Communities of small mammals in Kafue National Park and their response to fire, vegetation and land use

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Summary

Small mammals assume multiple and cardinal roles in ecosystem functionality. They are known to influence the composition and structure of plant communities through their herbivorous and seed predation activities, as agents of soil aeration through their burrowing activities, pest controllers as the consume large amounts of insects and plant material, and as food for a variety of prey. Yet, the understanding of small mammal ecology is overshadowed by studies of large mammals as small mammals have very little tourism appeal and are often viewed as vermin benefiting from human disturbances. Even so, many small mammals are known to be highly sensitive to anthropogenic factors.

This lack of information on small mammals also applies to the Kafue National Park (KNP), Zambia, including the Busanga Flood Plain as one of KNP's critical habitats and a wetland of international importance (RAMSAR site number 1659). Not much is known about small mammals in the KNP, much less the influence of anthropogenic and non-antropogenic factors on their communities. Given that KNP is a protected area where the human foot print is minimized, anthropogenic factors that act upon the communities of small mammals include bush fires, that occur repeatedly (annually) on wildlands. These are ignited by various stakeholders including park authorities that set fires in the early dry season (May to mid-July) in order to reduce incidences of fires in the late dry season, and to clear vegetation for photographic tourism. The other anthropogenic factor is habitat modification arising from infrastructure developments in the natural habitats of small mammals as given by the park's management zones. In order to come to a better understanding of the relationships between small mammals and some of the ecosystem components of KNP, the aims of the study were to (i) provide checklists of small mammals in KNP together with an assessment of their functional characteristics, (ii) investigate the interaction of small mammal communities with three major vegetation formations, land use and fire, and (iii) assess dietary resource-use and partitioning among small mammal species.

In a first step, a literature review provided a species list on which future studies could be based upon. This review identified termitaria, grassland and woodland as the three most important habitats for small mammals in the park. These

habitats were then used to assess relationships between small mammals, vegetation, land use and fire. Thus, during the dry season of 2014 and 2015, 6,273 trap nights were employed to trap 105 individuals of 16 species of small mammals in Miombo woodland, termitaria and grassland vegetation. In each of these vegetation types replicate sites were set in areas of low and high fire recurrence. Sites that experienced less than eight years of fire between the years 2000 and 2013 were classified as low fire recurrence sites and those that experienced eight or more, were classified as high fire recurrence sites. For each site, fire age was assigned based on the last time a site experienced fire. For dietary resource-use and partitioning, stable isotope biochemistry techniques were employed. These techniques provide quantitative records of an animal's feeding ecology based on the signatures of stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) found in an animal's tissues. Values of $\delta^{13}C$ in animals reflect the carbon source of food whilst $\delta^{15}N$ reflects the trophic position in a community. Linear models and multivariate analysis were used to asses the effect of vegetation, land use and fire on the community measures.

More than 50% of the small mammal species described in Zambia occur in KNP, which makes it an important conservation area for this group of mammals. These belong to the orders Rodentia, Soricomorpha and Macroscelidea. Of these, only one species, *Fukomys kafuensis* bears a high conservation status and is listed as vulnerable by the International Union for Conservation. Important habitats for small mammals include termitaria, woodland and grassland, with the former two being the habitats for *Fukomys kafuensis*.

Land use as prescribed by the management zones has no influence on the community structure and composition of small mammals. However, vegetation does and thus, conservation actions aimed at preserving vegetation formations would be more beneficial to small mammals than the large tracts of land assigned as management zones in the park. Termitarias proved to be important for small mammals particularly in areas prone to disturbance. In the Busanga Flood Plain, termitarias act as refugia for species during periods of disturbance as they provide shelter against fire, as it may be easier to dig in the mounds as compared to the hard-compacted soils in the grasslands after floods. Further in the wet season, in times of floods, they offer dry ground as they are elevated. This role, was corroborated by the large dietary space small mammal communities in termitarias occupied, that

encompassed almost all the dietary spaces of other communities in miombo and grasslands.

Although fire recurrence as a single factor had no significant impact on species richness its effect became significant when combined with the time elapsed since the last fire. This suggested adaptation of small mammal communities to the fire regimes in their environments, as areas that were burnt frequently, had fewer species irrespective of the time elapsed since the last fire had occurred. Further, the smaller sized species seemed to be more affected by recent burns than larger species that may have fewer problems escaping fire and recolonizing burnt areas. This response to fire by small mammals was also reflected in the difference in the dietary niche widths particularly for rodents. Rodents had broader dietary niches under high fire recurrence and may indicate relaxed competition under this regime because their populations do not reach the carrying capacity of the habitat, or reduced species numbers under high-versus-low fire frequency regimes. This is an important finding as it provides an understanding on the boundary conditions under which small mammals reach their carrying capacity in this ecosystem. For shrews, the opposite persists as they appear to have narrower dietary niches in areas under high fire frequencies and their dietary niche differentiation remains unresolved. Another important finding was that rodent communities appeared to be structured by size (differences in body mass between species of the same guild by a factor of two), dietary guilds (based on carbon isotopes) or trophic levels (based on nitrogen isotopes), suggesting mechanisms of coexistence to avoid competition.

In conclusion, small mammals are important components of the KNP, and their responses to the various environmental factors acting upon them, needs to be incorporated into the management plans of the park. Further, as competition appears to be an important component structuring rodent communities in the park, it signifies limiting resources. Since the limitations of dietary resources are likely to affect large and small mammals alike, studies of African savannas should use a broad approach to come to a comprehensive understanding of African ecosystems.

To my Lord Jesus Christ, for His unfailing love that has seen me through my seasons.

Contents

General Introduction

Conservation of biodiversity remains paramount on the global agenda, and has over 190 nations subscribed to its implementation (United Nations Environment Programme [UNEP] 2011). Biodiversity coined from 'biological diversity' refers to the variety of life (Sands and Galizzi 2004), whilst conservation refers to all actions taken to preserve flora and fauna and their natural habitats. Most nations have responded to conservation of biodiversity by setting aside large tracts of land, called protected areas, where various conservation actions are taken. In these protected areas, the human footprint is minimized and thus, pressure from anthropogenic and non-anthropogenic activities is ideally minimal. Despite the existence of these protected areas and their increase in surface area globally, biodiversity continues to decline and has been more so in the last four decades (Woodley and Langhammer 2017).

This discrepancy is thought to be related to the degree to which protected areas deliver biodiversity outcomes and the degree of representation of biodiversity in a protected area (Woodley and Langhammer 2017). This is the case for most of the protected areas in Zambia, where over thirty percent of the land estate is protected for purposes of biodiversity conservation (Government of the Republic of Zambia [GRZ] 1998), and yet they continue to underperform on ecological, economic and social terms (Lindsey *et al.* 2014). According to Lindsey *et al.* (2014) protected areas in Zambia are largely underfunded and are marred with illegal offtakes of various components of wild flora and fauna amidst pressure from human encroachment. The other major challenge compounding conservation is the lack of information on components of biodiversity, and their responses to their changing environment (Zambia Wildlife Authority [ZAWA] 2011).

The Kafue National Park, Zambia's largest protected area (~22,400km^2, Fig.1), is not exempt from these challenges and pressures. Illegal offtakes of game continue to undermine the efforts of conservation coupled with repeated bushfires (Siamudaala *et al.* 2009) that burn over fifty percent of the park annually, against the prescribed burns outlined in the Fire Management Plan of Kafue National Park (FMP-KNP). Given that the Kafue National Park lies within an ecosystem that has evolved with fire (Campbell *et al.* 2007; Chanda 2007; Kampamba *et al.* 2005), fire is considered as a natural phenomenon and therefore the FMP-KNP recommends a rest interval of 2-3 years for all vegetation types. This recommendation is rarely followed as extensive burns are conducted annually on the rangeland, mainly to reduce the impact of the late dry season fires ignited by illegal activities. Other reasons for burning include improved visibility for game viewing, to foster vegetation succession and to provide fresh fodder for game from the green reserve shoots afforded by grasses after burns (Chanda 2007; Green *et al.* 2015; Kampamba *et al.* 2005; National Parks and Wildlife Services /Japan International Cooperation Agency [NPWS/JICA] 1999; Parr & Chowan 2003).

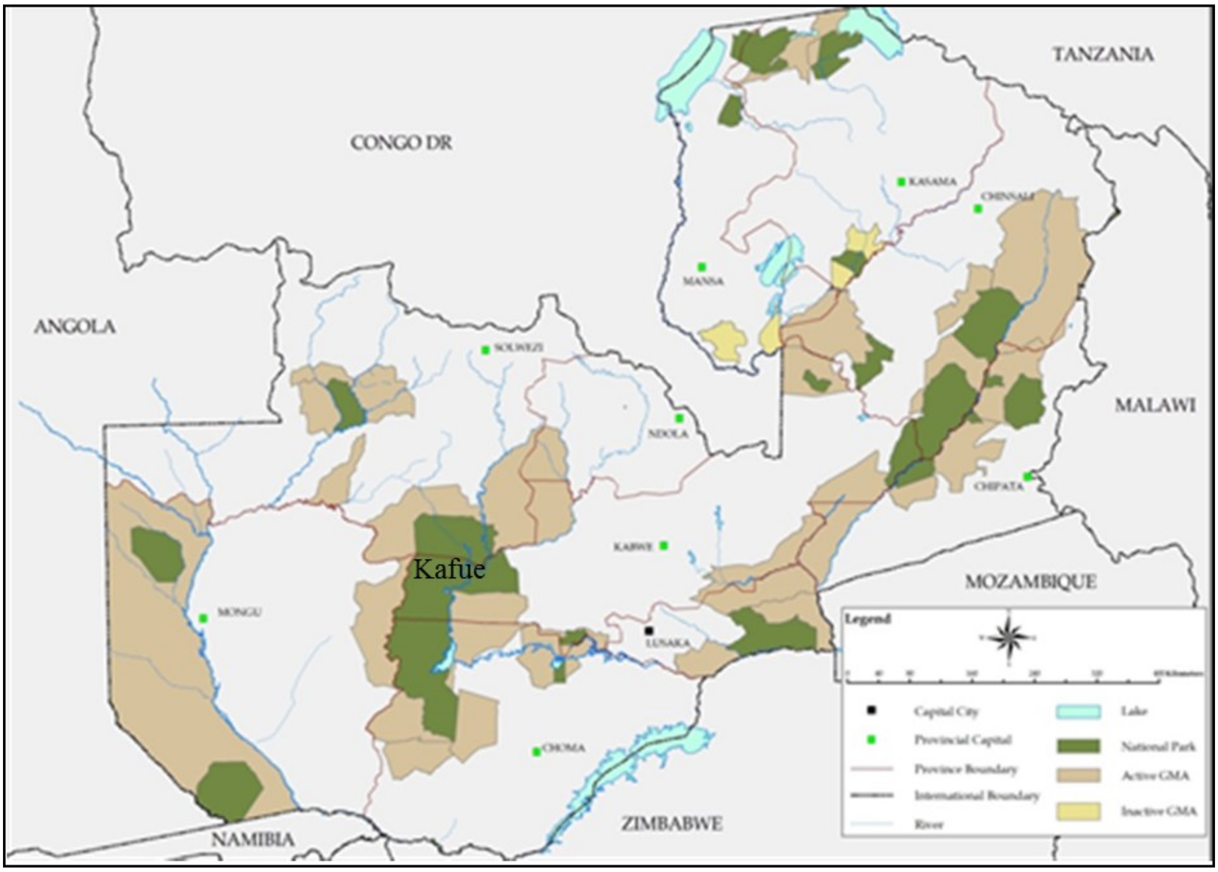

Fig 1. Kafue National Park in relation to other Parks in Zambia. (Source: United Nations Development Programme [UNDP] 2014).

As species response to repeated bushfires remains unclear, speculations persist. Some speculate a significant alteration in the range land to more open lands, soil erosion as soils are exposed to agents of dispersal i.e. wind & rain, reduced productivity of the rangeland (Chanda 2007; Moss 1973) and species loss particularly the non-conspicuous species that are largely under surveyed. Besides herpetofauna and invertebrates, small mammals is a group of taxa that is often overlooked and remains understudied compared to the large and charismatic species (ZAWA 2005) found in the park. They do not feature prominently in research or conservation plans (ZAWA 2005), and their lists in the park's management plans (NPWS/JICA 1999) are incomplete compared to larger mammals, birds and fish. Their size, cryptic nature, the large amount of effort required to study them (Barnett and Dutton 1995; Symes *et al*. 2013), and the fact that they are often viewed as pest or vermin to be controlled (Cudjoe 1994; Myllymäki 1979; Sieg 1987; Skonhoft *et al.* 2006; Swanepeol *et al.* 2017), could be the reasons why they are not prioritized in management plans and why information on their distribution remains scanty (NPWS/JICA 1999, ZAWA 2011).

Yet small mammals play cardinal roles in ecosystem functionality as they act as agents of pollination and dispersal through their mobile links (Johnson *et al*. 2001; Payne *et al.* 2016), soil aeration and creation through their burrowing activities (Kalies and Covington 2012; Martin 2003), pest control as they consume large amounts of vegetation and invertebrates (Sieg 1987; Timbuka and Kabigumila, 2006) and as food for a myriad of predator in the ecosystem (Apps 2012; Happold 2013; Happold & Happold 2013; Kingdon 1997; Skinner & Smithers 1990; Torre *et al.* 2010). This multiplicity of ecosystem functions assumed, makes them good indicators of environmental perturbations and it makes sense to have them studied in detail. In this dissertation, small mammals are defined as non-flying mammals, weighing less than one kilogramme and measuring less than a foot when adult.

Since Ansell's (1978) account of mammals in Zambia, very few attempts have been undertaken to detail small mammal communities. Instead, most studies have concentrated on specific species and on aspects of their ecology and zoonosis potential (e.g. Bennet and Aguilar 1995; Bennett *et al.* 2000; Burda *et al.* 1999; Chidumayo 1979, 1980; Colbo and Macleod 1976; Corti *et al.* 2005; Hutterer and Dippenaar 1987; Ishii *et al.* 2012; Bryja *et al.* 2012; McDonough *et al.* 2015; Mikula *et al.* 2016; Kawalika 2004; Kawalika and Burda 2007; Sichilima *et al*. 2008; Sasaki *et al.* 2014; Scharff *et al.* 1999; Wallace and Bennett 1998). Yet inventories that afford checklists are essential to conservation as they provide the basic information required for conservation actions. Inventories provide a finer view of biodiversity in an area that helps determine its significance or conservation value. Inventories form the basis of formulating preservation plans for species and their habitats. Having a full inventory of small mammals is undoubtedly essential as this would bring to the fore, threatened species that need protection and would contribute towards realizing their full ecological potential.

The latter would obvious need more than just species checklists, but an understanding of the biotic communities they form and their interactions with the environmental factors in which they exist. A community refers to a collection of species occurring in the same place and at the same time (Fauth *et al.* 1996). Its definition is bound to location and time where different species associate and interact. Several studies demonstrate the influence of environmental factors on small mammal communities in Africa. In the plains of Accra, Decher and Bahian (1999) demonstrated that small mammal communities were not only influenced by rainfall, soils and vegetation, but also by anthropogenic factors including the prevention or deliberate setting of fire. In the drier savanna regions (Kalahari savannah rangelands), Blaum *et al*. (2006), showed that species richness and abundances of small mammals was negatively affected by shrub encroachment, brought about by overgrazing, though grazing itself had no significant impact in a similar environment in Knersvlakte, South Africa (Bösing *et al.* 2014). Similar to the situation described by Blaum *et al.* (2006), fire as an environmental factor didn't have a direct impact on small mammals (Swanepoel, 1981; Yarnell *et al*. 2008) but acted through the animals' response to reduced cover to emigrate or avert predation. Further to this, Yarnell *et al.* (2007) described fire as having little impact on small mammal diversity, unless coupled with grazing and rainfall. Plavsic (2014) and Swanepoel (1981) described the effect of fire on small mammals as short lived and also associated with the removal of vegetation cover. Meanwhile, others describe it as having a positive impact on small mammal diversity, as species diversity is higher in areas where fire is a periodic disturbance (Bowland & Perrin 1993). This evidence, particularly on the influence of fire seems disconnected, and maybe difficult to apply to the current situation in Kafue National Park, given that the authors considered different environmental drivers in different combinations and carried out their work in different regions of Africa.

As in many African savanna systems small mammal communities in Kafue National Park are very diverse with many species occurring in sympatry. How these species come together or assemble to form communities is thought to be influenced by historic events (glacial and tectonic plate movements), non-random or random processes. The two dominating theories that try to explain community assemblage include assembly rules championed by Diamond (1975) and the neutral theory by Connor and Simberloff (1979). Assembly rules assume non-random processes where assembly is solely driven by competition. No two-species bearing the same traits can co-exist, thereby allowing only certain permissible combinations of species. If two similar species co-exist, the species unable to compete favourably for habitat resources is driven to extinction. Thus, communities are packed based on species gaps or traits. Contrary to this assumption are arguments by Connor and Simberloff (1979) that demonstrated community assembly as being driven by random processes and not by competition. They argued that species are distributed randomly based on the given number of species a habitat can accommodate irrespective of interspecific competition. In later years, Hubbell (2001) described random processes driving species diversity and abundance in communities as random dispersal, speciation and extinction.

Rules governing community assembly is still an important research focus for many ecologists (Gotelli 1999) and has been followed through by many studies (e.g. Brown *et al.* 2000; Fox and Brown 1993; Ganzhorn 1997). It is now widely accepted that both deterministic (non-random) and stochastic (random) approaches are useful in understanding community assembly. Deterministic approaches prevail under stable environment conditions, where populations within a community can grow up to carrying capacity of a habitat. In this scenario species are likely to compete over limiting resources and in order to avoid competition, species within a community will occupy different niches. A niche may be defined as a function or position that a species has or maintains in a given ecological habitat (Begon *et al.* 2006). Its differences are reflected in the variations of life history traits, activity patterns and in the partitioning of food resources and microhabitat separation. On the other hand, stochastic approaches prevail in unstable conditions that keep populations within a community, below their carrying capacity. Thus, species do not occupy exclusive niches as their co-existence is determined by spatial and temporal disturbances.

Given the protection accorded to biodiversity in the national parks in Zambia, organization of small mammal communities in Kafue National Park, is most likely a product of both deterministic and stochastic approaches. In areas set aside for purposes of attaining undisturbed natural resources namely, Wilderness and Special Conservation Zones (NPWS/JICA 1999), it would be expected that deterministic approaches would influence community composition and structure. However, this may not be the case, as there are other physical factors such as flood and fire that act as periodical disturbances and therefore, a combination of both approaches would be most likely. Meanwhile in areas where the human footprint is entertained to allow for visitor use and enjoyment (i.e. Wild and Intensive Utilization Zones), assembly of communities would follow stochastic approaches.

The heterogeneity of vegetation in Kafue National Park potentially provides a large variety of habitats for small mammal species in the park. This most likely influences their distribution, and their presence, absence and numbers is used to quantify or measure community properties. For instance, a habitat that supports a large number of species is more diverse than one with fewer species, and based on the multiplicity of roles small mammals assume in ecosystem functionality, this habitat would be more functionally diverse. However, most ecological studies and community comparisons between sites are often hampered by taxonomic issues, such as different species compositions or taxonomic uncertainties that make comparisons difficult. Instead, functional traits that dictate how an organism interacts with its environment are used. According to Violle *et al.* (2007) functional traits are the measurable attributes of an organism and these can be behavioral, morphological, phenological and physiological. For small mammals, these would include:

a. Social systems (solitary, paired or gregarious) as indication for the utilization of food resource and predator distribution, following the socio-ecological model for small mammal social organization (Ostfeld 1990).
b. Habitat utilization (i.e. terrestrial, arboreal, fossorial or aquatic), as indication for vertical resource separation.
c. Activity patterns (nocturnal [animals recorded as being active at dusk or dawn were assigned to the category "nocturnal"]; diurnal, and cathemeral [= can be active around the clock]), as an indication for temporal partitioning of resource use.
d. Diet i.e. insectivores/carnivore (insects, meat, fish, eggs, amphibians), omnivores (insects and plant material), herbivores (tree resins, grab roots, flowers and leaves) and granivores (seeds and fruit). Based on the diet composition, species were assigned to guilds of insectivores, omnivores, herbivores and granivores. These functional groups have been used in other studies to characterize small mammal communities (Fox 2011; Gonzalez-Salazer *et al.* 2014; Kelt *et al.* 1999).
e. Body size, as an indication of home range use and size (Fisher *et al.* 2011; Swihart *et al.* 1988).
f. Locomotion, an indication of habitat utilization in response to cover.
g. Litter size, and indication of resilience to disturbance (Plavsic 2014).

As most small mammals are cryptic, conventional studies that expound their functional traits are usually hampered by methodological problems associated with direct field observations (Symes *et al*. 2013). Unlike the large mammals, direct field observations are inappropriate for small mammals as they are small and will sometimes burrow or hibernate when inactive or taking cover from disturbance. Further, they occupy small home ranges than large mammals that can be observed from vehicles or aircrafts that allow a large coverage of areas. Instead, small mammals are trapped using traps specially designed to cater for their size and behaviour. Trapping is described by several authors as the most effective way of studying communities of small mammals (Stanley and Goodman 2011a, b;

Stanley *et al.* 2011; Torre *et al.* 2010), and owing to the different forms in which they occur a combination of traps is normally utilized. Pitfall, Sherman and Tomahawk traps are the three most commonly used live traps for small mammals and are species specific. Pitfall traps tend to favour small mammals belonging to the order Soricormorpha, for species that are too small to trigger closure of trap doors and for semi-fossorial species (Torre *et al.* 2010; Stanley and Goodman 2011a, b; Stanley *et al.* 2011). Captures from pitfalls are random as they are interceptive (Torre *et al*. 2010). Sherman and Tomahawk are widely used to trap small mammals belonging to the order Rodentia (Stanley and Goodman 2011a, b; Stanley *et al*. 2011).

Setting up pitfall traps requires a lot of effort especially in areas with hard compacted soils where specific depths need to be attained in order to increase the capture success. Capture success is dependent on the depth of pitfall traps (Torre *et al.* 2010). In shallow pitfalls, species that are good jumpers and climbers are more likely to escape than in deep pitfalls. Stanley *et al.* (2011) considers pitfalls of depths of at least 26 cm as effective in trapping shrews. Although Sherman and tomahawk traps are unable to capture multiple individuals like pitfalls, they account for high species diversity in many studies (e.g. Belant and Windels 2007; Francl *et al.* 2002; Torre *et al.* 2010). The fact that they are easier to set i.e. requiring no displacement of earth and require only to be laid or affixed, allows them to capture a variety of species utilizing different sections of a habitat i.e. arboreal and terrestrial species. They also come in different sizes thus, catering for a wide variety of body sizes. Their transportation is also easy as they are light and can be folded.

