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Section A: Peer-reviewed papers

Section B: Open articles

Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia

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ABSTRACT

The Skeleton Coast National Park in the northwest of Namibia supports a small population of African lions (*Panthera leo*) that are adapted to the harsh hyper-arid conditions. After a period of prolonged human-lion conflict during the 1980s lions disappeared from the Skeleton Coast for more than a decade. Due to favourable conditions, such as the development of communal conservancies and the growth of tourism in the area, lion populations started to recover along the Skeleton Coast in 2002. However, it took another 15 years for the lions to rediscover the rich marine food resources that their predecessors utilised in the 1980s. In 2017 two prides of lions started hunting cormorants (*Phalacrocorax* spp.) and Cape fur seals (*Arctocephalus pusillus*) on a regular basis. Over a period of 18 months, three young lioness of the Hoanib Floodplain pride killed two greater flamingos (*Phoenicopterus roseus*), 60 cormorants and 18 seals. The marine diet contributed to 79% of their food items and 86% of the biomass they consumed during this period. The marine resources along the intertidal zone of the Skeleton Coast provide an important source of energy and nutrients to lions that they could rely on when their terrestrial food resources are scarce.

Keywords: African lion; Cape fur seal; coastal habitat; cormorant; desert; marine diet; maritime mammal; Namibia; predation

INTRODUCTION

Predatory strategies are shaped by ecological constraints that may vary extensively between regions and habitats (Elliot & Cowen 1978, Sunquist & Sunquist 1989). The behaviour and ecological characteristics of predators are influenced by habitat and prey availability. More specifically, the density, distribution and richness of prey items in relation to habitat variations are key parameters that affect group size, home range size and behaviour of social predators (Macdonald 1983, Van Orsdol et al. 1985). Throughout its range the African lion (*Panthera leo*) is known to prey on a wide variety of species and the most abundant species generally form the mainstay of their diet (Hayward & Kerley 2005).

In the Namib Desert along the west coast of Namibia, lions have survived for centuries (Shortridge 1934, Ripple et al. 2014) and they have become uniquely adapted to the hyper-arid environment (Stander et al. 2018). The Skeleton Coast National Park (SCNP) was proclaimed by the Namibian authorities in 1971 to protect the unique habitat and its endemic animals and plants. Shortly thereafter officials reported evidence of lions living along the coastline that were feeding on seals and other marine-based food items. Bridgeford (1985) confirmed this during a short study and recorded 14 cases of lions feeding on Cape fur seals (*Arctocephalus pusillus*), as well as evidence of predation on white-breasted (*Phalacrocorax carbo*) and Cape cormorants (*P. capensis*). In 1985 an adult male lion was seen feeding on a beached pilot whale (*Globicephala melas*) (S Braine pers. com. 1986). These were the first records of lions living along the coast and feeding on marine organisms.

Terrestrial carnivores and other mammals are well known to utilise marine organisms at intertidal zones around the globe (Carlton & Hodder 2003). Termed ‘maritime mammals’ by Carlton & Hodder (2003), they play an important role in the flow of resources and energy between the land and the ocean. The utilisation of intertidal marine species by maritime mammals contribute to the transfer of energy between trophic levels, which is an important element of food webs (Polis et al. 1997). Four maritime mammals have been reported for the African coastline: chacma baboons (*Papio ursinus*) that feed on crustaceans and shellfish in South Africa (Avery & Siegfried 1980, McLachlan & Brown 1990), black-backed jackals (*Canis mesomelas*) that eat fish (*Mugil cephalus*) and mussels (*Bivalvia* spp.) along the Namibian coastline (Nel & Loutit 1986, Hiscocks & Perrin 1987), and brown hyaenas (*Hyaena brunnea*) have been recorded to eat crabs (*Brachyura* spp.; Stuart & Shaughnessy 1984) and to prey on Cape fur seal pups (Wiesel 2010).

Marine mammals and birds that breed on land are extremely vulnerable to predation by terrestrial predators. As a result, they select small islands, the

Arctic or Antarctic to avoid predation by large carnivores. The Namib coastline is unique in that it is the only place where seals form colonies and breed on a continent inhabited by several large carnivore species, and where the humans have lived at low densities for millennia (Small et al. 2011). It is only in the Arctic where a large terrestrial carnivore, the polar bear (*Ursus maritimus*), preys on seals (Stirling & Archibald 1977).

The land-use practices bordering the SCNP, during the 1980s, were not conducive to wildlife. In an area with tremendously high tourism value, local communities living just outside the narrow SCNP were attempting to survive from uneconomical and unsustainable livestock farming (Carter 1990). Conflict between lions and the farmers was inevitable. Lions raided livestock and farmers retaliated (legally) by shooting or poisoning lions. By 1990 all the known lions that lived in the SCNP had been killed (Stander et al. 2018). Several years later, in 1997, a small remnant group of approximately 20 desert-adapted lions (hereafter referred to as the Desert lion population) was discovered in a mountainous region on the eastern edge of the Namib, and the Desert Lion Conservation research project (DLCP) was launched. Much had changed since the 1980s: several years of good rainfall saw an increase in wildlife numbers; the Namibian tourism industry was growing and providing value to wildlife; local people derived benefits from wildlife and tourism through the communal conservancies system (Naidoo et al. 2016); and the conditions were right for lions to find their way back to the Skeleton Coast and the rich marine food resources.

METHODS

Study Area

The area studied by the DLCP covers 51,500 km^2 of arid habitat that falls in the Etendeka Plateau landscape of the northern Namib Desert, with an annual rainfall of 0-100 mm (Mendelsohn et al. 2002). The area is dissected by a series of ephemeral drainage lines that provide food, water and shelter to most of the large mammal species, including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*) and lion, that live here. The area includes a protected area (the Skeleton Coast National Park), tourism concessions (Palmwag, Etendeka and Hobatere Concessions), and communal conservancies where people live and farm with livestock (Figure 1).

