977b; Lock 1985; 1988). In addition, not only the quantity of thicket vegetation but also the diversity of species was increased, with much greater numbers of *Euphorbia candelabrum* and *Securinega* (*Fluggia) virosa*, a favorite elephant food, and an increase in vegetation at the lake margins creating a fringe of *Vossia cuspidata* around the lakes (Lock 1985, 1988). The increase in thicket and lakeshore vegetation in the park between the 1960s and 1980s was a result of reduced intake as a result of a reduction in the numbers of elephant, as well as buffalo, and hippo, according to census estimates from 1969 and 1989 (Lock 1993).

Impacts of Hippopotamuses

Hippopotamuses also have profound effects on vegetation when at high density due to their inefficient digestion, their size, and their limited movements from water to feed. As hippos graze on land at night, and return to permanent water by day, the impact that they have on vegetation within a zone of about 3 km from water is noticeable, and particular grassland types occur in zones according to their distance from permanent water (Lock 1972). During the dry season, this zone can be increased somewhat, as the quality of vegetation within the zone becomes poorer (Laws *et al*. 1975). Hippos prefer to graze short grass and maintain it as such. Longer grass is left untouched for as long as there is enough short grass. This results in characteristic 'hippo lawns' often surrounded by longer un-grazed grass of the same species. Constant use may lead to a degree of overgrazing and trampling depending on soil and climatic conditions. Once this process gets beyond a certain point, rainwater runoff erodes a ridge or a terrace at the edge of a lawn which may become undercut. This happens because the roots of the heavily grazed grass are less numerous than those of less grazed lawn and bind the soil less tightly (Laurie 1974). In one study where hippos were excluded from a grazing area for 2 years, the area that was originally a mosaic of short and tall grasses and bare patches of soil became relatively uniform (Lock 1972).

A decrease in the climax grass species of *Bothriochloa insculpta*, *Themeda triandra*, *Hyparrhenia filipendula* and *Hyperrhenia dissoluta*, and a change in species composition to *Heteropogon contortus* and *Sporobolus* spp. was evident in areas of high hippo grazing in QENP during the mid 1960s (Heady 1966). With even more intense grazing, the composition of the grass community changed further to be dominated by *Aristida*, *Eragrostis*, *Tragus* and *Sida* spp. as well as *Sporobolus stapfianus* and *Microchloa kunthii* . At the time of peak hippo grazing on the Mweya peninsula (1950s), the dominant vegetation was *Chrysochloa orientalis*, a low growing plant with low biomass but high surface cover (Eltringham 1999). Hippo grazing in this park also favours tussock forming strong-rooted grasses, principally *Sporobolus pyramidalis* (Lock 1972). These grasses are replaced by taller grasses under low grazing regimes. As the taller grasses take over there is also an increase in litter, which prevents erosion by protecting the soil from the direct impact of rain, and absorbing water that would otherwise run off immediately (Eltringham 1999). Upon removal of hippos from the Mweya peninsula in 1957-58, tall grasses increased and the creeping grasses decreased, and thus the number of other large mammals increased (Eltringham 1974). Heavy grazing also essentially fireproofs an area by removing the fuel (Heady 1966).

Moderate hippo grazing in QENP maintains a mosaic of short and long grasses that are utilized by other grazing species (Lock 1972). However, high population densities of hippos can lead to complete loss of the vegetation, resulting in high rates of erosion and low permeability of the soil (Thornton 1971). This deterioration of the habitat then decreases the carrying capacity of this grassland mosaic habitat for other species as well (Edroma 1981). Exclusion of herbivores from areas of QENP has provided insights on the effects of trampling. When herbivores were excluded for 20 years from grassland dominated by *S. pyramidalis*, with thickets dominated by *Capparis tomentosa* the result was that grass density, cover and root biomass increased when compared to adjacent areas that had been open to grazing (Lenzi-Grillini *et al*. 1996). The trampling of vegetation that happens in areas that are heavily used by grazers had a significant effect on root biomass (Lenzi-Grillini *et al*. 1996, and references in Edroma 1981). In addition, it is thought that the effect of grazing and trampling on the surface structure of the soil influenced the germination success of seeds (Lock 1972). Grassland areas that were grazed freely tended to have lower vegetation biodiversity (Lenzi-Grillini *et al*. 1996).

Impacts of fire

Fire is relatively common in savannas. In the 1970s for instance, up to 32.7% of QENP burned in one season, and 55% of the park had burned at one time or another during a 3-year study (Eltringham 1976). Fire damages vegetation in the immediate term and the extent of subsequent effects of fire on vegetation depends on the available fuel. When the burn occurs at the beginning of the second dry season (June-August), it promotes growth and diversity of herbaceous species in *Hyparrhenia-Themeda* grassland (Edroma 1977, 1984). As the dry seasons in the park are too short to allow total drying of the soil and grasses, the duration and intensity of fires when allowed to burn is relatively low. Management of fire has promoted early burning at the end of the wet season so that the fires are less intense. A number of smaller herb species such as the grasses *Microchloa kunthii*, and other herbs such as *Hibiscus aethiopicus* and *Rhamphicarpa* sp., flower after burning when the taller grasses have been removed, suggesting that they are at least partly dependant on fire for their survival (M. Lock pers. comm.). Burning stimulates uniform sprouting and growth of grassland (Edroma 1984), which in turn attracts herbivores (and thus their predators) to areas that had been abandoned due to the maturity of the grasses. Fire has been shown to stimulate germination of the buried seeds of *Themeda triandra* (Lock and Milburn 1971). Under usual conditions, fire seems to have more of an effect in maintaining existing vegetation structure than causing changes in the habitat structure of the park. Because fire has been a historical factor in the development of the vegetation community, plants have adapted to thrive with regular burning (Edroma 1977, Nangendo *et al.* 2006). In the absence of intensive action by elephants, fire does not cripple tree regeneration in woodland habitat Laws *et al*. (1970). Regular occurrence of fire also stimulates fresh growth of new grasses which are much more palatable to grazers than mature grasses (Wilson 1991). Fire also facilitates germination of certain woody species. Laboratory investigations of *Acacia sieberiana* seeds taken from an area affected by fire in QENP showed a much higher rate of germination than seeds that had not been exposed to fire, so it appears to be a necessary process for regeneration of this species (Sabiiti and Wein 1987). Seeds infested by bruchid beetle larvae are more sensitive to fire than are un-infested seeds, and thus the higher rates of germination in fire treated seeds are probably due to the destruction of the bruchid larvae (*Ibid.*). *Acacia gerrardii* is less resistant to fire than *A. sieberiana*, showing reduced germination rates when exposed to it (Mucunguzi 1995a; 1995b; Mucunguzi and Oryem-Origa 1996). This is likely due to their smaller and less protected seed (Mucunguzi and Oryem-Origa 1996). Thus *A. sieberiana* has a higher potential to survive in burnt areas.

While fire encourages or maintains vegetation community structure and composition under normal circumstances, under others its effects are more complex. At high fire frequencies when elephants are present, it promotes the establishment of trees that are fire-resistant and damages young trees, inhibiting regeneration and leading to lower vegetation diversity, especially of herbaceous plants (Smart *et al*. 1985). For example, *Acacia* trees are easily damaged by frequent fire at young growth stages although they require fire to germinate (e.g. Smart *et al*. 1985). In Kidepo Valley National Park, the presence of fire in the 1960s to early 1970s increased elephant browsing pressure on trees, as fire removed low browse, making it more likely that elephants would push over mature trees to browse on them (Harrington and Ross 1974). With increased grazing and browsing pressure in the park, it was forecast that this park would follow MFNP toward an increasing amount of grassland and decreasing amount of woodland. The role of fire in this process was threefold: 1) preventing *Acacia* woodland from regenerating in the wetter areas of the park, 2) preventing the development of extensive thicket in the drier parts of the park, and 3) limiting the montane woodland on the hills in Kidepo to isolated patches (Ross *et al*. 1976).

In the absence of elephant browsing, high fire frequency reduces species diversity by promoting fire-resistant (usually less palatable) species over the less resistant (usually more palatable) ones. In QENP, regular burning may result in dominance by fire-tolerant grass species, such as *Themeda triandra* and *Cymbopogon afronardus*, which sprout very quickly after fire (Wilson 1991). Because very long, mature grasses are absent when fires are frequent, thickets dominated by *Capparis tomentosa* increase under these conditions. These thickets and *Acacia sieberiana* trees are in greater density in areas where there is little or no browsing by elephants. High intensity or frequency of fires, caused by either significant increases or decreases in herbivory, can therefore alter the vegetation communities, generally causing them to become less diverse (Smart *et al.* 1984).

The preceding description of the pros and cons of fire in rangelands and its potential use in park management has been a subject of debate among scientists for many years and there are still disagreements. On the one hand, fire prevents regeneration in wooded grasslands and conversion of woodland to grassland, while in the open grasslands, it improves palatability and nutritional value of the new grass which springs up after the burn. On the basis of a decline in the area of woodland, probably due to both the action of elephants and fire, Eltringham (1976) recommended fire control in QENP using fire breaks and a controlled burning scheme to create fire breaks, especially between forested areas and grassland early in the dry season. However despite the best intentions these management recommendations were not implemented or did not succeed in reducing fire which is often set by people using the roads throughout the park, or which spreads from outside the park. Fire management measures were re-introduced in the park in 2005 by applying controlled early burning in selected areas. Jaksic-Born (2009a) made recommendations for fire management regimes in the park following an extensive study of the impacts of fire on large mammals in the northern sector of the park (Jaksic-Born, 2009b). This study showed that Uganda kob fed preferentially on burnt areas of grassland soon after the grasses had started to sprout and that these areas of short grass were important for this species. Likewise it showed that buffalo required areas of burnt grassland but fed in them at a later period when the grass was taller. The study also documented the spread of spear grass (*Imperata cylindrica*) in this part of the park and highlighted the problems of fire in the management of this species which appeared to be adapted to regular burning.

Methods used

Vegetation mapping

In June 2006 an aerial mapping survey was undertaken using Enso Mosaic over Queen Elizabeth and the savanna portions of Virunga National Park. Enso Mosaic comprises a digital camera linked to a GPS and computer which can be programmed to take photos at regular intervals to allow an aerial photo coverage to be obtained. The images are then orthorectified and a mosaic created which is georeferenced and can be imported into a GIS package (figure 2). Aerial photographs from a survey made in 1989/90 were also scanned into a computer at high resolution and then stitched together using Enso Mosaic. The aerial photographs used to map Uganda in 1954 were also located for the park and a third mosaic was created for this time period.

A 250 x 250 metre grid of cells was overlaid over this imagery in a Arcview 3.3 and then each cell assigned a vegetation type based upon visual interpretation by one observer (T. Akuguzibwe) to generate vegetation maps from these two time periods. The vegetation types that were assigned are given in table 1.

Table 1. Vegetation types, their codes and definitions assigned to aerial photo mosaics.

Code	Landcover Type	Description
PS	Papyrus Swamp	Dense Papyrus - more than 50% cover
OS	Other Swamp	Seasonally waterlogged areas with different vegetation - not papyrus
SF	Swamp Forest	Forest North of lake George that is permanently flooded
GL	Grassland	At least 20 m radius of grassland with no trees/shrubs
WG	Wooded Grassland	Between 10-50% woody cover - grassland under and between trees
WD	Woodland	More than 50% woody cover - grassland between trees
LF	Low Stature Forest	Trees and shrubs -at least 30% tree cover - trees generally less than 15 metres tall
HF	Tropical High Forest	Trees only and most canopy trees greater than 15 m
RF	Riverine Forest	Narrow strips of trees along streams and rivers
EU	Euphorbs	Euphorbia candelabra with at least 30% cover
SC	Bush / Scrub	Low stature bushes with little grass between - at least 50% cover
AB	Banana	Banana trees form at least 50% cover
AT	Tea	Tea forms at least 50% cover
AC	Coffee	Coffee/low stature tree crops form 50% cover
AP	Tree Plantation	Trees planted in rows - eucalyptus or pine
PG	Pastoralists grassland	Grassland used for grazing cattle, goats and sheep
AO	Other Agriculture	Any other short stature crops - cassava, potatoes etc
BE	Bare Earth	Less than 20% vegetation cover
SE	Settlement	Human habitation and bare earth/roadscovers at least 30% of land
SW	Salt Water	Saline Crater lakes
WT	Water	Other Lakes

Figure 2. Example of Enso Mosaic product for Mweya Peninsula in Queen Elizabeth National Park.

Animal densities

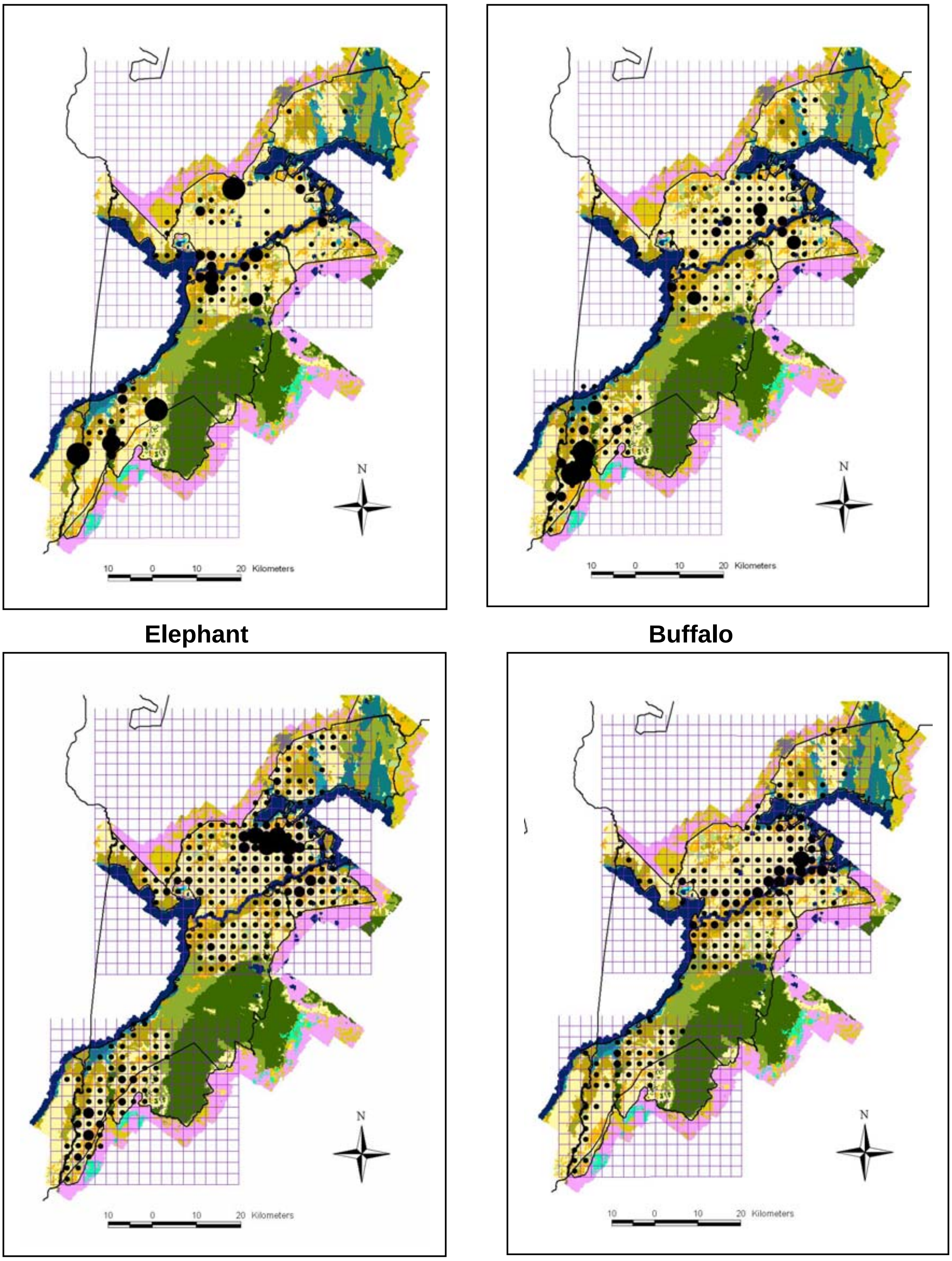
Since 1995 the Uganda Wildlife Authority has been undertaking aerial sample counts of wildlife in Queen Elizabeth National Park using a standardized grid flight system over the savanna areas of the park. The grid cell sizes are 2.5 x 2.5 km and the observers record all wildlife seen within each cell. During the processing of the aerial census data densities of different species are assigned to each grid cell as well as estimates for sectors of the park and the whole park.

Aerial sample counts have been undertaken in 1995, 1999, 2000, 2004, and 2006 using the same grid cells and it was therefore possible to calculate a mean density of each species per cell for these five censuses and also a mean was calculated for only animal densities from the three censuses from 2000-2006. Mean animal density was then plotted for these grid cells over the vegetation map to allow a visual assessment of relative abundance of the different species across the park (examples given in figure 3).

The vegetation map was created using 250 x 250 metre cells but the animal surveys use 2.5 x2.5 km cells. There are therefore 100 vegetation cells per animal survey cell. The number of cells of each vegetation type (equivalent to percentage) were then calculated for each animal survey cell using ArcView 3.3. This produced a file of percentage of each vegetation type per animal survey cell. The mean density of each animal species surveyed between 2000-2006 was then joined to this file, matching the field by Cell ID to produce one file with vegetation data and animal density data.

Fire mapping

Woods Hole Research Centre (WHRC) digitized all fire scars at the end of dry seasons (Dec-Feb and Jun-Aug) from 1973 to 2009 from Landsat Quick-look imagery. Burns, visible as dark swaths in relation to the vegetation on the satellite imagery, were heads-up digitized using the Landsat Quick-look data available from the USGS Global Visualization Viewer (http://www.glovis.usgs.gov). Normally, Quick-look data are not used for analysis since these images are simply "snapshots" of the data that allow analysts to assess image quality (ie., determine if the study area is cloud-free before purchasing the image). However, these data were deemed suitable for use since (1) the burn scars were easily discernable, (2) the images were free to download and provided a complete digital record of the study area since the Landsat program inception, and (3) the image file size was small (~50-300 kb), requiring very little bandwidth to download.



Elephant **Buffalo**

Uganda Kob **Waterbuck**

Figure 3. Relative abundances of four ungulate species in the Queen Elizabeth National Park, averaged over six aerial sample counts from 1995-2006.

WHRC digitized burn scars for every year where cloud-free imagery was available for the landscape from 1973 to 2009 with the following number of images digitized in each decade: 1970s-2 images; 1980s – 8 images; 1990s- 5 images; 2000s – 17 images. Years were separated into two dry seasons (Dry Season 1: December (year-1)-April, Dry Season 2: May-November) to make comparisons between years and seasons. Burns delineated from multiple images, but within the same burn season, were grouped together using a GIS analysis to provide one comprehensive dataset for each dry season. The grouping of data files affectively removed duplicate burns that may have been delineated on multiple occasions (ie., burns may be visible in multiple images throughout the dry season). (appendix 1).

The number of times an area burned was then mapped for the period 2001-2009 because this was the most continuous sequence of images (appendix 1).

The frequency of burning per 2.5 x 2.5 km grid cell was then calculated as follows. Only data from within the park was used by clipping the fire layer to the boundary of the park. Raster data sets were then created for each season's burning at a 30 x 30 m resolution (because this was the original image resolution for Landsat imagery) and assigned a 1 if burnt or 0 if not burnt. These were then summed for the 2001-2007 period to calculate a burn frequency over this time period. The mean number of times a 30 x 30 m cell burned was then calculated for cells within each 2.5 x 2.5 animal survey cell to produce a mean number of times burned. This value was then joined with the vegetation and animal census data.

Bird and Plant surveys

A survey of the vegetation of QENP was made in 1992 (Zandri and Viskanic, 1992) by establishing 137 plots across the park to create a vegetation map based on plant communities (as opposed to structural categories such as woodland, grassland etc). This study mapped the plots and marked them on a series of aerial photograps. Unfortunately we were unable to locate the original photographs but we were able to use the map of the plots locations and the description of the plots to identify their probable location on the 2006 aerial survey imagery (described above). Each plot was assigned a GPS coordinate from the imagery. We then overlapped the plots on the map of fire frequency in the park. We wanted at least 10 plots in each of the burn frequency categories from 0 no burning) to 12 (burnt in 12 dry seasons) so additional plots were located randomly in areas where there were insufficient to achieve this. These we numbered (501-568) to differentiate them from the original plots (appendix 2). The number of plots in each burn frequency category is given in table 2.