At community level, studying aspects of their diet is even more challenging. This information provides important evidence on the food intake of species and an indication to the potential competition amongst sympatric species. As direct observations are impossible and conventional dietary analysis (stomach content analysis) tedious, most researchers have adopted less tedious methods such as stable isotope analysis. Stable isotope biochemistry offers a method of identifying resource use of shy and elusive species (Crowley 2012; Fry 2008). This method provides quantitative records of an animal's feeding ecology based on the stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) found in animal tissues. These isotopes can remain stable for eons. Values of $\delta^{13}C$ in animals reflect the carbon source (primary producer consumed) whilst $\delta^{15}N$ reflects the trophic positioning in a community (Symes *et al.* 2013, van der Merwe & Hellgren 2016). In a stable community with several coexisting species, species separation based on the utilization of different dietary resources is detected by a difference between species of 2.0‰ to 2.5‰ of $\delta^{13}C$ and $\delta^{15}N$ in their isotope signature, respectively (Crowley 2012).

Unveiling the functional traits of an organism is not only tedious, but requires long-term commitment. Where resources do not allow for long term commitments, many studies opt to utilize the plethora of information on the natural history of species complied by various authors applicable to their regions. For frequently trapped species information on their distribution is generally adequate, but lacking in several aspects of their ecology. Yet for others and particularly the less trapped species only the location of where they were trapped, exists. These shortcomings are particularly prevalent for species that are endemic and for those found in areas that are under surveyed. Reliable records of species occurrence in Zambia are given by Ansell (1960, 1978), Benadie and Roche (2010), Burda *et al*. (1999), Chidumayo (1979, 1980), Kawalika (2004), Lancester (1951), Larson (1957), NPWS/JICA (1999) and ZAWA (2013), whilst their natural histories by Happold (2013), Happold and Happold (2013), Kingdon (1997). Depositories of specimen of some of these studies include Livingstone Museum (Livingstone), The National Museum of Bulawayo (Bulawayo), The Kaffrarian Museum (King Williams), Transvaal Museum (Pretoria), The Museum of Comparative Zoology (Boston), The American Museum of Natural History (New York), and the British Museum of Natural History (London).

Study site

I studied the community composition, structure, response to repeated bush fires, dietary resource-use and partitioning of small communities in Kafue National Park. Kafue National Park is located between 14º 03' S and 16 º 43' S and 25 º 13' E and 26 º 46' E (Fig.1). It lies within five districts in Zambia, namely; Kalomo, Namwala, Mumbwa, Kasempa and Kaoma (ZAWA 2011) and is the fifth largest park in Africa. It is principally drained by the Kafue River that forms the largest sub-basin of the Zambezi River (Information sheet on Ramsar Wetlands [RIS], 2002) and lies within the sub-tropical intermediate climate zone with annual rainfall of about 1,100 mm to the north and 700 mm to the south (NPWS/JICA 1999). The park is rich in faunal diversity and is host to 158 mammal species, 481 bird species, 58 fish species, 36 amphibian species and 69 reptile species. Habitats for wildlife range from the extensive woodlands that cover most of the park to the large alluvial flood plains in the north west and southern parts of the park.

For management purposes, the park is divided into zones that describe the land use of an area. These zones include, Special conservation, Wilderness, Wild and Intensive utilization. In the Special Conservation Zone, management protects outstanding natural ecosystems and resources from human disturbance, and in the Wilderness Zone large tracts of undisturbed land is conserved for research activities and for the wilderness experience of visitors, while the in the Wild Zone, large tracts of undisturbed land is conserved particularly for wildlife (NPWS/JICA 1999). In the Intensive Utilization zone, intensive development and use are permitted for visitor use and park administration. The Park is managed by two units namely: Ngoma Area Management Unit that is in charge of the southern section of the Park and referred to as KNP (South) and Chunga Area Management Unit, that is responsible for the northern section of the park referred to as KNP (North). Activities of both KNP (North) and (South) are coordinated by the Department of National Parks and Wildlife in Zambia, formerly known as the Zambia Wildlife Authority (ZAWA).

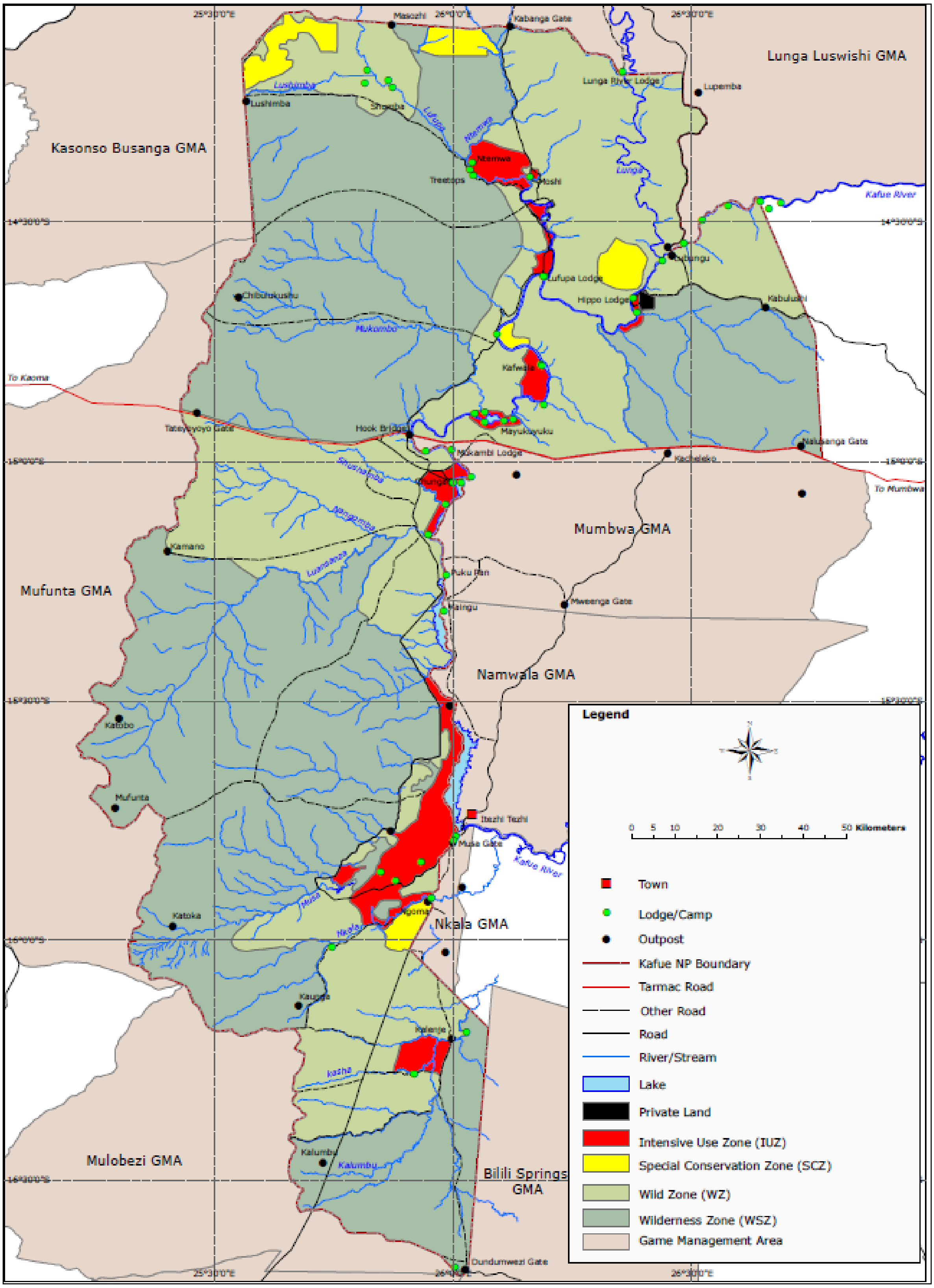

Fig 2. Kafue National Park management zones, river and road network systems. (Source: ZAWA 2011).

Aims of the study

In view of the possible importance of small mammals in the African ecosystem and the gaps in our knowledge of these groups of mammals, the objectives of this study were to:

1. provide checklists of small mammals in Kafue National Park, Zambia **(Chapter 1)**;
2. provide a preliminary assessment of functional characteristics of small mammals in Kafue National Park, Zambia **(Chapter 1)**;
3. investigate the interaction of small mammal communities with three major vegetation formations and ambient conditions in Kafue National Park, Zambia **(Chapter 2)**; and
4. assess dietary resource-use and partitioning among small mammal species found in grassland, termitaria and miombo of Kafue National Park, Zambia **(Chapter 3)**.

The specific questions and empirical data contributing towards meeting the aims of this dissertation were as follows:

Chapter 1

(1) Which species of small mammals occur in the habitats of Kafue National Park?

(2) Which species and functional traits of small mammals are associated with the different habitats in Kafue National Park?

Chapter 2

(1) What are the effects of vegetation types, fire recurrence and the time since the last fire (fire age) on the taxonomic composition and similarity of small mammal communities in the Busanga Flood Plain?

(2) What are the effects of vegetation types, fire recurrence and fire age on the species richness of small mammals in different communities in the Busanga Flood Plain?

(3) What are the effects of vegetation types, fire recurrence and fire age on body mass and functional traits of small mammal communities in the Busanga Flood Plain?

Chapter 3

(1) What is the dietary space available in the three habitats, as described by the $\delta^{13}C$ and $\delta^{15}N$ signatures of possible food items (grass, leaves of trees, invertebrates)?

(2) What is the dietary space realized by the small mammal communities in the three different habitats?

(3) Are small mammal assemblages within the same guild structured by size differences?

(4) In cases where no size differences are apparent: Do sympatric species differ in their trophic position within the community based on their $\delta^{13}C$ and $\delta^{15}N$ signatures?

(5) Do species broaden their dietary niche in areas of increased disturbance by fire?

The results should help to come to a better understanding of the small mammal communities, their structure and their roles witihin the ecosystems of Kafue National Park.

CHAPTER 1

Small mammals in Kafue National Park, Zambia

With Zook Muleya and Joerg U. Ganzhorn

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Abstract

Sustainable management of biological resources in protected areas is often limited by the lack of adequate inventories and baseline data. In these instances, inconspicuous species, such as small mammals are often overlooked as they tend to not draw attention from tourists. Yet they occupy important positions in the functionality of ecosystems. Small mammals in Kafue National Park (KNP) remain largely under surveyed, amidst speculations of their loss due to human activities. As a contribution to conservation, we compiled a checklist of the small mammals (Rodentia, Soricomorpha and Macroscelidea; without Chiroptera, Lagomorpha and galagos) for Kafue National Park. For this, we provide species lists, life history and functional traits and the species' habitat associations based on the available literature. Fifty species belonging to the orders Rodentia, Soricomorpha and Macroscelidea are described as occurring in KNP, representing over 50% of the species described for Zambia. This makes KNP an important conservation area for small mammals.

Keywords: Kafue National Park, Macroscelidea, Rodentia, species list, small mammals, Soricomorpha

Introduction

Kafue National Park (KNP) is Zambia's oldest and largest national park, founded in 1950 covering some 22,400 km². It has the greatest diversity of animal species in Zambia and hosts 158 species of mammals, a third (31.6%) of which (excluding bats, hares and galagos) consists of small mammals (ZAWA 2013). Small mammals perform various ecological functions that contribute towards proper ecosystem functionality. For instance, they are partly responsible for the regeneration of vegetation communities through their seed dispersal and burrowing activities (Laudenslayer and Fargo 2002), provision of essential food biomass that supports organisms at higher trophic levels (Starr 2010), contribute towards the control of pest outbreaks by consuming large quantities of arthropods (Flint and Dreistadt 1998), facilitate water infiltration through fossorial activities (Fleming *et al.* 2014 in Hayward *et al.* 2016) and can modify the characteristics of wildfire by reducing leaf litter and thus flame height and spread of fires (Hayward *et al.* 2016). Thus, small mammals might occupy important positions in the KNP ecosystems and most likely have profound influence on the organization of biodiversity and ecosystem processes as a whole.

Despite their possible importance in the ecological functioning of KNP, little is known about the distribution and abundance of small mammals in Zambia's oldest national park. This paucity of information can be attributed to the fact that they are not of primary importance for tourists and wildlife research in Kafue National Park (ZAWA 2005), and that they are inconspicuous, making them tedious to study. Instead, studies have focussed on birds, plants and on medium sized and large mammals (ZAWA 2005, 2013). The only exception was a preliminary study conducted by GREENFORCE (Kinahan 2003) which concentrated on the southern sector of KNP. Other records allude to species occurring generally in KNP (Benadie and Roche 2010; NPWS/JICA 1999; ZAWA 2013), or in Mumbwa, Itezhi tezhi, Kalomo and Kasempa districts (Ansell 1960, 1978; Lancaster 1951) in which KNP lies. Some of the first studies of small mammals in Zambia where conducted by Lancaster (1951) who listed over 70 species. His description of small mammals remained consistent with those of Barnett and Dutton (1995) that described small mammals as non-flying mammals weighing less than a kilogram when adult and measuring less than a foot (about 30 cm). The most extensive studies were conducted by Ansell (1978) who provided annotated lists of mammals in Zambia and their occurrence. Ansell (1978) described 81 species of small mammals now belonging to the orders Rodentia, Erinaceomorpha, Soricomorpha and Macroscelidea. Thereafter, studies of small mammals were generally site specific, i.e. covering only specific regions or areas in Zambia (Benadie and Roche 2010; Burda *et al.* 1999; Chidumayo 1979, 1980; Kawalika 2004; Kinahan 2003). Depositories of specimen of some of these studies include the Livingstone Museum (Livingstone), The National Museum of Bulawayo (Bulawayo), The Kaffrarian Museum (King Williams), the Transvaal Museum (Pretoria), The Museum of Comparative Zoology (Boston), The American Museum of Natural History (New York), and the British Museum of Natural History (London).

In order to provide the basis for future studies in KNP, we compiled lists of species of small mammals, their life history and functional traits and their habitat associations based on the available literature and compared the literature data with own trapping of rodents and shrews in three major habitats of KNP.

Methods

Study Site

KNP is located between 14º 03' S and 16 º 43' S and 25 º 13' E and 26 º 46' E and covers some 22,400 km² (Fig.1). It lies within five districts in Zambia, namely: Kalomo, Namwala, Mumbwa, Kasempa and Kaoma (ZAWA 2013) and is the fifth largest park in Africa. It is principally drained by the Kafue River that forms the largest sub-basin of the Zambezi River (RAMSAR 2009) and lies within the sub-tropical intermediate climate zone with annual rainfall of about 1,100 mm to the north and 700 mm to the south (NPWS/JICA 1999). For administrative purposes the park is managed by two units namely: Ngoma Management Unit that is in charge of the southern section of the Park and referred to as KNP (South) and Chunga Area Management Unit, that is responsible for the northern section of the park referred to as KNP (North). Activities of both KNP (North) and (South) are coordinated by the Department of National Parks and Wildlife in Zambia, formerly known as the Zambia Wildlife Authority (ZAWA).

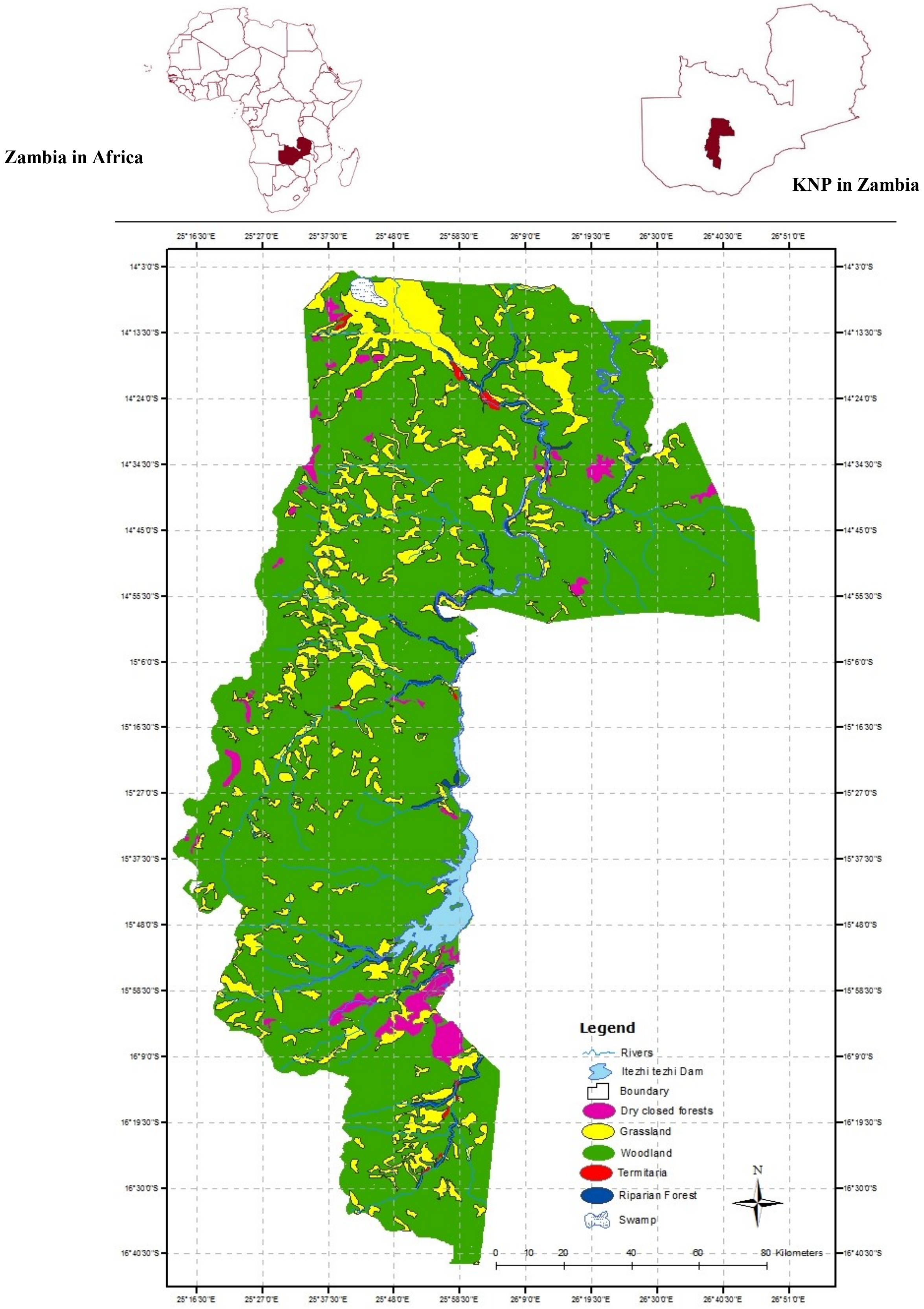

Fig 1. KNP and its habitat types

By now, eleven major vegetation types (miombo, mopane, Combretaceae, *Acacia, Baikaea*, grassland, wooded grassland, termitaria, riparian, thicket, shrubland) have been described as occurring in KNP (Mwima 2006). Since the present compilation of data is based on references published prior to the present vegetation classification, we distinguish six habitat types as they were used in the analysis by Ansell (1978; Fig. 1). His description of habitats of mammals was largely based on the vegetation classifications of Fanshawe (1971):

1. Dry closed forests are characterized by a closed canopy and are composed of *Baikaea* ("teak") and thicket vegetation types (Ansell 1978, Fanshawe 1967). This covers approximately 482 km^2 of KNP (Mwima 2006).
2. Riparian forests are classified as moist evergreen forests, herein referred to as Riparian and cover approximately 18 km^2 of KNP (Mwima 2006; Fig. 2A).
3. Woodlands are described as open forests with grass (Fanshawe 1967; NPWS/JICA 1999) and include miombo, mopane, kalahari and munga vegatation. Mwima (2006) reclassified the munga vegetation type to include *Acacia,* Combretaceae and shrubland. This covers approximately 16,733 km^2 of KNP (Mwima 2006; Fig. 2B).
4. Grasslands include those that are edaphic and montane. For the purpose of this paper the edaphic grasslands are referred to as 'grasslands'. This covers approximately 3,911 km^2 of KNP (Mwima 2006; Fig. 2C).
5. Swamps include rivers, streams and lakes. Busanga Swamps in the north western area of KNP is an example of the Ansell's (1978) habitat classification of swamps. In this paper this habitat is referred to as 'swamp' and covers approximately 94 km^2 of KNP (Fig. 2D).
6. Termitaria represent a special habitat characterized by mostly inactive termite mounds that take many different forms. These mounds provide shelter when the surrounding areas are flooded during the rainy season. All basic physiognomic types of vegetation from grassland to forest can be found on termitaria. This habitat type is most distinct along the flood plain of the Lufupa river, and covers approximately 79 km^2 of KNP (Mwima 2006; Fig. 2E).