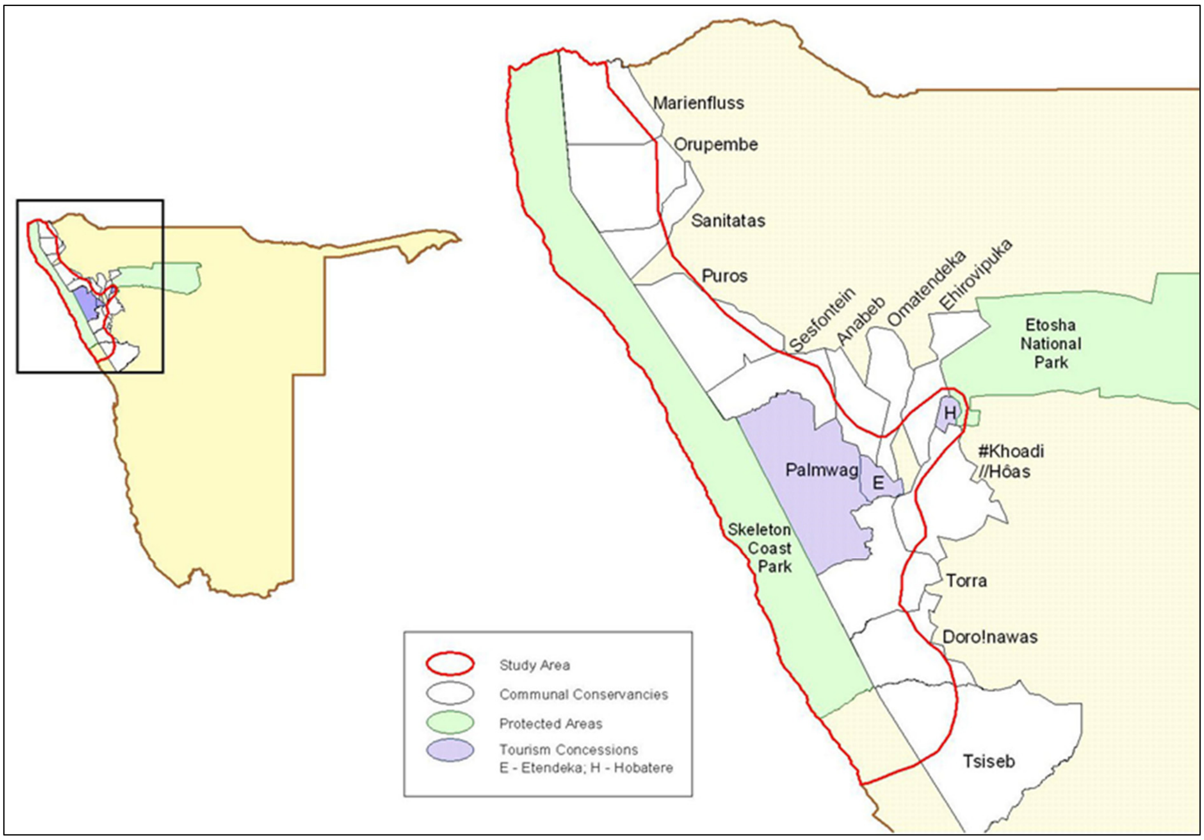

Figure 1: *The study area in the northwest of Namibia that includes the Skeleton Coast National Park, several tourism concessions and communal conservancies.*

Data collection

The study area was covered systematically by tracking spoor and using sound playbacks to locate and observe individual lions. All lions, including small cubs, were photographed, using high-quality equipment, and individually identified using vibrissae spot patterns (Pennycuick & Rudnai 1970). Some adult and sub-adult lions were captured and individually marked by fitting VHF, GPS or satellite radio collars.

Individual lions selected for radio-collaring were immobilised following procedures described by Smuts et al. (1977) and Stander and Morkel (1991), and according to Namibian veterinary requirements. Attempts were made to mark and individually recognise 75% of the population and population estimates were calculated using mark-recapture models. Fitting of GPS and satellite collars and the selection of individuals were based on group structure and individual records collected over several years. Adults that associate regularly with the rest of the pride/group (using a Matrix of Association Index) with large calculated home ranges were favoured.

Radio-collared animals were located by vehicle, with the use of RFID radio loggers or with an aircraft. All visual observations of lions, including hunting and feeding behaviour were done from a specialised vehicle using low-light binoculars, thermal-image night vision goggles and Infrared equipment. Lions were habituated to the observation vehicles and the same vehicle was used for extended periods (5-10 years per vehicle, n=3) to ensure that observations on their behaviour were not influenced by the vehicle. During observations on hunting behaviour, the vehicle remained stationary at a safe distance and care was taken not to disturb the lions or the prey animals that they approached. When aspects of their hunting or feeding behaviour could not be observed visually, the information was obtained through spoor reconstructions following the methods described by Liebenberg (1990), Bothma & Le Riche (1993) and Stander et al. (1997).

Home range analyses were based on the daytime resting spots of lions with at least 24 hours between fixes to ensure independence. Home range size was calculated using the Minimum Convex Polygon (MCP, Harris et al. 1990). Sufficiency of sample size was tested by determining whether or not or not an asymptote of home range estimate was reached. Spatial analysis of home range data and mapping was done using ArcView 3.2 (Johnston 1998).

In addition to monitoring the movements of radio-collared lions to determine the frequency with which they visited the coast, the coastal habitat itself was surveyed every quarter for lion tracks and other signs of lions utilising the habitat. When the Hoanib Floodplain pride began utilising marine food items along the coast in May 2017, a concerted effort was made to record an unbiased sample of the food items killed and consumed. During an 18-month period, between May 2017 and November 2018, the lions were observed for periods of between 24 hours and seven continuous days to record their food intake.

RESULTS AND DISCUSSION

Home ranges and movement patterns

After the demise of the Desert lion population that occupied the coastal habitat and utilised marine food resources during the 1980s, there were no resident lions in the SCNP for more than a decade, between 1990 and 2001. As the population recovered from the decline and numbers increased, their distribution expanded and by mid-2001 several prides began utilising sections of the SCNP (Stander et al. 2018).

The first record of lions returning to the ocean came early in 2002, when three lionesses from the Hoaruseb Pride started exploring the coastline. Gradually more lions ventured into the SCNP and by 2012 a total of five prides (the Ugab, Huab, Uniab, Hoanib Floodplain & Hoaruseb prides) occupied home ranges that included the coastline (Figure 2). All five prides lived in large home ranges that extended ≥100 km inland from the ocean, which they maintained over many years (Table 1). The coastal

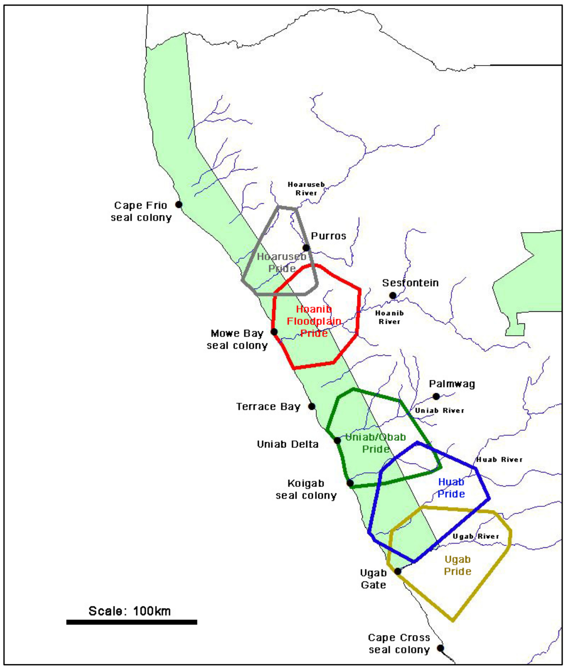

Figure 2: *The locations of four Cape fur seal colonies and the home ranges of five lion prides that utilised the coastal habitat in the Skeleton Coast National Park between 2002 and 2017*

Table 1: *The home range sizes, the proportion of coastal habitat in each home range and the duration of monitoring of five lion prides in northwest Namibia.*

Pride	**Home range size (km^2)^1**	**Coastal habitat (%)^2**	**Duration^3**	**No. of fixes**
Hoaruseb	2,850	1.5	4y 10m	1,761
Hoanib Floodplain	4,410	5.4	9y 5m	3,452
Uniab/Obab	4,730	6.9	8y 7m	3,120
Huab	5,770	1.5	4y 2m	1,531
Ugab	5,870	1.3	4y 10m	1,804
Mean **SD**	**4,726** **1,227**	**3.3** **2.6**	**6y 5m**	**2,334** **883**

[1] Home range size based on the Minimum Convex Polygon method.
[2] Coastal habitat area as a percentage of the pride's home range size.
[3] Duration in years and months of continuous monitoring with GPS or satellite collars.

habitat, however, only formed a small part (mean=3.3%) of their respective home ranges.