Table 2. The number of vegetation plots in the different burn frequency categories. It was not possible to locate 10 plots in the burn frequency category 13 because it was rare.

Burn frequency in 2000s	Total
0	51
1	18
2	14
3	14
4	16
5	15
6	13
7	10
8	10
9	11
10	9
11	11
12	12
13	2

At each plot point counts were made for birds. Two ornithologists visited the plot and waited five minutes before proceeding to make a point count of the birds over a five minute period, recording all species they saw or heard and the approximate distance to each one.

A team of botanists also visited each plot and measured the botanical composition of the plot in two ways:

1. In order to compare with the 1992 measurements plots of the same size were measured in September-November 2009. All trees were enumerated in a circular plot of 56 metre radius. Herbs were recorded in a nested plot of 2.8 metres radius and shrubs or lianas within a plot of 14 metre radius. Vegetation cover was recorded for the herbs, shrubs and lianas while the number of trees were recorded for each species in the plot. Vegetation cover was recorded on a modified Braun-Blanquet system as follows which replicated the cover measurements used in 1992 (Zandri and Viskanic, 1992):

1 – One or a few individuals
2 – Less than 5% of the sampled area
3 – Abundant but with low cover or less abundant but with higher cover; less than 5% of total cover
4 – Very abundant but less than 5% total cover
5 –5-12.5% cover
6 – 12.5-25% cover
7 – 25-50% cover
8 – 50-75% cover
9 – 75-100% cover

The aspect, slope and the number of termite mounds in the plot were also noted.

2. In order to compare the vegetation data with a series of surveys made by the Wildlife Conservation Society throughout the Albertine Rift we also measured the same plots using the following protocol: All herbs were collected within 2 metres radius of the GPS point and identified to species. In 10 metre radius plots all lianas larger than 1 cm DBH and saplings/shrubs between 2.5-10cm DBH were recorded. In a 20 m radius circle all trees were recorded to species. Species that could not be identified in the field were collected and pressed and identified at Makerere University Herbarium. Trees were classified into DBH intervals and the number recorded in each grouping: 2.5-10 cm; 10-30; 30-50; >50. Tree canopy height and cover was estimated for the 20 m radius plot as well as the percentage coverage of shrubs, grasses, herbs and bare earth.

The locations of the plots are given in appendix 3.

Statistical analyses

Large mammal associations with vegetation types

The combined data for vegetation, mean animal density and mean burn frequency for the 2.5 x 2.5 km grid cells was analysed in SPSS 9.0 in two ways:

1. A multiple regression model was created and all available predictive variables (vegetation and burn frequency) were entered to develop a model that would predict each species density

2. A stepwise multiple regression model was calculated that selected those variables that best predicted the density of a species of animal and eliminated those variables that were redundant. A 5% entry/exit level was used.

All data were normalized where necessary using a natural log transformation.

Biodiversity assessments

The number of bird and plant species per habitat types and per burn frequency groupings (0, 1-3, 4-6 and >6 times burnt in 2000s) was assessed using rarefaction in Biodiversity Professional. A cluster analysis using Jaccards measure of distance was also calculated to assess the relative similarity in species composition in the different habitat types and in the areas burnt at the same burn frequency groupings. The Shannon-Wiener and Alpha measure of diversity was also calculated for each habitat.

Plant associations and the impacts of large mammals and fire

Detrended Correspondence Analysis and Canonical correspondence analysis using CANOCO 4.5 (ter Braak and Smilauer, 2002) was used as a tool to tease out the relative effects of large mammals and burn frequency on the composition of plant species in QENP. The data used in the assessment included the plant plot data from the first method described above. Environmental variables used to try to explain plant distributions included:

1. altitude measured using a Garmin 60Csx GPS,
2. average large mammal biomass for the 2.5x2.5 km cell in which the plant plot occurred from all aerial surveys made,
3. average Elephant density in the 2.5x2.5 km cell in which the plot was located,
4. the distance to the nearest hippo pod mapped during the 2008 survey made by UWA was divided into distance categories which received a score from 1-6 (6=0-500m; 5=500-1000m; 4=1000-1500m; 3=1500-2000m; 2=2000-2500m; 1>2500m). Hippos are thought to graze up to 3 km from water at night in QENP (Lock, 1972).
5. the number of termite mounds at a plot which is thought to influence plant species composition (Olupot *et al.*, 2009),
6. rainfall derived from measurements taken across the park at 43 sites in the 1960s (data provided by M. Lock) and extrapolated to estimate rainfall across the park using Arcview 3.3 spatial analyst,
7. Habitat type (Forest-F; Bush – B; Woodland – W; Grassland – G).
8. Year of measurement (1992 and 2009)

The methods used are described in more detail under the presentation of the results.

Results

Fire frequency and area burnt

Fire frequencies in the in the landscape varied in different parts of the landscape. The areas that burnt frequently in the 2001-2009 period also burnt frequently in the 1970s, 80s and 90s (figure 4).

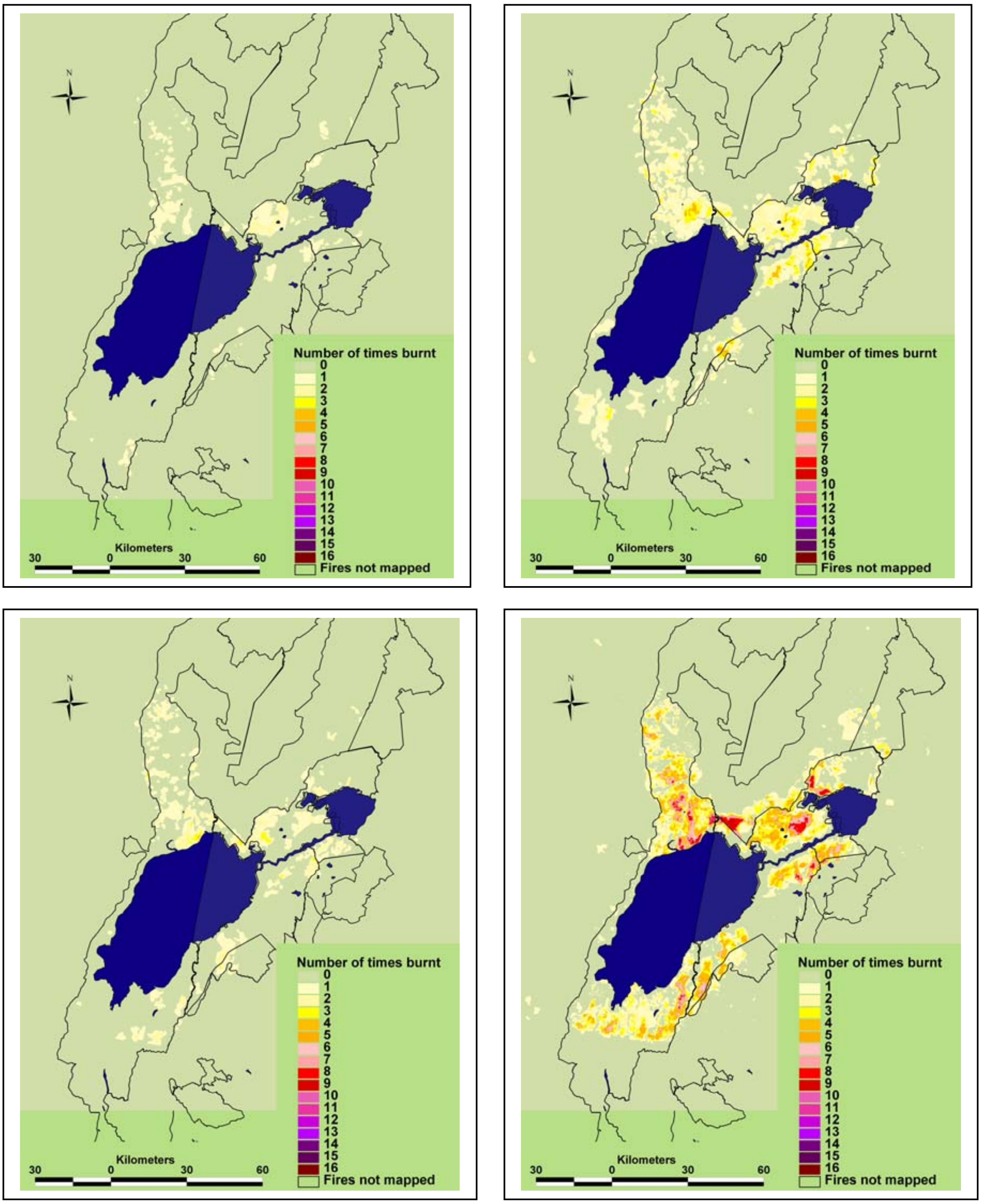


Figure 4. Burn frequencies in 1970s (top left – max possible burns=2), 1980s (top right – max possible burns=8), 1990s (bottom left- max possible burns=5) and 2000s (bottom left – max possible burns=17).

The area burnt in QENP varied between years from only 12.8 km^2 in the June-August dry season in 2007 to 533.8 km^2 in the December-February dry season of 2003 (figure 5). There were no significant differences between the average area burnt in the 1970s, 1980s, 1990s or 2000s (F=0.763, df=3,28, P=0.52). There is therefore no evidence of a difference in the average area burnt per season under fire management in QENP (1970s and 2000s) and when there was no active management (1980s and 1990s). Unfortunately we cannot tell from the images which burn scars are deliberately set for fire management (early burning) and which were natural or set by local people. This fact may explain why no differences in average area burnt occur between these decades.

The average area burnt in the December-February dry season was 258.2 km^2 (+/- 36.8 standard error; n=17) and in the June-August season was 136.8 km^2 (+/- 35.1 standard error, n=15). This is about 15.6% and 8.2% of the area of grassland and woodland that can burn in the park. The range of values is similar to those found by Eltringham (1976) from 1970-1973.The average areas burnt are significantly different between the two dry seasons (t=2.38, p=0.024). We also tested to see if there were differences in areas of savanna burnt in El Nino or La Nina years but there was no significant difference for the average area burnt per year per season. However if we separated seasons then there was a significantly larger area burnt in the Jun-Aug period in El Nino years (t=-3.34, P=0.002) and smaller area in La Nina years (t=4.01, p<0.001) but no difference for the Dec-Jan period for either El Nino or La Nina years.

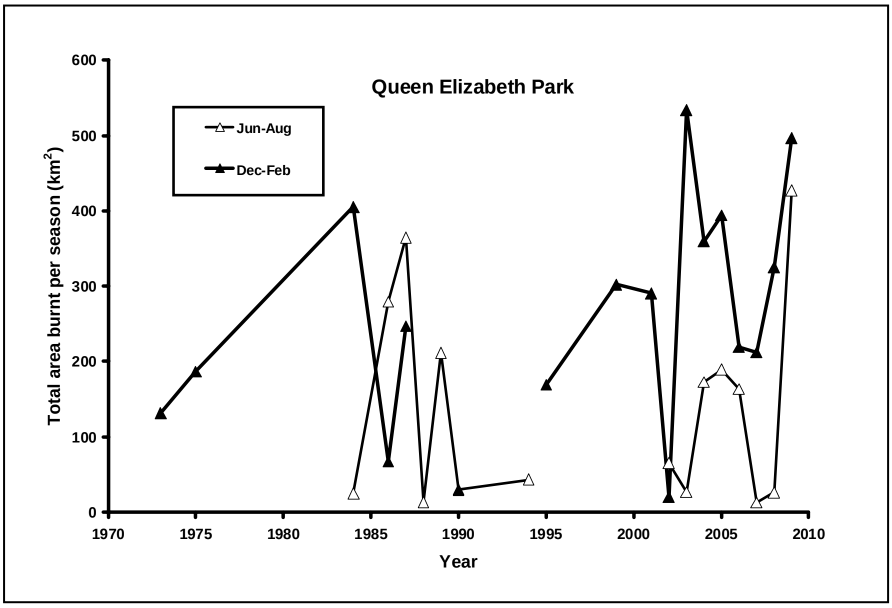


Figure 5. The area burnt in each dry season from images obtained between 1973 and 2009.

Burn frequency as measured from the satellite images (figure 4) is strongly related to the percentage cover of herbs and grasses (F=5.229, df=5,175, P<0.001), and negatively related to the cover of trees (F=3.084, df=5,178, P=0.011) and shrubs (F=11.206, df=5,178, P<0.001) at the vegetation plots we measured. Therefore as the vegetation cover changes over time the fire frequency will also change at that site. It is known that as hippopotamus abundance increases that the cover of grasses and herbs decreases and shrubs increase in cover and inversely with increases in elephant abundance the vegetation tends to decrease in tree and shrub cover and increase in grass cover (Lock, 1972; Eltringham, 1980; Olupot *et al.*, 2010). Therefore the changes in abundance of these animal species over time in this landscape has probably affected fire frequency and location. Unfortunately we don't have enough images from the early decades when animal numbers were high to assess where this effect may have occurred.

Vegetation changes since 1950s

The vegetation maps produced from the aerial photography imagery from 1954, 1989/90 and 2006 show a general increase in woody cover over the park following the decline in biomass of large herbivores in the 1970s and their gradual recovery up to the present day (figure 6).

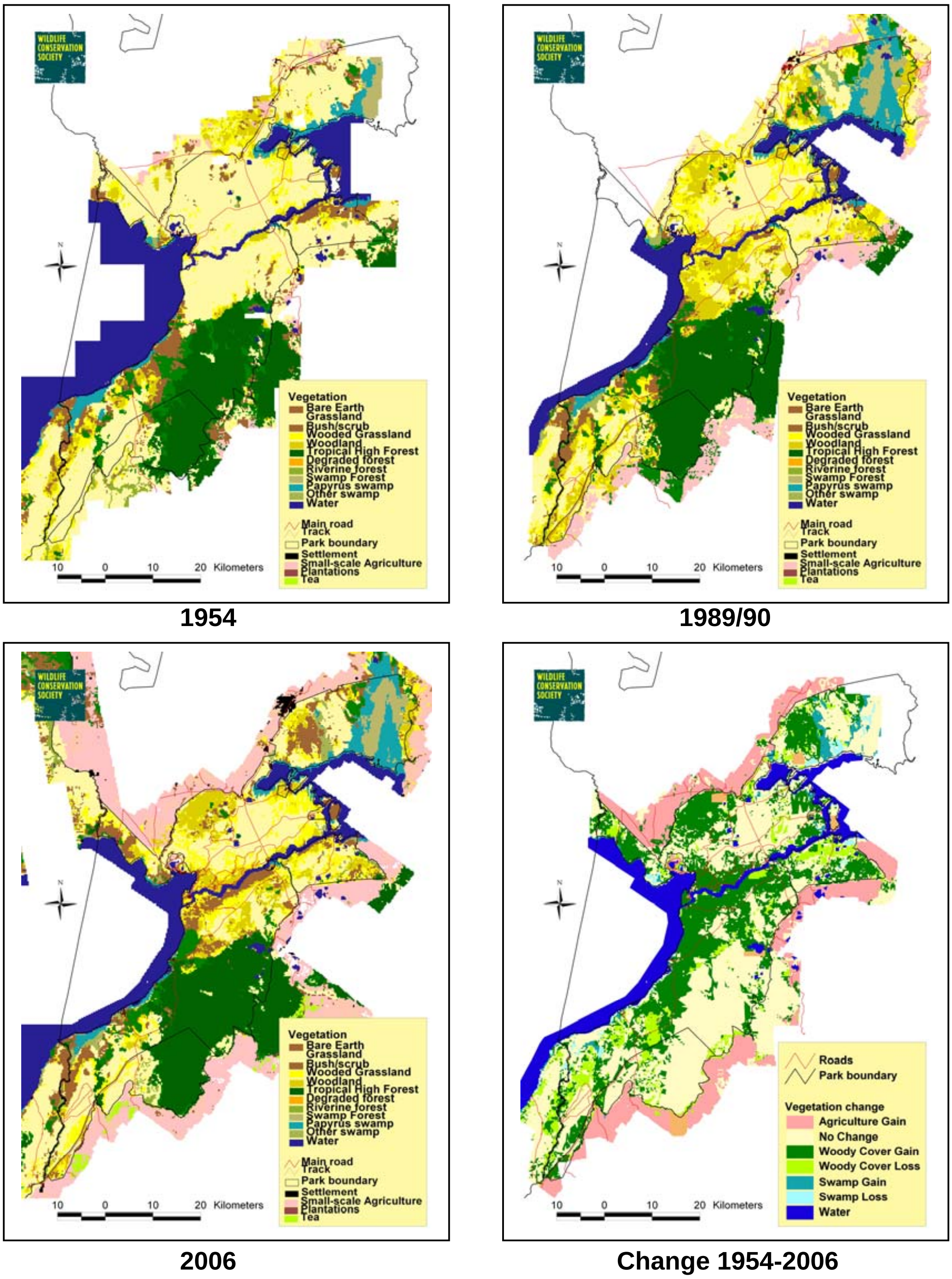


Figure 6. Vegetation cover in QENP in 1954, 1989/90 and 2006 and the change in vegetation cover between 1954 and 2006.

However, there are areas where woody cover has been lost between 1954 and 2006. This may have been a result of the increases in large mammal numbers between 1954 and 1970 before the major decline in the mid to late 1970s. The elephant population is known to have increased at this time and probably killed many trees and thickets before their decline in the 1970s. Swamp vegetation also tended to increase around the lake shore and along the Kazinga Channel with the decrease in large mammals.

The changes in woody cover between the two periods was calculated by summing the number of 250x250m cells that had changed. The results show that between 1954 and 2006 there was a large increase in woody cover of 1,021 km^2 but also a decrease in some areas of 260 km^2 (Table 3). By examining the changes between different dates we can see that most of the increase in woody cover occurred between 1954 and 1990 and that since 1990 woody decrease is not too different to woody increase.

Table 3. Changes in area of woody cover (increase, decrease, no change or human-induced change) between the three time periods (1954, 1990 and 2006). The differences in total areas is due to the fact that the aerial photo coverage differed between periods.

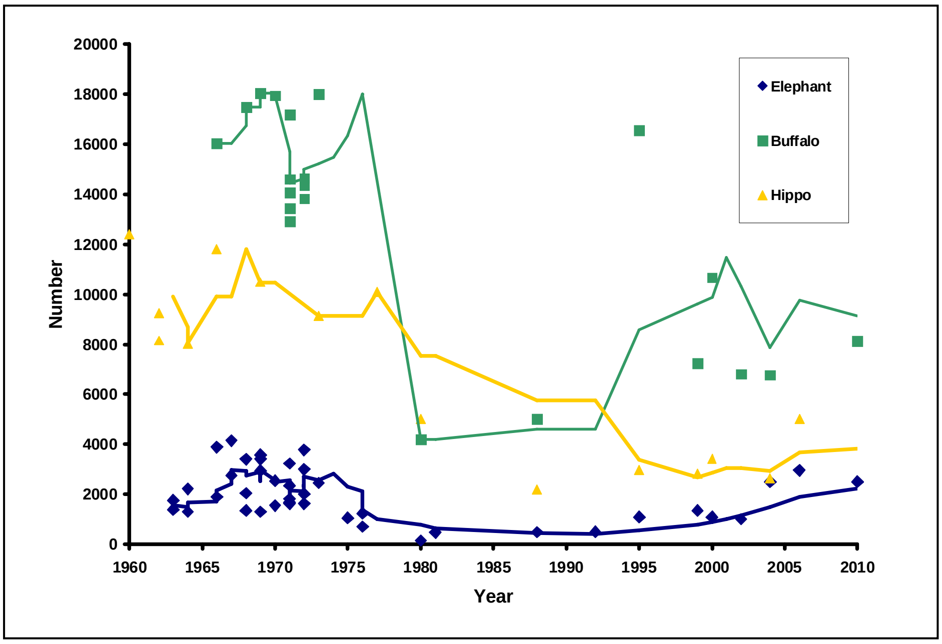
	Increase in woody cover Km^2 (%)	**Decrease in woody cover Km^2 (%)**	**No change Km^2 (%)**	**Human induced change Km^2 (%)**
1954-1990	1003 (29.9)	303 (9.0)	1793 (53.4)	258 (7.7)
1990-2006	437 (11.6)	316 (8.4)	2758 (73.0)	269 (7.1)
1954-2006	1021 (27.8)	260 (7.1)	1826 (49.8)	563 (15.3)

Large mammal population changes

Populations of the large mammals surveyed from aerial surveys have fluctuated between surveys which started in the 1960s. Most species experienced a major crash in numbers in the 1970s because of the intense poaching by the military at this time and then subsequently after the overthrow of the regime of Idi Amin in 1979 (figures 7 & 8).