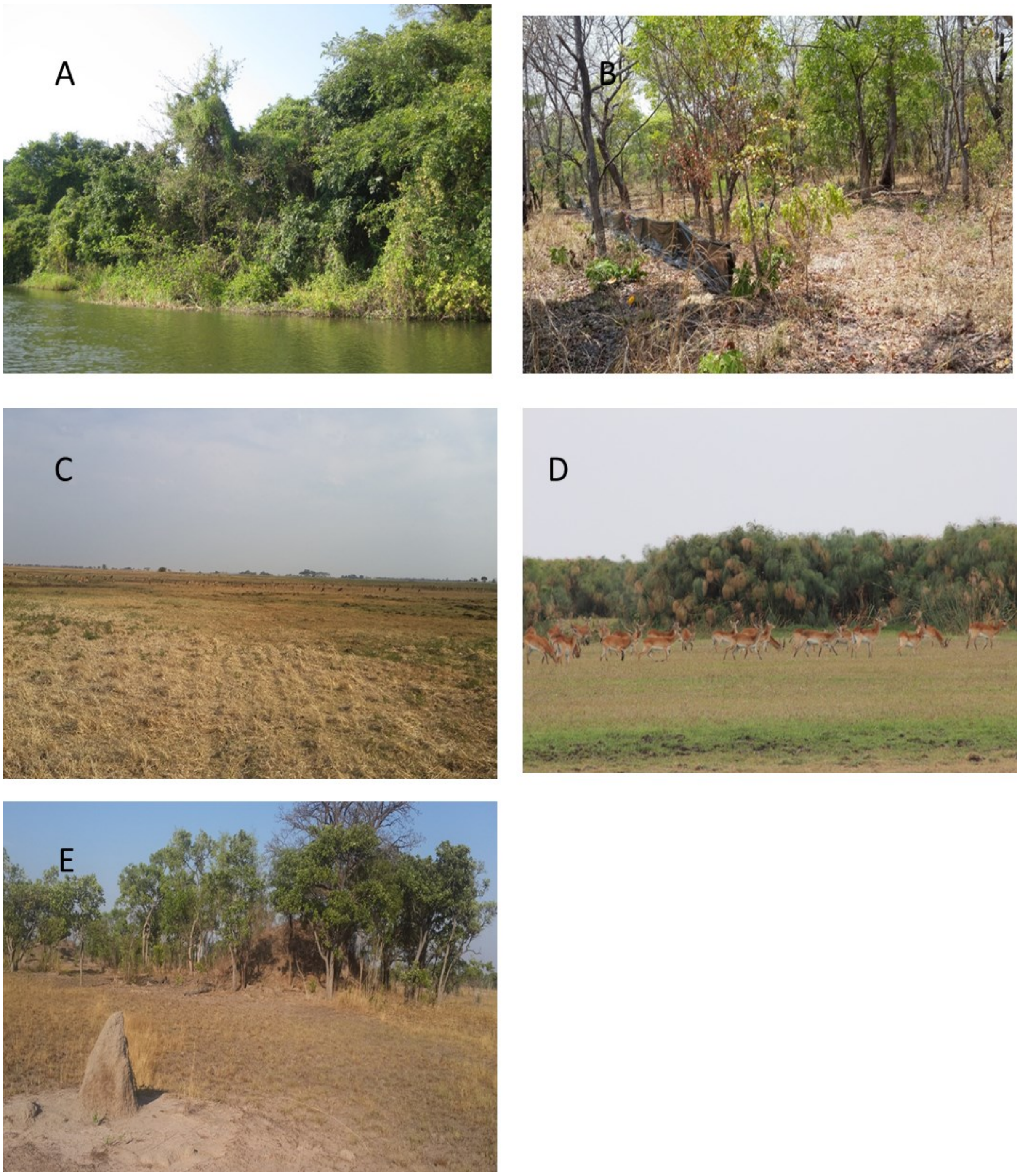

Fig 2. (A) Riparian forest along the Kafue River, (B) fence line along a pitfall line in woodland vegetation, in KNP, (C) grassland, bordered by woodlands in north western KNP, (D) Busanga Swamps of KNP, characterized by papyrus as the dominant vegetation cover, and (E) termitaria vegetation characterized by termite mounds with *Euphorbia ingens* and *Kigelia africana* as characteristic trees.

Species and their habitat associations

Taxonomy follows Kingdon et al. (2013) for elephant shrews, Happold & Happold (2013) for shrews and Happold (2013) for rodents. Lagomorpha, Chiroptera and Primates (galagos) were not considered here. Life history characteristics were taken from the original references listed in Tables 1 and 2. Species information of small mammals (Rodentia, Soricomorpha and Macroscelidea) recorded in Zambia was obtained from Ansell (1960, 1978), Benadie and Roche (2010), Bennet and Aguilar (1995), Bronner and Meester (1988); Burda *et al.* (1999), Chidumayo (1979, 1980), Happold (2013), Happold & Happold (2013), Kawalika (2004), Kingdon (1997), Kingdon *et al.* (2013), Lancester (1951), Larson (1957), NPWS/JICA (1999), and ZAWA (2013). For each species, their habitats of occurrence were recorded as given by Ansell (1960, 1978), Happold (2013), Happold and Happold (2013), Kinahan (2003), Kingdon *et al.* (2013) and Lancaster (1951). This together with their life histories (Apps 2012, Happold (2013), Happold & Happold (2013), Kingdon 1997, Kingdon *et al.* 2013, Skinner & Smithers 1990) was compiled to produce presence-absence data sheets. All species described as occurring in Kalomo, Namwala, Mumbwa, Kasempa and Kaoma districts, where considered as occurring in Kafue National Park.

Own inventories

We trapped twelve species of rodents and five shrew species in three habitats representing woodland (miombo), termitaria and grassland in KNP during the dry season of 2014 and 2015 (Namukonde *et al.* 2017). In each of these habitats six transects were laid and placed with 22 Sherman, eight Tomahawk and eleven pitfall traps for three nights. Traps were checked every morning (06-07hrs) and evening (16-17hrs). Pitfall traps were employed to capture shrews whilst Sherman and Tomahawk traps were set for rodents. Details of the trapping procedures are described by Namukonde *et al.* (2017).

Functional traits

We assigned species to functional groups based on:

a. Social systems (solitary, paired or gregarious) as indication for the distribution of food and predators, following the socio-ecological model for small mammal social organization (Ostfeld 1990).
b. Habitat utilization (i.e. terrestrial, arboreal, fossorial or aquatic), as indication for vertical niche separation.
c. Activity patterns (nocturnal [animals recorded as being active at dusk or dawn were assigned to the category “nocturnal”]; diurnal, and cathemeral [= can be active around the clock]), as an indication for temporal partitioning of resource use.

d. Diet i.e. insectivores/carnivore (insects, meat, fish, eggs, amphibians), omnivores (insects and plant material), herbivores (tree resins, grab roots, flowers and leaves) and granivores (seeds and fruit). Herbivores and granivores can be combined into plant feeders. Based on the diet composition, species were assigned to guilds of insectivores, omnivores, herbivores and granivores. These functional groups had also been used to characterize other small mammal communities and were retained here to allow further comparisons (Fox 2011; Gonzalez-Salazer *et al.* 2014; Kelt *et al*. 1999).

Results

Species and their habitat associations

A total of 50 small mammal species have been recorded from the wider area of Kafue National Park and are likely also to occur within the park. These include 39 rodents belonging to nine families (Nesomyidae, Bathyergidae, Thryonomyidae, Hystricidae, Pedetidae, Muridae, Anomaluridae, Sciuridae, Gliridae), nine species of shrews belonging to one family (Soricidae) and two species of Macroscelidea. Of these only one species is listed as vulnerable (*Cryptomys kafuensis*) and one as data deficient (*Mus neavei*). Most species (88%) occur in two or more habitats save for *Gerbilliscus boehmi, Thallomys paedulcus, Elephantulus brachyrhynchus* that occur only in woodlands, and *Gerbilliscus validus, Dendromus mystacalis, Dendromus nyikae* that occur only in grassland. *Crocidura flavescens* has been listed by ZAWA (2010) as possibly occurring in KNP while Happold and Happold (2013) assign it to areas close to the coast of South Africa. The form from KNP is thus likely to represent a different species.

Species trapped in the three habitats (miombo [3 rodent species, termitaria [9 rodent, 2 shrew species] and grassland [five rodent, 5 shrew species]) by Namukonde *et al.* (2017), remained consistent with the habitat associations described by Ansell (1960, 1978), Apps (2012), Happold (2013), Happold and Happold (2013), Kinahan (2003), Kingdon *et al.* (2013), Lancaster (1951) and Skinner and Smithers 1990). Appendices 1 and 2 provide species lists with their life history traits and habitat associations.

Functional traits

Several information gaps exist on the life-history traits of small mammals in KNP. The most severely affected are traits associated with their social systems and reproductive events, where only 58% and 54% of species are accounted for, respectively. Nonetheless, a large proportion of the small mammal species in KNP are classified as solitary, nocturnal, terrestrial and omnivorous (Table 3). Across the six habitats, woodland had the highest number of individuals belonging to the functional groups ascribed, whilst the lowest number has been recorded from the dry closed forest.

Table 3. Distribution of functional traits of small mammal communities among different habitats of KNP.

Functional group	Riparian	Swamp	Grassland	Termitaria	Woodland	Dry closed forest	Total pool of species
Social system							
Solitary	6	4	10	10	15	5	**16**
Paired	2	2	5	4	3	1	**6**
Gregarious	2	1	5	1	6	1	**7**
Daily activity pattern							
Dirunal	1	1	3	3	5	2	**6**
Nocturnal	11	8	24	16	26	5	**31**
Cathermal	1	2	1	1	2	1	**3**
Habitat use							
Terrestrial	11	11	31	19	27	4	**37**
Aboreal	4	0	0	3	6	5	**7**
Others (Aquatic, semi-aquatic & Subterranean)	1	3	3	0	2	0	**4**
Trophic guild							
Omnivore	7	4	12	10	14	4	**21**
Granivore	2	3	5	4	5	1	**5**
Herbivore	2	4	10	4	12	4	**13**
Insectivore/Carnivore	5	3	4	7	6	1	**10**
Number of species	**16**	**14**	**35**	**23**	**37**	**10**	**50**

Even though many species occur in more than one habitat, the different vegetation formations seem to be perceived by some of the species as distinct habitats. This can be illustrated by species-area relationships where the extent of the different vegetation types is plotted against the number of species reported from these habitats (Fig. 3). The relationship is suggestive but not significant (Spearman rank correlation: $r_s = 0.60$, $p = 0.21$, $n = 6$).

Habitat specificity is obvious as arboreality as a functional trait is absent in grassland and swamp (Table 3; Fig. 4), as these habitats lack trees. Further, granivorous species are found mostly in grasslands and in wooded grasslands where grasses are abundant. Diurnality is more pronounced in larger sized species (> 50 g), a trait that might favour species that are better able to escape predators in more closed habitats (Joubert and Ryan 1999).

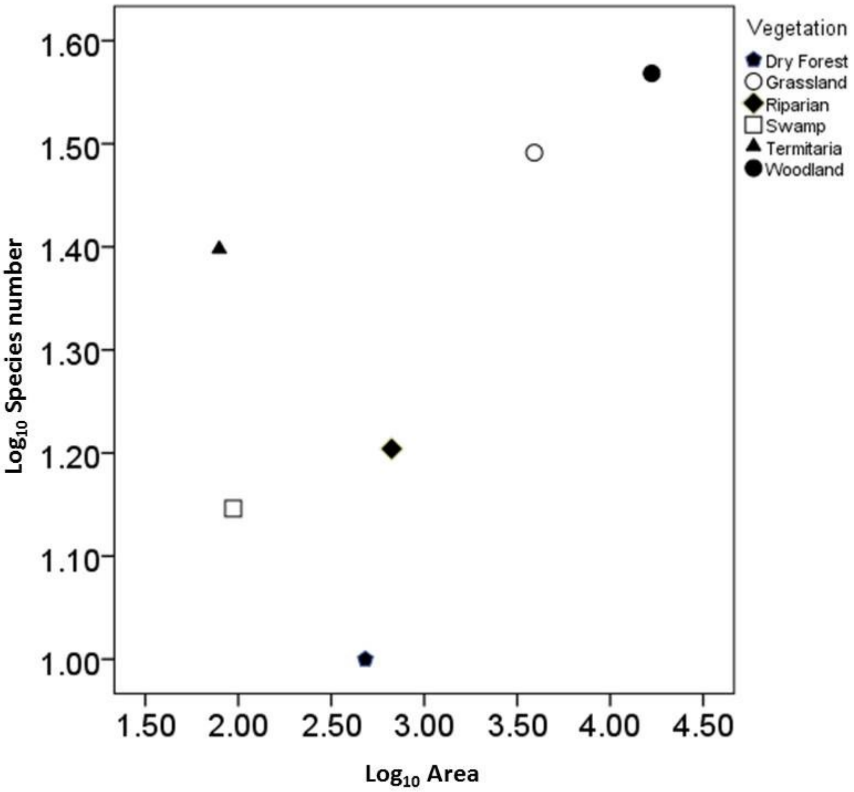

Fig 3. Species number of small mammals in relation to the spatial extent of different habitats in KNP.

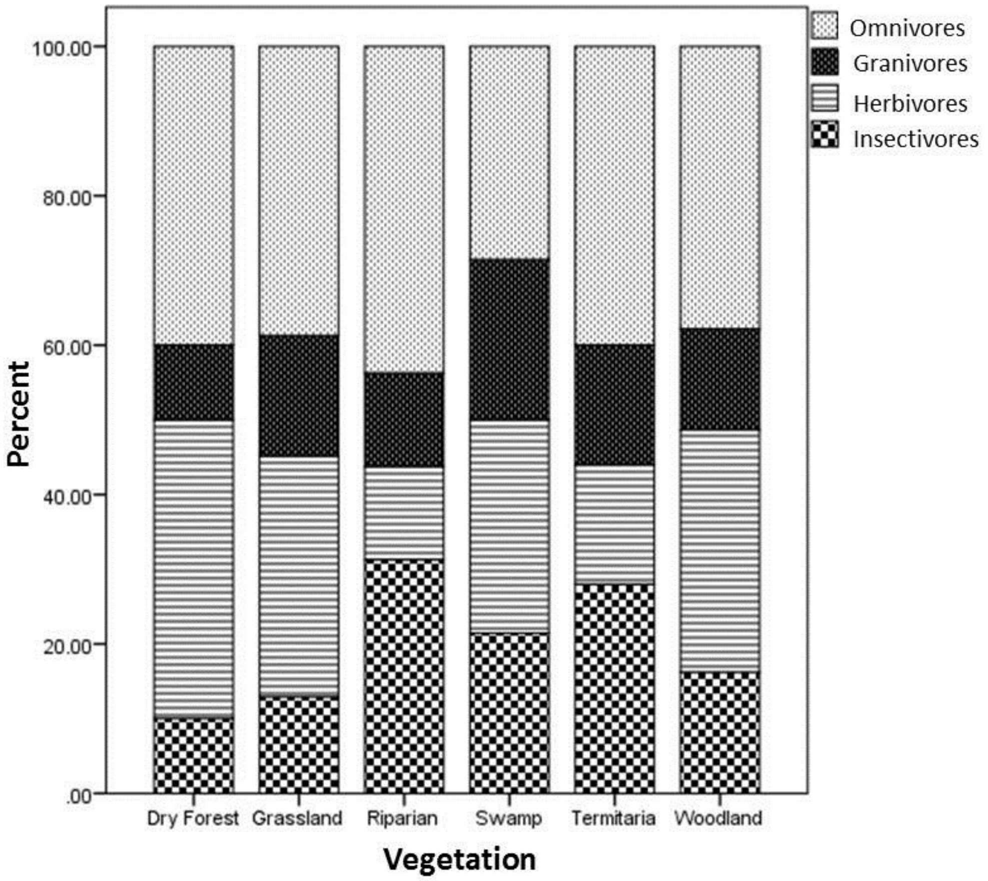

Fig 4. Representation of trophic guilds in different habitats of KNP as per data summarized in Appendices 1 and 2.

Discussion

The species lists presented in this paper represents more than 50% of the small mammal species described as occurring in Zambia. This makes KNP an important conservation area for small mammals. Kawalika (2004) using Ansell's (1978) publications only, described 12 species of rodents as occurring in KNP, which according to his spatial description is KNP (South). Kinahan (2003) listed 17 species of rodents and 5 of shrews from the preliminary studies conducted by GREENFORCE in KNP (South). Namukonde *et al.* (2017) listed 16 species (11 rodents and 5 shrews) from own trapping studies conducted during two dry seasons in grassland, termitaria and miombo in the Busanga Flood Plain of KNP.

In general, the number of small mammal species reported from the different habitats tends to be related to the spatial extent of the habitats in the region (Fig. 3). Small mammal species richness is highest in grassland and woodland which are the dominating habitats of the region (Mwima 2006). While the species-area-relationship seems to follow a straight line for the main vegetation formations, the number of species recorded from termitaria is remarkably high and for the closed dry forest it is very low. The former may be due to high structural and floristic diversity of termitaria compared to the surrounding grassland and also due to the fact that the plains are flooded during the wet season when termitaria provide dry refuges for small mammals. The low species number in dry forest is unlikely to reflect insufficient sampling of the dry closed forests of the region. Using standardized and identical trapping efforts in woodland, grassland and termitaria, Namukonde *et al.* (2017) also had caught significantly fewer small mammal species in the miombo forest than in grassland and termitaria. Therefore, it seems more likely that the low number of species in forest habitats results from the evolution of the small mammal assemblages as adaptations to grassland and open woodland. The woodlands in KNP are mainly dominated by trees of miombo, mopane, kalahari and munga vegetation types, whilst the closed dry forest is dominated by *Baikaea plurijuga* and *Baphia massaiensis* which occurs in very few patches in the park. The low species number in dry closed woodland might then be a consequence of environmental filters that prohibit species having evolved in a different habitat (grassland and woodland) to colonize the dry closed forest. On-site studies would be needed to evaluate the importance of environmental filters, in the evolution of the small mammal communities found in Kafue National Park.

Acknowledgements

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Appendix 1. Species list of rodents in Busanga Swamps, their habitat association, functional groups and live history traits

	Species	**Habitat**						**Social systems**			**Daily Activity**			**Habitat use**			**Diet**																								**References**
		Riparian forest	Swamp	Grassland	Termitaria	Woodland	Closed dry forests	Single	Paired	Gregarious	Dirunal	Nocturnal	Cathemeral	Terrestrial	Aboreal	Other	Insects	Meat	Fish	Other invertebrates	Amphibians	Seeds & fruits	Lizards	Eggs	Flowers	Leaves & stems	Mushroom	Tree resins	Tree grub/bark	Roots	Trophic guild	Mass (g)	Total length (mm)	Tail (mm)	Ear (mm)	Head length (mm)	Hind foot (mm)	# of Reproductive	Av.Litter size	Conservation status	
	Order: Rodentia																																								
	Family: Nesomyidae																																								
	Subfamily: Cricetomyinae																																								
1	*Saccostomus campestris* Peters, 1846			x	x	x		x				x		x								**x**									G	48.5	164	50	14	30.7	21	3.8	5.1	LC	Ansell (1978); Apps (2012); Larson (1957); Kinahan (2003); Kingdon *et al*. (2013); Namukonde *et al*. (2017); ZAWA (2010)
2	*Cricetomys gambianus* Waterhouse, 1840	x		x	x	x	x	x				x		x			x					x									O	786	678	352	37	66.4	62		3	LC	Ansell (1978); Kingdon *et al.* (2013); Larson (1957); ZAWA (2010)
	Subfamily: Dendromurinae																																								
3	*Steatomys pratensis* Peters, 1846			x	x	x		**x**				x		x			?					**x**									G	39.7	139	44	15	24.6	16			LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon *et al.* (2013); Lancaster (1951); Larson (1957); Namukonde *et al*. (2017); NPWS/JICA (1999); ZAWA (2010)

4	*Steatomys krebsii* Peters, 1852		x	x	x	x	x	x				x		x			?					x									G	21.4	49.6	87.4	14.9	24.4	17.8		4.5	LC	Ansell (1978); Kingdon *et al.* (2013); ZAWA (2010)
5	*Steatomys parvus* Rhoads,1896	x	x	x		x						x		x			?					x									G*	13.3	116	40	14	22.6	15			LC	Kingdon *et al.* (2013)
6	*Dendromus mystacalis* Heuglin, 1863			x					x			x		x			x					x									O	8.7	145	84.3	9.3	20.2	17.4		3.5	LC	Ansell (1978); Kingdon et al. (2013); ZAWA (2010)
7	*Dendromus melanotis* Smith 1834	x	x	x	x	x		x				x		**x**								x									G	7.4	158	90	16	20.1	18		5	LC	Ansell (1978); Kingdon et al. (2013); ZAWA (2010)
8	*Dendromus nyikae* Wroughton, 1909			x										**x**			x					**x**									O	10.5	153	86.4	14	21.8	16.7		4	LC	Kingdon *et al.* (2013); ZAWA (2010)
	Family: Bathyergidae																																								
9	*Cryptomys kafuensis* Burda et al. 1999			x		x										x														x	H*	95	121	16.7	0	33.5	23.1			VU	Kingdon *et al*. (2013)
10	*Cryptomys mechowi* (Peters, 1881)		x	x		x				x						x														x	H	370	193	27.8	0	52	35.3	3	2.6	LC	Ansell (1978); Bennet et al. (1994); Kingdon *et al.* (2013); NPWS/JICA (1999); ZAWA (2010)
	Family: Thryonomyidae																																								
11	*Thryonomys swinderianus* (Temminck, 1827)		x	x								x				x										x					H	4500	903	188	35	90.6	94	2	3.5	LC	Ansell 1978; Kingdon *et al* (2013); Lancaster (1951); NPWS/JICA (1999) & (ZAWA 2010)

	Family: Hystricidae																																								
12	*Hystrix africaeaustrials* Peters, 1852			x	x	x			x			x		x								x							x	x	H	22600	760	105	40	161	99	1	1.5	LC	Ansell (1978); Kingdon *et al.* (2013); Lancaster (1951); NPWS/JICA (1999); ZAWA (2010)
	Family: Pedetidae																																								
13	*Pedetes capensis* (Forster, 1778)			x	x	x		x				x		x								x				x				x	H	3260	830	429	75	88.6	161	12	1	LC	Ansell (1978); ZAWA (2010)
	Family: Muridae																																								
	Subfamily:Otomyinae																																								
14	*Otomys angoniensis* Wroughton, 1906		x	x		x		x			x			x								x				x			x		H	96.6	241	86	20	37.5	26	12	3.1	LC	Bronner and Meester (1988); Kingdon *et al.* (2013); Lancester (1951); Namukonde *et al.* (2017)
	Subfamily: Gerbillinae																																								
15	*Gerbilliscus validus* (Bocage, 1890)			x						?		x		x			x									x				x	O	129	324	157	21.8	41.7	34	2	4	LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon *et al.* (2013); ZAWA (2010)
16	*Gerbilliscus boehmi* (Noack,1887)					x						x		x			x					?			?	?			?	?	O	146	378	216	24.3	43.5	40.8			LC	Ansell (1978); Lancaster (1951); ZAWA (2010)
17	*Gerbilliscus leucogaster* (Peters, 1852)			x		x				x		x		x			x					x				?			?	?	O	69.8	277	149	21	37.3	33.5	4.5	5	LC	Ansell (1978); Apps (2012); Chidumayo (1980); Kinahan (2003); Kingdon *et al.* (2013); Namukonde *et al.* (2017); ZAWA (2010)