With an average size of 4,726 km^2, lions from the desert population in the northwest of Namibia have the largest recorded home ranges for the species (Celesia et al. 2010, Loveridge et al. 2009, Van Orsdol et al. 1985, Schaller 1972). This, however, is to be expected because ranging behaviour of animals is affected by a number of ecological factors (Gittleman & Harvey 1982, East 1984). Amongst social carnivores, home range size is influenced by the distribution and availability of food items (Macdonald 1983) where the scarcity of resources may lead to larger ranges (Mills & Knowlton 1991). This is especially relevant when the distribution of food resources is heterogeneous (Macdonald & Carr 1989). The arid environment of the Northern Namib supports low densities of suitable prey animals for lions that are also highly variable in their distribution. Lions have to be resourceful by hunting a range of different prey species in a wide variety of habitats in their home range, and by expanding their range when food is scarce.

Since the distribution of prey animals in the heterogeneous habitat of the Northern Namib is a function of patchy and unpredictable rainfall (Sharon 1981, Viljoen 1989, Lu et al. 2016), it is to be expected that the movement patterns of lions will not be uniform (Macdonald & Carr 1989). The behaviour of adult lions in the established prides suggested that they maintain a mental map of the food resources in their home ranges, and that they visit these food patches at particular intervals. Two of the prides (Hoanib Floodplain and Uniab/Obab), where the coastal habitat formed >5% of their respective home ranges, visited the coast at irregular intervals.

The Hoanib Floodplain pride visited the coast on eight occasions between August 2014 and November 2015 (Figure 3a & b). On average they spent 7.5 days (range: 4-14 days) along the coast, where they captured mainly gemsbok that are attracted to the fresh-water springs and green grass at the mouth of the Hoanib River. In between these visits the lions moved inland, up to 62 km from the mouth of the Hoanib River, for an average of 55.7 days (range: 12-156 days, n=7).

The Uniab/Obab pride visited the coastal habitat at the mouth of the Uniab River on six occasions between January and November 2015 (Figure 4a & b). They fed on gemsbok and ostrich (Struthio camelus) that are attracted to green grass and several small fresh-water springs at the Uniab Delta. The lions spent an average of 23.3 days (range: 7-60 days) in the coastal habitat at the Uniab Delta. In between these visits they moved inland, up to 38.9 km from the mouth of the Uniab River, for an average of 20 days (range: 5-41 days, n=5).

Predation and consumption of marine food items

The first confirmed evidence of lions utilising marine food items along the Skeleton Coast came in March 2006 when lionesses from the Hoaruseb pride were observed feeding on a Cape fur seal on a beach north of the Hoaruseb River. During the next ten years, lions were observed feeding on adult seals on a total of nine occasions. Similar to the findings by Bridgeford (1985) from the early 1980s, most of the incidents occurred in the vicinity of the Hoanib and Hoaruseb Rivers with two records from the Uniab River and one from the Huab River (Figure 2). At least three seals were killed by lions and since the cause of death of the remaining six seals was not confirmed, they may have been scavenged.

Up until the end of 2016 the killing and/or scavenging of seals by lions in the SCNP was opportunistic and sporadic. There are four Cape fur seal colonies situated within reach of where lions were distributed during that period (Figure 2). Based on the movements of radio-collared lions and spoor surveys along the coast, none of the lions visited the colonies, nor did they appear to be aware of the rich food resources on offer.

Early in 2017, when conditions for lions throughout the Desert population were difficult due to poor rainfall, the Hoanib Floodplain pride and the Uniab/Obab pride started using the rich marine food source along the coast. They were also the two prides with the largest proportion of coastal habitat in their respective home ranges (Table 1) and that visited the coastline most often.