Some species such as elephants, buffalos and waterbuck have recovered to relatively healthy populations since the 1970s but others such as hippopotamuses, warthogs and topi have remained at lower levels compared to the 1960s estimates. Uganda kob increased up to the early 2000s but have declined greatly since then and are now at their lowest level ever.

A closer look at the elephant data shows that there were great fluctuations between counts in the 1960s. Some of this could be explained by movement of elephants across the border into Virunga Park in the Democratic Republic of Congo but it is also due to variation in the counts with more animals being missed during some censuses (figure 9).



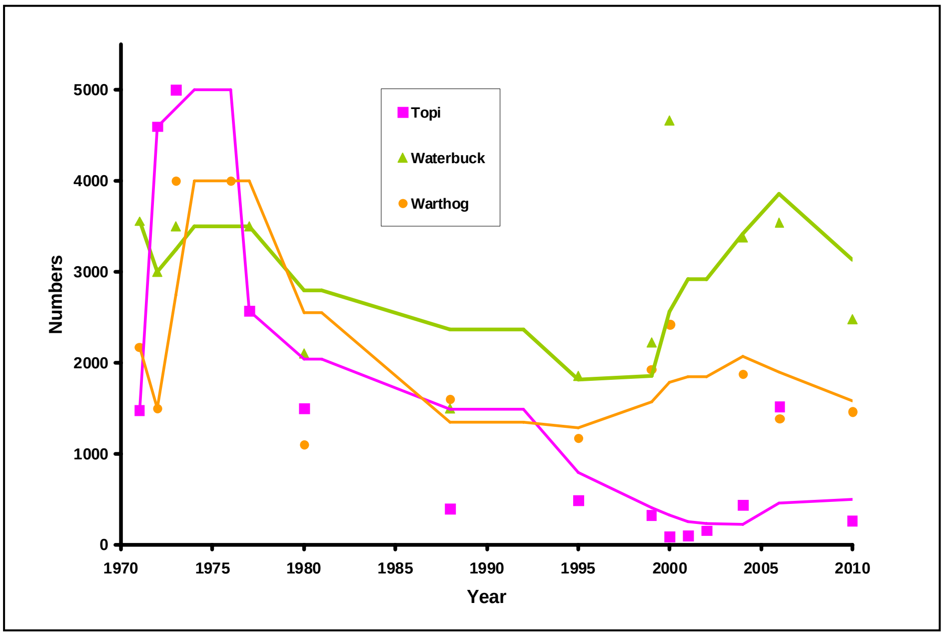


Figure 7. Population changes in the mega herbivores (top) and large antelopes and warthogs (bottom) since surveys started for these species. Five-survey running means are plotted to smooth the fluctuations between surveys.

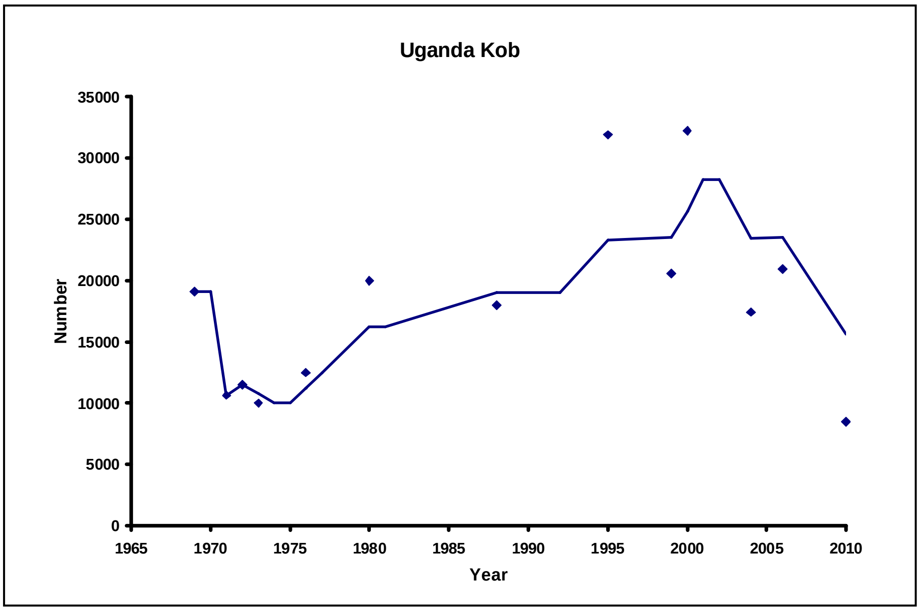


Figure 8. Population changes in the most abundant ungulate species, the Uganda Kob. A five-survey running mean is plotted to smooth the fluctuations between surveys.

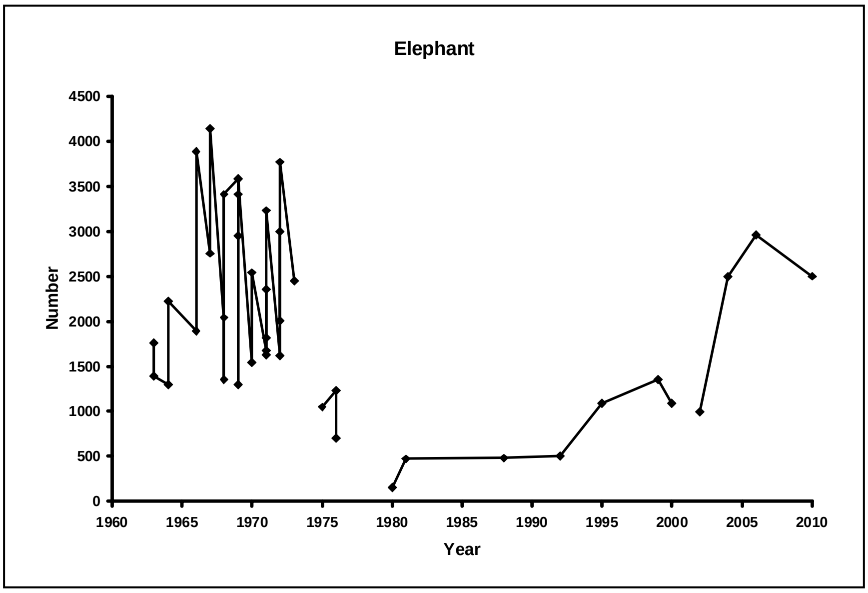


Figure 9. Fluctuations in elephant numbers over the years since surveys began.

Biodiversity assessments

Species and habitats

A total of 249 bird species were recorded from the point counts at each plot. QENP has a bird list of 620 species so that despite 206 plots being visited the surveys only found 40% of the bird species. The 2009 plots also contained 495 plant species out of a total of 950 species recorded for the park (Plumptre *et al.*, 2007), 52% of recorded plants. However if the 1992 plots are included 859 plant species were identified in total (94%).

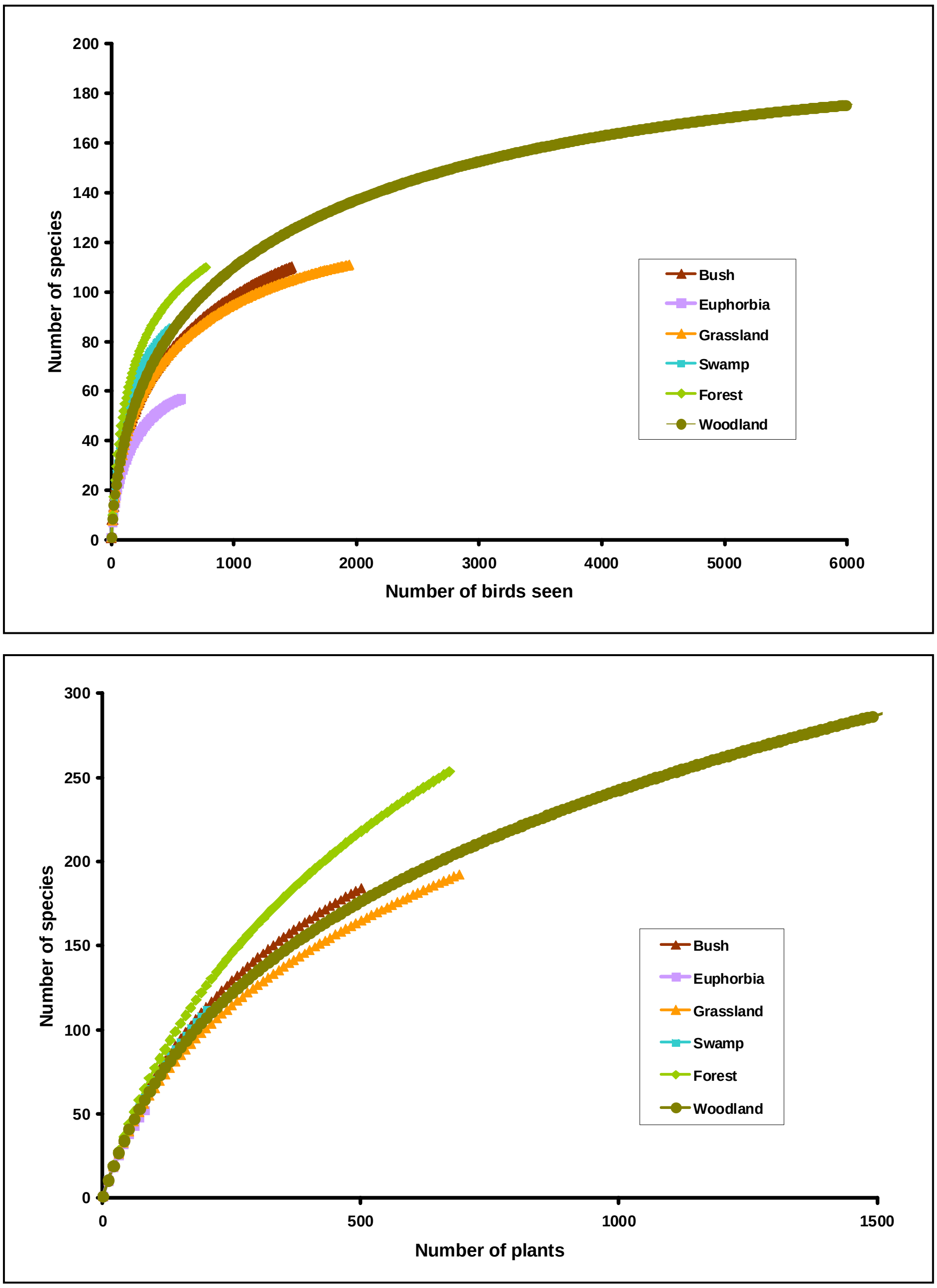


Figure 10. Rarefaction curves for each habitat for birds (top) and plants (bottom)

Figure 10 shows the rarefaction curves for birds and plants for each of the main habitat types in which plots were located. Not surprisingly forest habitat has more species for both plants and birds. Woodland and Swamp also has a higher abundance of species of birds compared with other habitats. Euphorbia dominated woodland had the lowest diversity of birds. Plant species diversity was similar in the other habitats but all were lower than forest. A cluster analysis showed that for birds woodland, bush, forest and grassland the species composition was not that different but was different to species found in swamp and Euphorbia woodland. For plants there was a more regular difference in similarities between the different habitat types (figure 11).

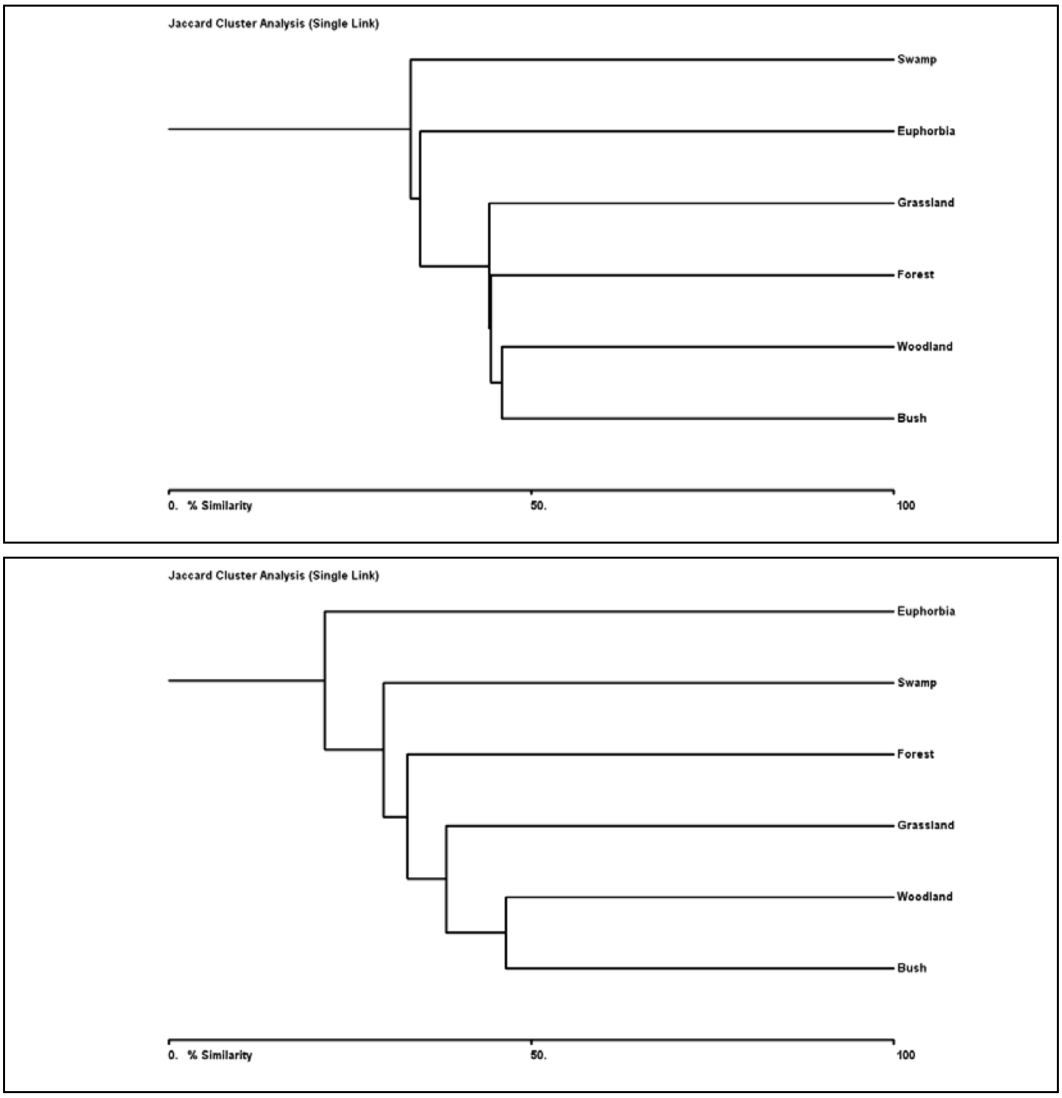


Figure 11. Similarities in species composition in the different habitats for birds (top) and plants (below).

Shannon Wiener and Alpha diversity values also show that forest diversity is highest and show a similar pattern (table 4).

Table 4. Shannon-Wiener and Alpha diversity values for birds and plants in the different habitat types in Queen Elizabeth Park.

Habitat	Bush	Euphorbia	Grassland	Swamp	Forest	Woodland
Plants						
Shannon-Wiener	2.119	1.66	2.051	1.954	2.246	2.165
Alpha	105.066	63.172	88.394	104.184	148.163	105.701
Birds						
Shannon - Wiener	1.512	1.24	1.447	1.694	1.825	1.58
Alpha	27.53	15.754	25.539	29.883	34.971	33.764

Table 5. Shannon-Wiener and Alpha diversity values for birds and plants in the different burn frequency categories for the plots in Queen Elizabeth Park.

Burn frequency:	0	1-3	4-6	>6
Plants				
Shannon - Wiener	2.227	2.284	2.16	1.961
Alpha	129.908	140.992	126.901	71.911
Birds				
Shannon - Wiener	1.841	1.609	1.478	1.466
Alpha	47.374	33.127	30.981	23.91

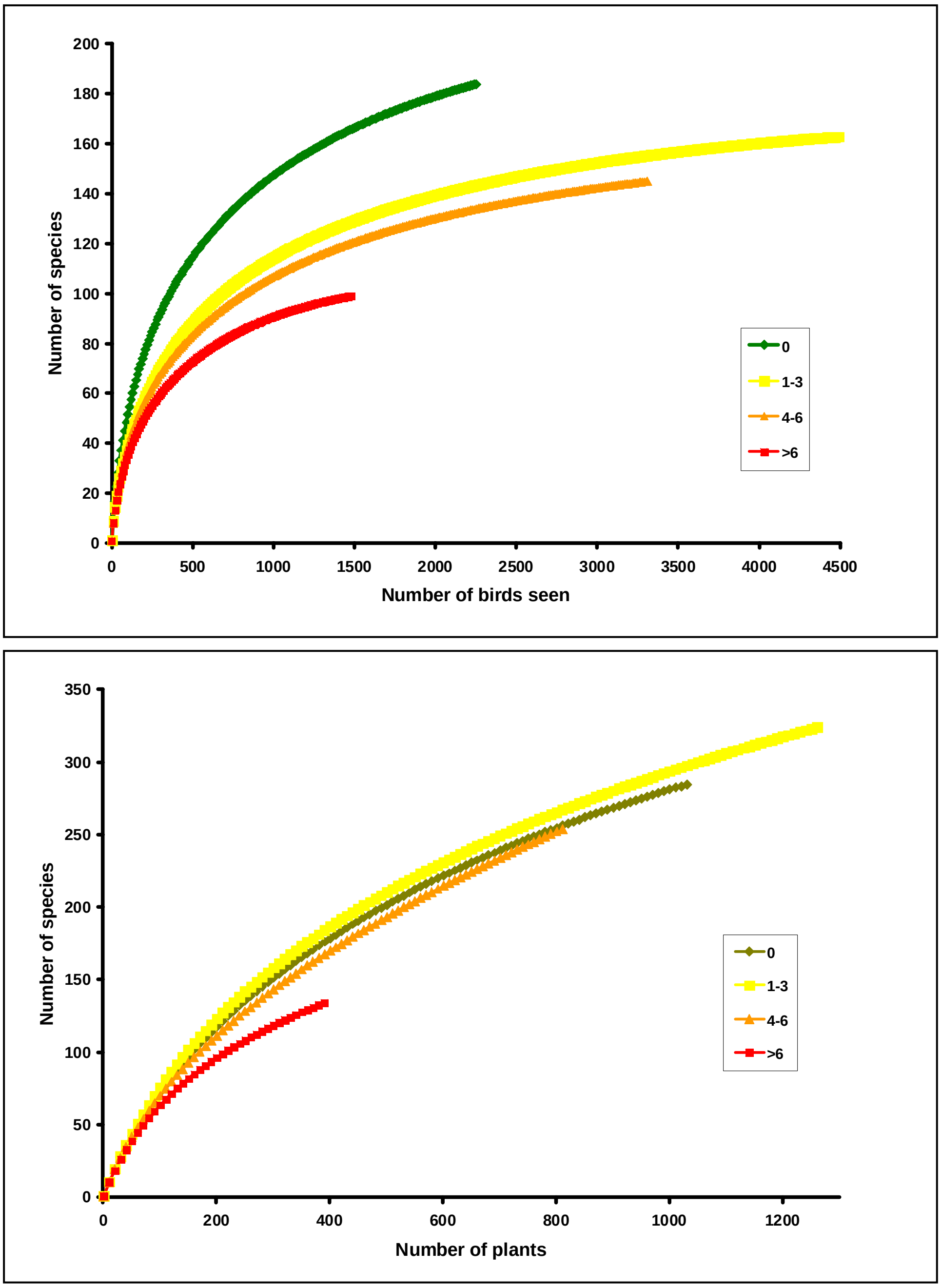
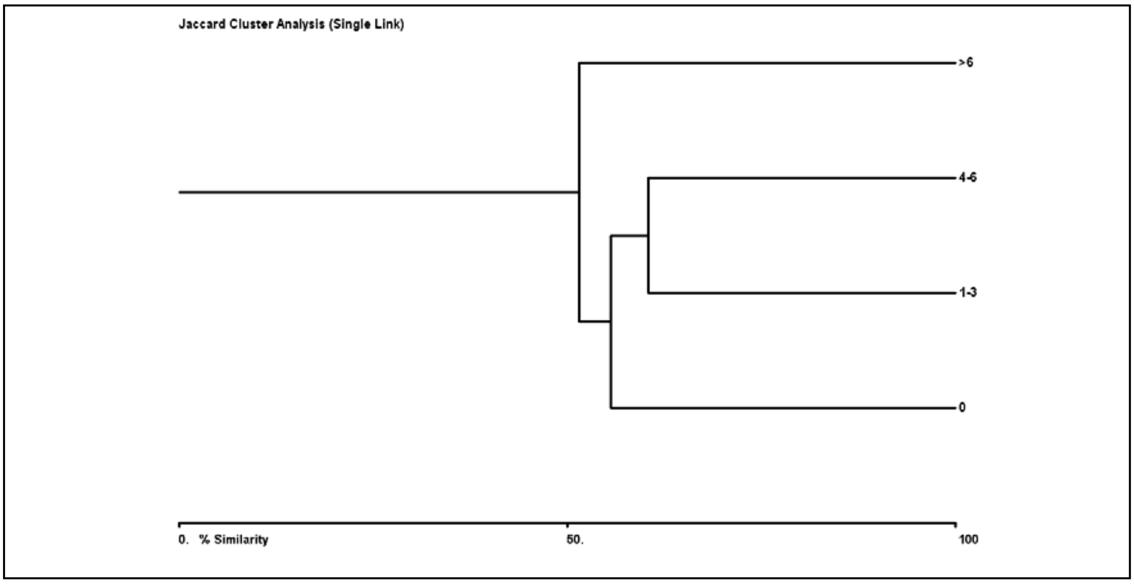


Figure 12. Rarefaction curves for plots that have experienced different burn frequencies from no burning (0), 1-3 times, 3-6 times or burnt greater than 6 times for birds (top) and plants (bottom).