	Subfamily: Murinae																																								
18	*Pelomys fallax* (Peters, 1852)		x	x	x	x	x			?			x	x								x				x				x	H	105	280	133	9.2	35.1	32		5.5	LC	Ansell (1978); Apps (2012); ; Kinahan (2003); Kingdon *et al.*(2013); Larson (1951); ZAWA (2010)
19	*Aethomys chrysophilus* (de Winton, 1897)	x		x	x	x			x			x		x			x					x				x				?	O	75	294	156	20	36.1	20		3-4	LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon et al. (2013); Larson (1951); Namukonde *et al.* (2017); ZAWA (2010)
20	*Aethomys kaiseri* (Noack, 1887)	x			x	x						x		x			x					?				?			?	?	O	95.5	266	120	22.7	36.4	25.2		2.6	LC	Ansell (1978); Kingdon *et al.* (2013); Lancaster (1951); ZAWA (2010).
21	*Aethomys nyikae* (Thomas, 1897)			x	x	x				?		x		x			x					x				x				x	O*	90.2	309	166	20.6	35.1	28.6			LC	Ansell (1978); Kingdon et al. (2011); Namukonde et al. (accepted); ZAWA (2010)
22	*Arvicanthis niloticus* (E. Geoffroy, 1803)			x		x				x	x			x			x					x				x					O	110.8	281	130	17.8	32.9	31.5	12	4.3	LC	Ansell (1978); Kingdon et al. (2013); ZAWA (2010)
23	*Acomys spinosissimus* Peters, 1852	x		x						x		x		x			x					x								x	O	26	165	77	14	25.7	16	3.2	3	LC	Ansell (1978); Apps (2012); Kinahan (2003): Kingdon et al. (2013); Lancaster(1951); Larson (1957)
24	*Mastomys natalensis* (Smith, 1834)			x	x	x						x		x			x					x				x					O	37.5	216	108	17.2	28.5	22.3		10-12	LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon et al. (2013); Lancaster (1951); Namukonde et al. (accepted)
25	*Grammomys dolichurus*	x				x	x			x		x			x							**x**				**x**			x		H	40	279	166	17	28.9	24	12?	4.6	LC	Kingdon et al. (2013); Larson (1957)

	(Smuts, 1832)																																								
26	*Mus musculoides* Temminck, 1853			x		x				x		x		x								x				x					H	8.5	104	43.6	9.6	19.3	13.6	12	3.38	LC	Kingdon et al. (2013).
27	*Mus minutoides* Smith, 1834		x	x	x	x			x			x		x			x					x				x					O	6.2	95.8	41	8.5	18.8	12.5	12?	4.5	LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon *et al.* (2013); Lancaster (1951); Namukonde *et al*. (2017); ZAWA (2010);
28	*Mus neavei* (Thomas, 1910)				x	x																									DD		127	38.4	11	18.5	13			DD	Ansell (1978); Kingdon *et al.* (2013); Larson (1957); ZAWA (2010)
29	*Mus triton* (Thomas, 1909)		x	x	x							x		x			x					x									O	12.1	130	54	12.7	21.8	15.9	2	4.5	LC	Ansell (1978); Kingdon *et al.* (2013); Namukonde *et al.* (2017); Thomas (1909); ZAWA (2010)
30	*Dasymys incomtus* (Sundervall, 1847)	x	x					x					x			x	x									x					O	158	311	146	20	37.9	33		3 (2-4)	LC	Ansell (1978); Kingdon *et al.* (2013)
31	*Lemniscomys griseilda* (Thomas, 1904)			x		x	x																								H*		256	135	14	31	28			LC	Ansell (1978); Apps (2012); Kinahan (2003); Kingdon *et al.* (2013); Larson (1951); ZAWA (2010)
32	*Lemniscomys rosalia* (Thomas, 1904)			x	x	x		x			x			x								x									H	55.8	269	132	11.3	31.9	26.9		6.1	LC	Apps (2012);Kinahan (2003); Kingdon et al. (2013); Lancaster (1951); Namukonde *et al.* (2017)
33	*Thallomys paedulcus* (Sundevall, 1846)					x				?		x			x							x			x	x					H	72.3	307	166	20.8	32.8	25.3	5	2.7	LC	Ansell (1978); Kingdon *et al.* (2013); ZAWA (2010)

34	*Zelotomys hildegardeae* (Thomas, 1902)		x	x		x						x		x			x	x				x									O	59.8	214	87.9	14.6	31.4	22.5		5	LC	Ansell (1978); Kingdon *et al.* (2013); Lancaster (1951); ZAWA (2010)
	Family: Anomaluridae																																								
35	*Anomalurus derbianus* (Gray, 1842)	x				x	x	x				x			x							x			x	x			x		H	595.3	590	284	40	58.7	56		1-3	LC	Ansell (1978); Kingdon *et al.* (2013); ZAWA (2010)
	Family: Sciuridae																																								
36	*Heliosciurus gambianus* (Olgilby, 1835)				x	x	x	x			x				x		x					x	x	x							O	220	411	214	15.3	47.3	44.5	1-2	5	LC	Ansell (1978); Lancaster (1951); ZAWA (2010)
37	*Paraxerus cepapi* (A. Smith, 1836)				x	x				x	x				x		x					x		x	x	x		x			O	193.3	345	169	19	44	43	1	2	LC	Ansell (1978); Larson (1957); Namukonde *et al.* (2017); ZAWA (2010)
	Family: Gliridae																																								
38	*Graphiurus microtis* (Noack, 1887)	x			x	x	x	x				x			**x**		x	x				x									O	29.5	174	75.2	15.5	27.4	16.9	3-4	3-7	LC	Apps (2012); Kinahan (2003); Kingdon *et al* (2013); Lancaster (1951)
39	*Graphiurus murinus* (Desmarest, 1822)	x					x			?					**x**		x			x		x			x	x					O	17	168	76.6	13.3	26.4	18.5	3-4	1-5	LC	Apps (2012); Kinahan (2003); Kingdon *et al* (2013); Lancaster (1951)

Appendix 2. Species list of moles and shrews in Busanga Swamps, their habitat association, functional groups and live history traits

	Species	**Habitat**						**Social systems**			**Daily Activity**			**Habitat use**			**Diet**									**Morphology**							**References**
		Riparian	Swamp	Grassland	Termitaria	Woodland	Dry closed forests	Solitary	Paired	Gregarious	Diurnal	Night	Cathemeral	Terrestrial	Aboeral	Other (aquatic, semi	Insects	Meat	Fish	Other invertebrates	Amphibians	Seeds & fruits	Eggs	Fungus	Trophic guild	Mass (g)	TL (mm)	Tail (mm)	Ear (mm)	# of Reproductive events	Litter size	Conservation status	
Order: Soricomorpha																																	
1	*Crocidura fuscomurina*			x	x	x		x				x		x			x								I	5.7	105	43	9		3-4	LC	Ansell (1978); ZAWA (2010); Kinahan (2003); Skinners & Smithers (1990); Hutterer & Dippenaar (1987); Kinahan (2003).
2	*Crocidura hirta*			x	x							x		x			x	x		x					I/C	16	140	50	9	2	5	LC	Apps (2012); Skinners & Smithers (1990); Smithers (2012); Larson (1951; 1957), Ansell (1978): ZAWA (2010); Kinahan (2003); Namukonde et al. (submitted).
3	*Crocidura turba*	x		x		x								x											I*	-	155	56	8.1	-	-	LC	Lancaster (1951); Ansell (1978); ZAWA (2010). Kingdon et al. (2013).

4	*Crocidura mariquensis*	x	x	x								x		x			x			x					I	9-12	140	56	9		3-4	LC	Apps (2012); Skinners & Smithers (1990); Smithers (2012); Ansell (1978); ZAWA (2010), Namukonde *et al.* (2017).
5	*Crocidura flavescens*	x				x		x				x		x			x	x		x					I/C	16-22.2	140-163	55	11	2	4	LC	Apps (2012); Skinners & Smithers (1990); Smithers (2012); ZAWA (2010).
6	*Crocidura cyanea*			x		x		x				x		x			x								I	9	130	5	9			LC	ZAWA (2010); Skinners & Smithers (1990); Kingdon *et al.* (2013).
7	*Crocidura gracilipes*		?											x			x								I*	-	117	52	6.5	-	-		Ansell (1978); ZAWA (2010).
8	*Suncus lixus*	x		x	x	x								x			x			x					I	8	11.5	4.5		1	2-5	LC	Ansell (1978); ZAWA (2010); Kinahan (2003); Lancaster (1951); Apps (2012); Skinner & Smithers (1990); Kingdon (1997); Smithers (2012); Kingdon *et al.* (2013).
9	*Suncus varilla*		x	x	x				x					x			x			x					I	25	127	30	6.9			LC	Kinahan (2003): Kingdon *et al.* (2013).
Order: Macroscelidea																																	
10	*Petrodromus tetadactylus*	x					x		x		x			x			x								I	120-200	350	163	35	2	1	LC	Apps (2012); Skinner & Smithers (1990); Kingdon (1997); Smithers (2012); Larson (1951); Ansell (1978); ZAWA (2010); Kinahan (2003).
11	*Elephantulus brachyrhynchus*					x		x					x	x			x					x			O	43	210	100	20	5	2	LC	Apps (2012); Skinners & Smithers (1990); Smithers (2012); Ansell (1978); ZAWA (2010).

CHAPTER 2

Differential effects of fire on small mammal communities in the Busanga Flood Plain, Zambia

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Abstract

We assessed effects of vegetation and fire on small mammals in open vegetation formations of the Busanga Flood Plain (Kafue National Park, Zambia) in areas of low and high fire recurrence. The impact of fire was related further to the time elapsed between the last fire and the time of trapping (fire age). Sampling sites covered three management zones: intensive utilization (tourist areas), wild (less used), and wilderness (no road access). Vegetation type, fire recurrence, fire age, and management zone were independent variables. Communities were similar in grassland and on termitaria but differed from miombo. Species richness was highest on termitaria, followed by grassland and miombo. Species numbers declined with increasing fire frequency but were unaffected by fire age. In contrast, the average body mass of species occurring at any one site (only adult individuals considered) declined with the time elapsed between the time of capture and the last fire (the longer the time interval, the lower the body mass of species averaged over the species found at the site). This response implies higher vulnerability of the smaller species to fire and slower recolonization potential of smaller species after fire. The interactions between fire, vegetation characteristics, and small mammals need to be reviewed, given their importance in the functionality of this ecosystem.

Key words: Busanga flood plain, Zambia, small mammals, fire recurrence, fire age, fire effect, grassland, miombo

Introduction

Fire is an integral part of African savannah ecosystems (Green *et al.* 2015; Parr and Chowan 2003; Plasvic 2014; Salvatori *et al.* 2001; Swanepoel 1981). In concert with grazing by large herbivores, it determines the physiognomy of large tracts of land. Apart from being a natural phenomenon, fire is widely used as a management tool in protected areas in Africa. The purpose of its use ranges from clearing vegetation for photographic tourism to fostering pastures for wildlife (Chanda 2007; Green *et al*. 2015; Kampamba *et al.* 2005; Parr and Chowan 2003). In the Kafue National Park (KNP), Zambia, fire is predominately used during the early dry season (May to mid-July) as a means of reducing the probability of catastrophic fires, and to improve visibility for tourists to view and photograph game. Fires are set along the boundaries, access roads and fire breaks. Other management objectives for fire include: inducing fresh forage flush for wildlife grazing, fostering natural succession of fire sensitive vegetation, reducing soil erosion in the event of late season fires, and controlling insect pests

(Chanda, 2007; NPWS/JICA 1999). Whilst most early fires are started by management, unplanned fires at any time of the year outnumber them (Chanda 2007). These were earlier thought to originate from local communities in the Open and Game Management Areas bordering KNP (Chanda 2007), but recent evidence alludes to fires beginning and occurring more frequently in the park as opposed to the Game Management Areas or open areas (Kelly 2014). In fact, the park has the largest proportion of areas with high fire recurrence (Figure 1) even in critical habitats such as the Busanga Flood Plain.

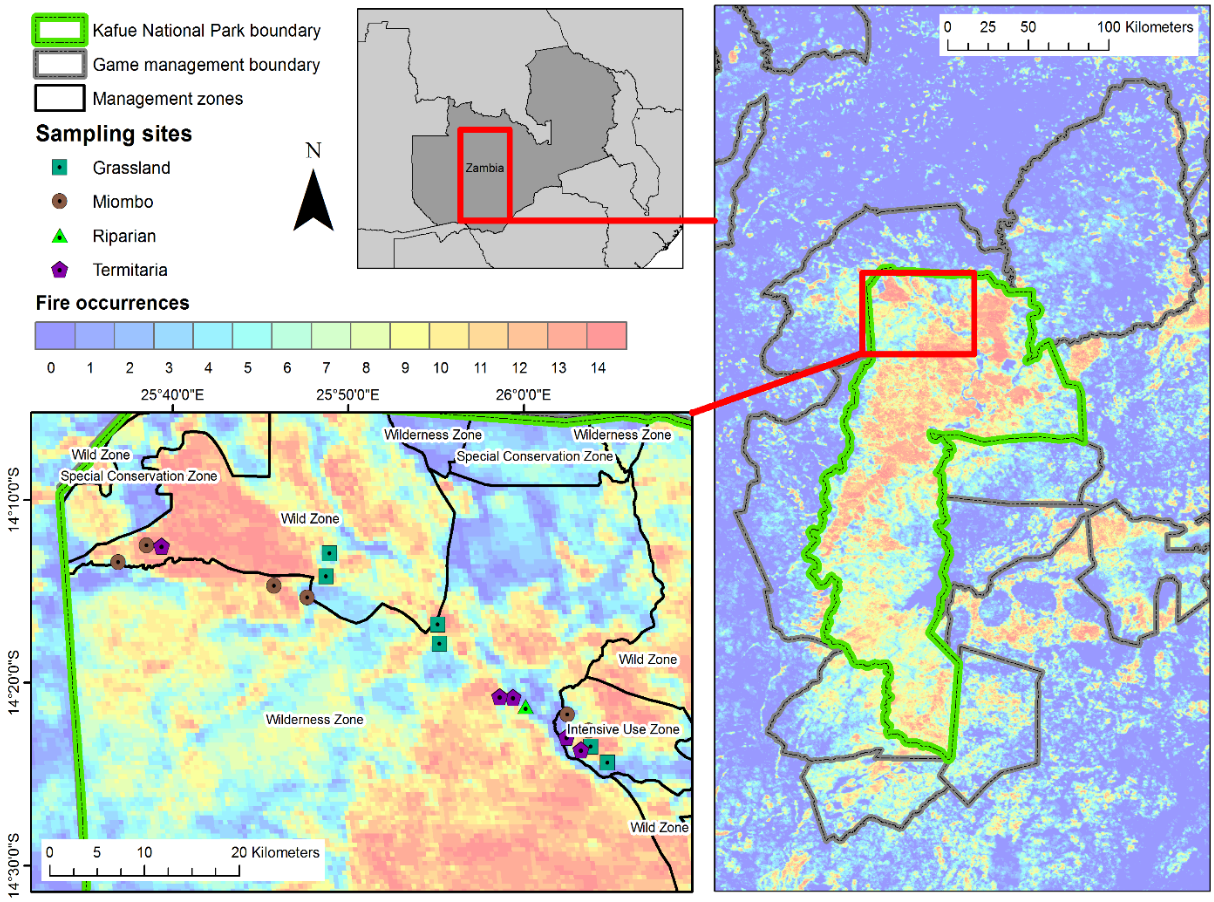

Fig 1. Sampling sites depicting the vegetation, fire recurrence, and management zones in the Busanga Flood Plain, north–west of Kafue National Park. Fire occurrences indicate the number of years with fire between 2000 and 2013 (base map from Kelly, 2014)

Given the size of KNP (22,400 km2) and the lean resources available to manage it, (NPWS/JICA 1999; ZAWA 2011) unplanned fires remain a major challenge to conservation. Most of the Park’s rangeland is burnt annually, despite the prescribed rest interval of 2 to 3 years in its fire management plan. Furthermore, early burning as per current practice does not favor all wildlands. For instance, in areas such as the Busanga Flood Plain (predominately a grassland), early fires are thought to interfere with processes such as rooting, seeding, and seed dispersal for grasses (Moss 1973). The extent of interference is thought to directly depend on the amount of rainfall received. In a wet year (>1,000 mm), most areas remain moist till the mid dry season (July to August), thereby inhibiting the spread of early fires. The rainy season in Zambia ends in April and paves way for the dry season which begins in May and lasts to early November (ZAWA 2011).

Very little is known about the influence of the current fire regime on biodiversity in KNP (Kinahan 2003). Stakeholders speculate on a significant alteration in the vegetation structure that would result in reduced fodder and cover for species (Parr and Chowan 2003). Small mammals are a matter of concern, as faunal studies in KNP tend to focus on larger species (ZAWA 2005). Yet, small mammals (rodents and shrews) play a cardinal role in ecosystem functionality. They occur at several trophic levels, consuming substantial amounts of plant material, insects, and arthropods; serve as prey; and are important for perturbation of the soil (MacFadyen *et al.* 2012; Timbuka and Kabigumila 2006).

While several studies demonstrated the impact of fire and vegetation cover on small mammal communities, the evidence for fire effects is inconsistent. Some authors have described fire as having little impact on small mammal diversity, unless coupled with grazing (Salvatori *et al*. 2001) and rainfall (Yarnell *et al.* 2007). Others describe its effects as short lived and associated with the removal of vegetation cover (Plavsic 2014; Swanepoel 1981). Yet others describe it as having a positive impact on small mammal diversity, as species diversity is higher in areas where fire is a periodic disturbance (Bowland and Perrin 1993). In the drier savanna regions (Kalahari savannah rangelands), species richness and abundances of small mammals had been negatively affected by shrub encroachment, brought about by overgrazing (Blaum 2006), though grazing itself had no significant impact (Bösing, *et al.* 2014).

Similar to the situation described for grazing, fire as a single factor didn't have a direct impact on small mammals (Swanepoel 1981; Yarnell *et al*. 2007) but acted through the animals' response to reduced cover to emigrate or avert predation. Diurnal species seem to be more affected by the removal of vegetation cover as nocturnal species, as the former would be more prone to predation than the nocturnal species, whose predators rely on hearing or smell to detect prey (Hauptfleisch *et al.* 1999). For the time being, it seems premature to try synthesizing these disconnected results, as the different studies consider different environmental drivers in different combinations and have been carried out in different regions. Yet, they provide the basis and framework to add on to.

Ecological studies and community comparisons between sites are often hampered by taxonomic issues, such as different species compositions or taxonomic uncertainties that make comparisons difficult. Functional and life history traits can be used to replace species names and thus replace site specific taxonomies by generalizable characteristics that facilitate comparisons between sites (Fox 2011; Violle *et al*. 2007). As illustrated by the different predation risk of diurnal versus nocturnal species (Hauptfleisch and Avenant 2015; Joubert and Ryan 1999), the survival or persistence of species after disturbances of their habitat can often be linked to its life history or functional traits (Plavsic 2014). Since body mass shows allometric relationships to a large number of life history traits (e.g., mobility, home range size,resistance to variation, and reproductive traits), it can be used as a proxy for life history traits that are favorable or unfavorable under different disturbance regimes (e.g., Brown 1984; Stearns 1992).

In order to fill some of the gaps in our knowledge of small mammal interactions with vegetation formations and ambient conditions, we addressed the following questions:

(i) What are the effects of vegetation types, fire recurrence, and the time since the last fire (fire age) on the taxonomic composition and similarity of small mammal communities in the Busanga Flood Plain?
(ii) What are the effects of vegetation types, fire recurrence, and fire age on the species richness of small mammals in different communities in the Busanga Flood Plain?
(iii) What are the effects of vegetation types, fire recurrence, and fire age on body mass and functional traits of small mammal communities in the Busanga Flood Plain?

Methods

Study site

The Busanga Flood Plain is located between about 25 25’ E/1345’ S to 26 10’ E/14 25’ S and covers some 750km^2 (NPWS/JICA, 1999). It is a wetland of international importance listed as Ramsar site no. 1659 of the Ramsar Convention of Wetlands of International Importance (Information sheet on Ramsar Wetlands [RIS] 2002). It is principally drained by the Lufupa River that constitutes the middle catchment area of the Kafue river basin (RIS 2002). This basin is the largest subbasin of the Zambezi River (156,995 km^2) and lies entirely within Zambia. The Kafue Basin is often described as the lifeline for most of

Zambia (ZAWA 2011), as it is the main provider of water for major cities and most of Zambia's wildlife estate. Annual rainfall is around 1,100 mm and begins to fall in November, ending in April the following year. The dry season (May to November) is divided into two seasons; cool, dry (May to August), and hot, dry (September to November; ZAWA 2011).

Trapping sites

Trapping sites where categorized based on vegetation type, management zone, fire regime, and fire age (Table 1). These characteristics were used as independent variables in the analyses. Based on the vegetation descriptions by Mwima (2006), management zones (NPWS/JICA 1999), and fire recurrence (Kelly 2014), 17 sampling sites were established by stratified random assignments. The initial intention was to achieve a balanced design of capture sites for the vegetation types of grassland, termitaria, and miombo forest. Since we could not find a termitaria site with low fire recurrence in the wild zone, we achieved only an unbalanced design for termitaria. Sites could not be stratified systematically with respect to fire age.

Table 1. Characteristics of capture sites.

Characteristic	Description
Vegetation types	There are at least nine vegetation types within the Busanga Flood Plain, with grassland being the most predominant, followed by termitaria and miombo woodland (Mwima 2006). According to Mwima (2006) grassland is characterized by a distinct expanse of grass cover whose layer is comparatively well developed than the herb and sub shrub layer, that cover less than five percent. Termitaria has the distinct characteristic of being associated with large termite mounds that can rise up to 6 m with widths of up to 10-15 m (Walker 2015). Mwima (2006) describes termitaria as bearing a tree, shrub and grass layer, with the latter two being generally sparse. Characteristic tree species include *Acacia nigrescens, Markamia obtusiforlia, Cassia abreviata, Adonsonia digitata, Euphorbia ingens, Kigelia Africana* and *Diospyros mespiliformis.* Miombo woodland has an open canopy of trees, with a herb, sub-shrub and grass layer that is sparse but very diverse (Mwima, 2006). Characteristic tall trees include *Brachystegia spiciformis, B. boehmii, Julbernardia paniculata, Isoberlina angoiensis, Burkea africana, Parinari curatellifolia, Erythrophleum africanum* and *Sclerocarya birrea.* As compared to termitaria, miombo has higher tree densities.
Management zones	Four management zones have been prescribed and include zones of intensive utilization by tourism, wild (less used) zones, wilderness (no road access) and special zones (NPWS/JICA 1999; ZAWA 2011).
Fire regime	The area is subject to different fire management regimes with different frequencies of burning (Kelly, 2014). "Low fire recurrence" refers to areas where fires occurred in seven or fewer years during the time period from 2000 to 2013. "High fire recurrence" refers to areas with 8 - 14 fires between the year 2000 and 2013. The different types of fire recurrence represent long-term effects of fire. Fire recurrence data was obtained from Kelly (2014) for the period 2000-2013 (Figure 1). This period was considered, as this is where most reliable data on fire extents in KNP existed prior to the study.
Fire age	In order to assess short-term effects of fire, trapping sites were further classified based on the time elapsed since the last fire (termed "fire age"). Four categories of fire age were assigned to sampling sites: (1) very recent burn occurring in the mid fire season of the same year of trapping; (2) area burnt during the early fire season in same year of trapping; (3) area with fire scars from the previous years' burning season; (4) area without or with very few fire scars from several years ago. The fire history of the sites was based on our own field observations during data collection, verified by park staff and tour operators in the area.