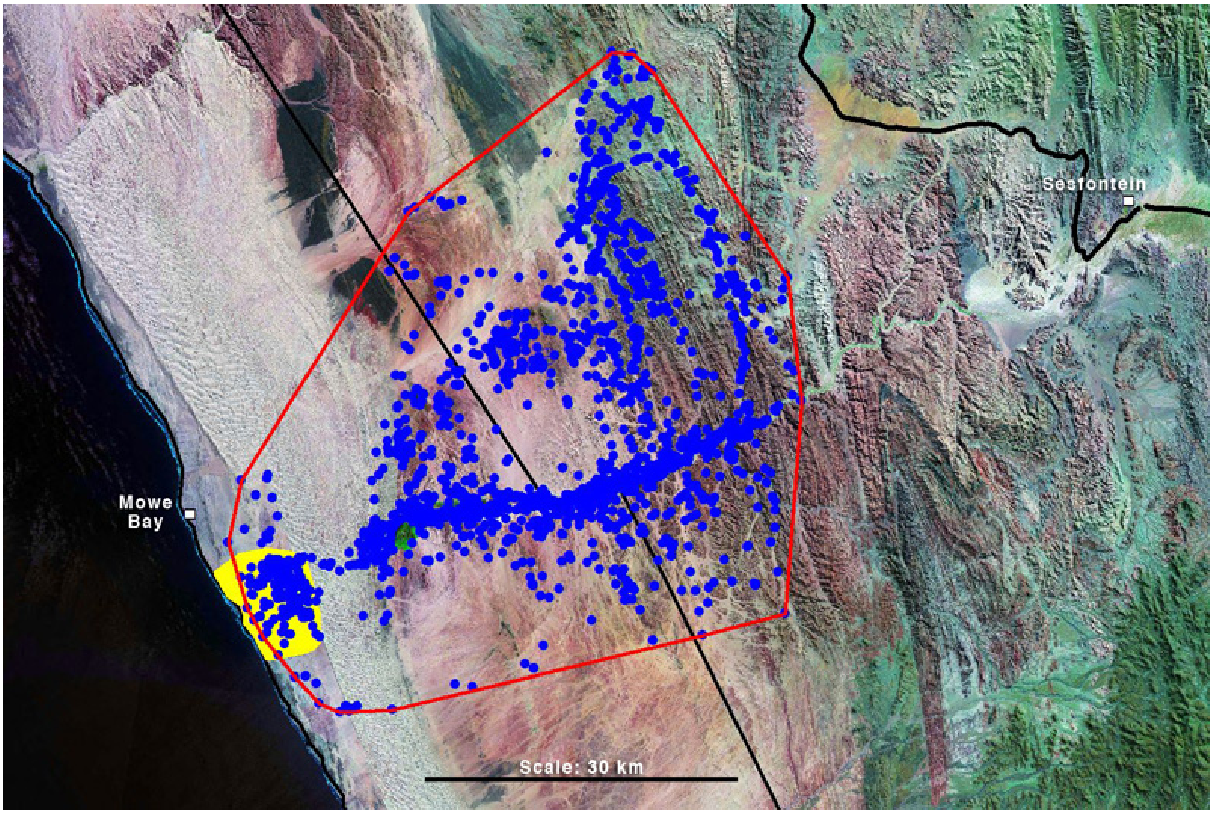

Figure 3a: *The home range area and movements of the Hoanib Floodplain pride in relation to the coastal habitat around the mouth of the Hoanib River (yellow area) between August 2014 and November 2015 (See Figure 3b).*

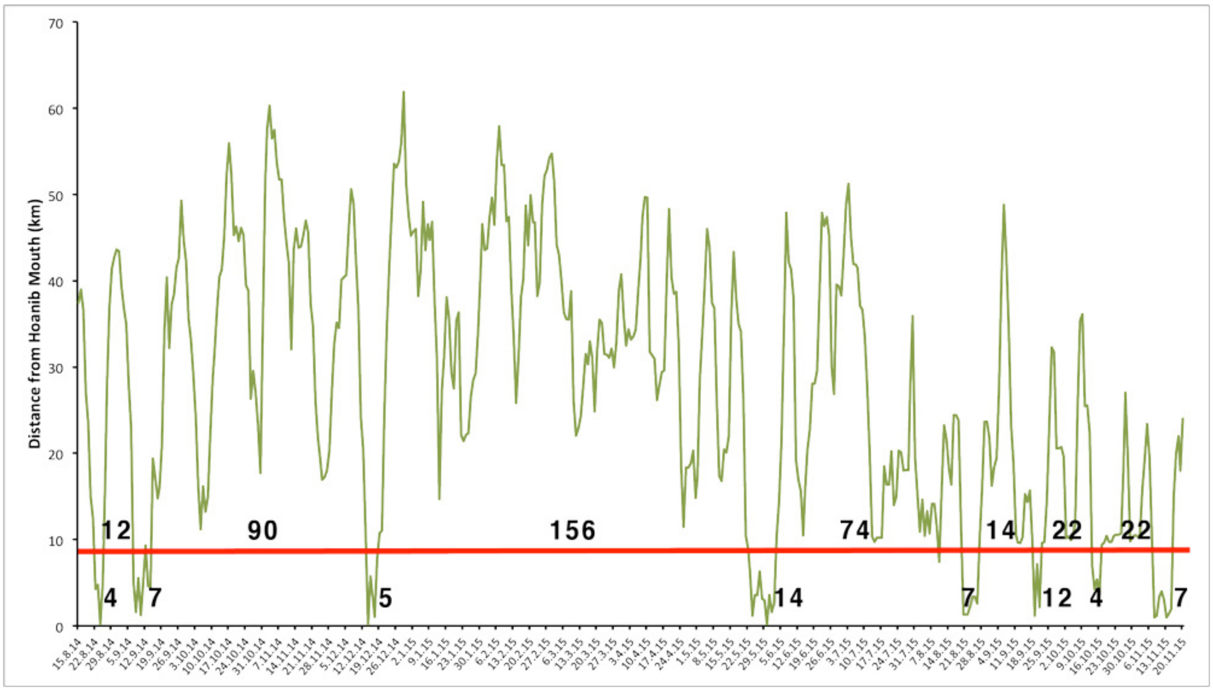

Figure 3b: *The movements of the Hoanib Floodplain pride displayed as sequential distances from the coastal habitat around the mouth of the Hoanib River between August 2014 and November 2015. The yellow area on the map (see Figure 3a) and the area below the red line on the graph denote the coastal habitat at the mouth of the Hoanib River. The numbers of days that the Hoanib Floodplain pride spent at the coast are indicated by the numbers below the red line and the number of days further inland by the numbers above the red line.*