Species and burn frequency of the plots between 2001-2009

The diversity of birds decreases with burn frequency category (table 5 and figure 12). Fewer birds are therefore likely to be seen on the most frequently burnt parts of the park. This is probably linked to the habitat however, with the more frequently burnt areas also being those with most grassland, least woody cover and consequently less structural diversity.

However plant diversity does not seem to be so affected by burn frequency, with similar diversity values for those plots that never burnt and those with burn frequencies of 1-3 or 3-6 times in 8 years between 2001 and 2009. The plots that burnt more than 6 times during this period had a lower diversity however (figure 13).



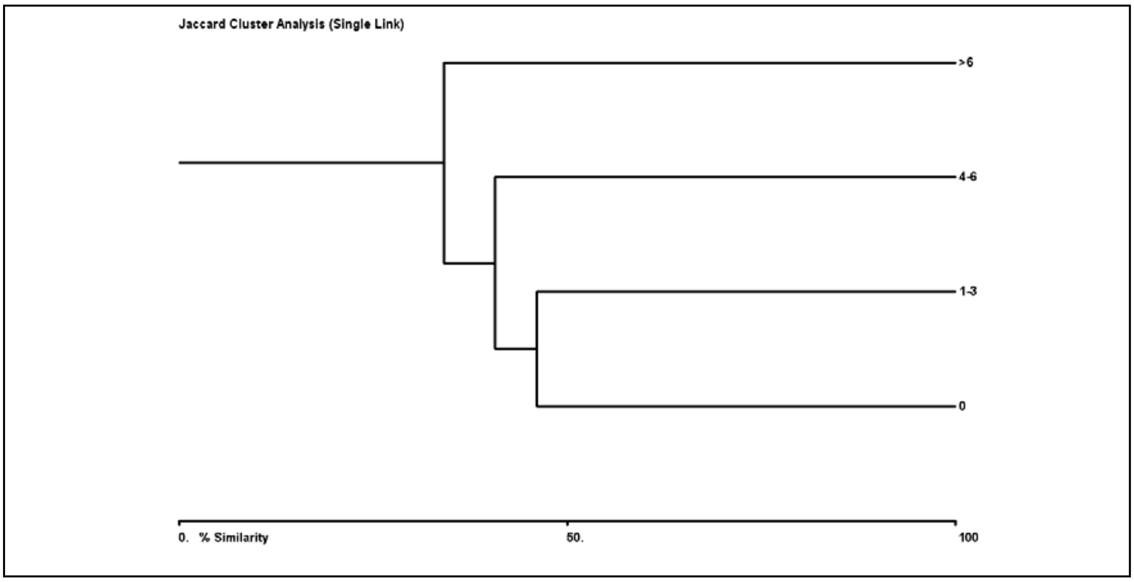


Figure 13. Similarities in species composition of the bird (top) and plant (bottom) communities in the plots which have been burnt at different frequencies.

The similarities in bird and plant species composition also showed a fairly regular pattern with burn frequency with those species in the plots burnt more than 6 times between 2001 and 2009 being most different to the other plots (figure 11). Interestingly, plots that burn 1-3 or 3-6 times were more similar in bird species composition compared with those that had never burnt.

Spatial distribution of species richness

The distribution of species richness for birds, all plants and trees was plotted for each plot surveyed in the park (figure 14). The results show that birds are fairly evenly distributed across the park but that the areas to the east of the park tend to have higher numbers of plant and tree species, particularly in Kyambura Wildlife Reserve and to the south of Kyambura gorge.

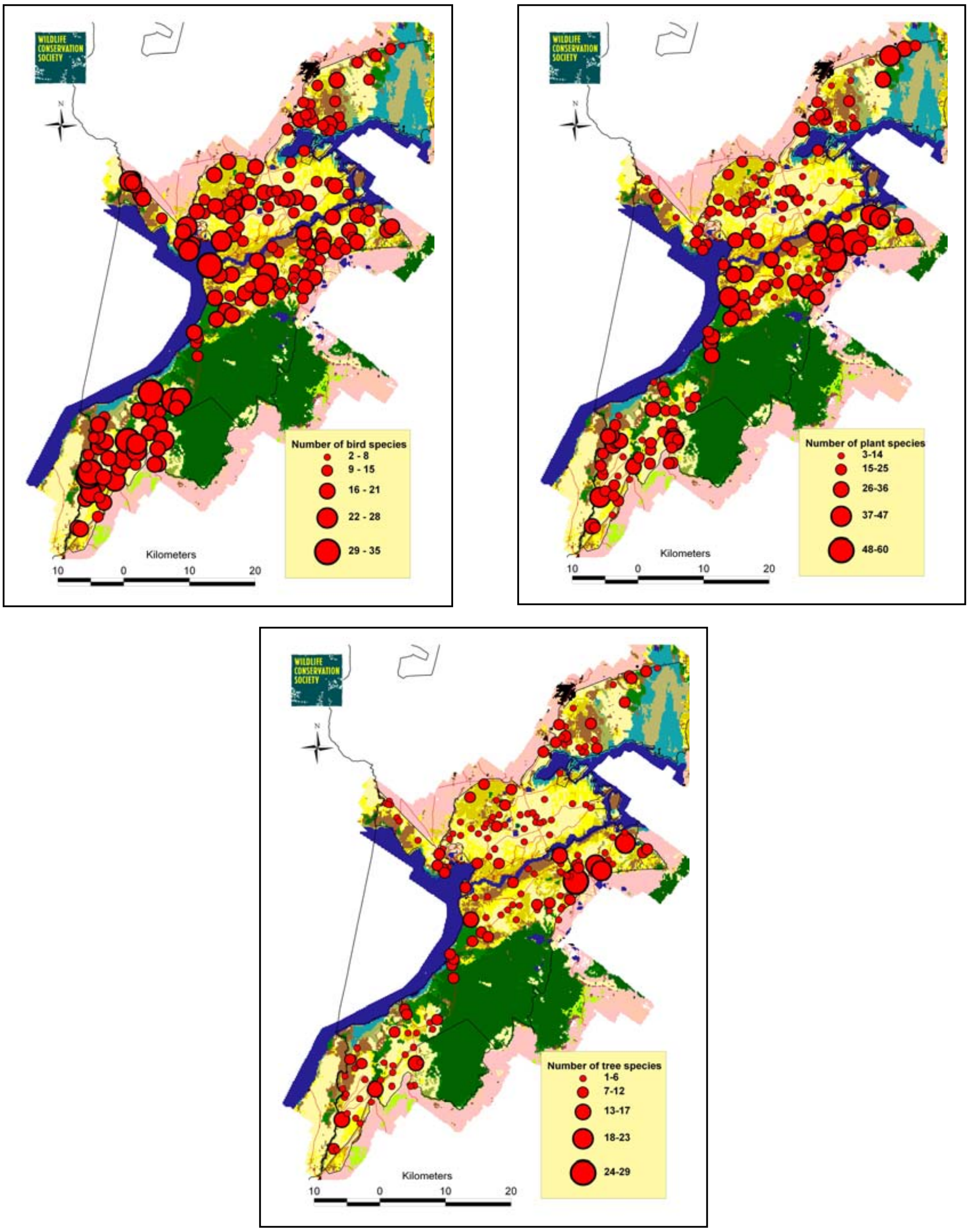


Figure 14. Relative species richness of birds (top left), all plants (top right) and trees (bottom) for each of the plots measured in the park.

Large mammal associations with vegetation

The results of the two regression models are summarized for each species and model in table 6. These show that the two regression models did not differ greatly except for Topi where the full entry of all variables was not significant. Topi only occur in the southern half of the park and only data from this region was used and the number of cells was therefore considerably fewer.

Table 6. Results of the regression models for each animal species. The R^2_{adj} value is equivalent to the proportion of the variation in density explained by the model.

Species	Model	R2 adj	F value	df	P
Elephant	1	0.080	3.03	15,337	<0.001
	2	0.093	9.95	4,347	<0.001
Buffalo	1	0.154	5.23	15,337	<0.001
	2	0.144	12.89	5,347	<0.001
Uganda Kob	1	0.421	18.07	15,337	<0.001
	2	0.416	36.76	7,345	<0.001
Topi	1	0.014	1.09	15,75	ns
	2	0.062	6.86	1,89	<0.01
Waterbuck	1	0.148	5.09	15,337	<0.001
	2	0.190	21.61	4,347	<0.001
Warthog	1	0.188	6.416	15,337	<0.001
	2	0.244	23.68	5,346	<0.001

Table 7. The variables selected in the stepwise regression model as being most strongly associated (positively or negatively) with the density of the animal species. Variables in italics were selected if distance to water was omitted as a variable.

Species	Variables selected in regression model	
	Positively associated	*Negatively associated*
Elephant	Bush/Scrub	Grassland
	Wooded Grassland	Grassland with pastoralists
Buffalo	Grassland	Grassland with pastoralists
		Tropical High Forest
		Papyrus swamp
		Bush/Scrub
Uganda Kob	Burn frequency	Grassland with pastoralists
	Grassland	Low stature forest
	Settlement	Papyrus swamp
Topi	Wooded grassland	
Waterbuck	Wooded Grassland	Papyrus swamp
	Proximity to water	Grassland with pastoralists
		Burn frequency
Warthog	Wooded grassland	Grassland with pastoralists
	Proximity to water	Low stature forest
		Bush/Scrub
		Burn frequency

The stepwise regression models selected a subset of variables that best predicted species densities (table 7). Those that were positively associated (selected), and those negatively associated (avoided) with species density. For Uganda kob burn frequency was an important predictor variable together with vegetation types but topi, buffalo and elephant did not appear to be distributed in relation to burn frequency. Warthog and waterbuck tended to be found in close proximity to water but if this variable was excluded then burn frequency was selected as a variable that was negatively associated with their distribution.

Assessment of plant community dynamics and causes of changes

Ordination analyses were made in CANOCO using Detrended and Canonical correspondence analyses. We analysed the herb and tree communities separately, primarily to avoid the confusion of the many names in the biplots but also because we believed that the two communities might respond to the environmental factors differently. We therefore present the results here for each analysis for these two groups. We do not give the background theory to ordination (unconstrained and constrained) here as there are good reference books that cover this type of analysis (Leps and Smilauer, 2003; ter Braak and Smilauer, 2002). In brief though both methods allow an analysis of community composition when you have data with many zero values as it does not rely on normally distributed data. It also allows an analysis of the combined impacts of environmental factors on the whole plant community which is not possible with other statistical techniques.

Detrended Correspondence Analysis

Initially a Detrended Correspondence Analysis (DCA) was made of the herb and tree communities to assess plant associations and the strength of the differences between different associations. DCA is an ordination method that identifies axes of the greatest variability in the community composition (the ordination axes) for a set of samples and to visualize the variation using ordination plots (usually of the first and second axes which identify the greatest variability. In these DCA analyses detrending by segments was used which creates a measure of standard deviation in species turnover along the axes generated by the analysis (figure 15 & 16). Environmental variables (listed in the methods) were overlaid passively on the ordination plot to assess their relative strengths and associations with species. In all these plots the nearer a species is to the arrow head of an environmental variable (or point of categorical environmental variables) the more likely it is to be associated with high values of that variable.

<u>Herbs</u>

The DCA for herbs used the cover values which are on an approximate log scale and as such there was no need to transform the data. The environmental variables (although passively entered) explained 27.3% of the variation in species composition of these herbs (figure 15). Gradient lengths were 9.09 for Axis 1 and 6.18 for axis 2. Anything greater than 4 (standard deviations) is usually judged to have plant communities at either ends of the axis that do not co-exist anywhere (Leps and Smilauer, 2003). Of the environmental variables the burn frequency and the distance to hippos were both strongly correlated with the variation in the species distributions. Burn frequency is opposite to Hippo distance because where hippos are grazing heavily (ie. low distance to hippos and a high distance category value) there is little fuel available to burn and so fires will be rare.

<u>Trees</u>

The DCA of trees in QENP used a square root transformation on the tree count values as recommended by ter Braak and Smilauer (2002). Gradient lengths were 7.20 for axis 1 and 4.15 for Axis 2, again indicating different communities of tree species that rarely are found together. Those species near to each other in the ordination plots are more likely to be found together and those furthest apart are the least likely to be associated with each other. The environmental variables explained about 49.2% of the variation in species composition. Altitude, rainfall, burn frequency and distance to hippos were the four strongest environmental variables correlated with the DCA axes (figure 16).

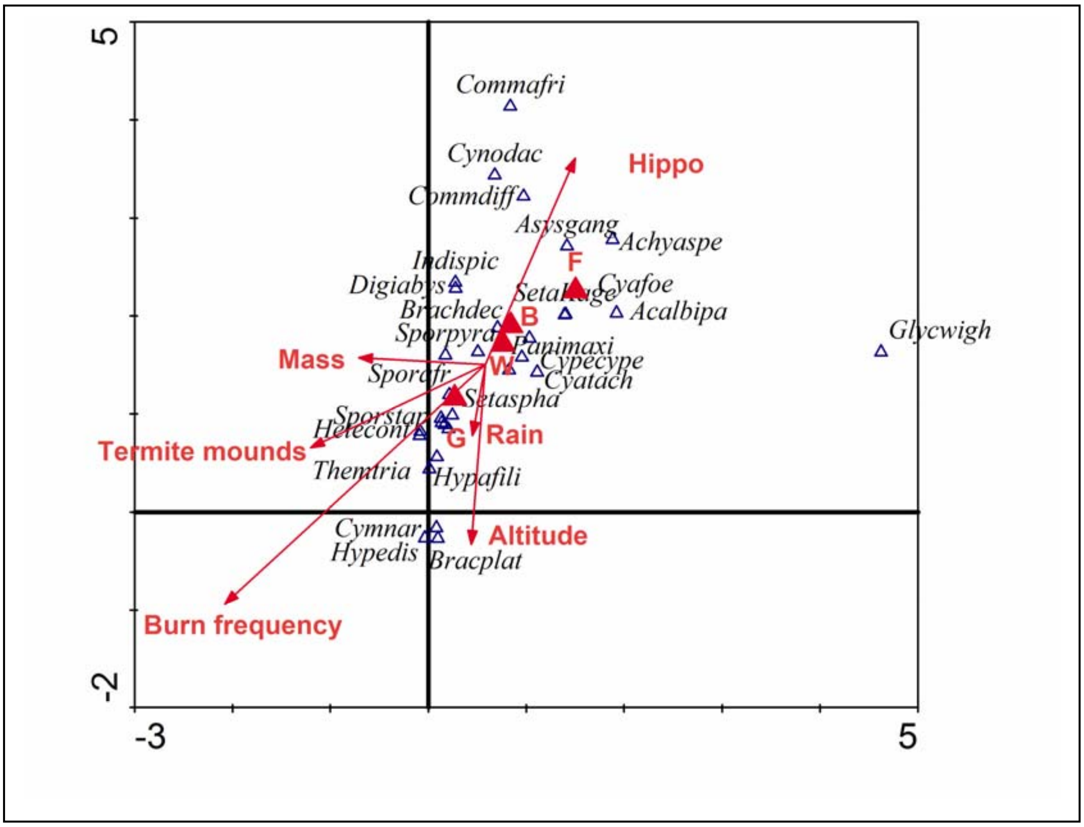


Figure 15. DCA of the herb communities in QENP from the 2009 plot data.
Species: *Acalbipa - Acalypha bipartite; Asysgang- Asystasia gangetica; Achyaspe - Achyranthes aspera; Brachdec - Brachiaria decumbens; Bracplat - Brachiaria platynota; Commafri – Commelina africana; Commdiff-Commelina diffusa; Cyafoe- Cyanotis foecunda; Cyatach - Cyathula achyranthoides; Cymnar - Cymbopogon nardus; Cynodac – Cynodon dactylon; Cypecype - Cyperus cyperoides; Digiabys - Digitaria abyssinica; Glycwigh - Glycine wightii; Hetecont - Heteropogon contortus; Hypafili - Hyparrhenia filipendula; Hypedis - Hyperthelia dissoluta; Indispic - Indigofera spicata; Panimaxi – Panicum maximum; SetaKage - Setaria kagerensis; Setaspha - Setaria sphacelata; Sporafr - Sporobolus africanus; Sporpyra - Sporobolus pyramidalis; Sporstap - Sporobolus stapfianus; Themtria – Themeda triandra.* Only the most dominant species of the 394 possible herb species are plotted here. Environmental Variables: *Hippo – distance category to hippos; Mass – average biomass of large mammals from surveys between 1996 and 2006; Termite mounds – number of termite mounds; Rain –rainfall; Altitude –altitude in metres a.s.l; Burn frequency – number of times plot burned between 2001 and 2009; F-Forest; B-Bush; W-Woodland; G-Grassland.*

Canonical Correspondence Analysis

DCA gives a good measure of the association between the different species and the difference in plant communities in the park. However it does not give a good measure of the impact of the various environmental factors on the different plant species. For this Canonical Correspondence Analysis (CCA) or Redundancy Analysis (RA) can be used, both techniques that are direct gradient analyses and aim to determine the effects of environmental gradients. RA assumes a linear response of the plant species to environmental factors whereas CCA assumes a Gaussian response curve along a gradient. Usually if a DCA has axes longer than 3 standard deviations then a CCA should be used as the response of species is more likely to be unimodal with long gradients (or high beta diversity).

In this study we used some environmental factors in a CCA direct gradient analysis after partitioning out the effects of several other factors (or covariables). These covariables included the effects of geographic position in the park (latitude and longditude coordinates) and the effect of the different global habitat types in which the plot was located (forest, bush, woodland or grassland).