Data Collection

All data were collected during the dry seasons (August to October) of 2014 and 2015. Wet season captures were not possible as the Busanga Flood Plain is flooded during the wet season and is not accessible till the mid dry season. Each site consisted of three transects spaced 300 to 500 m apart, each containing 22 Sherman traps, 11 pitfall traps, and 8 Tomahawk traps. Procedures for setting these traps followed protocols described by Stanley, Goodman, and Hutterer (2011) and Stanley and Goodman (2011a, 2011b), who demonstrated the effectiveness of trap and pitfall lines to trap insectivores and medium sized rodents. For rodents, 22 Sherman Live Traps (Large Folding Aluminum Treadles and Doors Galvanized traps [LFA-TDG] 7.5x9x23 cm) were placed every 5 m on the ground along a 110 m transect. Eight collapsible Tomahawk traps (four traps of 41x13x13 cm and four traps of 48x15x15 cm size with one door) were set 5 to 10 m perpendicular to the Sherman trap line. For shrews and rodents that are too small to release the Sherman traps, 50 m pitfall lines were established (Stanley et al., 2011). Each pitfall line consisted of 11 buckets, set 5m apart, and buried in the ground with the top of the bucket flush with the ground. The 15-l buckets measured 26 cm high, 26 cm in upper diameter, and 24 cm in lower diameter. Traps were exposed for 3 days and nights and were checked twice per day (morning 06–07 hr and evening 16–17 hr), resulting in 99 trap nights for pitfall traps and 270 trap nights for Sherman and Tomahawk traps per site (3 transects x 30 Sherman and Tomahawk traps x 3 nights). Sherman and Tomahawk traps were baited with oats and peanut butter. Pesola precision spring scales (accurate to 0.1 g) were used to measure body mass. Some animals were sacrificed and specimen was deposited in the collection of Copperbelt University, Zambia. Individuals who were released were marked by fur cuttings to avoid recounting them in case of recaptures. Recaptures were not considered in any of the analyses. Body mass was considered as a proxy for body size. Both measures show allometric relationships to various aspects of animals' ecology and physiology (Brown 1984; Iskjaer *et al.* 1989).

Analyses

All data were collated in Microsoft Excel and later uploaded into SPSS 22.0 for statistical analysis. The data from the three transects per site were pooled for statistical analyses. The dependent variables ''species richness'' and ''log body mass'' were tested for deviations from normality using Kolmogorov–Smirnov one sample tests. Neither variable deviated from normality (p=.2 for both variables).

Composition and Similarities of Small Mammal Communities

Small mammal communities per site were characterized by taxonomic community composition, species richness, body mass, and functional groups. Taxonomic community composition was described with nonmetric dimensional scaling (NMDS). NMDS integrates community measures, that is, dissimilarity, diversity, and abundance to generate matrices. Differences in species composition between vegetation types and fire effects were determined by permutational multivariate analyses of variance (perMANOVA) used in the function adonis() in R package vegan (Oksanen *et al.* 2015). The analyses were based on community dissimilarity matrices by calculating Bray–Curtis dissimilarities of relative abundance data (Nopper *et al.* 2017). Sites that did not have any species captured were excluded from the analysis. Stress of matrices attained was 0.08. PerMANOVA was used to test for significant dissimilarities between communities in relation to vegetation types, management zones, and fire.

Species Richness

Species richness was used to describe community composition. General linear models were employed to determine whether vegetation types, management zones, and fire recurrence as fixed factors and fire age as continuous variable had an impact on species richness and on the mean body mass of the small mammal community per site. Due to small sample size, it was not possible to include all factors in a single model. We combined vegetation type, fire recurrence, and management zone in various combinations to determine their combined influence on species richness (i.e., vegetation type fire recurrence; vegetation type management zone; fire recurrence management zone). To account for effects of vegetation types without having to enter ''vegetation type'' as an additional factor, we z transformed species number per vegetation type. This transformed species numbers per vegetation type to z values with a mean of zero and unit variance.

Body Mass and Functional Traits

Body mass and diet were considered as proxies for life history and functional traits. We assessed the influence of vegetation types and fire (recurrence and age) on body mass by calculating the average body mass for each species using only adult animals collected at all sampling sites. Given the small number of individuals caught at most sites, we did not attempt to use body mass as a proxy for body condition or reproductive success that could be used if we had considered juveniles or some kind of measure for body condition. Rather, the average body mass for each species was applied uniformly to the species caught at each of the sampling sites. The mean body mass of the small mammal community per site (=mean of the species body mass of on all species caught at a site) was calculated as the unweighted mean of the body mass of the species caught per site. Mean body mass per site could not be calculated for two sites of miombo, as no animals had been caught there. Logarithmic transformation to the base of 10 was carried out on mean body mass prior to statistical analyses to achieve normality. To account for effects of vegetation types without having to enter ‘‘vegetation type’’ as an additional factor, we z transformed the mean body mass per vegetation type. This transformed the body mass of species averaged over the species occurring there to z values with a mean of zero and unit variance. Statistical analyses were performed as for species richness. Pearson’s correlations were used to assess relationships of fire age to species richness and body mass in the two fire recurrence areas. Kruskal–Wallis analysis of variance was used to determine differences in the representation of dietary guilds between vegetation types.

Functional traits have been compiled from the literature for all small mammal species (Rodentia, Soricomorpha, and Macroscelidea) known from KNP. Species information was obtained from Ansell (1960, 1978); Benadie and Roche (2010); Burda *et al.* (1999); Chidumayo (1979, 1980); Happold (2013); Happold and Happold (2013); Kawalika (2004); Kingdon (1997); Kingdon *et al*. (2013a, b); Lancester (1951); Larson (1957); NPWS/JICA (1999); and ZAWA (2013). The information for all species recorded from the region so far has been summarized by Namukonde *et al.* (in press). Given the large number of possible combinations of life history traits, the number of species captured in the present study was too low to analyze associations of most of these traits quantitatively in the context of this study. With the exception of dietary categories, we therefore describe only some traits qualitatively as they seem important to interpret the results of the study.

Results

Composition and Similarity of Small Mammal Communities

During the dry seasons of 2014 and 2015, we captured 105 small mammals belonging to 16 species (11 rodent and 5 shrew species) in the 51 transects assigned to 17 different sites. Even though the inventories were likely to be incomplete, the standardized trapping efforts at all sites should allow robust comparisons between sites and conditions (Tables 2 and 3). The number of individuals caught per site did not differ between vegetation types (Kruskal–Wallis test: $\chi^2=3.31$; $p=.19$; $df=2$), and the number of individuals caught was not correlated with species richness at the sites: (Spearman correlation $r_S=.42$; $p=.12$; $n=15$; the correlation was calculated without the two sites were no animals had been caught).

Table 2. Trapping sites with three trap lines per site installed in the Busanga Flood Plain. Trapping sites are listed using the code names used in the field; Iz = intensive utilization zone, W = wild zone, Wz = wilderness zone.

Trapping sites	Habitat	Fire regime	Fire age	Trapping dates	No. of species/no. of individuals	No. of shrew species/ no. of individuals	No. of rodents species/ no. of individuals	Coordinates
Iz0H1	Termitaria	Low	4	15-18 Aug. 2014	3/10	1/4	2/6	S14° 22' 57" E26° 02' 26"
Iz7H1	Termitaria	High	2	22-25 Aug. 2014	2/3	0	2/3	S14° 23' 39" E26° 03' 16"
W7I3	Termitaria	High	2	18-21 Oct. 2015	4/5	1/1	3/4	S14° 12' 31" E25° 39' 22"
Wz0H1	Termitaria	Low	3	22-25 Oct. 2014	4/6	0	4/6	S14° 20' 47" E25° 59' 23"
Wz7H1	Termitaria	High	1	26-29 Aug. 2014	5/9	1/1	4/8	S14° 20' 44" E25° 58' 37"
Iz0C13	Grassland	Low	2	18-20 Sept. 2015	2/9	0	2/9	S14° 24' 21" E26° 04' 46"
Iz7C14	Grassland	High	2	27-30 Sept. 2015	3/21	0	3/21	S14° 23' 28" E26° 03' 49"
W0C10	Grassland	Low	4	10-13 Aug. 2015	4/9	3/5	1/4	S14° 12' 54" E25° 48' 56"
W7C10	Grassland	High	3	6-9 Aug. 2015	1/2	0	1/2	S14° 14' 09" E25° 48' 44"
Wz0C13	Grassland	Low	3	14-17 Sept. 2015	3/8	1/3	2/5	S14° 17' 50" E25° 55' 12"
Wz7C10	Grassland	High	2	3-6 Aug. 2015	2/3	1/1	1/2	S14° 16' 48" E25° 55' 05"
Iz0D7	Miombo	Low	2	24-27 Sept. 2015	2/2	0	2/2	S14° 22' 35" E26° 03' 41"
Iz7D7	Miombo	High	3	20-23 Sept. 2015	1/3	0	1/3	S14° 21' 43" E26° 02' 29"
W0D1	Miombo	Low	2	21-24 Oct. 2015	1/3	0	1/3	S14° 12' 28" E25° 38' 31"
W7D1	Miombo	High	2	15-18 Oct. 2015	0	0	0	S14° 13' 23" E25° 36' 53"
Wz0D5	Miombo	Low	1	12-15 Oct. 2015	2/12	0	2/12	S14° 14' 40" E25° 45' 45"
W70D1	Miombo	High	2	25-29 Oct. 2015	0	0	0	S14° 15' 19" E25° 47' 39"

*Per site: Number of pitfall traps/trap nights =33/99 and number of traps/trap nights =90/270 in all sampling sites

Table 3. Transect characteristics and small mammal captures in the Busanga Flood Plains in 2014 and 2015. Captures reflect numbers of individuals; recaptures are not considered. Habitat: T = Termitaria, G = Grassland, Mi = Miombo woodland; Fire recurrence: L = low, H = high; Fire age: (1) very recent burn occurring in the mid dry season of the same year of trapping; (2) area burnt during the early fire season in same year of trapping; (3) area with fire scars from the previous year; (4) area without or with very few fire scars from several years ago; Management zone: Iz = intensive utilization by tourism, W = wild zone (rarely used), Wz = wilderness (no access). Abbreviations for trophic guilds: O=Omnivore, G=Granivore, H=Herbivore, I=Insectivore, I/C=Insectivore/Carnivore (*) denotes data deficient but classified based on taxonomic affiliation. Trapping sites are listed using the code names used in the field.

Trapping sites	Vegetation type	Fire recurrence	Firge age	Management zone	*Mus minutoides*	*Mastomys natalensis*	*Saccostomus campestris*	*Paraxerus cepapi*	*Lemniscoyms rosalia*	*Mus triton*	*Aethomys nyikae*	*Steatomys pratensis*	*Gerbilliscus leucogaster*	*Aethomys chrysophilus*	*Otomys angoniensis*	*Crocidura fuscomurina*	*Suncus lixus*	*Crocidura cyanea*	*Crocidura mariquensis*	*Crocidura hirta*	Species number	Ominvore	Herbivore	Granivore	Insectivore / carnivore
Iz0H1	T	L	4	Iz	3	3										4					**3**	2			1
Iz7H1	T	H	2	Iz		2	1														**2**	1		1	
W7I3	T	L	3	Wz		3				1	1	1									**4**	2		1	
Wz0H1	T	H	1	Wz	2	2		3	1							1					**5**	3	1		1
Wz7H1	T	H	2	W		2	1							1						1	**4**	1		2	1
Iz0C13	G	L	2	Iz		8					1										**2**	1			
Iz7C14	G	H	2	Iz		1							19		1						**3**	2	1		
W0C10	G	L	4	W		4												2	1	2	**4**	1			3
W7C10	G	H	3	W		2															**1**	1			
Wz0C13	G	L	3	Wz	1	4										3					**3**	2			1
Wz7C10	G	H	2	Wz		2											1				**2**	1			1
Iz0D7	Mi	L	2	Iz				1					1								**2**	2			
Iz7D7	Mi	H	3	Iz									3								**1**	1			
W0D1	Mi	L	2	W									3								**1**	1			
W7D1	Mi	H	2	W																	**0**				
Wz0D5	Mi	L	1	Wz		1		11													**2**	2			
Wz7D1	Mi	H	2	Wz																	**0**				
Total					**6**	**34**	**2**	**15**	**1**	**1**	**2**	**1**	**26**	**3**	**1**	**8**	**2**	**2**	**1**	**3**					
Body mass (g)					3.57	24.20	59.00	189.30	43.00	23.00	97.50	20.00	101.64	30.00	112.00	3.06	10.75	8.00	12.00	15.00					
SD					0.59	5.26	7.07	22.13			48.50		36.50	1.41		0.84	0.35	1.41		2.65					
Trophic guild					O	O	G	O	H	O	O*	G	O	O	H	I	I	I	I	I/C					

Of the 105 individuals captured (recaptures were not considered here), we caught 52 (49.52%) in grassland, 33 (31.42%) in termitaria, and 20 (19.05%) in miombo. The species caught in these vegetation types represent a sub_sample of species known from the region (Namukonde et al., in press). The most abundant species, *Mastomys Natalensis*, was captured in all habitats with varying abundances. Its abundance was lowest in miombo, where only one (corresponding to 2.9% of all individuals caught in this vegetation type) individual was trapped. Grassland had the highest abundance of *M. natalensis* (21 individuals, 61.8% of captures), followed by termitaria (12 individuals, 35.3% of captures). The species is known as a generalist that can cope with all kinds of disturbances but seems to be less prone to enter extended forested habitats, as it was caught at all grassland and termitaria sites but was found at only one transect with only one individual in miombo (Table 3).

Mus minutoides is the smallest rodent and *Crocidura fuscomurina* is the smallest of the shrews caught in the present study (both about 3–4 g). Both species were caught mostly on termitaria and in one grassland transect. Species captured in only one vegetation type included *Crocidura cyaena, C. mariquensis* and *Otomys angoniensis* in grassland and *Steatomys pratensis, Mus triton, Lemniscoyms rosalia,* and Saccostomus campestris in termitaria. All species, except for *C.mariquensis* (that is associated with marshes) can be considered generalists that are expected in a wide range of habitats.

The small mammal communities differed significantly between vegetation types (perMANOVA: *F*=3.34; *p*<.01; Figure 2). Communities in grassland and termitaria were rather similar while communities of miombo were set apart. This is due to the low number of species caught in miombo, the lack of insectivores caught in this vegetation type and the frequent occurrence of arboreal squirrels (*Paraxerus cepapi*; though squirrels were also caught on one termitaria site). Communities did not differ significantly with respect to management zone, fire recurrence or fire age (*F*<1.18; *p*>.24 for all three analyses).

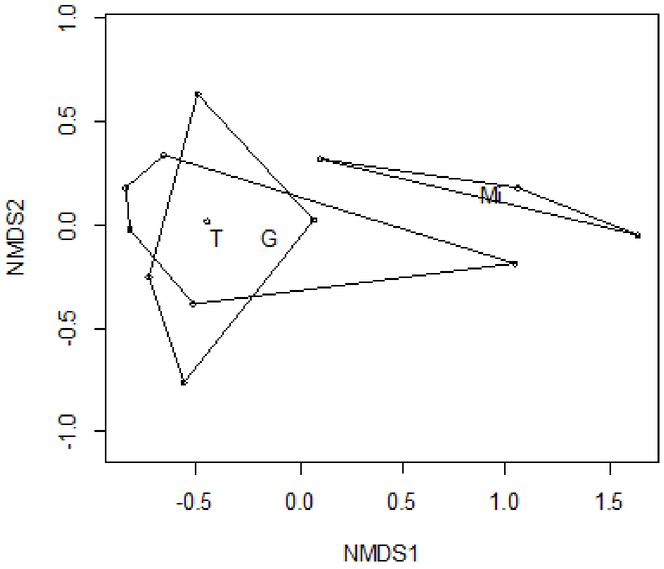

Fig 2. Non-metric dimensional scaling of the small mammal communities in different vegetation types of the Busanga Flood Plain.

Species Richness

The most species rich vegetation type was on termitaria (nine rodent species, two shrew species; mean and standard deviation: 3.6 ±1.1 species/site; *n*=5), followed by grassland (five rodents, five shrews; 2.5±1.0 species/site; *n*=6) and miombo (three rodents, no shrews 1.0±0.9 species/site; *n*=6; Figure 3). Species richness differed significantly between vegetation types (analysis of variance: *F* (2, 14) = 8.97; *p*=.003. All subsequent statistical analyses were based on species richness after z transformation per vegetation type to account for differences between vegetation types.

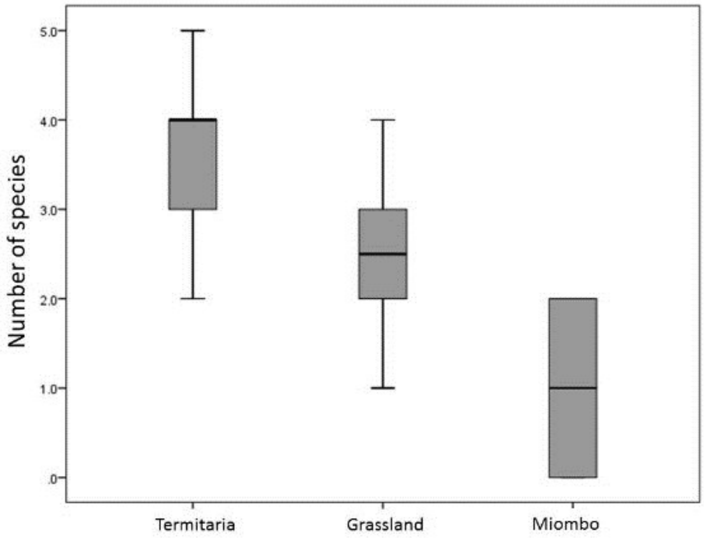

Fig 3. Small mammal species richness in different vegetation types. Values are medians, quartiles and ranges; N = 5, 6 and 6 sites for termitaria, grassland and miombo, respectively.

Species richness did not differ between management zones ($F_{2,14} = 0.34; p = .72$). In single factor analysis, there was a tendency but no significant difference of small mammal species richness between the low and high fire recurrence areas ($F_{1,15} = 7.77; p = .07$). As a single factor, fire age was also uncorrelated with species richness (Pearson correlation: $r = -.08; p = .75; n = 17$). When combining fire recurrence and fire age, the effect of fire recurrence became significant while fire age remained non-significant (GLM: Fire age: $F = 1.02; p = .33$; Fire recurrence: $F = 4.66, p = .049$; Model: $F = 2.40, p = .13$; Figure 4).

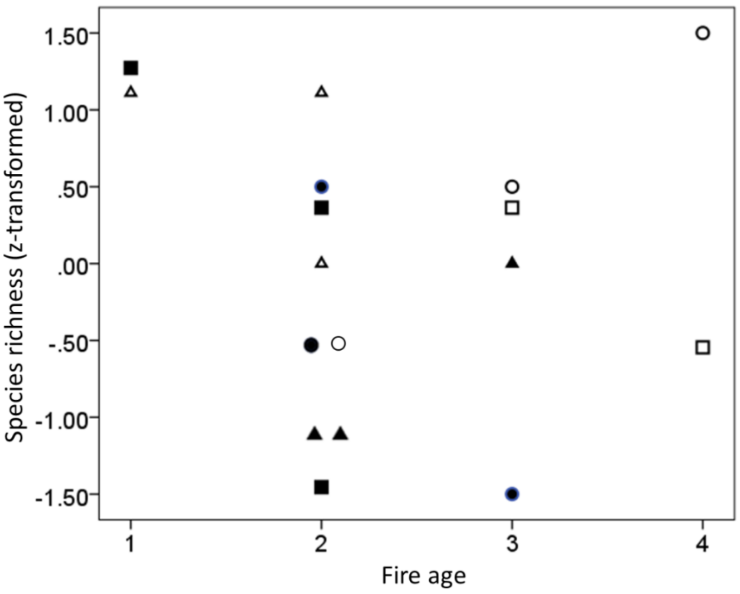

Fig 4. Relationship between fire age and small mammal species richness at sites subject to low or high fire recurrence. Species numbers were z-transformed per vegetation type. Categories of "Fire age": 1: very recent burn from the mid fire season of the same year of trapping; 2: area burnt during the early fire season in same year of trapping; 3: area with fire scars from the previous years' burning season; 4: area without or very few fire scars from several years ago. O = grassland, □ = termitaria, Δ = miombo; open symbols: low fire recurrence, filled symbols: high fire recurrence.

Body mass and Functional Traits

Based on literature classification of life history traits, small mammals of Kafue National Park are predominately omnivorous and nocturnal with body mass ranging from 3.06 g (*Crocidura fuscomurina*) to 189.30 g (*Paraxerus cepapi*) (Table 3). The percentage of omnivorous and granivorous species differed significantly between vegetation types (Kruskal-Wallis-Test: Omnivores: $H = 7.56; p = .02$; Granivores: $H = 6.90; p = .03$; Figure 5). Granivores were only captured on termitaria and were represented by two species (*Steatomys pratensis* and *Saccostomus campestris*) that shelter in burrows excavated by themselves or by spring hares or aardvarks, in sandy soils or termite mounds (Kingdon et al., 2013a). In the absence of sandy soils as is the case in the Busanga Flood Plain (Mwima, 2016), these two species will most likely burrow in termite mounds.