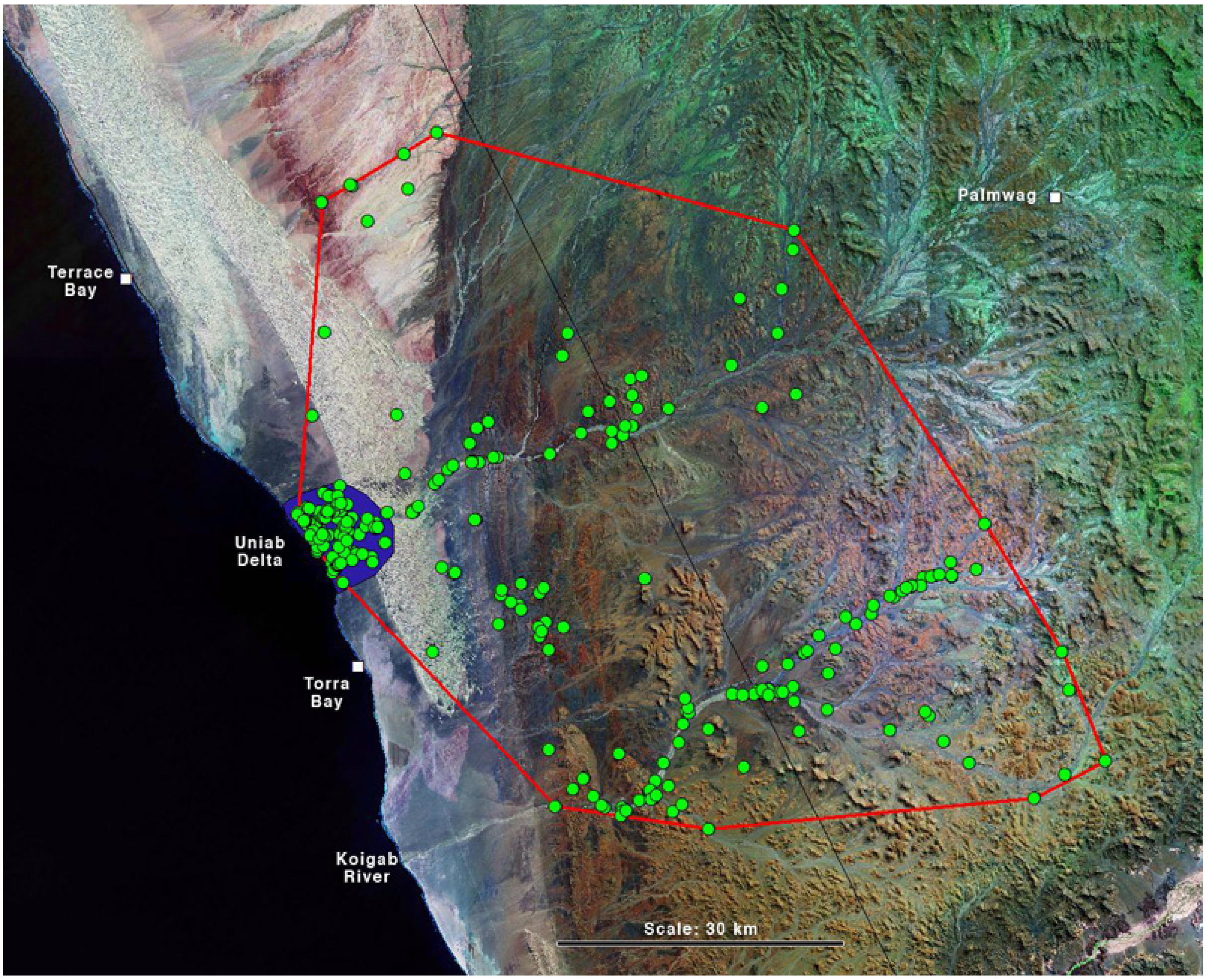

Figure 4a: *The home range area and movements of the Uniab/Obab pride in relation to the coastal habitat at the Uniab Delta (yellow area) between January and November 2015 (See Figure 4b).*

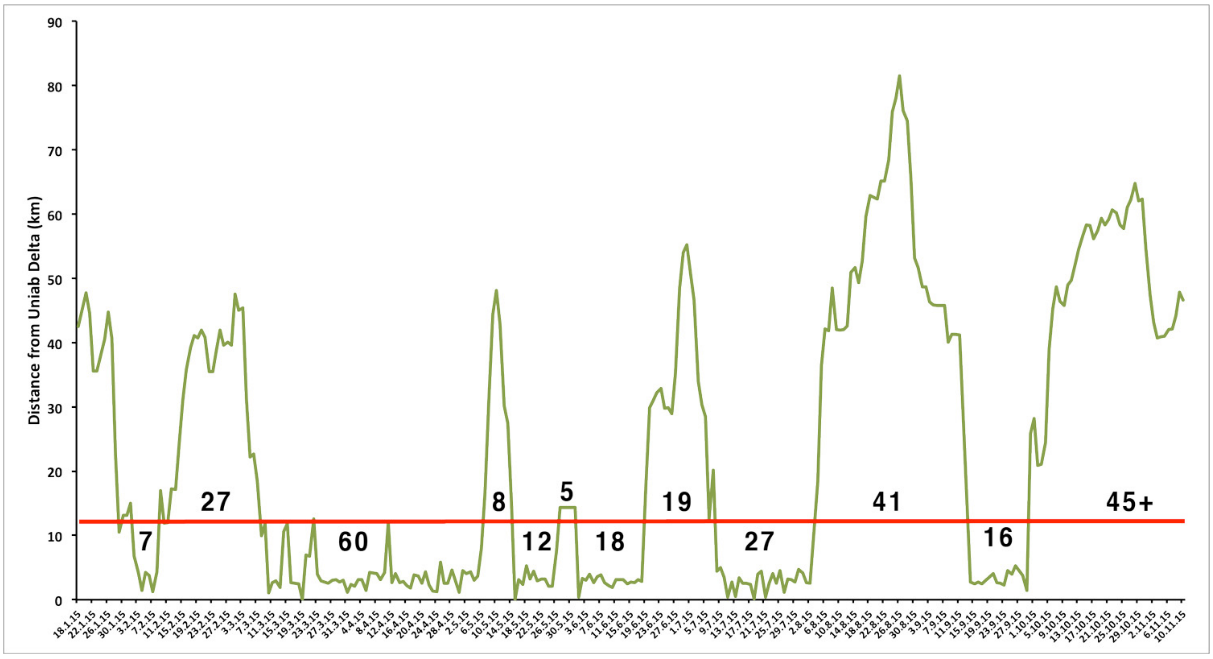

Figure 4b: *The movements of the Uniab/Obab pride displayed as sequential distances from the coastal habitat at the Uniab Delta between January and November 2015. The yellow area on the map (see Figure 4a) and the area below the red line on the graph denote the coastal habitat at the Uniab Delta. The number of days that the Uniab/Obab pride spent at the coast are indicated by the numbers below the red line and the number of days further inland by the numbers above the red line.*

Lions from the Uniab/Obab pride have been visiting the Uniab Delta on a regular basis since 2014. They moved along the coastal zone between Torra Bay and Terrace Bay and fed primarily on gemsbok and ostriches. In April 2017 one lioness that was in poor condition started killing cormorants at Torra Bay. During a two-day period, she was observed catching and consuming six white-breasted cormorants, four Cape cormorants and one adult brown hyaena. The lioness then moved further south along the coast and started to prey on Cape fur seals from the Koigab colony. Over a period of four weeks she killed and consumed a minimum of eight adult seals.

At the mouth of the Hoanib River three young lionesses from the Hoanib Floodplain pride began depending on a marine diet in March 2017. Their mother died of natural causes when the lionesses were barely a year old. Driven by hunger and desperation, the young lionesses found their way over the dunes and swam onto an island at a fresh-water spring near the coast. Here they started killing cormorants that roost on the island at night (Figure 5a). They became skilled in hunting a wider range of wetland birds, including flamingos and red-billed teals (*Anas erythrorhyncha*). The large numbers of resident Cape and white-breasted cormorants provided them with a nutritious and reliable marine diet. The lionesses began following the large flocks of cormorants and hunting them at night on the mud-flats and along the coastline (Figure 5b). This brought them into contact with Cape fur seals from the Möwe Bay colony that rest on the beaches. At first the lions scavenged seal carcasses that they found along the beaches (n=5), and then they expropriated seal carcasses from brown hyaenas (n=2). Early in 2018 the lionesses started killing seals themselves. Initially they took only juveniles of less than a year old, but as they became more experienced they selected larger seals of >50kg, including a few adult females (Figure 5c & d).

During visual observations on 62 days and supplemented by spoor reconstructions in the coastal habitat between May 2017 and November 2018, the lionesses killed and consumed a total 89 animals of eight different species (Table 2). The majority of their food items were cormorants (n=60) and seals (n=13). The 89 food items provided an estimated 701 kg of edible biomass that the lionesses consumed. Marine species (seals, cormorants and flamingos combined) contributed 79% of the food items and 86% of the biomass that the lionesses consumed during the observation periods. On numerous occasions the lionesses were observed exploring the intertidal zone and investigating items in shallow water (Figure 5c). But it was not possible to determine whether or not they utilised any other marine organisms.