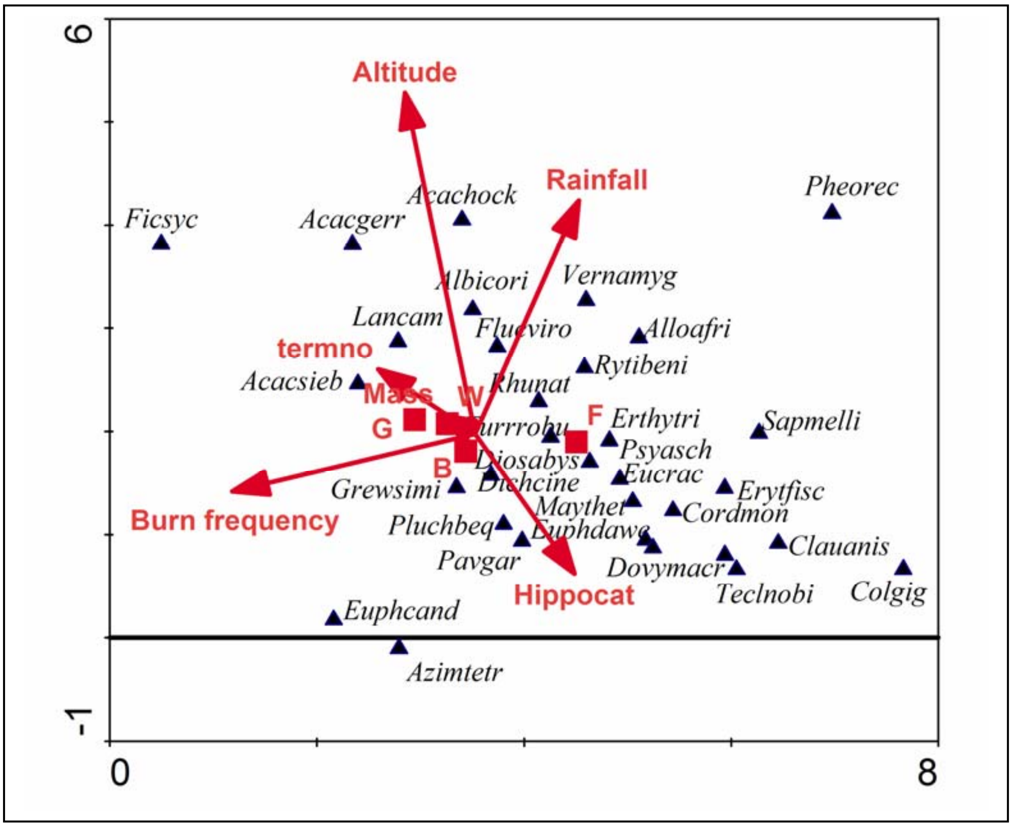


Figure 16. DCA of tree communities in QENP using the 2009 plot data.
Species: *Acacgerr – Acacia gerrardii; Acachock – Acacia hockii; Acacsieb – Acacia sieberiana; Albicori - Albizia coriaria; Alloafri - Allophylus africanus; Azimtetr - Azima tetracantha; Clauanis – Clausena anisata; Colgig – Cola gigantea; Cordmon - Cordia monoica; Dichcine - Dichrostachys cinerea; Dioabys – Diospyros abyssinicus; Dovymacr – Dovyalis macrocalyx; Erytfisc - Erythroxylum fischeri; Erthytri - Erythrococca trichogyne; Eucrac - Euclea racemosa; Euphcand – Euphorbia candelabra; Euphdawe – Euphorbia dawei; Ficsyc - Ficus sycomorus; Flueviro - Flueggea virosa; Grewsimi – Grewia similis; Lancam - Lantana camara; Maythet - Maytenus heterophylla; Pavgar - Pavetta gardeniifolia; Pheorec - Phoenix reclinata; Pluchbeq - Pluchea bequaertii; Psyasch - Psydrax schimperianum; Rhunat - Rhus natalensis; Rytibeni - Rytigynia beniensis; Sapmelli - Sapium ellipticum; Teclnobi –Teclea nobilis; Turrobu - Turraea robusta; Vernamyg – Vernonia amygdalina.*
Only the most dominant species of the 97 possible tree species are plotted here.
Environmental Variables: *Hippocat – distance category to hippos; Mass – average biomass of large mammals from surveys between 1996 and 2006; Termite mounds – number of termite mounds; Rain –rainfall; Altitude –altitude in metres a.s.l; Burn frequency – number of times plot burned between 2001 and 2009; F-Forest; B-Bush; W-Woodland; G-Grassland.*

Herbs

A CCA of the 2009 plot data for QENP shows that certain species are strongly associated with particular environmental factors (figure 17). *Sporobolus pyrimidalis* and *S. africanus* occur where ungulate biomass is high together with *Heteropogon contortus*. Grasses such as *Panicum maximum* and *Imperata cylindrica* occur at higher altitudes and where rainfall is generally higher. *Cynodon dactylon* and *Cyanotis foecunda* occur in close proximity to hippo pods and probably where grazing is most intense. The environmental factors were entered with the forward selection method available in CANOCO and using a Monte-carlo permutation test to test the significance of the factor. Each of the factors was significant at P<0.06. The environmental variables explained about 80.7% of the variation in the fitted species data in the first four axes and 54.9% in the first two axes.

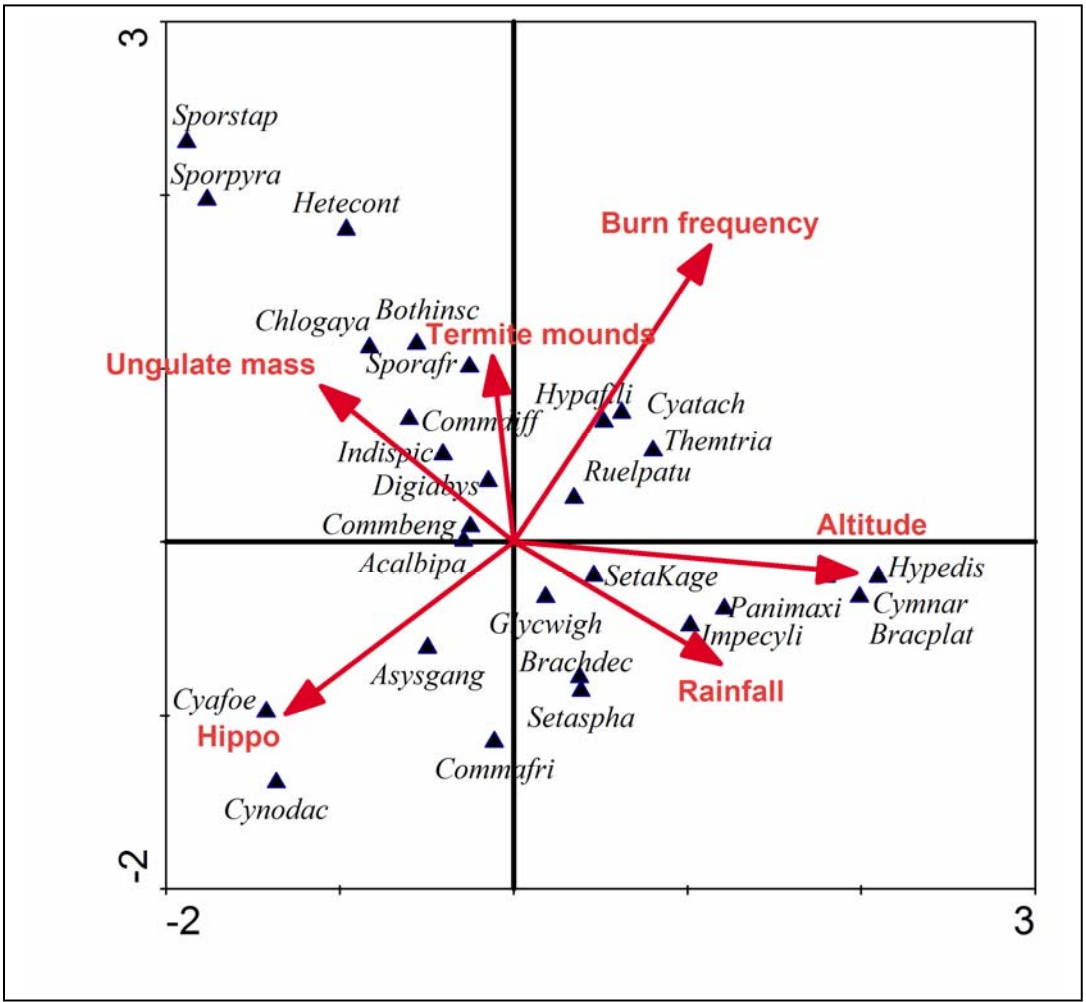


Figure 17. CCA of the herb communities in QENP from the 2009 plot data.
Species: *Acalbipa - Acalypha bipartite; Asysgang- Asystasia gangetica; Bothinsc - Bothriochloa insculpta; Brachdec - Brachiaria decumbens; Bracplat - Brachiaria platynota; Chlogaya - Chloris gayana; Commafri – Commelina africana; Commbeng - Commelina benghalensis; Commdiff- Commelina diffusa; Cyafoe- Cyanotis foecunda; Cyatach - Cyathula achyranthoides; Cymnar - Cymbopogon nardus; Cynodac – Cynodon dactylon; Digiabys - Digitaria abyssinica; Glycwigh - Glycine wightii; Hetecont - Heteropogon contortus; Hypafili - Hyparrhenia filipendula; Hypedis - Hyperthelia dissoluta; Impecyli – Imperata cylindrica; Indispic - Indigofera spicata; Panimaxi – Panicum maximum; Ruelpatu - Ruellia patula; SetaKage - Setaria kagerensis; Sporafr - Sporobolus africanus; Sporpyra - Sporobolus pyramidalis; Setaspha - Setaria sphacelata; Sporstap - Sporobolus stapfianus; Themtria – Themeda triandra.* Only the most dominant species of the 394 possible herb species are plotted here. Environmental Variables: *Hippo – distance category to hippos; Ungulate Mass – average biomass of large mammals from surveys between 1996 and 2006; Termite mounds – number of termite mounds; Rainfall –rainfall; Altitude –altitude in metres a.s.l; Burn frequency – number of times plot burned between 2001 and 2009.*

Trees

A CCA of the 2009 tree count data (also square root transformed) was also made with forward selection of the environmental factors. In this case only altitude, distance to hippos, rainfall and the burn frequency were significant at P<0.05. The number of termite mounds and mammal biomass were not significant. Distance to hippos, altitude and burn frequency had the strongest correlations with the tree community composition (figure 18). The first two axes explained 65.1% of the species environment relations.

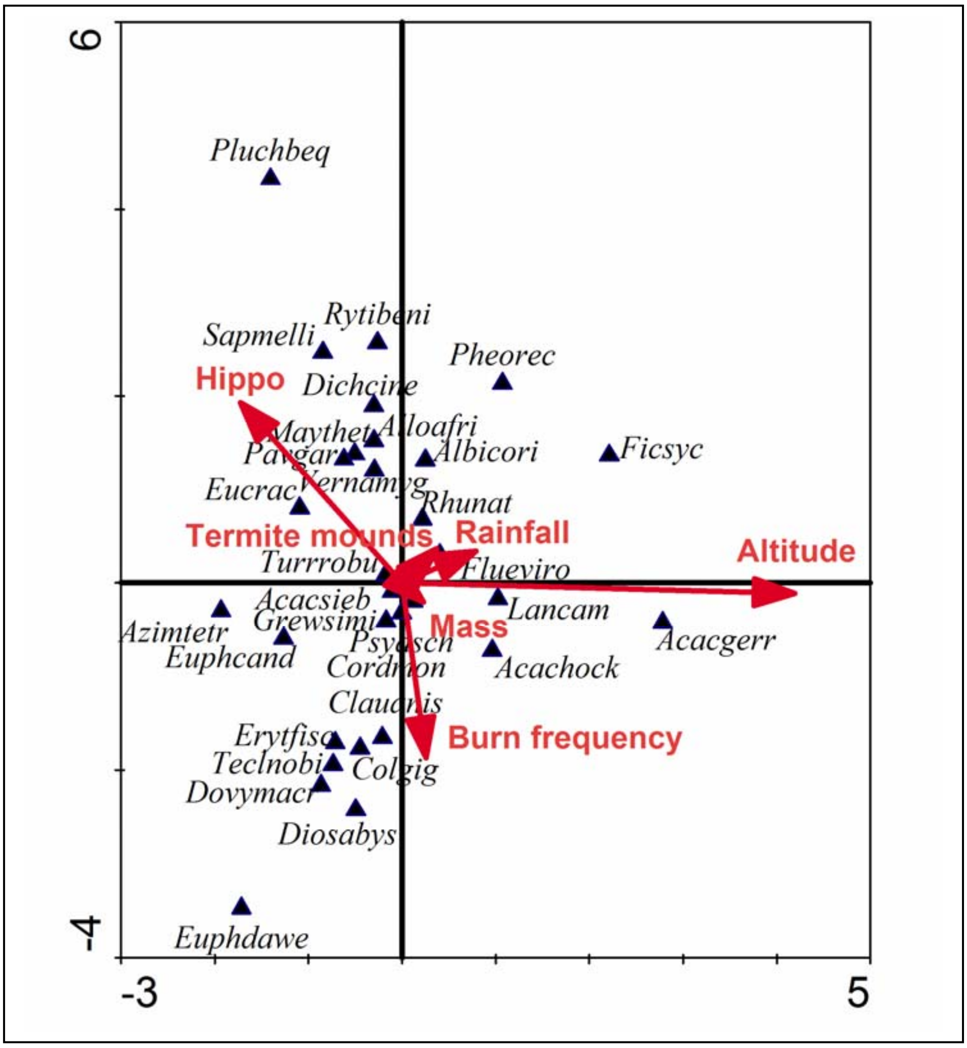


Figure 18. CCA of tree communities in QENP using the 2009 plot data.
Species: *Acacgerr – Acacia gerrardii; Acachock – Acacia hockii; Acacsieb – Acacia sieberiana; Albicori - Albizia coriaria; Alloafri - Allophylus africanus; Azimtetr - Azima tetracantha; Clauanis – Clausena anisata; Colgig – Cola gigantea; Cordmon - Cordia monoica; Dichcine - Dichrostachys cinerea; Diosabys – Diospyros abyssinicus; Dovymacr – Dovyalis macrocalyx; Erytfisc - Erythroxylum fischeri; Euphcand – Euphorbia candelabra; Euphdawe – Euphorbia dawei; Ficsyc - Ficus sycomorus; Flueviro - Flueggea virosa; Grewsimi – Grewia similis; Lancam - Lantana camara; Maythet - Maytenus heterophylla; Pavgar - Pavetta gardeniifolia; Pheorec - Phoenix reclinata; Pluchbeq - Pluchea bequaertii; Psyasch - Psydrax schimperianum; Rhunat - Rhus natalensis; Rytibeni - Rytigynia beniensis; Sapmelli - Sapium ellipticum; Teclnobi –Teclea nobilis; Turrrobu - Turraea robusta; Vernamyg – Vernonia amygdalina.* Only the most dominant species of the 97 possible tree species are plotted here.
Environmental Variables: *Hippo – distance category to hippos; Mass – average biomass of large mammals from surveys between 1996 and 2006; Termite mounds – number of termite mounds; Rain –rainfall; Altitude –altitude in metres a.s.l; Burn frequency – number of times plot burned between 2001 and 2009;*

CCA’s show the relationship between environmental factors and particular species but interpreting the data is not easy. Does burn frequency determine the presence of *Euphorbia dawei* for instance in figure 18 or does this tree occur in areas where burning is likely to occur? It is not possible to assess this by using the CCA of the 2009 data alone. However, we have two data sets from plots at the same site in 1992 and 2009. It is possible to undertake a third CCA that assesses the changes that have taken place between these time periods and relate them more directly to the environmental factors.

CCA factoring- in the changes between 1992 and 2009.

In order to factor-in the effects of changes between the two time periods the plots are entered for both years as separate plots. Year the plot was measured is then entered as a co-variable (together with latitude, longditude, and the four habitats; F, B, W, G) and the combined effect of year multiplied by the factor is entered as the environmental variable (ter Braak and Smilauer, 2002). We did this analysis for the herbs (figure 19) and the trees (figure 20).

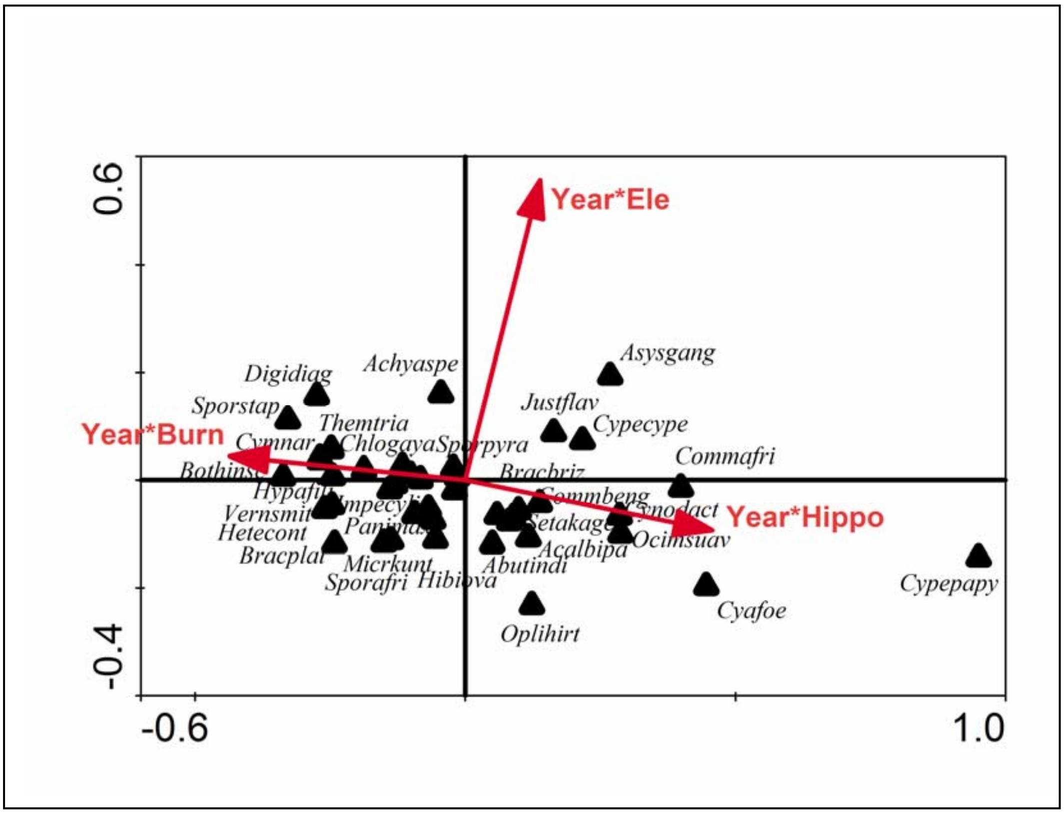


Figure 19. CCA with measurements of the herbs in the plots in 1992 and 2009 entered and year of measurement entered as a co-variable. Environmental factors are then entered as the product of year and the environmental variable to assess their effects on the changes in plant composition. The species near the arrow heads are those that have increased cover over time in relation to that environmental factor. Species: *Abutindi - Abutilon indicum; Acalbipa - Acalypha bipartite; Achyaspe - Achyranthes aspera; Asysgang- Asystasia gangetica; Bothinsc - Bothriochloa insculpta; Bracbriz – Brachiaria brizantha; Bracplat - Brachiaria platynota; Chlogaya - Chloris gayana; Commafri – Commelina africana; Commbeng - Commelina benghalensis; Cyafoe- Cyanotis foecunda; Cymnar - Cymbopogon nardus; Cynodac – Cynodon dactylon; Cypecype - Cyperus cyperoides; Cypepapy - Cyperus papyrus; Digidiag - Digitaria diagonalis; Hetecont - Heteropogon contortus; Hibiova - Hibiscus ovalifolius; Hypafili - Hyparrhenia filipendula; Impecyli – Imperata cylindrica; Justflav - Justicia flava; Micrkunt - Microchloa kunthii; Ocimsuav – Ocimum suave; Oplihirt – Oplismenus hirtellus; Panimaxi – Panicum maximum; SetaKage - Setaria kagerensis; Sporafri – Sporobolus africanus; Sporpyra - Sporobolus pyramidalis; Sporstap - Sporobolus stapfianus; Themtria – Themeda triandra; Vernsmit - Vernonia smithiana.* Only the most dominant species of the 554 possible herb species are plotted here. Environmental Variables: *Year x distance to hippos; year x density of elephants and year x burn frequency.*