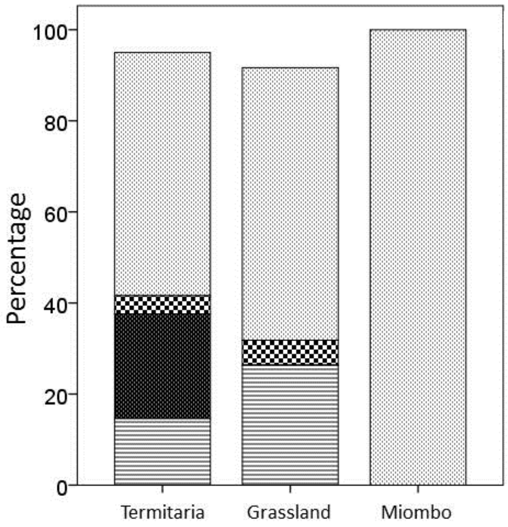

Fig 5. Relative representation of species in different trophic guilds in different vegetation types. Finely dotted = omnivores, checkerboard = herbivores, black = granivores, striped = insectivores.

In grassland 100% of the species caught were terrestrial and small. On termitaria, most of the small species from the grassland were present, plus a few other small terrestrial species. In addition, the large arboreal squirrel *Paraxerus cepapi* has been caught at one termitaria site. None of the small shrews and only one of the smaller rodent species have been captured in miombo (Figure 6).

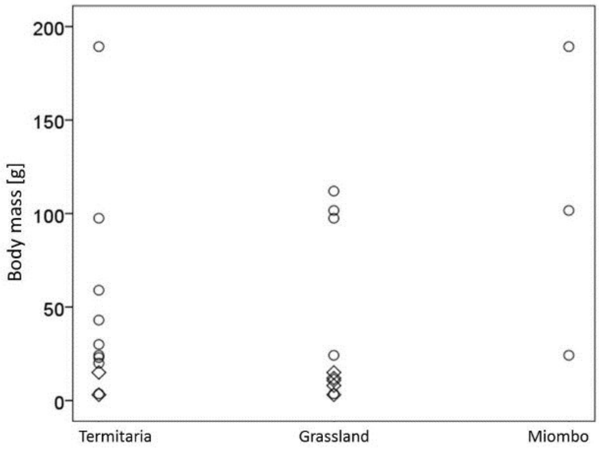

Fig 6. Body mass of species caught in different vegetation types of the Busanga Flood Plain. Each entry marks one species. All individuals of a given species were assigned the same body mass in all vegetation types; O = rodents, ◊ = shrews.

The squirrel *Paraxerus cepapi* is the only species classified as truly arboreal. Since, on average, more species were caught at termitaria sites than at miombo sites and since *P. cepapi*, was caught only at one termitaria site but at two miombo sites, the relative contribution of this one arboreal species for the termitaria community was lower than for miombo communities, where *P. cepapi* was one of three species species (= 33% of the species) caught in miombo. Due to this unequal representation and since *P. cepapi* has a substantially higher body mass than any of the terrestrial species, average body mass of the small mammal species per site was significantly higher in miombo than at the other sites ($F_{2, 12} = 6.74; p = .01$; Figure 7).

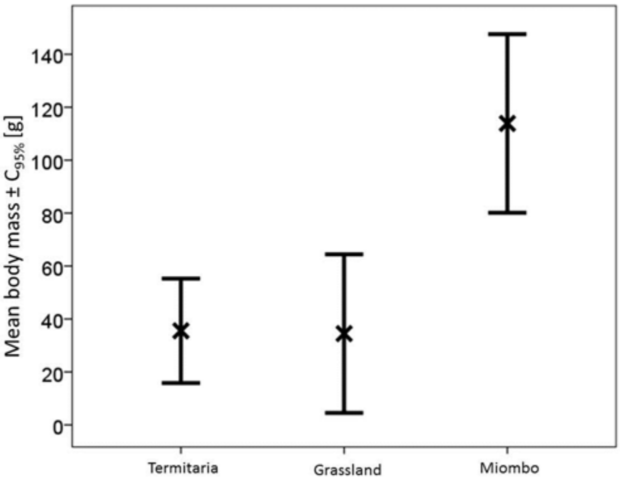

Fig 7. Mean body mass of species per site in different vegetation types of the Busanga Flood Plain. Values are means and 95% confidence intervals. N = 5, 6 and 4 sites for termitaria, grassland and miombo, respectively.

The allometric relationship between body mass and arboreality would bias any analysis of body mass in relation to environmental variables. Therefore, all subsequent statistical analyses were based on mean body mass after z-transformation per vegetation type to account for differences between vegetation types. Z-transformed mean body mass did not differ between management zones ($F_{2, 12} = 0.98; p = .40$) and fire recurrence ($F_{1, 13} = .49; p = 51$). Two-way analysis of variance indicated no significant interactions of these factors on body mass (fire recurrence x management zone: $p > .05$). Overall, the mean body mass of small mammal species caught per site decreased significantly with the time elapsed since the last fire (Pearson correlation: $r = -0.57; p = .03; n = 15$). When combining fire recurrence and fire age, the effect of fire age remained significant (GLM: Fire age: *F = 5.17, p = .04*; Fire recurrence: *F = 0.02, p = .88*; Model: *F = 2.91, p = .09*; Figure 8).

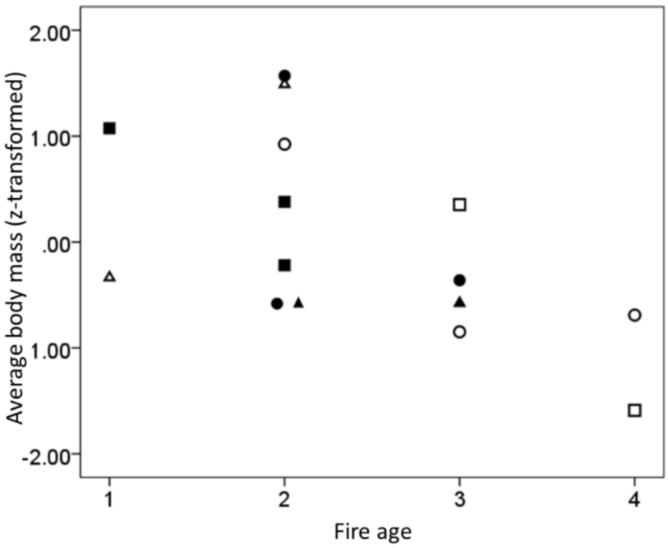

Fig 8. Relationship between fire and averaged body mass of small mammal species at sites subject to low or high fire recurrence. Average body mass of small mammal species was z-transformed per vegetation type. Categories of "Fire age": 1: very recent burn from the mid fire season of the same year of trapping; 2: area burnt during the early fire season in same year of trapping; 3: area with fire scars from the previous years' burning season; 4: area without or very few fire scars from several years ago. O = grassland, □ = termitaria, Δ = miombo; open symbols: low fire recurrence, filled symbols: high fire recurrence.

Discussion

Fire is an important component of African savannah ecosystems and often used as a management tool for conservation and tourist activities. Yet, the interplay between vegetation and fire and their effects on the diversity and structure of small mammal communities is not understood and studies yielded differing results (e.g., Blaum et al. 2006; Bösing et al. 2014; Decher & Bahian 1999; Hauptfleisch and Avenant 2015; Joubert and Ryan 1999; Yarnell *et al.* 2008). In view of their possible importance for ecosystem processes, we assessed the composition and traits of small mammal communities in the three major vegetation types of the Busanga Flood Plain and assessed the influence of fire (recurrence and age) on their community characteristics. In the Busanga Flood Plain, termitaria mainly occur as interspaced elevated patches in grasslands that provide islands of refuge in times of floods during the wet season. During the dry season, they might also provide more shelter against fire as it is easy to dig holes in the previous termite mounds while the surrounding floodplain can be extremely hard to dig in once the soil has dried out. Thus termitaria are likely to serve as refuge and source for recolonization of areas after disturbance during the wet as well as during the dry season (Bowland and Perrin 1993; Parr & Chowan 2003). This might explain the higher species richness and greater variety of dietary guilds on termitaria than in the neighboring grassland that might need to be recolonized repeatedly during the course of the year.

Miombo occurs at the fringes of the Busanga Flood Plain and as it is structurally enriched with more trees than found in grassland. Due to the increased heterogeneity of the vegetation we had expected greater species richness of small mammals. Yet this was not the case. While our traps were not designed to catch larger species, the lack of small sized species in miombo is startling. This is even more so as a review of the small mammal inventories in KNP based on published reports had indicated higher species richness for woodlands (Namukonde *et al.* in press.). Miombo is considered a vegetation formation growing on poor soil and thus not being very productive (East 1984; Desanker *et al.* 1997; Campbell *et al.* 2007) while termitaria are characterized by good soil conditions that promotes plant growth (Otieno *et al.* 2011). While high productivity soil results in high biomass across trophic levels, the link between productivity and species diversity remains unclear despite decades of research and seems to depend on local conditions, including habitat structure that is likely to obscure productivity – diversity relationships when considered across different vegetation types (Liang *et al*. 2016; Simons *et al*. 2017; Socher *et al.* 2012, 2013; Srivastava and Lawton 1998). Thus, miombo might be as rich in small species as the other two vegetation types, the densities of the terrestrial small mammals might be lower. If so, our results (low species richness in miombo) might not so much be a consequence of low species numbers occurring in miombo, but might be due to low densities of species and therefore low capture rates.

Effects of fire were quite variable. While we were able to estimate fire frequencies, fire intensity could not be measured, though it is likely to be important. Early dry season fires (such as prescribed by the management plan) are less intense and severe than late dry season fires owing to the seasonal differences in the fuel moisture levels and loads (Govender *et al.* 2006; Smit *et al.* 2016). It is to be assumed that fire intensity has pronounced effects on the distribution and composition of small mammal communities in different habitats. Despite the important role of fire, and probably due to the difficulties in measuring fire properties (such as intensity), the interactions between fire, grazing and precipitation are still not understood well for large herbivore communities, let alone for small mammals (e.g., Archibald 2008; Archibald *et al.* 2005). Integrating some kind of indicator for fire intensities at ground level and in the canopy (where applicable) might be a valuable addition to future analyses of fire effects.

To make the analyses more complex, fire does not only act directly simply by burning, but also indirectly through reduction in vegetation cover, through reduction in food availability, or fire history can impart demographic legacies on vegetation structure and dynamics, such as documented in Kruger National Park (Levick *et al.* 2015). On the level of species richness, areas that are burnt frequently in contradiction to the prescriptions of fire management plan of the area, had fewer species irrespective of the time elapsed since the last fire had occurred. This might indicate restrictions by fire regimes imposed upon small mammals and might reflect a similar phenomenon as described by Rowe-Rowe (1995) who suggested that species of small mammals are adapted to either frequent or infrequent burning. Despite the extensive trapping effort we could not identify any species, traits or combination of traits that would allow describing a pattern in the phenomenon of declining species numbers with increasing fire frequency. The phenomenon seems real, but our data are too scant to allow for interpretations of this phenomenon based on species identities or species traits.

The representation of species with different body mass found in communities at different times since the last fire has gone through the area might be easier to interpret. As time goes by after a fire, more smaller species were represented in the community (Figure 8). Thus, smaller species seem to be more affected by burning than larger species. A possible explanations could be that smaller species have more problems than larger species to escape fire and once they are gone, there are very few left to recolonize burnt areas. Also, given that body mass correlates positively with mobility and home range size (Lindstedt *et al.* 1986; Lomolino and Perault 2006; Swihart *et al.* 1988), larger species have larger home ranges, are more likely to utilize the escape routes provided by the intervening termitaria and to recolonize the area again after fire. Certainly, other traits could also be responsible for the observed differences, such as diet, which determines a species ability to make use of the food resources available after a fire, locomotion, which is linked to the ability to escape disturbance (Golley *et al.* 1975), or litter size and the number of litters per year, which determines a species ability to counter fire induced mortalities (Plasvic 2014). Yet, for the Busanga Flood

Plain, the information on life history traits of small mammals is too scant to allow further analyses of the interactions between species and environmental characteristics.

Implications for Conservation

Our study demonstrated different responses of different small mammals to the current fire regimes in the Busanga Flood Plain. Specifically, it demonstrates the impact of repeated bushfires on small mammal communities outside the prescriptions of the Kafue National Park's Fire Management Plan. It also revealed substantial gaps in our knowledge on fundamental properties of small mammal species, let alone their interactions within this ecosystem. If small mammals react differently to different fire regimes, either due to the direct fire effect or due to indirect effects, such as changes in vegetation characteristics, these different regimes might have long-term consequences that are far from being understood. Further, the vulnerability of small mammal communities to repeated bush fires in the Busanga Flood Plain may increase given the predicted changes in climate to drier and warmer conditions (GRZ 2007; Kalantary 2010; MacFadyen *et al*. 2012) that pertain in the late fire seasons and are likely to increase under the current climate scenarios. Given the possible importance of fire and small mammals in ecosystem processes, their interactions will need to be reviewed in more detail.

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Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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CHAPTER 3

Dietary niche separation of rodents and shrews in a Zambian flood plain

With Chuma Simukonda and Joerg U. Ganzhorn

In revision with *BIOTROPICA*

Abstract

While niche separation and relationships with environmental conditions of large mammals of the African savanna have been studied intensively, less conspicuous components have not received similar attention. This is the case of Kafue National Park (KNP), Zambia, where mechanisms supporting the coexistence of rodents and shrews remain unclear, much less the influence of fire on their dietary-resource use. Here we use stable carbon and nitrogen isotopes to assess dietary resource-use and partitioning among rodents and shrews found in three vegetation formations of KNP. According to the nitrogen isotope signatures, rodents are one to two trophic levels above primary production, save for *Mus triton* that is above by two to three. Shrews are two trophic levels above primary production. Among shrews, factors allowing coexistence of similar sized species could not be resolved. Rodent species of the same assemblage either differ in body mass by a factor of two (following Hutchinson's rule) or similar sized species occupy different trophic levels or dietary guilds based on their isotopic nitrogen or carbon signatures. At sites with frequent fires, rodents have broader dietary niches than at sites with low fire frequencies. This could either indicate relaxed competition under high fire frequencies as rodent populations do not reach the carrying capacity of the habitat, or it could reflect reduced competition due to lower species numbers under high versus low fire recurrence regimes. The results indicate competition as an important component structuring rodent communities in Zambian savannas, thus suggesting limited resources.

Key words: rodents, shrews, competition, savanna ecosystem, fire, Zambia

Introduction

African savanna ecosystems are mostly known for their diverse assemblages of large mammals. Studies of the ecology of these species and their interactions have a long history and mechanisms that allow the persistence of these species-rich communities in a seemingly rather homogenous habitat are well documented (McNaughton 1983, Owen-Smith *et al*. 1993, Sinclair & Arcese 1995, Kiffner *et al*. 2014). In contrast, very little is known of the equally diverse communities of small mammals, though small mammals play important roles in ecosystem functionality, such as consumption of primary and secondary production, seed predation and dispersal, burrowing or serving as food for higher trophic levels (Timbuka & Kabigumila 2006, Hoffmann *et al*. 2010, MacFadyen *et al*. 2012, Symes *et al*. 2013).

Coexistence of multi-species assemblages can be facilitated by frequent disturbances that keep species populations below the carrying capacity of the habitat. In this scenario, species do not need to occupy specific and exclusive niches, because coexistence is facilitated by temporal and spatial disturbances. These aspects can be summarized in the context of stochastic community processes (Begon *et al*. 2006). Deterministic processes prevail under more stable conditions when species can establish populations up to the carrying capacity of the habitat. In this scenario, species are likely to compete over limited resources. As a result, and in order to avoid competition, they occupy different niches. Therefore, species should be morphologically and dietarily dissimilar in order to be able to coexist (MacArthur & Levins 1967). The deterministic approach has allowed formulating assembly rules that reflect the constraints of similarities but also reveal cases where such deterministic processes do not operate or are poorly understood. Niche differences can be reflected in partitioning of food resources, microhabitat separation, temporal separation due to different activity pattern, or different life history traits that are often linked to body size by allometric relationships (Brown & West 2000). Separation of species by trophic specializations has been documented by a variety of mammal communities across different scales and across continents (e.g., Bell 1971, Jarman 1974, Geist 1974, Demment & van Soest 1985, Ganzhorn 1989, 1997, Fox 2011, Dammhahn *et al*. 2013). A classic example for small mammals is the pattern of body size distribution in communities of seed eating desert rodents in the Sonoran and Great Basin Deserts (Brown 1995). This example illustrates Hutchinson's rule (Hutchinson 1959), where species can co-exist if they differ in body mass by a factor of two or more or in linear body size dimensions by a factor of 1.4. Body size is linked to different aspects of an animal's life (Lindstedt *et al*. 1986, Iskjaer *et al*. 1989) and plays a major role in community structure and dynamics through differences in metabolism, reproductive traits and foraging behavior (Swihart *et al.* 1988, Ernest 2005, Lomolino & Perault 2000, Fisher *et al.* 2011), and can therefore be used as a proxy for a combination of traits.

While the deterministic component of community assemblages is intuitively clear, many ecosystems are subject to disturbances that do not allow a system to reach equilibria. In African savanna systems fire is considered such a factor. Though fire is such an integral part of savanna ecosystems, that it should not be considered a "stochastic disturbance" component (Bell 1971), its effect on small mammals is still poorly understood. Small mammal communities respond differently to repeated bush fires, indicating that they are constrained in various manners by the frequency of habitat disturbance (Rowe-Rowe 1995, Namukonde *et* *al*. 2017). If small mammal communities were structured by interspecific competition (as implied by the above considerations) and fire would act as a disturbance agent, it is to be expected, that they would broaden their niche with increasing disturbance. This phenomenon has been described for Galapagos finches under the impact of El Nino events (Grant & Grant 2006).

Conventional studies on dietary niche differentiation of small mammals have been hampered by methodological problems associated with gut content analysis and direct field observations of feeding strategies (Symes *et al*. 2013). Stable isotope biochemistry offers a method of identifying resource use by secretive species (Fry 2008, Crowley 2012). This method provides quantitative records of an animal's feeding ecology based on the stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) found in animal tissues. Values of $\delta^{13}C$ in animals reflect the carbon source (primary producer consumed), whilst $\delta^{15}N$ reflects the trophic positioning in a community (Symes *et al*. 2013, van der Merwe & Hellgren 2016). In a stable community with coexisting species, taxon separation based on different dietary resources is detected by variation between species of 2.0‰ to 2.5‰ of $\delta^{13}C$ and $\delta^{15}N$ in their isotope signature, respectively (Crowley 2012).

Kafue National Park (KNP) is Zambia's largest protected area and an important conservation area for small mammals, which excluding bats, has recorded 50 species representing nearly 50% of the small mammal species known from the country (Namukonde *et al.* 2017, in press). One of the major challenges faced in understanding their role and conserving these taxa, is the lack of precise information on their habitat requirements in terms of food resource utilization, mechanisms supporting their coexistence and their response to anthropogenic disturbances such as bushfires (e.g., Nakagawa *et al.* 2007, Crowley *et al.* 2012, 2013, Dammhahn *et al*. 2013, Codron *et al*. 2015). Using rodent and shrew communities of termitaria, grassland and Miombo woodland as the three most species rich habitats of KNP in Zambia, we employ the conceptual framework of competition over limited resources resulting in limiting similarities (MacArthur & Levins 1967) and reconstruction of diet composition based on stable isotopes to investigate the following questions. (1) What is the dietary space available in the three habitats, as described by the $\delta^{13}C$ and $\delta^{15}N$ signatures of possible food items (grass, leaves of trees, invertebrates)? (2) What is the dietary space occupied by rodent and shrew communities in the three different habitats? (3) Are rodents and shrews within the same guild structured by size differences? (4) In cases where no size differences are apparent: do sympatric species differ in their trophic position within the community based on their δ^{13}C and δ^{15}N signatures? (5) Do species broaden their dietary niche in areas of increased disturbance by fire?

Methods

Study area

The study was conducted in the northwestern part of KNP, specifically the Busanga Flood Plain (25º 25' E / 13º 45' S to 26º 10' E / 14º 25' S, Fig. 1). KNP measures about 22,400 km^2 and receives about 1100 mm of rain per year. The Busanga Flood Plain is an important conservation area that is home to a wide variety of game (Information sheet on Ramsar Wetlands [RIS] 2002, Zambia Wildlife Authority [ZAWA] 2013), which is inundated annually during the rainy season (Nov. - April), and is dominated by grasslands, that are surrounded by woodlands. The Miombo woodland is the most dominant vegetation type in KNP and followed by grasslands. Termitaria occur as intervening patches within the grasslands and can rise up to 6 m with widths of up to 10-15 m (Walker 2015, Fig. 2). Termitarias are thought to act as refugia for small species during floods and fire (Namukonde *et al*. 2017).

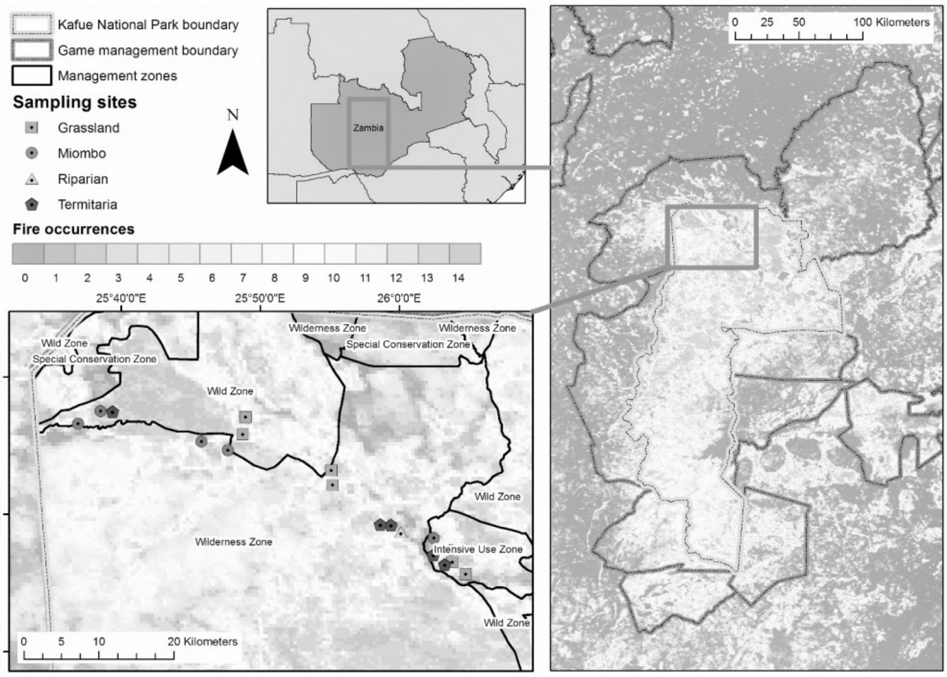

Fig 1. Sampling sites depicting the vegetation and fire recurrence in the Busanga Flood Plain, northwestern Kafue National Park. Fire occurrences indicate the number of years with fire between 2000 and 2013 (base map from Kelly 2014).