Figure 5: *Lionesses foraging along the Namibian coastline: (a) catching cormorants on a small island, (b) hunting cormorants at the Hoanib Lagoon, (c) foraging along the intertidal zone, and (d) feeding on a Cape fur seal.*

Table 2: *The number of recorded prey species killed and the estimated biomass consumed by the Hoanib Floodplain pride in the Skeleton Coast National Park, between May 2017 and November 2018.*

Species	**Number**	**Biomass (kg)**[1]
Gemsbok *Oryx gazella*	1	65
Porcupine *Hystrix africaeaustralis*	2	19
Black-backed jackal *Canis mesomelas*	4	12
Cape fur seal *Arctocephalus pusillus*:		
Juvenile (<1 year)	13	273
Sub-adult & adult (>50 kg)	5	240
Cape cormorant *Phalacrocorax capensis*	47	61
White-breasted cormorant *Phalacrocorax carbo*	13	26
Red-billed teal *Anas erythrorhyncha*	2	1
Greater flamingo *Phoenicopterus roseus*	2	4
Total	**89**	**701**

[1] Edible biomass was calculated by subtracting the percentage inedible biomass from the mass of the prey animal or the known mass of an adult female of the species.

The use of marine food resources by lions in the SCNP is an adaptation to the constraints imposed by their environment. Apart from the information presented by Bridgeford (1985) for lions from the same area during the 1980s, there is no evidence of lions utilising marine species anywhere else throughout their range (Carlton & Hodder 2003, Hayward & Kerley 2005). There are also currently no free-ranging lions that utilise or are resident in coastal habitats (Riggio et al. 2013, Ripple et al 2014). Specialising on unusual prey species, however, is not uncommon and in some areas lion prey on porcupines (Eloff 1984), rhinoceroses (Brain et al. 1999, Matipano 2004) and elephants (Ruggiero 1991).

The role of maritime mammal predation on marine intertidal communities in the transfer of energy between trophic levels is generally poorly understood, but recent studies have demonstrated the importance of landward flow of energy between the sea and the land (Polis et al. 1997). Furthermore, marine resources are an important source of energy and nutrients to many maritime mammal populations (Stapp et al. 1999). When lions identified the value and availability of marine foods along the Namibian coastline in May 2017, they began utilising the resource. The Hoanib Floodplain pride, in particular, currently derive a substantial proportion of their food items and biomass from marine resources. In other arid areas and ecosystems with high seasonal fluctuations in food availability many coastal carnivore populations rely on a marine diet when their terrestrial food items are scarce (Suraci et al. 2006), such as coyotes (*Canis latrans*) in the arid areas of Baja California that feed on a range of marine species, including mammals, sea turtles and birds (Rose & Polis 1998), Arctic foxes (*Alopex lagopus*) at the Bering sea (Fay & Stephenson 1989) and many examples of bears (*Ursus* spp.) in British Columbia, Canada & Alaska (Carlton & Hodder 2003).

The marine resources along the Skeleton Coast are potentially a valuable and reliable source of nutrients and energy to the Desert lion population. When the Skeleton Coast lions of the 1980s were killed, their knowledge of the marine food resources along the coast was lost as well. Once conditions changed and became favourable again in 1997, the population recovered within four years and repopulated several of their former ranges in the SCNP. For the next 15 years, lions moved to the ocean occasionally and inspected the coastline, but they did not forage along the intertidal zones, as their predecessors of the 1980s did. The knowledge of the rich marine food resource was only regained in 2017. The importance of marine resources to the survival of many terrestrial mammals, including the Skeleton Coast lions, may have been overlooked (Stapp et al. 1999). In the arid environment of the Northern Namib, with its variable rainfall patterns and unpredictable distribution of food items, the rich marine resources along its coastline can provide an important and reliable source of food to the lion population.

CONCLUSION

After an absence of more than 35 years, lions have returned to the coastal habitat of the SCNP to prey on marine organisms. As a species, lions are now on the list of maritime mammals, as the largest of the coastal carnivores, that prey on marine organisms.

Conflict between livestock farmers and lions during the 1980s resulted in a considerable decline in the population and lions were absent from the SCNP for more than ten years. Once conditions had improved by 1997, the Desert lion population recovered and repopulated the SCNP within four years. Five distinct prides utilised sections of the coastline. Due to the constraints imposed by the hyper-arid environment they occupied large home ranges – the largest yet recorded for the species. The coastal habitat formed a small proportion of their large home ranges, but data from two prides revealed that the lions visited the coast regularly.

Following the recovery of the population and the return of lions to the coast, the incidents of predation or scavenging on Cape fur seals appeared opportunistic and occurred sporadically for more than a decade. In 2017, lions from two prides began to forage along the coastal habitat and the intertidal zone, where they mainly preyed on cormorants and Cape fur seals. The lions had found a rich and reliable marine resource that can provide then with an important source of energy. Preliminary observations of lions investigating and foraging along the intertidal zones suggest that they may learn to prey on other marine organisms, like shellfish, crabs or sea turtles. The intertidal zones along the Skeleton Coast provide a rich source of energy that the Desert lion population could rely on when their traditional terrestrial food resources are low.

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REFERENCES

Avery G, Siegfried WR (1980) Food gatherers along South Africa's sandy shore. *Oceans* 13:37.

Bothma JD, Le Riche EAN (1993) Disturbance bias when tracking Kalahari leopards *Panthera pardus* by spoor. *Koedoe - African Protected Area Conservation and Science* 36(2).

Bridgeford PA (1985) Unusual diet of the lion *Panthera leo* in the Skeleton Coast Park. *Madoqua* 14: 187-188.

Carlton JT, Hodder J (2003) Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256: 271-286.

Carter LA (1990) *The wildlife survey of Skeleton Coast Park, Damaraland, Kaokoland, north-west Namibia May/June 1990*. Report to the Commission of the European Communities, Windhoek, Namibia.

Celesia GG, Townsend Peterson A, Kerbis Peterhans JC & Gnoske TP (2010) Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology* 48: 58-71.

East R (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* 22: 245-270.

Elliot JP, Cowan IM (1978) Territoriality, density and prey of the lion in Ngorongoro Crater, Tanzania. *Canadian Journal of Zoology* 56: 1726-1734.

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behaviour Ecology and Sociobiology* 10: 57-63.

Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20: 97-123.

Hayward MW, Kerley GIH (2005) Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, London 267: 309-322.

Hiscocks K, Perrin MR (1987) Feeding observations and diet of black-backed jackals in an arid coastal environment. *South African Journal of Wildlife Research* 17: 55-58.

Johnston CA (1998) *Geographic Information Systems in Ecology*. Blackwell Science, Oxford, UK.

Liebenberg L (1990) *The Art of Tracking: The Origin of Science*. David Philip. Cape Town, South Africa.

Loveridge AJ, Valeix M, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32: 953-962.

Lu X, Wang L, Pan M, Kaseke KF, Li B (2016) A multi-scale analysis of Namibian rainfall over the recent decade – comparing TMPA satellite estimates and ground observations. *Journal of Hydrology: Regional Studies 8*: 59-68.