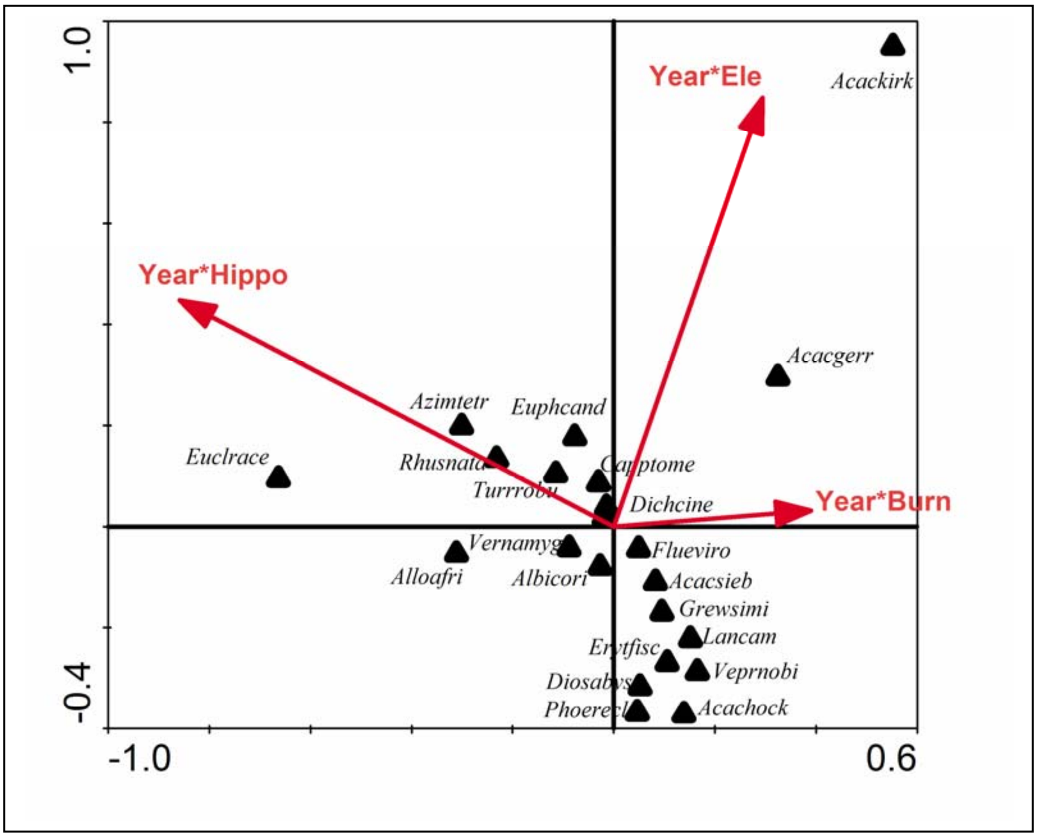


Figure 20. CCA with measurements of the trees and shrubs in the plots in 1992 and 2009 entered and year of measurement entered as a co-variable. Environmental factors are then entered as the product of year and the environmental variable to assess their effects on the changes in plant composition. The species near the arrow heads are those that have increased cover over time in relation to that environmental factor. Species: *Acacgerr – Acacia gerrardii; Acachock – Acacia hockii; Acackirk – Acacia kirkii; Acacsieb – Acacia sieberiana; Albicori - Albizia coriaria; Alloafri - Allophylus africanus; Azimtetr - Azima tetracantha; Capptome – Capparis tomentosa; Dichcine - Dichrostachys cinerea; Diosabys – Diospyros abyssinicus; Erytfisc - Erythroxylum fischeri; Euclrace – Euclea racemosa; Euphcand – Euphorbia candelabra; Flueviro - Flueggea virosa; Grewsimi – Grewia similis; Lancam - Lantana camara; Pheorec - Phoenix reclinata; Rhusnata - Rhus natalensis; Turrrobu - Turraea robusta; Veprnobi – Vepris nobilis; Vernamyg – Vernonia amygdalina.* Only the most dominant species of the 154 possible tree species are plotted here. Environmental Variables: *Year x distance to hippos; year x density of elephants, and year x burn frequency.*

In both analyses Monte Carlo tests were made of the significance of each of the environmental variables entered using a split plot design for the test (effectively comparing changes in the paired plots in 1992 and 2009) and a stepwise process was used to enter the Year x Factor variable. For the herbs all three factors (Burn frequency x year, Hippo distance category x year and elephant density x year) were significant at $P<0.05$. For the trees elephant density and hippo distance category were both significant at $P<0.05$ but burn frequency was only significant at $p=0.14$ after the other two variables had been fitted. We can therefore be fairly confident that these factors have had an impact on the changes shown in these two figures.

It is possible to use the same method to assess the changes in species at plots that had different burn frequencies using a CCA combining those areas that burnt rarely (1-4 times between 2001-2009), more frequently (>4 times) and that never burned (figure 21).

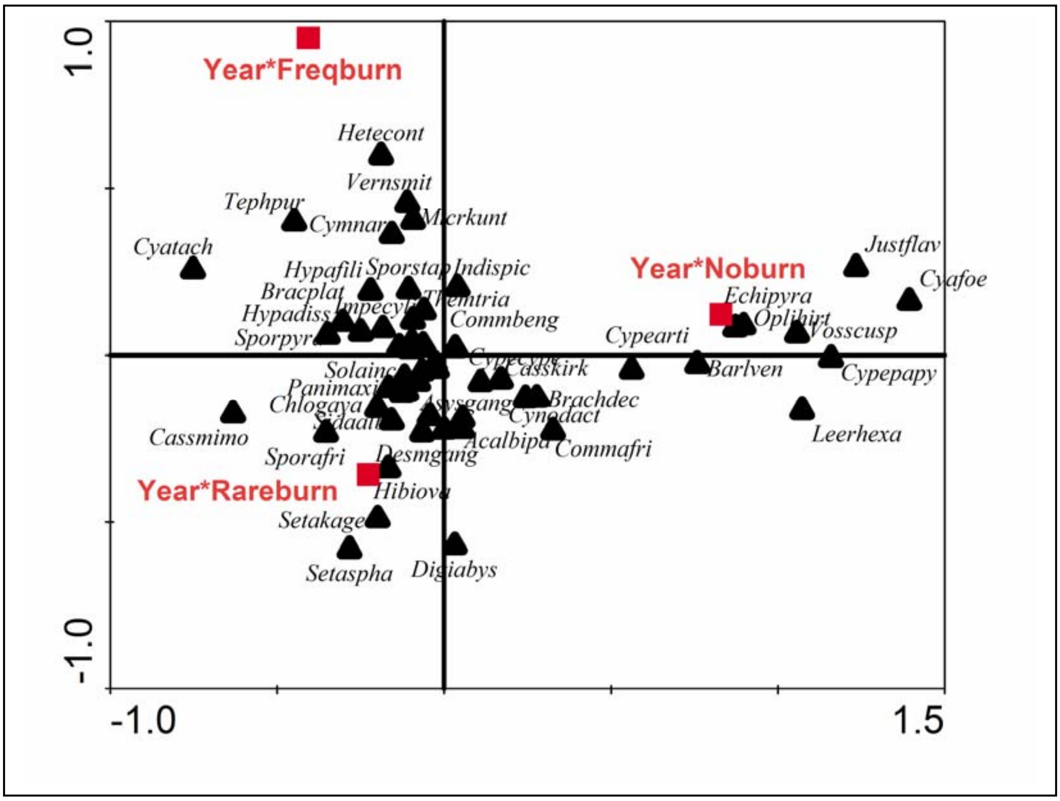


Figure 21. CCA with three categories of burn frequency entered as environmental variables. Year was entered together with GPS position and habitat type as covariables and then year was multiplied by the three environmental variables to show how species have increased under the three burn frequencies between 1992 and 2009. Areas which never burned (no burns), those that burned 1-6 times (rare burns) and those that burned >6 times (frequent burns) were entered as the three environmental variables. Species: *Acalbipa - Acalypha bipartite; Asysgang- Asystasia gangetica; Barlven – Barleria ventricosa; Brachdec – Brachiaria decumbens; Bracplat - Brachiaria platynota; Casskirk – Cassia kirkii; Cassmimo – Cassia mimosoides; Chlogaya - Chloris gayana; Commafri – Commelina africana; Cyafoe- Cyanotis foecunda; Cyatach - Cyathula achyranthoides; Cymnar - Cymbopogon nardus; Cynodac – Cynodon dactylon; Cypecype - Cyperus cyperoides; Cypearti – Cyperus articulatus; Cypepapy - Cyperus papyrus; Desmgang – Desmodium gangenticum; Digiabys - Digitaria abyssinica; Echipyra – Echinochloa pyramidalis; Hetecont - Heteropogon contortus; Hibiova - Hibiscus ovalifolius; Hypadiss – Hyperthelia dissolute; Hypafili - Hyparrhenia filipendula; Impecyli – Imperata cylindrica; Indispic – Indigofera spicata; Justflav - Justicia flava; Leerhexa – Leersia hexandra; Micrkunt - Microchloa kunthii; Oplihirt – Oplismenus hirtellus; Panimaxi – Panicum maximum; SetaKage - Setaria kagerensis; Setaspha – Setaria Sphacelata; Sidaalba – Sida alba; Solainca – Solanum incanum; Sporafri – Sporobolus africanus; Sporpyra - Sporobolus pyramidalis; Sporstap - Sporobolus stapfianus; Tephpur – Tephrosia purpurea; Themtria – Themeda triandra; Vernsmit - Vernonia smithiana; Vosscusp – Vossia cuspidata.* Only the most dominant species of the 554 possible herb species are plotted here. Environmental Variables: *Year x no burning; year x rare burning (1-4 years between 2001-2009) and year x frequent burning (4-8 times between 2001-2009).* In this case environmental variables are nominal (1 or 0) and are represented as centroids.

Responses of particular species to factors

We also plotted the species response curves of particular species of interest using a Generalised Additive Model to generate the curve in CANODRAW. Only those species that had a significant fit of the curve are included (figure 22). These results show that *Heteropogon contortus*, *Chloris gayana* and *Bothriochloa insculpta* are more abundant where burning is frequent. *Cynodon dactylon* is more abundant where hippos are present. Interestingly *Imperata cylindrical* (Spear grass) is more abundant at low hippo presence but at a medium burn frequency.

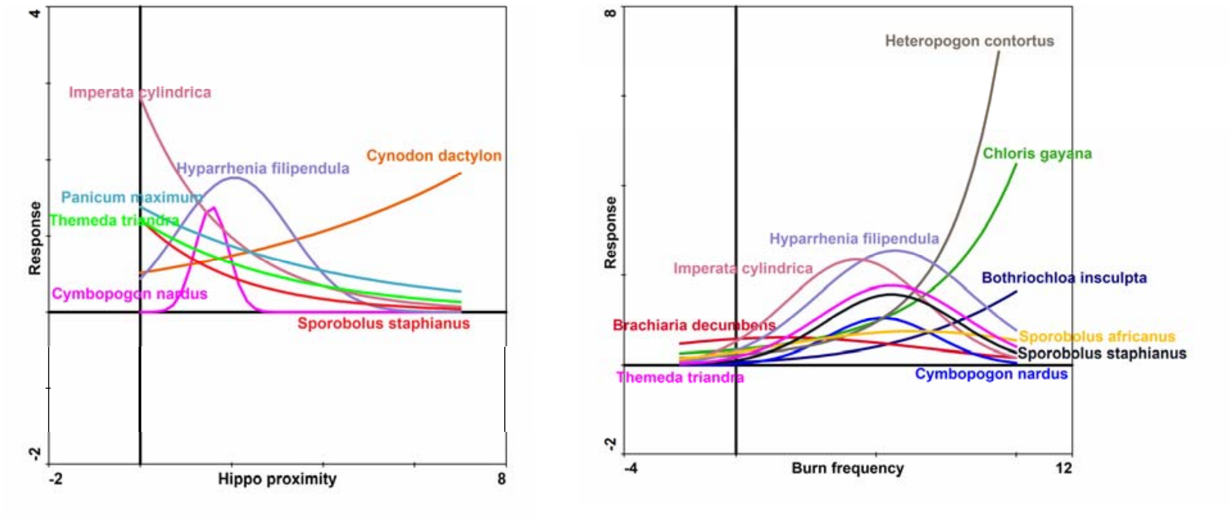


Figure 22. Response curves of grass species to hippo distance category (left) and burn frequency (right).

Another species that is of management concern is *Lantana camara*, an introduced invasive species. This species was tested with generalized additive models with elephant density, hippo distance category and burn frequency but none of them was significant. However there is a trend to higher abundance where these factors are low (figure 23).

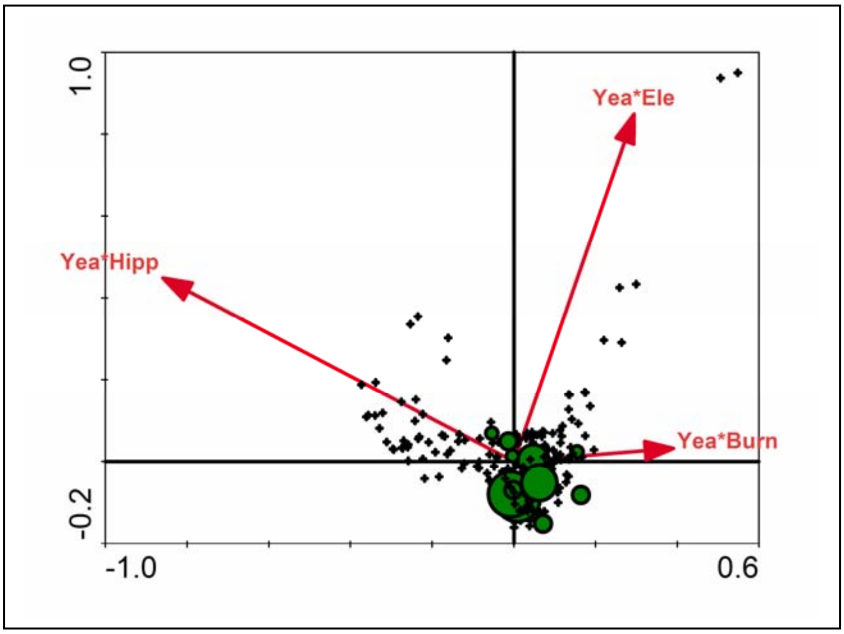


Figure 23. Distribution of *Lantana camara* in relation to the CCA analysis in figure 19. Circle size is related to relative abundance of this species and crosses are positions of plots where the species did not occur.

We mapped the distribution of this invasive species by walking around the regions of the park where it occurs relatively abundantly. A total of 66 km^2 of the park is invaded by this species (Figure 24).

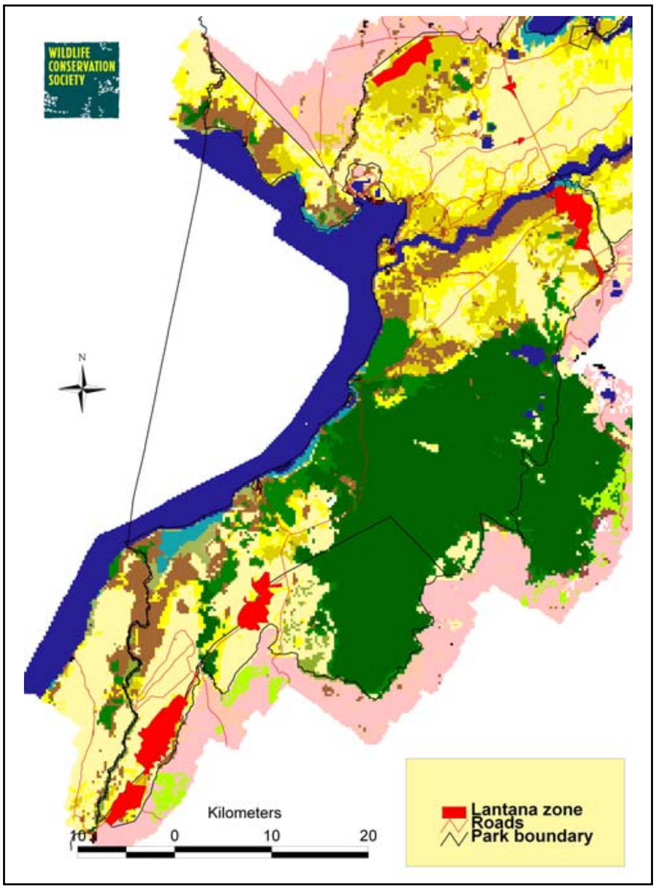


Figure 24. Map of Queen Elizabeth National Park showing the 2006 vegetation types (figure 6) with the locations of *Lantana camara* highlighted in red.

Discussion

This report aimed to pull together much of the information that has been collected on the distribution of large mammals, birds and plants in Queen Elizabeth National Park, the changes that have taken place in the park since the 1950s, and to assess how the impacts of large mammals and fire have affected these changes in habitats and species. Without the establishment of a rigorous sampling procedure and controls since the 1950s it is difficult to be totally certain of the cause and effect of the relationships we describe here. For instance does increased fire frequency occur where there is greater herb/grass cover (and reduced fire frequency where there is greater tree and shrub cover) because fire causes this habitat or because this habitat tends to burn better and so encourage fire. With fire and large mammals influencing the vegetation types and species composition at the same time it is also difficult to tease out the respective impacts of each process. The CCA's when assessing the plant community dynamics aimed to get at some of these changes while controlling for other factors that might affect species composition. We here summarise the main findings and then develop some management recommendations from the results.

Habitat changes

It is clear that the habitat in the park has changed considerably since the 1950s. In fact we know changes have been taking place over a much longer time period. Preliminary results of pollen analyses from lake sediments in and around the park indicate that from the mid to late 1800s there was a large increase in woody vegetation in the region of the park. This may have been linked to increased rainfall, or a result of the ivory trade which caused large reductions in elephant numbers around this period. Subsequently the vegetation changed back to more open habitat during the early 1900s up to the 1950s (D. Verschuren, pers.comm., presentation at Mweya Research Symposium Sep 2010). What has driven the changes in vegetation since the 1950s to the present time is uncertain but is likely to be a combined effect of fire, the loss of the large mammal biomass from the park in the 1970s and early 1980s, followed by the recovery of species such as elephants and hippopotamuses which have differing impacts on the vegetation as outlined in the introduction of this report. We can see that woody vegetation has increased in abundance in areas where animal density is relatively low (comparing figures 3 and 6) and that some of these areas also have a low frequency of fire (figure 4), although some have intermediate fire frequencies. We overlaid the average large mammal biomass from the aerial surveys between 1995 and 2006 over the woody change between 1954/1990 and 2006 and the results show that woody cover increased in areas where large mammal biomass is lower (figure 25). The biomass in this figure does not include the mass of hippopotamuses, however.

These results do seem to confirm that habitat changes are affected by the impacts of a large mammal biomass and to a lesser extent fire. It supports the findings made in this park in the 1950s-1970s that elephants and hippopotamuses can have significant impacts in determining the structure of the vegetation of the park and it also shows that the vegetation types in the park are in a constant state of change over time and that large mammal populations will need to be managed to promote particular vegetation types in future.

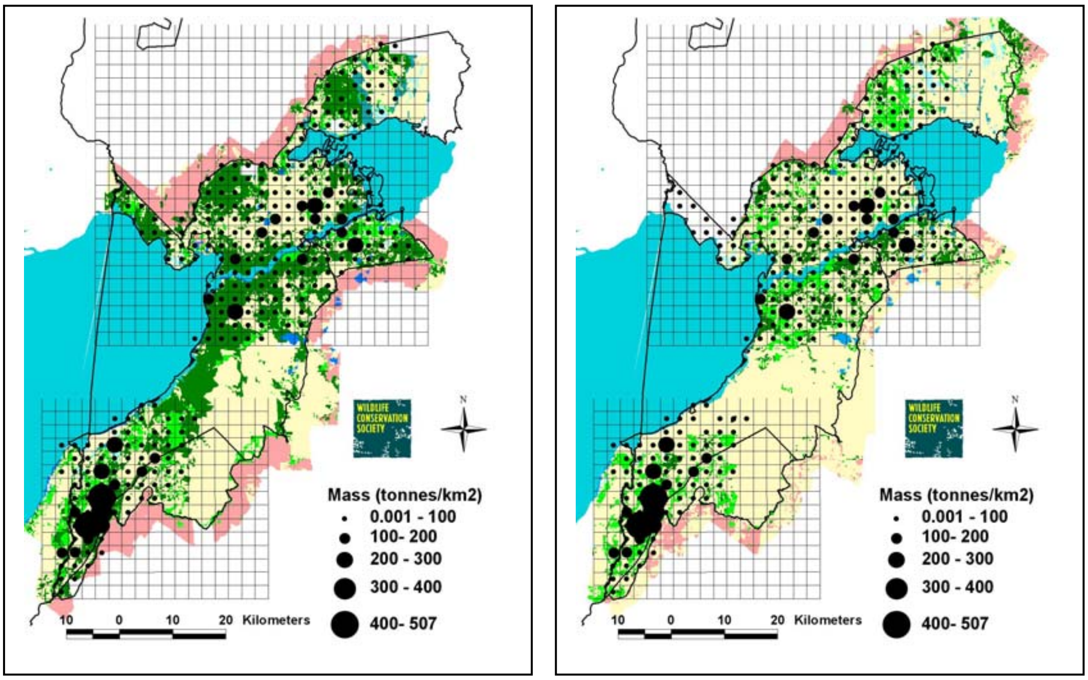


Figure 25. Large mammal biomass (tones/km^2) mapped per 2.5 x 2.5 km grid cell used in the aerial surveys and overlaid on the vegetation changes from 1954-2006 (left) and 1990-2006 (right). Dark greens show an increase in woody cover and light greens a decrease. Cream is where there is no change in habitat.