Data collection

We considered species of rodents (Rodentia) and shrews (Soricomorpha) that weigh less than a kilogram and measure less than thirty centimeters as adults as defined by Barnett & Dutton (1995) and adopted by Namukonde *et al*. (2017) for the Busanga system. Elephant shrews (Family Macroscelidae) are also present but could not be captured in the present study. The sampling program was established to assess the influence of habitat types and fire frequencies on rodent and shrew communities. We trapped rodents and shrews in three vegetation types (grassland, Miombo woodland and termitaria), each with sites representing areas of high (3 sites) and low fire recurrence (3 sites), and in each site we laid three trapping transects 300 – 500m apart. Trapping results were pooled for the three transects per site. Sites classified as low fire recurrence had experienced less than eight fires between the years 2000 and 2013 and those with high fire recurrence more than eight fires during this period (Kelly 2014). For termitaria, we could locate only two out of the three planned sites for low fire recurrence, hence termitaria had five sites (3 under high and 2 under low), whilst Miombo woodland and grassland each had six sites (3 high and 3 under low). In each of these sites, three transect lines were installed with Sherman (22 LFA-TDG 7.5 x 9 x 23 cm) and Tomahawk (four TH 41 x 13 x 13 cm and four TH 48 x 15 x 15 cm sized) live-traps baited with peanut butter and oats, following methods outlined by Stanley & Goodman (2011 a, b) and Stanley *et al.* (2011). These traps were placed perpendicular to pitfall lines and spaced 5 m apart along a 100 m transect. Pitfall lines consisted of buckets (11 x 15l, 26 cm height, 26 cm in upper diameter, and 24 cm in lower diameter) placed in the ground, at intervals of 5 m, with the top of the bucket flush with the ground surface. A drift fence consisting of opaque black plastic was constructed for the 50 m pitfall line, running over the buckets (Fig. 2). Traps were open for three days and three nights. They were checked twice per day (after sunrise and before sunset).

Fig.2 Miombo woodland, grassland and termitaria in Kafue National Park, including fence lines constructed along a pitfall traps.

Species were identified using species description by Ansell (1978), Apps (2012), Kingdon *et al*. (2013a, b), and Skinner & Smithers (1990). The mass of all adult individuals trapped was attained using Presola Spring balances. Body mass was not used to indicate body condition, but as a proxy for body size. This is described as a reasonable measure for body size as it is allometrically related to an animals' ecology and physiology (Iskjaer *et al.* 1989). Pregnant females were encountered mostly in squirrels. Since these species are substantially larger than the others, the increase in body mass due to pregnancy should not affect the overall conclusions. Sample size was too small to assess seasonal changes in body mass or food composition. Since traps were set in high and low fire recurrence sites in subsequent weeks per habitat and habitats were trapped in no specific order, seasonal changes should also not affect the comparisons between fire regimes and habitats.

With clean scissor, hair samples were taken by clipping a tuft of hair from the lower back, as close to the skin of trapped individuals: these marks remained evident to identify recaptured animals, which were not resampled. Voucher specimen were deposited in the collection of Copperbelt University. Hair samples were stored dry until analysis. In order to characterize stable isotope signatures of the habitats, leaves of dominant tree and grass species were collected from each of the sampling sites in a random manner and invertebrates were collected from pitfall traps. These samples were sun dried and stored for analyses.

Isotope analysis

Isotope analysis was conducted at the Biozentrum Klein Flottbek of the University of Hamburg. This analysis presented the differences in ratios between heavy ($^{15}{}_{7}N$, $^{13}{}_{6}C$) and light ($^{14}{}_{7}N$, $^{12}{}_{6}C$) isotopes of nitrogen and carbon. Both nitrogen and carbon occur naturally in several stable forms and persist for eons after they are formed (Fry 2008). This difference in mass is presented as a ratio of heavy to light isotopes, expressed as parts per thousand (‰) and with the notation δ. International standards for $\delta^{15}N$ are based on atmospheric nitrogen (AIR), and $\delta^{13}C$ to PeeDee Belemnite (PDB) (Fry 2008, Crowley 2012).

Prior to analysis, all samples were dried in an oven for three days to eliminate any remaining moisture. Leaves of plants were crushed into powder using a motorized mill (Retsch MW 400 mill), followed by crushing with a mortar and pestle if the material had not been homogenized. Duplicate samples of each specimen, were weighed using a precision microbalance (~2 mg of plant, and ~1 mg of hair and arthropod material), and placed in 4 x 6 mm tin cups (HEKAtech, Germany) that were compressed into a small ball using a forcep. These samples were stored in a vacuum prior to analysis. Samples were then combusted in a mass spectrometer (EURO-EA 3000, Euro Vector, and Italy). BBOT (2, 5-bis (5-tert-butyl-2-benzoxazol-2-yl) thiophene (6.51% N; 72.52% C; HEKAtech, Germany), KNO_3 and coffein were used as internal standards. Samples were analyzed in duplicates by Mathis Gersthage and Christoph Reisdorff from University of Hamburg.

Data analysis

All data was collated in Microsoft Excel and then latter uploaded to SPSS 22.0 for analysis. The baseline of δ^{13}C and δ^{15}N signatures of food available in the different habitats was established by the analysis of plant material (leaves of grasses and trees), as well as invertebrates. The dietary space available and the trophic space occupied by rodent and shrew communities were characterized using δ^{13}C and δ^{15}N bi-plots based on group means (in case of leaves and invertebrates) and species means for small mammals (Layman *et al*. 2007).

Niche widths were calculated using standard deviation of δ^{13}C and δ^{15}N of species that had more than two individuals trapped. To analyze differences of means within the food sources (grasses, leaves and invertebrates), we used Analysis of Variance (ANOVA) and explored differences that arose using Least Significant Differences (LSD) tests. We determined statistical differences between plant food sources (trees and grasses) using t-tests for samples with equal variance difference. Sign test was used to test for consistent differences between rodent and shrew niches respectively, in high and low fire recurrence sites.

We expected that sympatric species of similar body sizes of rodents and shrews respectively, would differ in trophic level and basal resource use. First, we examined the occurrence of species with different body mass for each vegetation type. In cases where species did not differ in body mass by a factor of about 2, we checked, whether or not co-occurring species of similar body mass differed in their isotope signatures, with the assumption that average trophic differences of 2.5‰ in δ^{15}N would reflect different trophic levels, and differences of 2.0‰ in δ^{13}C would reflect reliance on different basal resources (Crowley 2012).

Results

Hair samples from 110 individuals representing 16 species (11 rodents and five shrews) were analyzed. Leaves for 43 tree and 19 grass samples, and 97 invertebrates were analyzed for their stable isotope concentrations. The raw data are provided in the Supplementary Material.

Dietary space available in the three habitats

Possible food sources for small mammals were derived from grass, tree leaves and invertebrates. Values for δ^{13}C signatures for grasses averaged -14.54 ± 3.35 (mean ± standard deviation; N = 19) while those of trees averaged -27.63 ± 1.35 (N = 43). Mean values for δ^{15}N were 2.31 ± 1.77 for grasses and 1.35 ± 1.35 for trees. There were no significant differences in the signatures of grass and tree leaves between the three vegetation types (ANOVA: grass (N = 19), δ^{13}C: *F = 1.948, P = 0.175;* δ^{15}N: *F = 0.048, P = 0.954*; trees (N = 43): δ^{13}C: *F = 1.700, P = 0.196*; δ^{15}N: *F = 0.217, P = 0.806*). The signatures of δ^{13}C and δ^{15}N differed significantly between grasses and tree leaves (t-tests for samples with equal variance: δ^{13}C: *t = 22.052, df = 60, P < 0.001*; δ^{15}N: *t = 2.358, df = 60, P = 0.022*).

The invertebrate signatures differed widely between taxa and averaged -20.12 ± 3.21 for δ^{13}C and 6.02 ± 2.03 for δ^{15}N (N = 97). In the model including all three vegetation types, the means of δ^{13}C differed significantly between vegetation formations (*F = 8.198, P = 0.001*). This difference was due to lower values of invertebrates in Miombo woodland which were significantly lower than the values for grassland or termitaria (LSD posthoc test: *P < 0.01* for either vegetation type). Grassland and termitaria did not differ in their δ^{13}C values. The means of δ^{15}N also did not show any difference between the three habitats (*F = 0.687, P = 0.505*).

Dietary space realized by the small mammal communities in the three different habitats

Rodents fell within the δ^{13}C signatures of invertebrates and grasses whilst those of shrews were within the signatures of invertebrates. Communities consisting of rodents and shrews associated with termitaria covered the largest dietary space and almost encompassed the dietary spaces of those found in the other two vegetation types. (Fig. 3A). Rodents occupied the lowest and the highest trophic positions (lowest: *Otomys angoniensis*: δ^{15}N = 3.43, found only in grassland; highest: *Mus triton*: δ^{15}N = 9.42, found only in termitaria). On average shrews occupied a higher trophic value (7.16) than rodents (5.64), even though their dietary space was engulfed by rodents due to the high δ^{15}N values found in *M. triton* (Fig. 3B).

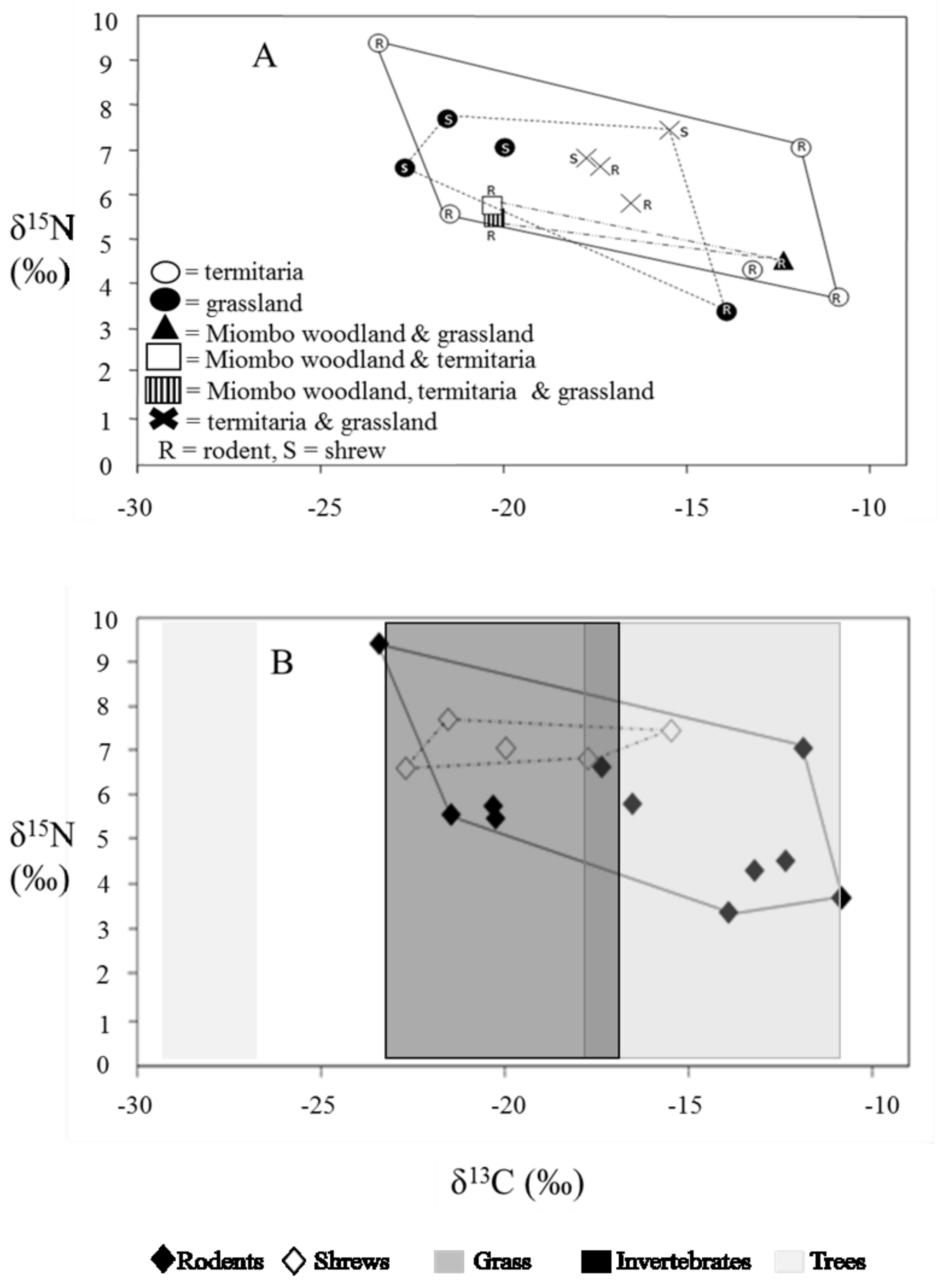

Fig 3. (A) Habitat specific dietary space of rodents and shrews in termitaria, Miombo woodland and grassland. Each symbol represents the isotope signature of a rodents and shrews occurring in one or several vegetation types. (B) Dietary space for rodents and shrews in all habitats combined (termitaria, Miombo woodland and grassland). Standard deviations of $\delta^{13}C$ signatures of grasses, invertebrates and trees are depicted in shaded areas accordingly.

Small mammal assemblages within the same guild structured by size differences

Among rodents, there was a clear arrangement of species within a given vegetation type with body mass of sympatric species differing by at least a factor of 2 with the exception of some rodent species with body mass between 20-30 g in termitaria and with 97.5-112 g in Miombo woodland. Body mass of shrew species differed widely in termitaria, but in grassland at least four species with body masses of 8-15 g occurred.

Trophic differences in sympatric species of similar body size

Sympatric species with similar body sizes in termitaria differed either in the trophic level (by ca. 2.5‰ in $\delta^{15}N$) or in the basal resource use (by ca. 2.0‰ in $\delta^{13}C$; Fig 4). In grassland, these differences were not pronounced for rodents particularly *Gerbilliscus leucogaster* and *Otomys angoniensis* (Fig 4). Shrews in grassland all belonged to the same trophic level and differed only in basal resource use, except for *Crocidura cyanea* that appears to show trophic overlap with the similar sized *C. mariquensis* and *Suncus lixus* (Fig 4).

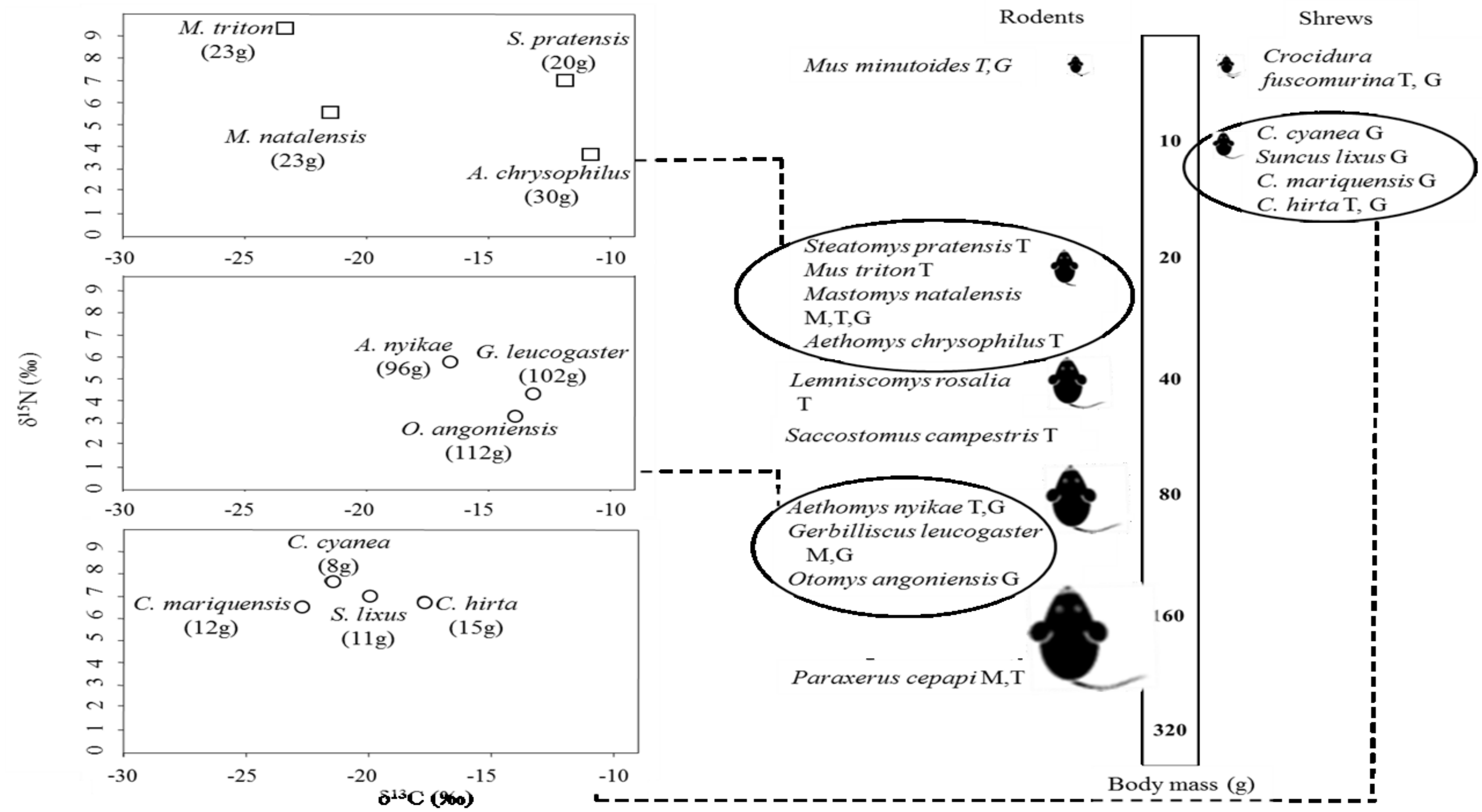

Fig 4. Body mass distribution of small mammal communities in the Busanga Flood Plain and the trophic and dietary guilds of similar sized rodents and shrews. M, G and T indicate the occurrence of species in Miombo woodland, grassland and termitaria respectively. The scale indicating body mass reflects Hutchinson's concept that species belonging to the same guild should differ in body mass by a factor of 2 in order to avoid competition. □ = termitaria, ○ = grassland.

Species dietary niche in areas of increased disturbance by fire

For the shrew *Crocidura fuscomurina* niche width, as indicated by the standard deviation of $\delta^{13}C$ and $\delta^{15}N$ was smaller for these isotopes in the high fire recurrence areas than in the low fire recurrence areas (Fig. 5A, B). For rodents, the standard deviations of $\delta^{15}N$ and $\delta^{13}C$ signatures were larger in high fire than in low fire recurrence areas for all species, the exception being for *Mus minutoides* that had a smaller standard deviation in $\delta^{13}C$ in areas of high than in areas of low fire frequencies. In combination, rodent niches as measured by their variance, were broader in seven out of eight comparisons ($P = 0.035$, Sign test). Analyzing single species separately, significant differences were attained in termitaria for *M. minutoides* (F-test: $\delta^{15}N$: $F = 10.954, p = 0.030$) and for *Mastomys natalensis* ($\delta^{13}C$: $F = 5.294, p = 0.042$; Fig. 5A, B).

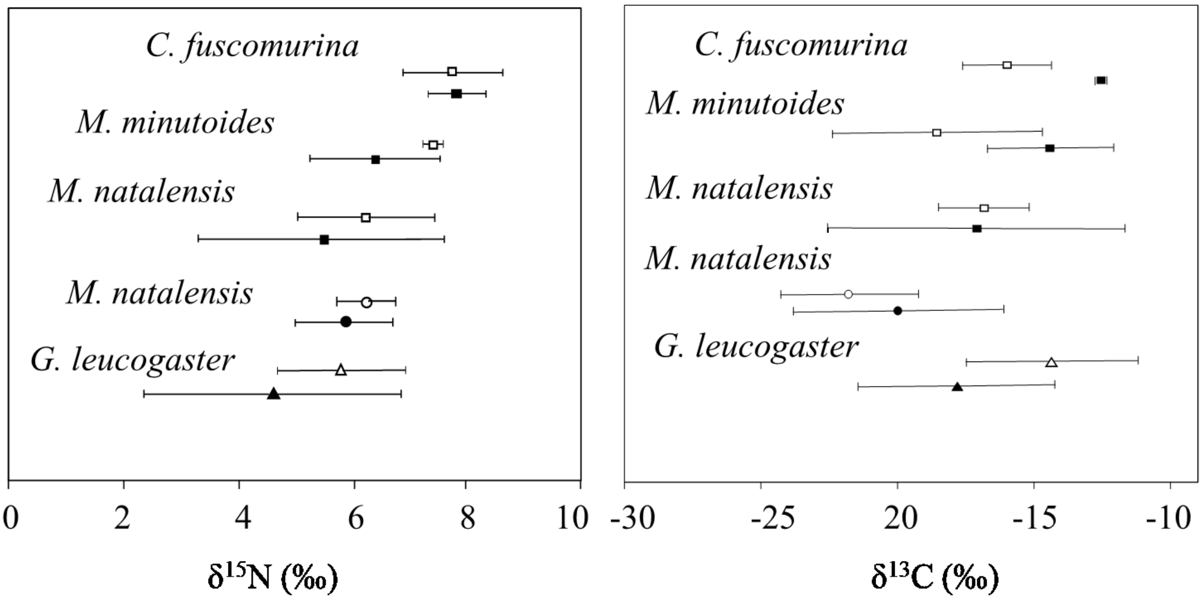

Fig 5. Niche width indicated by $\delta^{15}N$ (A) and $\delta^{13}C$ (B) in high and low fire recurrence areas. □ = termitaria, ○ = grassland and Δ = Miombo woodland; open symbols: low fire recurrence, filled symbols: high fire recurrence. Values are means and standard deviation. Full species names are shown in Figure 4.