Macdonald DW (1983) The ecology of carnivore social behaviour. *Nature* 301: 379-384

Macdonald DW, Carr GM (1989) Food security and the rewards of tolerance. Comparative Socioecology: *The Behavioural Ecology of Humans and Animals* 8: 75-99.

McLachlan A, Brown AC (2006) *The Ecology of Sandy Shores*. Elsevier Inc. Cape Town, South Africa.

Mendlesohn J, Jarvis A, Roberts C, Robertson T (2002) *Atlas of Namibia: A portrait of the Land and its People*. David Philip Publishers, Cape Town, South Africa.

Mills LS, Knowlton FF (1991) Coyote space use in relation to prey abundance. *Canadian Journal of Zoology* 69: 1516-1521.

Naidoo R, Weaver LC, Diggle RW, Matango G, Stuart-Hill G, Thouless C (2016) Complementary benefits of tourism and hunting to communal conservancies in Namibia. *Conservation Biology* 30: 628-638.

Nel JA, Loutit R (1986) The diet of black-backed jackals Canis mesomelas, on the Namib desert coast. *Cimbabasia* 8: 91-96.

Pennycuik CJ, Rudnai J (1970) A method of identifying individual lions, *Panthera leo*, with an analysis of the reliability of identification. *Journal of Zoology, London* 160: 497-508.

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289-316.

Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, Funston P, Groom R, Henschel P, de Longh H et al. (2013) The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation* 22: 17-35.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.

Schaller GB (1972) The Serengeti Lion. University of Chicago Press, Chicago.

Sharon D (1981) The distribution in space of local rainfall in the Namib Desert. *Journal of Climatology* 1: 69-75.

Shortridge GC (1934) *The Mammals of South West Africa*. William Heinemann Ltd., London, UK.

Small C, Nicholls RJ, Summer F, Smallt C (2011) A global analysis of human settlement in coastal zones. *Journal of Coastal Research* 19: 584-599.

Smuts GL, Whyte IJ, Dearlove TW (1977) A mass capture technique for lions. *East African Wildlife Journal* 15: 81-87.

Stander PE, Ghau //, Tsisaba D, #oma //, |ui | (1997) Tracking and the interpretation of spoor: a scientifically sound method in ecology. *Journal of Zoology, London* 242: 329-341.

Stander P, Morkel PV (1991) Field immobilization of lions using disassociative anaesthetics in combination with sedatives. *African Journal of Ecology* 29: 138-148.

Stander P, Steenkamp W, Steenkamp L (2018) *Vanishing Kings – Lions of the Namib Desert*. HPH Publishing, Johannesburg, South Africa.

Stapp P, Polis GA, Sánchez Piñero F (1999) Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature* 401: 467-469.

Stirling I, Archibald WR (1977) Aspects of predation of seals by polar bears. *Journal of the Fisheries Research Board of Canada* 34: 1126-1129.

Sunquist ME, Sunquist FC (1989) Ecological constraints on predation by large felids. In: Gittleman JL (ed.) *Carnivore Behavior, Ecology and Evolution* 283-301. Cornell University Press, Ithaca, NY.

Suraci JP, Clinchy M, Zanette LY (2017) Do large carnivores and mesocarnivores have redundant impacts on intertidal prey? *PLoS ONE* 12(1).

Van Orsdol KG, Hanby JP, Bygott JD (1985) Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology, London* 206: 97-112.

Viljoen PJ (1989) Spatial distribution and movements of elephants (Loxodonta africana) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology, London* 219: 1-19.

Wiesel I (2010) Killing of Cape fur seal (*Arctocephalus pusillus pusillus*) pups by brown hyenas (*Parahyaena brunnea*) at mainland breeding colonies along the coastal Namib Desert. *Acta Ethologica* 13: 93-100.

Euphorbia otavimontana (Euphorbiaceae), a new species from Namibia

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ABSTRACT

Euphorbia otavimontana Swanepoel, here described as a new species, is a robust, spiny, succulent shrub endemic to the Otavi Mountains and surrounding areas in northern Namibia. It is probably most closely related to *E. ingenticapsa* from western Angola. Diagnostic characters for the new species include the variably shaped stem segments with greyish white or grey margins, the obconic involucre with the glands spreading in the central initial cyathium and erect or suberect in lateral cyathia, the papillate bifid styles and the obtusely trigonous or 3-lobed capsule which lacks turgid sinuses when developing. A comparative table with diagnostic morphological features to distinguish between *E. otavimontana* and *E. ingenticapsa* is provided. Based on IUCN Red List categories and criteria, a conservation assessment of “Endangered” is recommended for the new species.

Keywords: Euphorbieae, *Euphorbia otavimontana*, Karstveld, limestone, new species, Namibia, Otavi Group, succulents, taxonomy

INTRODUCTION

Hitherto seven large, spiny, succulent shrub or tree species of *Euphorbia* Linnaeus (1753: 450) with ± candelabriform habit have been recognised from Namibia (Germishuizen & Meyer 2003, Klaassen & Kwembeya 2013). In this contribution, an eighth candelabriform species of *Euphorbia* is described for Namibia.

In 2008 during a botanical excursion to the Otavi Mountains and surrounding areas in the Karstveld (region dominated by limestone) of central northern Namibia, the author encountered an unusual large, spiny, succulent, shrub *Euphorbia*, with a candelabriform habit belonging to subg. *Euphorbia* sect. *Euphorbia* (Bruyns et al. 2006). Initially it was thought to represent *E. virosa* Willdenow (1799: 882), but careful examination showed that it differs from this species in several characters and is in fact more closely related to *E. ingenticapsa* Leach (1971: 356) from western Angola. Plants were found at four localities and are here proposed as representing a distinct new species. A study of the *Euphorbia* holdings in the National Herbarium of Namibia (WIND) revealed one other collection of the taxon, filed under the name *E. venenata* Marloth (1930: 337, 339), a synonym of *E. avasmontana* Dinter (1928: 96) (Bruyns 2012).

Populations of the new species were studied in the field and morphological states described in the present contribution are based on live plants, fresh flowering material and mature fruit. For *E. ingenticapsa* and the other species mentioned in the text, diagnostic features were obtained from field observations and/or the original descriptions.

TAXONOMIC TREATMENT

Euphorbia otavimontana Swanepoel, *sp. nov.* (Figures 1-9)

Euphorbia otavimontana resembles *E. ingenticapsa*, but is easily distinguished from this species by, amongst others, the stem segments being more variable in shape, namely elliptic, narrowly elliptic, ovate, trullate, lanceolate, spathulate or suborbicular, rarely oblong (*vs.* more or less trullate, elliptic or suborbicular), with margins greyish white or grey (*vs.* pale brown), not hump-like at base of spines (*vs.* hump-like at base of spines); 1-5 cymes produced per flowering eye (*vs.* 1-3); involucre obconic (*vs.* bowl-shaped); glands spreading in initial cyathium, erect or suberect in lateral cyathia (*vs.* spreading in all cyathia); male flowers 16-48 per involucre (*vs.* ± 70), pedicels shorter, 1.8-3.6 mm (*vs.* ± 5 mm), filaments longer, 1.2-2.0 mm (*vs.* ± 1 mm); female flowers with ovary ovoid or trigonous (*vs.* subglobose), styles shorter, 2.6 mm (*vs.* ± 5 mm), stigmas papillate, bifid (*vs.* capitate, rugulose, emarginate); capsule ± obtusely trigonous or 3-lobed, smaller, 9-13 × 6-9 mm, developing sinuses not turgid (*vs.* 3-lobed, larger, 26-28 × 11-13 mm, developing sinuses turgid).