Habitat associations of large mammals, birds and plants

The models relating large mammal species density to the availability of different habitat types and fire frequency predicted between 6-42 % of the variation in animal densities of the individual species. Uganda Kob density were predicted best with 42% of the variation accounted for by their model (table 6) followed by warthog (18%), buffalo (15%) and waterbuck (14%). There is a need to identify other variables that may be important in predicting species distributions to better refine these models. Distance to water is potentially of importance for some of these species.

The frequency with which the park burns does deem to be important for some species and was selected in three of the stepwise regression models. Uganda Kob are found in the areas that burn most frequently while warthogs and waterbuck tend to be at higher density in areas that burn infrequently or are close to water (table 7). This is probably linked to the vegetation composition of these areas.

Bird species richness tended to be higher where there was more woody vegetation in habitats such as forest and woodland (figure 10) and lower where fires were frequent (figure 12). Plant species richness was higher in forest but fairly similar in woodland, grassland and bush/scrub in comparison with the birds (figure 10). It was also fairly similar in sites where there was rare burning frequency or none but decreased in sites where burning occurred about once every year (figure 12). However, the Detrended Correspondece Analyses (figures 15 and 16) show that plant species differ in areas where burning is more frequent compared with areas that rarely or never burn. The similarity in plant species composition between sites that burn frequently, rarely or never was also small (less than 50%), with decreasing similarities when comparing sites which never burn with those that burn more frequently (only 24% similar with sites that burn each year).

Plant species responses to large mammals and fire

These analyses showed that certain species become more abundant where large mammals are at a high biomass density and where fire is more frequent. We here summarise some of the responses:

Hippopotamus impacts

Where hippopotamuses are relatively abundant the vegetation tends to be dominated by *Cynodon dactylon*, *Commelina diffusa*, *Commelina africana*, *Asystasia gangetica*, *Cyanotis foecunda*, and *Achyranthes aspera* (figures 15 and 17). When comparing changes that have taken place between 1992 and 2009 species such as *Cyanotis foecunda*, *Cynodon dactylon*, *Commelina africana*, *Ocimum suaveolens, Oplismenus hirtellus*, *Cyperus papyrus*, and *Cyperus cyperoides* have increased where hippopotamuses are more abundant (figure 19). The increase of the two *Cyperus* species is surprising but may have occurred in areas where distance to hippopotamus pods was short but the numbers of hippopotamuses in each pod was low or the overall density of animals was low so that swamp vegetation continued to increase despite the presence of some animals.

Grasses that were more abundant where hippos were not present included *Sporobolus stafianus*, *Panicum maximum*, *Themeda triandra*, and *Imperata cylindrical* (figure 21). Species that showed a decline were hippopotamuses where more abundant (or an increase where they were rare) included *Bothriochloa insculpta, Digitaria diagonalis*, *Cymbopogon nardus*, *Sporobolus stapfianus*, *Hyparrhenia filipendula*, and *Themeda triandra* (figure 19). Lock (1972) showed many of these same species to increase in exclosure plots designed to keep hippopotamuses out.

Elephant/large mammal biomass impacts

Sporobolus pyramidalis, *Sporobolus stapfianus*, *Chloris gayana*, *Sporobolus africanus*, and *Bothriochloa insculpta* were all more abundant where ungulate biomass was high (CCA – figure 17). This is probably because these species are common food species in the diets of many of the ungulates in this park (Field, 1972). Large mammal biomass did not have a significant relationship with tree species distribution (figures 16 and 18), possibly because of the long lag time that occurs in the regeneration of trees following large mammal declines. The distribution of large mammal biomass between 1995 and 2006 may not necessarily be the same as it was in the 1950s, 60s and 70s. However, there appears to be in increase in the number of trees for *Acacia kirkii* and *Acacia gerradii* (figure 20) between 1992 and 2009 where elephant density is higher. Unfortunately the data from the plots measured in 1992 only recorded the number of trees and there was no measure of diameter size classes which could be compared with data collected from the same plots in 2009. It is possible the numbers of trees have increased but size classes decreased as was observed in Tarangire with increases in browsing by elephants (Van de Vijver, Foley and Olff, 1999). The herbs *Asystasia gangetica*, *Achyranthes aspera*, and *Justicia flava* have also increased in abundance where elephants are more abundant in QENP.

Burn frequency

It is clear that this park has fire adapted vegetation. Plant species richness does not change greatly until very regular burning takes place and which point diversity declines. Species of herb that increased with increasing burn frequencies included *Digitaria diagonalis*, *Cymbopogon nardus*, *Chloris gayana; Sporobolus stapfianus*, *Bothriochloa insculpta*, *Vernonia smithiana*, *Microchloa kunthii*; *Hyparrhenia filipendula*, and *Heteropogon contortus*. Species such as *Brachiaria decumbens*, *Cynodon dactylon*, *Cyanotis foecunda*, *Cyperus articulatus*, *Justicia flava*, and *Oplismenus hirtellus* generally occurred where burn frequency was very low or never occurred between 2001 and 2009. These species tended to be consistently found in these patterns whichever analysis was used to assess the impact of fire and some of them have been found to do well in areas of the park that regularly burn (Jaksic-Born, 2009a).

Management of vegetation change

It is clear that the vegetation of Queen Elizabeth Park continues to change following the assessments of Lock (1985, 1988 and 1993). What should park managers do to try and control the spread of the less palatable grasses which seems to be taking place, particularly *Imperata cylindrica*, and the change in vegetation to more bush/scrub and forest? Large mammals and fire are both having an impact on the vegetation but their effects are synergistic and depend on the grazing and browsing biomass as well as the fire frequency and intensity. Assessing the result we obtained here as well as the literature that exists of work on the impacts of fire and large mammals on African savannas more generally and in Queen Elizabeth Park specifically we can recommend the following:

1. Early burning is useful in some of the *Themeda triandra*, *Bothriochloa insculpta*, *Hyparrhenia filipendula, Heteropogon contortus*, *Sporobolus pyrimidalis*, and *S. stapfianus* grasslands and should be continued. However attempts should be made to burn every 2-3 years and to burn smaller areas so that a patchwork of areas of different age of grass is maintained.
2. Lock (1988) suggested that the deliberate lighting fires should take place in the evening and early in the dry season as the winds are light and the fires will tend to die out overnight. As a result smaller areas will be burnt. UWA should aim to only burn about ¼ of the park each dry season.
3. In *Imperata cylindrica* grassland, this species germinates quickly after fire and flowers early to seed the soil. During the early period of re-sprouting it is visited by large mammals that graze the young shoots but when older is avoided. In order to reduces the spread of this species two alternative strategies could be tested:
    a. Burn small areas to encourage large mammals to visit the area and spend time grazing here. If small areas of the young grass occur within a larger mosaic of less palatable grass animals will remain here and keep the grass grazed low. This will encourage a shift to other grass species at this site and the creation of grazing lawns (Archibald et al., 2005).
    b. Burn this grassland late in the dry season so that firstly the fire is more intense and may kill the grass and secondly it doesn't have time for the plant to flower before the wet season growth of other species can take place. This may provide more competition from other plant species which may replace the grass over time.
4. It is likely that the increase in large mammals that has been taking place in QENP since the early 1990s will lead to a reduction in the spread of woody vegetation. The data from 1990-2006 show that there is more of a balance now between woody vegetation increase and woody vegetation loss (table 3). We don't therefore believe that the woody vegetation component should be managed actively but that the large herbivores should continue to be conserved and their numbers continue to increase, particularly the elephants. At present hippopotamus numbers are not as high as they used to be in the 1960s (up to 21,000) and range around 4,800 in the last two surveys in 2006 and 2008 (M.dricuru pers. comm.) and their impacts on the vegetation are probably not too damaging. As numbers increase there may be a

need to consider culling, which could provide meat and some revenue to local communities and increase their support for the park.

5. The recent decrease in Uganda kob from about 35,000 animals in the early 2000s to about 8,000 (figure 8) is a real concern. The population is now at its lowest level since censuses began. Why there has been such a decline is unclear. It could be that poaching has been much higher than had been estimated and this has significantly reduced their numbers. The area they frequent is also used to graze livestock from the fishing villages and it is possible that livestock are competing for pasture with them. There is a need for a research project to look at what is causing the population to decline. There must also be a concerted effort to make sure cattle do not graze in the Kasenyi area of the park where they are most abundant.
6. All efforts should be made to remove exotic species in the park. While this survey did not find many of the known exotics in the park, because sampling was not around sites of human habitation, there is a need to remove those that have been identified. Lock (1988) listed several species which included:
    a. *Lantana camara* – This species is widespread and particularly problematic. We estimated it occurred over 66 km^2 of the park. It is unpalatable to all large mammal species and is therefore reducing the availability of suitable habitat for the large mammal fauna. It is hard to eradicate and is best done so with poisons that kill the root stock. However repeated cutting of the plants can also kill them. It is probably possible to employ ex-poachers to harvest these regularly until the plant is eradicated, thereby providing some employment for the poachers as well as removing the plant.
    b. *Parthenium hysterophorus* (Congress weed) – this species is very invasive and should be removed as soon as possible. Currently it occurs along the channel track and is on the peninsula, particularly in the old workshop. All efforst should be made to remove it before it spreads further.
    c. *Opuntia* (Prickly pear cactus) – Most of the areas where this species occurred have been cleared since 1988. There is a need to monitor these sites and ensure it does not re-appear.
    d. *Tecoma stans* – This is a plant at Mweya with long yellow flowers and long pods with winged seed that was planted by people in the gardens there. It should be uprooted and burned as it was spreading in the late 1980s and is probably still doing so.
    e. *Thevetia peruviana* – This plant was planted as hedges at Mweya and has yellow flowers with roundish fruits containing a hard stone-like seed. It has milky latex which exudes when it is cut. All plants not growing in gardens should probably be destroyed by cutting and burning and over time the hedges should be planted with native species.

    There are a few other species that have been grown as ornamentals in the grounds of Mweya lodge and around UWA staff housing at Mweya. On a more general note all lodges in the park should be discouraged from planting non-native plants around their sites.
7. With the improvements and access to high resolution satellite imagery it is likely that it will be possible to regularly map vegetation types across the park in the future. If this is not possible it should be possible to repeat the aerial surveys that were made in 2006 to obtain another coverage of the park after about 10 years to assess woody cover changes.
8. The burn scar mapping should also be kept updates so that we have a measure of fire frequency and extent over time as management plans are re-establihsed.
9. The vegetation plots established in 1992 and the additional plots established in this study should be monitored at 10 year intervals also to assess changes that will take place in the future and which will allow monitoring of the vegetation communities over time. A complete set of the vegetation data will be provided to UWA with this report as well as a copy kept at the WCS offices in Uganda.

10. The US Forest Service recently conducted an assessment of fire management needs in the Greater Virunga Landscape (DeMeo, Barnett and Small, 2010) and plan to give training in fire control methods as well as help Uganda Wildlife Authority (UWA), Institut Congolais pour la Conservation de la Nature (ICCN) and the Rwanda Development Board/Tourism and Conservation (RDB) develop fire management plans. At present the planning in this document separates savannas and forests as two zones in the whole landscape and yet there is a clear need to think of the savannas as a patchwork which needs more detailed management in order to maintain the diversity of grasses and other herbs. Similarly fire in the alpine habitats may need specific management attention as fires have taken place on Mt Muhabura and in the Rwenzori mountains in the recent past, burning much of the alpine vegetation. To what extent some of the alpine flora may be adapted to fire is not known.

Conclusions

This study has summarized much of the historical information on changes in large mammal populations, changes in vegetation and changes in burning frequency in the Queen Elizabeth National Park since scientists first started collecting information from this park. These show that as the large mammal numbers crashed in the 1970s the vegetation became more wooded with an increase in woody vegetation over 1,021 km^2 of the park by 2006. As large mammals have increased again the change in vegetation appears to have slowed and the park is more in equilibrium now as a result of their impacts on the trees and shrubs, particularly elephants. Fire frequency has not changed greatly and is an important component of the park ecology. Plant species are adapted to burning and the diversity of plant species is similar at sites which never burn or burn at rare-medium frequencies. It is only at high frequencies of burning that diversity declines. However for birds, species diversity declines with burn frequency.

It is clear that the changes that are taking place are a result of several factors which include large mammal biomass, effects of hippopotamuses and elephants, fire, rainfall and also other factors such as the impacts of termites. Each of these factors does not occur in isolation and their effects may be synergistic or antagonistic. This study aimed to try and tease out the relative impacts and importance of each of these factors and shows that hippopotamus proximity, burn frequency, large mammal biomass and rainfall (which is correlated with altitude) are the dominant factors that can explain the variation in species composition in the park. These factors explained about 27% of the variation in herb distribution and 49% of the variation in tree distributions in the park. It is possible soil type which was not measured is an important factor also and their impact should be investigated.

Fire management in Queen Elizabeth National Park is not a simple process, simply using early or late burning to control grassland and woodland vegetation. Fire management actions to date have tended to rely on early burning to stop intense fires. There is a need to think about controlling fire extent, frequency and intensity and varying this depending on the grassland type found in the park. More research is needed to see how different grassland types can be managed by fire, with experimental manipulation of fire type, grazing pressure and time of burning. This should be a priority research topic in *Imperata cylindrica* (spear grass) grassland which is spreading in the park but at present it is unclear what the reasons for this are.

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Appendices

Appendix 1. Summary of imagery used to derive statistics of fire extent in Elizabeth National Park.

Landsat Image Tile 173_60
Statistics for entire tile (not just within Queen Elizabeth NP boundary)
Burn Season 1 = December (y-1) – April
Burn Season 2 = May - November

1970s

Burn Season	# of Burns	Min. Burn Area (km^2)	Max. Burn Area (km^2)	Avg. Area (km^2)	Total Area Burnt (km^2)	# of Images Used	Image Date(s) - dd/mm/yyyy
Season 1 – 1973	61	0.34	45.72	6.63	404.20	1	2/4/1973
Season 1 – 1975	50	0.30	152.96	9.87	493.29	1	3/12/1975

1980s

Season 1 – 1984	25	1.09	208.24	28.78	719.59	1	2/12/1984
Season 2 – 1984	18	0.45	8.32	3.64	65.54	1	5/26/1984
Season 1 – 1986	10	1.35	46.85	13.93	139.25	1	1/8/1986
Season 2 - 1986	65	0.15	141.77	9.14	594.04	3	6/1/1986, 7/19/1986, 8/4/1986
Season 1 - 1987	42	0.03	61.68	14.98	629.23	3	1/27/1987, 2/28/1987, 3/16/1987
Season 2 - 1987	97	0.22	57.15	8.87	860.41	6	5/3/1987, 5/19/1987, 6/7/1987, 8/7/1987, 9/8/1987, 10/2/1987
Season 2 – 1988	7	0.72	23.74	6.00	41.99	1	5/29/1988
Season 2 - 1989	120	0.47	34.98	5.37	644.88	4	7/3/1989, 8/4/1989, 8/20/1989, 9/21/1989

1990s

Season 1 – 1990	24	0.44	17.23	3.88	93.17	1	4/17/1990
Season 2 – 1990	33	0.56	12.47	3.34	110.26	1	6/4/1990
Season 2 – 1994	24	1.45	27.63	6.74	161.76	1	8/10/1994
Season 1 - 1995	92	0.40	52.62	6.36	585.15	3	1/17/1995, 2/2/1995, 2/18/1995
Season 1 – 1999	32	1.75	78.73	17.14	548.58	1	2/13/1999

2000s

Burn Season	# of Burns	Min. Burn Area (km^2)	Max. Burn Area (km^2)	Avg. Area (km^2)	Total Area Burnt (km^2)	# of Images Used	Image Date(s) - dd/mm/yyyy
Season 1 - 2001	36	0.72	66.19	15.84	570.39	2	3/14/2001, 1/9/2001
Season 1 - 2002	6	1.14	12.37	3.54	21.22	1	12/11/2001
Season 2 - 2002	19	0.55	26.86	5.86	111.30	2	7/23/2002, 10/11/2002
Season 1 - 2003	65	0.60	220.64	13.90	903.46	4	12/30/2002, 1/15/2003, 1/31/2003, 3/4/2003
Season 2 - 2003	4	11.26	92.56	40.38	161.51	1	10/14/2003
Season 1 - 2004	58	0.86	62.29	13.18	764.62	5	12/17/2003, 2/19/2004, 3/6/2004, 3/22/2004, 4/7/2004
Season 2 - 2004	23	1.17	38.49	12.20	280.67	2	10/6/2004, 12/7/2004
Season 1 - 2005	115	0.26	127.78	11.02	1266.74	4	1/4/2005, 1/20/2005, 2/5/2005, 2/21/2005
Season 2 - 2005	64	0.51	64.46	9.88	632.21	5	6/13/2005, 6/29/2005, 7/15/2005, 9/1/2005, 9/17/2005
Season 1 - 2006	76	0.85	97.32	10.87	825.79	3	12/22/2005, 1/23/2006, 2/8/2006
Season 2 - 2006	73	0.64	39.69	7.64	557.46	5	7/2/2006, 8/19/2006, 9/4/2006, 9/20/2006, 10/6/2006
Season 1 - 2007	33	0.82	59.98	13.25	437.18	3	1/26/2007, 2/27/2007, 3/15/2007
Season 2 - 2007	33	0.08	36.00	4.06	133.89	3	7/21/2007, 8/6/2007, 11/26/2007
Season 1 - 2008	68	0.00	82.58	4.79	325.46	3	1/13/2008, 2/14/2008, 4/18/2008
Season 2 - 2008	20	0.01	4.52	1.33	26.63	1	8/24/20008
Season 1 - 2009	173	0.00	36.91	2.87	496.89	4	12/14/2008, 1/15/2009, 1/31/2009, 2/16/2009
Season 2 - 2009	214	0.00	52.21	2.00	427.15	5	6/8/2009, 6/24/2009, 8/11/2009, 8/27/2009, 9/28/2009

Appendix 2. Location of plant plots and frequency of burning between January 2001 and September 2009.