Discussion

In the Afrotropics, rodents and shrews have been studied mostly in the context of a "response variable" to habitat characteristics or various kinds of disturbance, such as fire, grazing or the demise of large mammals in savanna systems (e.g., Eccard *et al.* 2000, Timbuka & Kabigumila 2006, Keller & Schradin 2008, Hoffmann *et al.* 2010, MacFadyen *et al.* 2012, Bösing *et al.* 2014, Young *et al.* 2015, Namukonde *et al.* 2017). However, interactions between rodent and shrew species, their ecological needs and the structure of these communities remain poorly known for most parts of the tropics (Amori & Luiselli 2011, Dammhahn *et al.* 2013, Symes *et al.* 2013, Abu Baker & Brown 2014). This lack of information impedes an understanding of African ecosystems, as small mammals have important ecosystem functions. Among other issues, it might be important to understand the boundary conditions under which rodents and shrews reach their carrying capacity in these ecosystems, as this will affect higher as well as lower trophic levels. Proxies indicating competition, such as niche differentiation could be interpreted as signs of limited resources and, thus, populations approaching carrying capacity of the respective habitat. The idea that resources are limited is supported by a study that showed compensational population growth of small mammals after the decline of large herbivores (Young *et al.* 2015), or the responses of small mammal assemblages to artificial feeding (Schoepf *et al.* 2015). Though feeding niches of rodents and shrews are difficult to define based on field observations, isotope analyses provide insights to assess these aspects with reference to differentiation of dietary niches of sympatric species over time and different environmental conditions (e.g., Rakotondranary *et al.* 2011, Crowley *et al.* 2012, 2013, Dammhahn *et al.* 2013, Codron *et al.* 2015).

The differences in the isotopic signatures of grasses and trees were anticipated, given their different photosynthetic pathways. Grasses are C_4 photosynthetic pathway plants, whose average $\delta^{13}C$ value is -14‰, and range from -12‰ to -16‰ (Crowley 2012). Trees sampled followed C_3 photosynthetic pathways with $\delta^{13}C$ values ranging between -30 and -20. The $\delta^{13}C$ signatures of rodents coincided with those of invertebrates and grasses or were between the $\delta^{13}C$ signatures of trees and grasses, reflecting different proportions of these food resources in their diets. For shrews, the different $\delta^{13}C$ signatures are likely to reflect diets composed of invertebrates or small vertebrates that in turn feed on different plant material, resulting in largely different $\delta^{13}C$ signatures of most shrew species.

According to the $\delta^{15}N$ signatures, rodents spanned a large range of $\delta^{15}N$ signatures with most rodents being one or two trophic levels above primary production. A remarkable exception is represented by *Mus triton* that deviated from primary production by about 8‰, representing 2-3 trophic levels. Shrews were rather uniform in their $\delta^{15}N$ signatures and were about 6‰ higher than the plant nitrogen signatures, corresponding to about two trophic levels.

The overarching trophic structure of the rodent and shrew communities of the Kafue National Park suggests a high diversity, of trophic traits most of which are found associated with termitaria that may function as a source from which other communities draw their trophic traits. This corroborates the earlier perceived role of termitaria to act as island refugia from which certain species recolonize other habitats after floods and fire (Namukonde *et al.* 2017). Termitaria are characterized by large termite mounds that can rise up to 6 m with widths of up to 10-15 m (Walker 2015) and occur as interspaced patches in the grasslands of the Busanga Flood Plain. Under periods of high water after heavy seasonal rains the Busanga Flood Plains are inundated but the termite mounds and the immediate area around the mounds are not flooded. Fire might have less effects on rodents and shrews living in and around termitaria, that tend to have friable soils as compared to the hard soil of grassland on dried up floodplains (similar to the bush-clumps in savanna systems; Whittington *et al*. 2008). In any case, the termitaria might provide underground shelter in case of fire.

The most obvious form of species separation is based on size differences. Body size is linked to many ecological and physiological processes of mammals in allometric relationships and plays a major role in community structure and dynamics (Lindstedt *et al.* 1986, Swihart *et al.* 1988, Iskjaer *et al.* 1989, Ernest 2005, Lomolino & Perault 2000, Fisher *et al.* 2011). Similar to findings in other regions, species size distribution in the three rodent communities (termitaria, grassland, Miombo woodland) contain a strong signal of community structuring by body mass. This is well illustrated by the Miombo woodland community, where three rodent species differ in body mass sufficiently to allow coexistence (*Mastomys natalensis*: 24 g, *Gerbilliscus leucogaster*: 102 g, *Paraxerus cepapi*: 189 g; Fig. 4). The situation is less clear in termitaria and grassland for rodents and in grassland for shrews. Here, rodents cluster in body mass ranges that approach separation by a factor of 2 (3 g, 20 – 30 g, 43 – 59 g, 98 – 112 g, 189 g, Fig. 4), but four similar sized rodents with body mass between 20 and 30 g coexist on termitaria, and three similar sized rodent species with body mass around 100 g coexist in grassland. Similarly, the smallest shrew species (*Crocidura fuscomurina*) with a body mass of 3 g is distinct from other shrew species, but four similar sized shrew species with body mass between 8 and 15 g coexist in grassland (Fig. 4). According to Levin *et al.* (2009), these species should either differ in niche space or have narrow niche overlap with other species. This clearly holds for rodents with body mass of 20 to 30 g in termitaria. Niche separation seems to be achieved among these four species by feeding on different trophic levels (separation of *Mus triton* versus *Mastomys natalensis* and of *Steatomys pratensis* versus *Aethomys chrysophilus* based on nitrogen isotopes), while species with similar nitrogen signatures appear well separated based on carbon signatures, indicating that they rely on different portions of available foods (Fig 4). For the three sympatric rodent species in grassland (*A. nyikae*, *Gerbilliscus leucogaster* and *Otomys angoniensis*) niche separation is not as evident, at least not for the latter two species. Their coexistence could be facilitated by differences in their spatial and temporal distribution of their activity patterns: *O. angoniensis* is diurnal while *G. leucogaster* is nocturnal (Skinner & Chimimba 2005, Kingdon *et al.* 2013b).

An unexpected finding was the dietary space of shrews being encompassed by rodents. Whilst we expected rodents to occupy larger dietary space as most are omnivorous and forage on food sources of shrews, we did not expect that they would occupy the highest trophic position. Shrews are insectivores and some with carnivorous tendencies (Skinner & Chimimba 2005, Kingdon *et al.* 2013b), and would ordinarily occupy the highest trophic level. However, *Mus triton* is described as a rodent that is predominately insectivorous (Skinner & Chimimba 2005, Kingdon *et al.* 2013b) and possibly feeds on insects that are carnivorous in nature or on other insectivorous vertebrates not captured in this study; hence, it has a high δ^{15}N value that is almost one trophic level greater than that shrews. Yet, *M. triton* is unlikely to compete directly with shrews as it is substantially larger (23 g) than most shrew species, except of *C. hirta* (15 g). The three sympatric species of shrews (*C. mariquensis, C. cyanea and Suncus lixus*) found in grasslands do not seem to have a clear separation in dietary regimes, space or time. Thus, while several findings support the idea that rodent communities are structured by competition and their occupied niches are shaped by past or present competition over limited resources, this is not supported for shrews.

The response of rodents and shrews towards fire as an element of disturbance also supports the idea that rodent communities are under different selection pressures than shrew communities. Repeated bush fires may depress populations below carrying capacity. If so, avoidance of competition by niche separation would be less reinforced in areas of high fire recurrence while niche separation might become important in more stable conditions, specifically areas of low fire recurrence. This seems to be the case for rodents as all species investigated have broader trophic niches in high than in low fire areas. The exception being *Mus minutoides,* with a wider niche in areas of low than in areas of high fire recurrence (Fig.

5B). However, since the number of species is lower under high fire frequencies than under low fire frequencies (Namukonde *et al.* 2017), the broader niches under high fire frequencies could also indicate competitive release in species-poor communities. But both interpretations imply competition as an important component in rodent communities of Kafue National Park, as found in other parts of southern Africa (Codron *et al.* 2015). *Crocidura fuscomurina* shows the opposite pattern (wider niche under low than under high fire recurrence). As this the smallest shrew species at the study site (body mass 3 g), and it is clearly separated from other shrews by body mass following Hutchinson's rule (Hutchinson 1959), its niche shape should not be affected by competition through the other shrew species. For the shrew species of similar body mass (*C. mariquensis, C. cyanea and Suncus lixus*), the factors allowing coexistence remain elusive.

In conclusion, stable isotope analyses provided insights into environmental constraints and species interactions in rodent and shrew communities that are otherwise difficult to study. The data presented herein, indicate that at least rodent communities are constrained by competition over limited food resources. In concert with the finding that small mammal assemblages show density compensations after the decline of large herbivores (e.g., Young *et al.* 2015), these results call for a simultaneous integration of large and small herbivores community studies in order to have a more comprehensive understanding of the African savanna ecosystems.

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Data availability statement

All data are provided in the supplement.

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General Discussion

Large mammals have long been the cornerstone of conservation in Africa. Despite the centre stage they occupy in African conservation, they continue to decline amidst human induced pressures that have profound influence on community composition, structure and ecosystem function (Young et al. 2015). Even though large mammals have been studied intensively (McNaughton 1983, Sinclair & Arcese 1995, Kiffner *et al*. 2014) and that their diversity is highest in conservation sites as is the case for small mammals (Decher and Bahain 1999; Young *et al.* 2015), their responses to environmental factors cannot act as surrogates for all fauna and particularly for the small mammals that are under studied. This does not relegate the interplay between large and small mammals alike, but stresses the need to integrate small mammals in savanna studies as they assume multiple roles in ecosystem functionality (e.g. shaping of vegetation communities, soil aeration and creation, water filtration, pest control, etc.). While several small mammal species are known to benefit from anthropogenic changes (Young *et al*. 2015; Sieg 1987; Myllymäki 1979), others are highly vulnerable and thrive in conservation sites where they occur in high species numbers.

Conservation sites for small mammals in Africa are protected areas that are mainly set aside for large wildlife. In Zambia these include national parks and game management areas. Game management areas are partially protected areas that lie immediately adjacent to national parks where resource extraction is allowed for economic interest for the local inhabitants (Caro 1999; Namukonde and Kachali 2015). Kafue National Park in Zambia is an important conservation area for small mammals as over fifty percent of the small mammal species described in Zambia are found in this park. As is the case for large mammals, research activities aimed at monitoring changes in community properties of small mammals needs to be integrated into the management plans of the park, for this taxon to contribute towards realizing its full ecological potential.

Whilst many factors influence the community properties of small mammals in Kafue National Park, I choose to investigate the influence of land use as prescribed by its management plan, bushfires and vegetation. Given the protection status of Kafue National Park, these and climate (rainfall) whose influence has been shown to impact diversity and abundance of small mammals (Decher and Bahian 1999) were thought to be the most important factors that would be acting on small communities. Climate was not investigated in the present study as this was considered to act uniformly under the isohyets of 1,100mm

(McIntyre 2017) in the Busanga Flood Plain. Land use of the park as prescribed by the management zones namely, Wild, Wilderness and Intensive Utilization Zones, has no influence on the community composition and structure of small mammals. Instead they are influenced by vegetation type that defines their compositions and structure. This is an important finding, and points to the conservation of vegetation for small mammals, instead of the large tracts of land assigned as management zones.

Important habitats for small mammals are woodlands, grassland and termitaria that together host all the small mammal species known to occur in Kafue National Park, except for *Dasmys incomtus* that favors water logged areas i.e. swamp and riparian and *Graphiurus murinus* found only in closed habitats of riparian and closed dry forests. These habitats are also important for *Fukomys kafuensis*, the only species in Kafue National Park listed with a conservation status of high concern. *Fukomys kafuensis* is listed as vulnerable under the IUCN Red List of Threatened Species (Cotterill and Maree 2008).

Given the number of studies that have demonstrated a high species diversity of small mammals in conservation areas as opposed to other land uses (Caro 1999; Decher and Bahain 1999; Timbuka and Kabigumila 2006; Young *et al.* 2015), this measure and other community characteristics could serve as indicators to changes in land use if monitored regularly. Also, their abundance, could serve as signals to large mammal activity, as they are seen to undergo compensational population growth after the decline of large herbivores (Young *et al.* 2015). This might also explain the dismal captures of small mammals in miombo woodlands. I expected to capture far more species from miombo given that it was more structurally enriched than termitaria and grassland, and that it had more tree species. After the population of elephants in southern and central parts of the park, the next largest is found in the Busanga Flood Plain (Frederick 2009). Elephants spend large amounts of time in the woodlands of the Busanga Flood Plains than in any other vegetation.

The park itself is under very little pressure to conversion into agriculture landscapes than its surround game management areas that have in recent years been under immense pressure from human encroachment (Fig 1). But even if this status quo is maintained in the park, profound shifts in the ecology of the biotic communities are likely, given the continued decline of large wildlife to illegal harvests and the influence of physical factors such as fire whose impacts are expected to increase under the influence of the anticipated changes in climate. The black rhinoceros, that once roamed Kafue National Park in the thousands (Chansa and Matandiko 2011) serves as an example of the drastic loss of large wildlife.

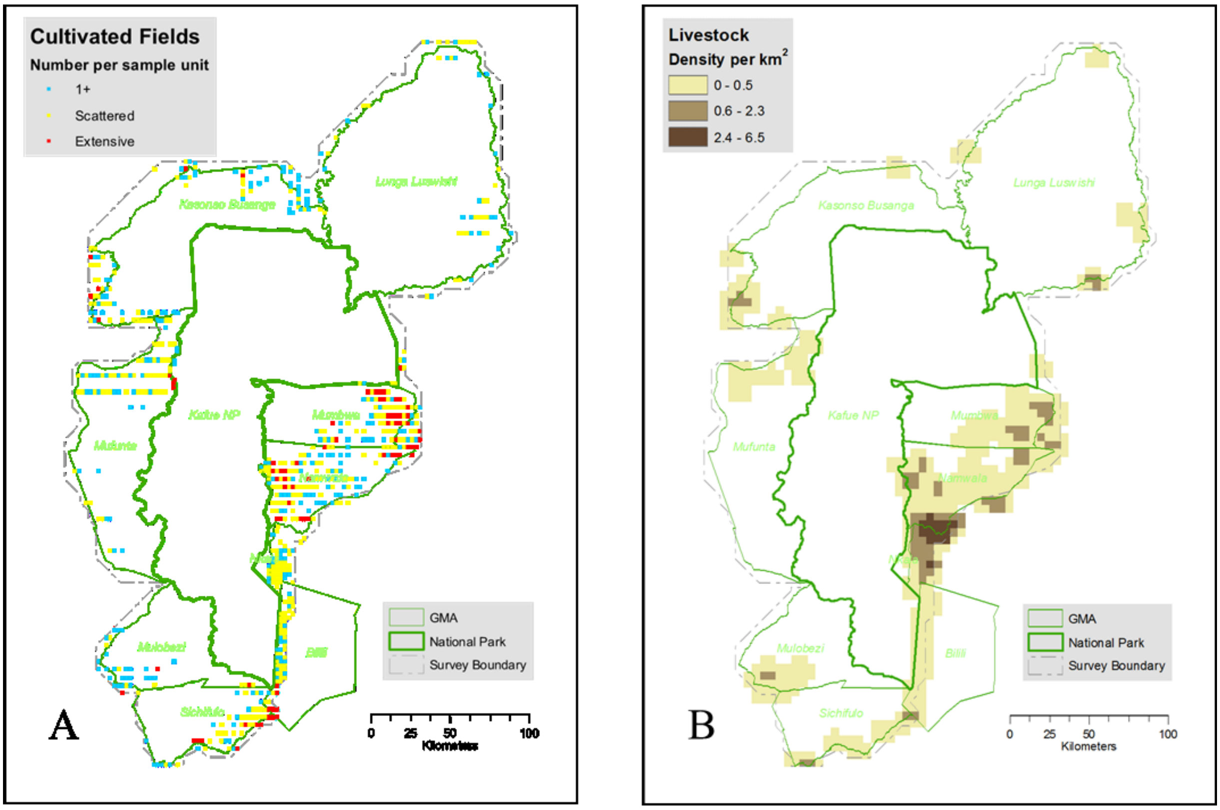

Fig 1. Agriculture activities in and around Kafue National Park. (A) Distribution and intensity of cultivation and (B) Distribution and intensity of livestock (combined cattle, sheep and goats (Source: Frederick 2011).

Whilst most large mammals seem adept to fires (Green *et al.* 2015), small mammals are seemingly affected by its effect to reduce cover (Yarnell *et al.* 2007, 2008, Swanepoel 1981). Their communities respond to such land transformations by favoring certain combinations of species (Young *et al.* 2015) and will also react differently to the different fire frequencies (Rowe-Rowe 1995, Namukonde *et al*. 2017). This supports the predictions in the shift of community composition and structure of small communities in Kafue National Park based on the evidence pointing to the significant differences in primary productivity between frequently burnt areas and areas that aren't (Kuebler 2016). According to Moss (1973) and Chanda (2007) fires occurring in areas of high fire recurrence have the potential to alter the range land into more open areas. Thus, based on the foregoing and considering the lean resources available to manage fires in the park, perhaps emphasis should be placed on important habitats such as termitaria whose perceived role as refugia for species from disturbance and recolonization, is reaffirmed by the overarching structure of the dietary space assumed by its small mammal communities over those in miombo and grassland.

This study supports the approach taken by several authors (e.g. Plavsic 2014, Fox 2011) to describe the response of small mammals to environmental factors and their habitat association using a suite of life history traits. For small mammals these traits include body size, social systems, activity patterns, diet, habitat utilization, locomotion and litter size (Namukonde *et al*. 2017, in press). This approach provides an in depth understanding of the response of species to environmental factors acting upon their communities as defined by their resource use and behavior (Violle *et al.* 2007; Fox 2011; Plavsic 2014). Studies on species interactions and ecosystem functioning are further advanced in other parts of the world (as summarized e.g. by Fox 2011; Gonzalez-Salazer *et al*. 2014; Kelt *et al*. 1999) and community properties may be characterized by functional traits rather than species. For, the traits (body size & diet) that I was able to explain species response to fire, the evidence points to the smaller sized species as being more affected by the current fire regime. These tended to favor areas that are not frequently burnt and entails that their existence is under more threat than the larger ones that have larger home ranges and have less problems to escape fire and recolonize areas after. This is supported by Schoepf *et al.* (2014), who described an individual's home range size as a determinant to its access to resources and its fitness. For diet, species particularly of rodents, tended to broaden their dietary niches in areas of high fire frequencies than under low fire frequencies. This indicated relaxed competition under high fire frequencies because small mammal populations did not reach their carrying capacity of the habitat, or that species numbers reduced under high-versus-low fire frequency regimes.

Evidence of competition amongst rodents as yielded from the analysis of their isotopic signatures of carbon and nitrogen signifies limited resources, an indication of populations reaching carrying capacity. Considering Young *et al.* (2015) correlation of large mammal activity and small mammal abundance, this might signify a low activity of large mammals in this ecosystem corroborating the evidence from studies that have asserted the large mammal population of Kafue National Park as functioning far below its carrying capacity (UNDP 2014, Frederick 2009, 2011; ZAWA 2011). For shrews, the mechanisms supporting their community organizations remains unclear, as all the similar sized and co-occurring species trapped (*Crocidura mariquensis, C. cyanea and Suncus lixus*) did not have a clear separation in food composition, space or time. Further, the only shrew (*Crocidura fuscomurina*) trapped in high and low fire recurrence areas showed no evidence of competition as it had a wider dietary and resource niche under low than under high fire recurrence areas. But since this was the smallest shrew species (body mass 3 g), there does not seem to be a need for niche changes due to competition with other shrew species.

The response of rodents and shrews towards fire as an element of disturbance also supports the idea that rodent communities are under different selection pressures than shrew communities. Repeated bush fires may depress populations below carrying capacity. If so, avoidance of competition by niche separation would be less reinforced in areas of high fire recurrences while niche separation might become important in more stable conditions (low fire recurrence areas). However, since the number of species is lower under high fire frequencies than under low fire frequencies (Namukonde *et al.* 2017), the broader niches under high fire frequencies could also indicate competitive release in species-poor communities. But both interpretations imply competition as an important component in rodent communities of Kafue National Park. This matches the results described in other parts of southern Africa (Codron *et al.* 2015).

Future Directions

This study revealed substantial gaps in the knowledge of the fundamental properties of small mammals. A lot more still needs to be unveiled with regards to their functional characteristics based on behavior and resource use. Specifically, more onsite studies are needed that evaluate the importance of environmental filters, phylogenetic constraints and biological history of their evolution in Kafue National Park. Further, as most of the records of species occurrence in the park are nearly 40 years old, more extensive and repeated surveys should be conducted in order to monitor the influence of anthropogenic and non-anthropogenic factors on their communities. This will need to be urgently fulfilled, given the anticipated changes in climate that will affect the range land regardless of the conservation actions in place.

Conclusion

This project has shown how small mammal communities are composed, structured and respond to fire. It has demonstrated their susceptibility to some of the environmental factors acting upon their communities. Their conservation can no longer continue to be over shadowed by the large and charismatic species as they respond to environmental factors differently. There is now need to integrate their conservation into the management plans of the park, and of immediate concern is the current Fire Management Plan for the park. This needs to be reviewed to consider the response of the smaller sized species that are more affected by the annual repeated burns on the wildlands, for tourism purposes and reduction of late dry season fires. This is a matter of urgency given that the climate predictions for the region suggest warmer and drier conditions that promote more fierce fires.

Further, the approach taken to conserve large tracts of land based on utilization will also need to be reviewed as small mammal community composition and structure is influenced by vegetation formations, rather than the land use assigned by management. As there is evidence of competition structuring small mammal communities, interventions by management that further limit resources shared by the larger and the small mammals alike, may have profound influence on species, as they promote behaviors that may favor only those that are adaptable to disturbance.

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Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe nur unter Verwendung der angeführten Literatur angefertigt habe.

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Ngawo Namukonde

Erklärung zum Promotionsvorhaben Hiermit erkläre ich, dass ich zuvor noch keiner Promotionsprüfung unterzogen wurde, sowie ich mich noch um keine Zulassung an der Universität Hamburg bzw. einer anderen Universität beworben habe. Weiterhin habe ich noch keiner Universität oder ähnlichen Einrichtung eine Dissertation vorgelegt.

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