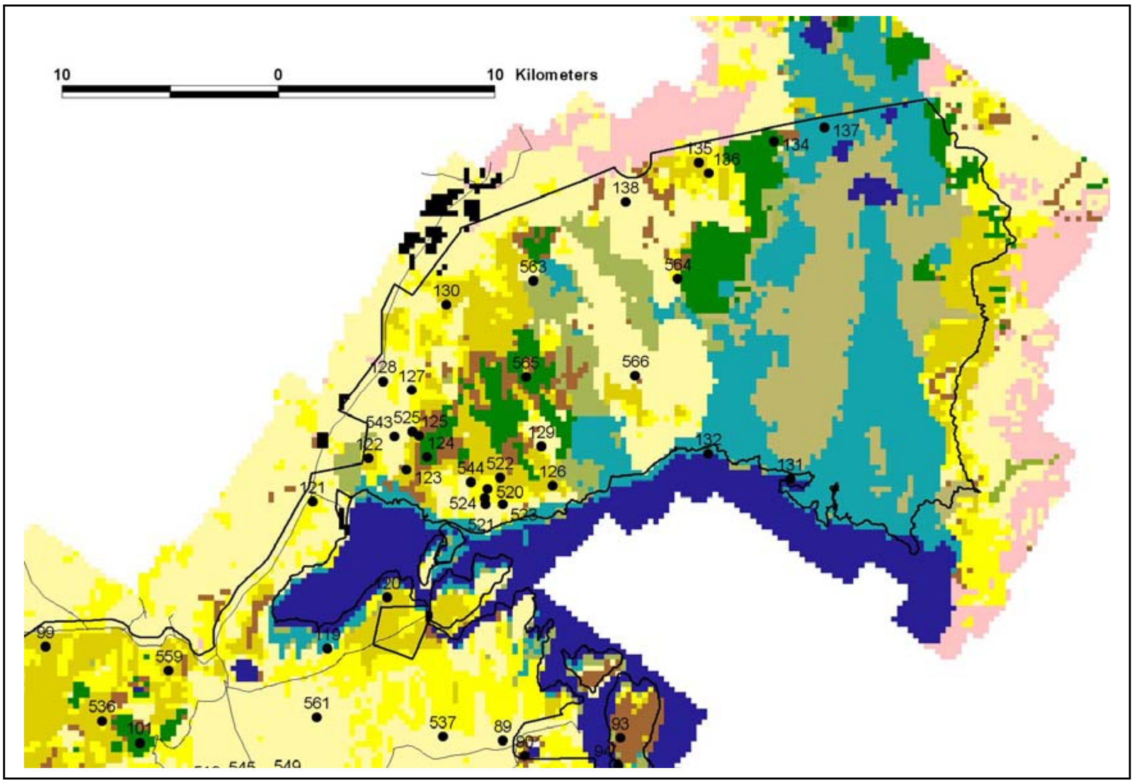
Plot number	Burn frequency in 2000s	Longditude	Latitude
1	1	29.648963	-0.682375
2	2	29.654377	-0.684467
3	4	29.697548	-0.634297
4	4	29.686541	-0.660912
5	4	29.690389	-0.604634
6	1	29.663562	-0.627886
7	4	29.673437	-0.616004
8	0	29.718301	-0.594102
9	0	29.725876	-0.569776
12	1	29.736041	-0.552872
13	2	29.688021	-0.531016
14	2	29.693963	-0.526293
15	2	29.700814	-0.521422
16	1	29.668870	-0.584691
17	1	29.671600	-0.578557
18	0	29.664874	-0.568024
19	0	29.669276	-0.545774
20	0	29.685133	-0.511036
21	0	29.691930	-0.491945
21b	0	29.694253	-0.485463
21c	0	29.687330	-0.488871
22	0	29.690523	-0.480377
23	0	29.698360	-0.474399
24	0	29.679214	-0.483654
25	0	29.679051	-0.513226
26	5	29.742051	-0.519759
27	3	29.786776	-0.464634
28	5	29.796993	-0.491080
29	0	29.780893	-0.420445
30	0	29.784698	-0.429315
31	1	29.802635	-0.464632
32	4	29.827391	-0.444713
33	2	29.840960	-0.439228
34	7	29.758023	-0.538888
35	0	29.765793	-0.419824
36	0	29.763730	-0.411627
40	0	29.868741	-0.336256
41	0	29.871496	-0.360942
41	0	29.865045	-0.316438
42	0	29.872214	-0.325986
44	3	29.923616	-0.275401
45	0	29.906667	-0.291801
46	10	29.951220	-0.256688
47	5	29.781444	-0.504421
48	4	29.800263	-0.511862
49	3	29.801507	-0.521045
50	2	29.809076	-0.519041
51	4	29.798854	-0.562764
52	4	29.791599	-0.563688
53	3	29.797418	-0.534368
54	4	29.996549	-0.202558
55	1	29.934545	-0.208036
58	8	30.012775	-0.192875
59	8	29.981438	-0.223551
60	6	30.002658	-0.205290

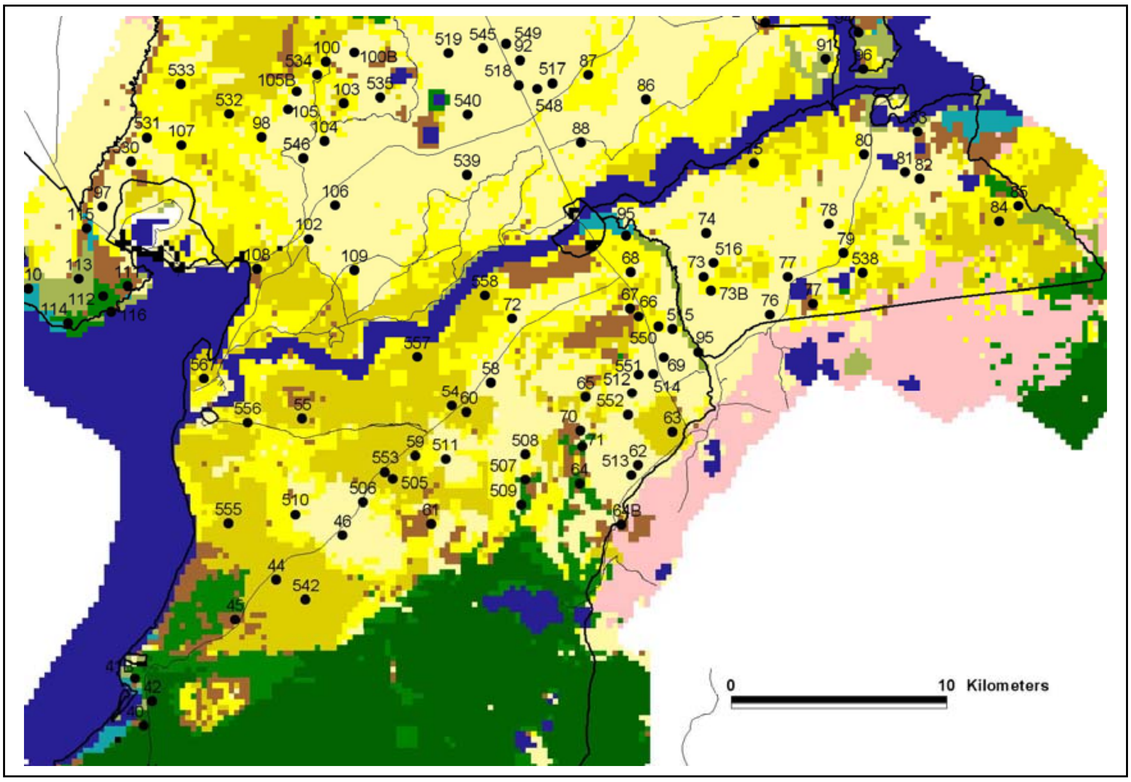
Plot number	Burn frequency in 2000s	Longditude	Latitude
61	1	29.988037	-0.252075
62	10	30.073980	-0.227311
63	8	30.088166	-0.213471
64	0	30.049673	-0.235086
64b	0	30.066954	-0.252406
65	1	30.052136	-0.198819
66	6	30.074218	-0.164946
67	6	30.070639	-0.161762
68	7	30.070883	-0.146454
69	8	30.084767	-0.182220
70	0	30.050105	-0.212982
71	0	30.050785	-0.219628
72	4	30.021655	-0.165857
73	9	30.101296	-0.148314
73	8	30.104196	-0.154207
74	6	30.102403	-0.130123
75	1	30.122079	-0.100746
76	3	30.128750	-0.164277
77	6	30.136029	-0.148460
77	1	30.146641	-0.159724
78	6	30.153170	-0.126203
79	6	30.159280	-0.138591
80	2	30.167789	-0.097140
81	2	30.184754	-0.104653
82	2	30.190986	-0.107570
83	0	30.190173	-0.087748
84	0	30.223990	-0.125141
85	0	30.232006	-0.118854
86	1	30.077290	-0.074106
87	2	30.053288	-0.063917
88	3	30.050147	-0.092323
89	3	30.117512	-0.035789
90	3	30.126637	-0.042018
91	2	30.151684	-0.057393
92	12	30.025035	-0.057713
93	0	30.166243	-0.034479
94	0	30.165503	-0.046092
95	9	30.098895	-0.179879
95b	0	30.069028	-0.131274
96	1	30.167414	-0.061491
97	7	29.851542	-0.119162
98	6	29.917560	-0.090087
99	8	29.928163	0.003394
100	8	29.956307	-0.054428
100b	4	29.944460	-0.058458
101	5	29.967349	-0.036651
102	2	29.937247	-0.132506
103	7	29.951741	-0.075909
104	8	29.943787	-0.091753
105	7	29.928789	-0.078216
105b	6	29.932369	-0.070827
106	3	29.948100	-0.118572
107	7	29.884364	-0.093391
108	0	29.915777	-0.145178
109	1	29.956061	-0.145622
110	0	29.820756	-0.153390
111	0	29.862038	-0.152319
112	0	29.851921	-0.156466

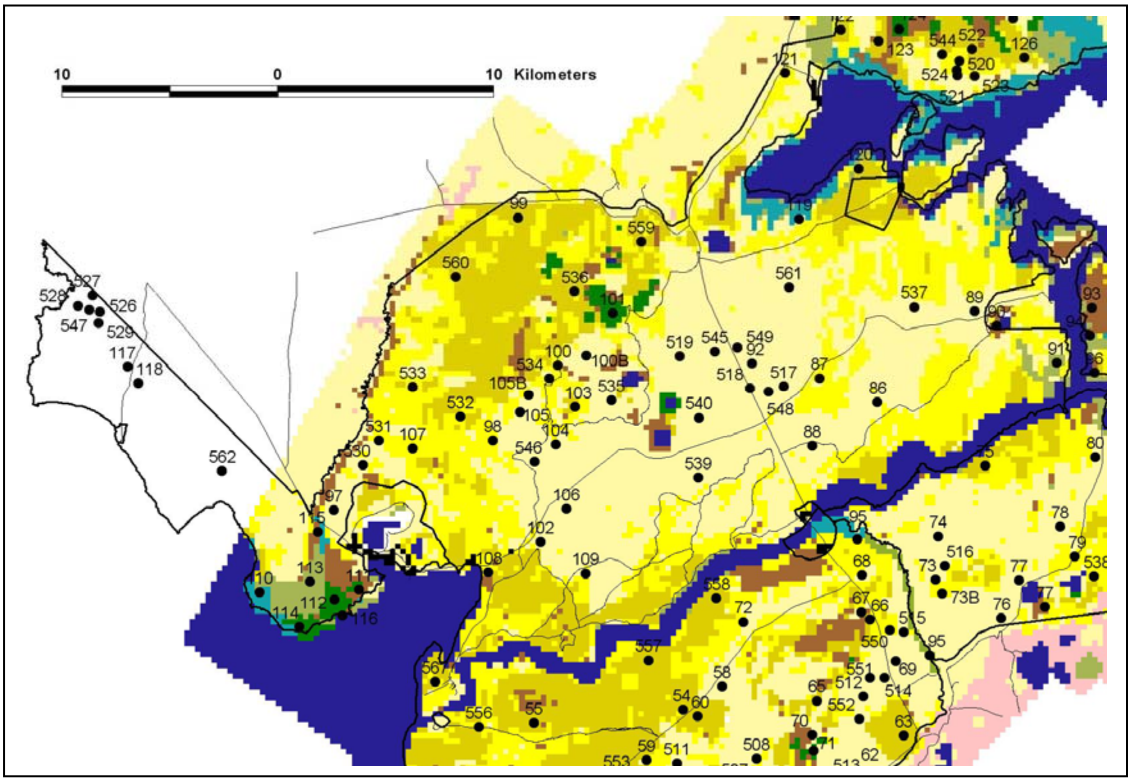
Plot number	Burn frequency in 2000s	Longditude	Latitude
113	0	29.841679	-0.149139
114	0	29.837173	-0.167865
115	0	29.845066	-0.128289
116	0	29.855127	-0.163125
117	2	29.766076	-0.059126
118	1	29.770519	-0.065881
119	0	30.044776	0.002607
120	0	30.069575	0.023901
121	4	30.038856	0.063816
122	2	30.062049	0.081844
123	6	30.077658	0.077188
124	5	30.086112	0.082340
125	6	30.082782	0.091280
126	8	30.138174	0.070410
127	10	30.079760	0.110351
128	8	30.067978	0.114023
129	3	30.133488	0.086644
130	4	30.094199	0.146117
131	0	30.236749	0.073147
132	0	30.202637	0.083766
134	0	30.229867	0.214210
135	1	30.198772	0.205289
136	3	30.202963	0.200934
137	0	30.250777	0.220098
138	4	30.168358	0.188900
501	10	29.758513	-0.525344
502	4	29.706444	-0.552115
503	4	29.761977	-0.462665
504	7	29.832370	-0.457524
505	11	29.972163	-0.233297
506	10	29.959665	-0.242862
507	9	30.027076	-0.233486
508	9	30.027078	-0.223032
509	7	30.025489	-0.244117
510	7	29.931681	-0.247993
511	7	29.993989	-0.224974
512	11	30.071427	-0.197110
513	11	30.071210	-0.231597
514	11	30.080255	-0.189283
515	11	30.088244	-0.170242
516	10	30.105272	-0.142527
517	11	30.038447	-0.067410
518	11	30.024367	-0.068256
519	11	29.995157	-0.054714
520	13	30.111326	0.069049
521	13	30.110342	0.062770
522	12	30.116468	0.073786
523	12	30.117673	0.062550
524	12	30.110123	0.065193
525	12	30.080140	0.092730
526	11	29.754380	-0.035979
527	12	29.751505	-0.029188
528	9	29.745312	-0.033530
529	9	29.753937	-0.040767
530	9	29.863536	-0.100232
531	9	29.870173	-0.090100
532	9	29.904130	-0.080192
533	9	29.884222	-0.067719

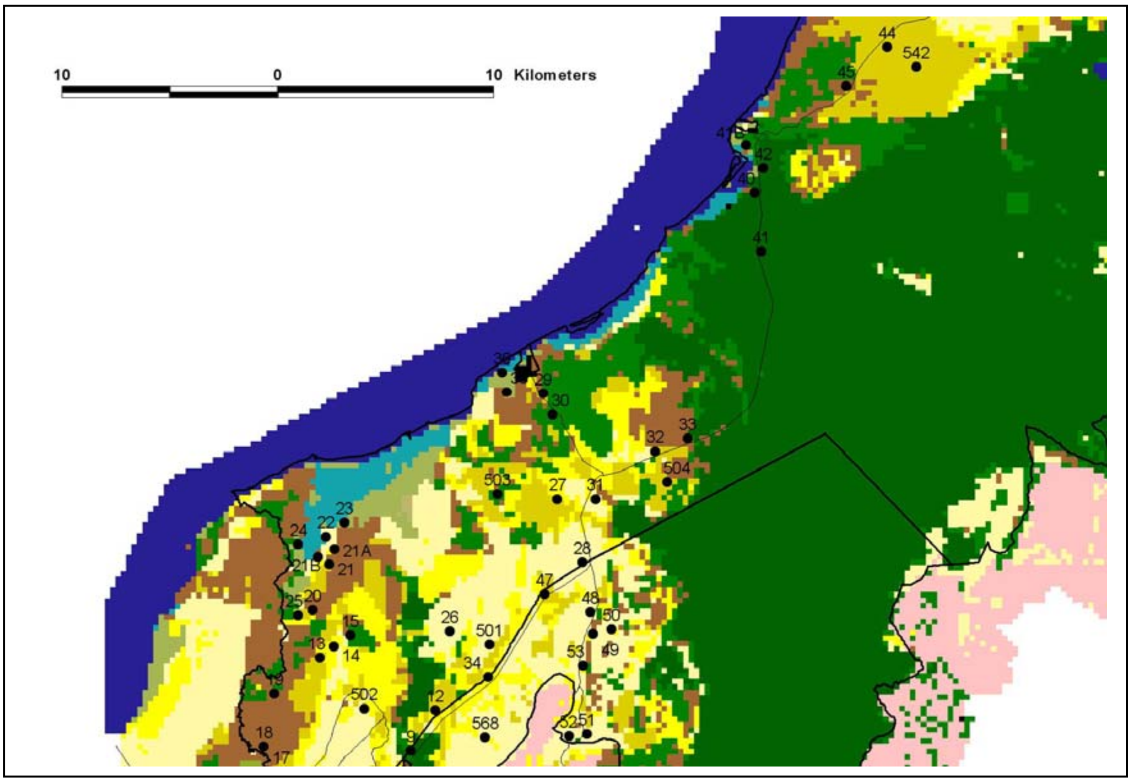
Plot number	Burn frequency in 2000s	Longditude	Latitude
534	5	29.940854	-0.064048
535	5	29.966848	-0.073292
536	5	29.951546	-0.027523
537	5	30.092658	-0.033985
538	5	30.167263	-0.146836
539	5	30.002853	-0.105691
540	5	30.003193	-0.080542
541	5	29.689426	-0.624881
542	5	29.935868	-0.283604
543	11	30.072585	0.090854
544	11	30.104247	0.071769
545	10	30.009636	-0.052760
546	10	29.934906	-0.098894
547	10	29.749957	-0.035333
548	12	30.032091	-0.069624
549	12	30.019207	-0.050908
550	12	30.082516	-0.169327
551	12	30.074229	-0.189339
552	12	30.069808	-0.206387
553	12	29.968936	-0.230271
554	3	29.696907	-0.587353
555	0	29.903739	-0.251778
556	0	29.911797	-0.209744
557	0	29.982234	-0.181902
558	0	30.010411	-0.156075
559	9	29.979230	-0.006658
560	6	29.902260	-0.021345
561	6	30.040609	-0.025906
562	3	29.805169	-0.102873
563	3	30.130158	0.155944
564	1	30.190036	0.156966
565	0	30.127143	0.115926
566	1	30.172429	0.116437
567	0	29.893691	-0.191002
568	5	29.756731	-0.564175

Appendix 3. Maps showing the location of each of the plots overlaid on the 1990 habitat map derived from aerial photographs.






10
0
10 Kilometers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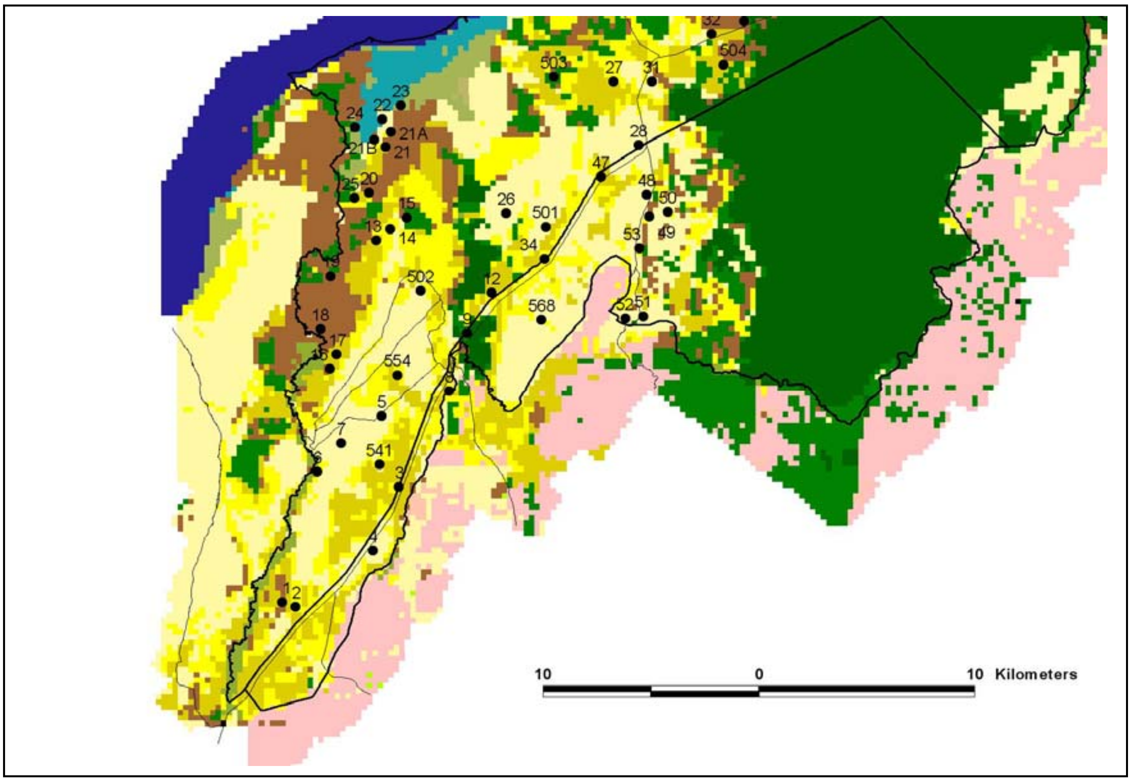
10 Kilometers


10
0
10 Kilometers