Figure 1: Euphorbia otavimontana. *Terminal branch segment with flowering eyes.*

Figure 2: Euphorbia otavimontana. *Terminal branch segment with fully developed cyathia.*

Figure 3: Euphorbia otavimontana. *Almost mature fruit.*

Type:

NAMIBIA. Otjozondjupa Region: Otavi Mountains, Farm Auros 595, hillside opposite farmhouse, 1,880 m, 1917DA, 1 July 2008, *Swanepoel* 349 (holotype WIND!; isotype South African National Biodiversity Institute, PRE!).

Description:

Succulent, candelabriform, ± flat-topped, spiny, small to large shrub with height and diam. up to 2.5 m, appearing acaulous. *Central stem* reduced, branching from base and up to 0.6 m above ground. *Branches* numerous, arcuate-ascending, rarely decumbent, densely whorled on central stem, persistent, constricted into segments, 4-7(8)-winged, up to 2.8 m long, occasionally rebranched at or towards apex, green or glaucous-green, sometimes with yellow-green bands radiating more or less to flowering eyes, often grey towards base; segments variable in shape, elliptic, narrowly elliptic, ovate, trullate, lanceolate, spathulate, or subcircular, rarely oblong, 20-150 mm long, 30-130 mm diam. over broadest part, 20-70 mm diam. over narrowest part, rarely twisted; wing-like angles usually much compressed, deeply grooved in between with continuous, ± even, sinuate, dentate, crenate or irregular, rarely undulate horny margin, often slightly decurrent; margin initially green or maroon becoming greyish white or grey, 3.5-10.0 mm wide, often widened at flowering eyes, armed with spines at apex of crenations. *Spines* paired, stout, ± straight, alternating with flowering eyes, 1-16 mm long, longest on broadest part of wings, spaced at 3-25 mm intervals, diverging at 20-160 degrees or parallel, ± perpendicular to margin or slightly pointing upwards or downwards. *Secondary branches* produced from wing margin at broadest part of segment or just below, single or whorled. *Leaves* sessile, ovate, ovate-triangular, ovate-pentagonal, triangular or pentagonal, in t/s concave or flat adaxially, convex abaxially, apex obtuse or acute, often apiculate, base cuneate or parallel-sided, thick, fleshy; flanked by pair of fleshy, soon withering, obtusely angular or conical prickles with drawn-out apices, marcescent, 15-50% as long as lamina; caducous, leaving often an inconspicuous, crescent-shaped or semi-circular leaf scar shortly above spine pairs, 1.5-3.9 × 1.6-4.1 mm long, margin entire, irregularly denticulate or crenate, dentate or irregular. *Inflorescences* cymose, glabrous, (1-)3(-5) horizontally arranged cymes arising above lower of two spine pairs, solitary cymes usually on smaller plants, on new growth a pair of thin, triangular or subquadrate, leaf-like caducous prickles at base of flowering eye, up to 0.9 × 0.8 mm long, margins unequally laciniate or irregularly dentate; flowering eyes at 30-60% the distance between adjacent pairs. *Cymes* pedunculate, glabrous, each with 3 vertically arranged cyathia, central initial cyathium male marcescent, sessile, laterally compressed by bisexual lateral cyathia, laterals borne on cyme branches. *Peduncle* bibracteate, stout, laterally compressed when more than one cyme at flowering eye, tapering to base, sometimes obscurely grooved vertically on sides between branches, light green, 1.5-3.4 mm long, 1.2-2.0 mm diam. at base, 4.5-5.5 mm at apex; bracts ovate or triangular-ovate, clasping peduncle, slightly keeled, light green, light yellow or orange-red, soon withering, thin and papery towards margin, margin entire, denticulate towards apex, 2.2-3.5 × 3.1-4.3 mm. *Cyme branches* bibracteate, stout, tapering to base, vertically ridged opposite adjacent cymes, light green, 2.1-4.3 × 4.3-5.5 mm diam.; bracts similar to those on peduncle, clasping involucre, leaving conspicuous broad v-shaped scar on cyme branch. *Involucre* obconic, glabrous, light green, in initial

Figure 4: Euphorbia otavimontana*. Plant in natural habitat, farm Auros, E of Otavi (type locality)*

Figure 5: Euphorbia otavimontana*. Plant in natural habitat, farm Nimitz, NE of Outjo*

Figure 6: Euphorbia otavimontana*. Plant in natural habitat, Lake Otjikoto, NW of Tsumeb*

Figure 7: Euphorbia otavimontana*. Plants in natural habitat, Lake Otjikoto, NW of Tsumeb*

Figure 8: Euphorbia otavimontana*. Plants in natural habitat, Lake Otjikoto, NW of Tsumeb*

male cyathium usually laterally compressed by laterals, 4.2-4.5 mm long, 5.2-7.2 mm diam. including glands, in lateral cyathia ± 3.6 mm long, ± 7.1 mm diam. including glands, laterally compressed when developing; *glands* (4)5(6), transversely oblong, elliptic-oblong or reniform, spreading in initial male cyathium, erect or suberect in lateral cyathia, thick, coriaceous, contiguous, rarely separate, obscurely peltate, green becoming yellow, smooth, margin entire; convex to flat adaxially and in t/s, in male cyathium 3.9-4.7 × 1.1-2.5 mm, *lobes* (4)5(6), erect, glabrous, transversely rectangular, subquadrate or flabellate, basally prominently longitudinally ridged abaxially, apex irregularly fimbriate, 1.1-1.5 × 1.1-2.2 mm. *Male flowers* 16-48, well exserted from involucre, subtended by filiform bracteoles, arranged opposite lobes in (4)5(6) bracteate fascicles of 4-8 flowers each, glabrous; *fascicular bracts* broad, unequally deeply laciniate, irregularly fimbriate, 3.0-3.8 mm long; *bracteoles* filiform or filiform-laciniate, 0.9-2.9 mm long; *pedicels* filiform, pale green, apices exerted beyond glands, when fully developed 1.8-3.6 mm long, 0.2-0.4 mm diam.; *filaments* terete, pale green, 1.2-2.0 mm long; *anther thecae* ellipsoid or subglobose, flattened, pale yellow, 0.4-0.7 mm diam., pollen yellow. *Female flowers* erect, glabrous; *ovary* ovoid, trigonous, three-locular, green, ± 1.6-1.8 mm high, 1.3-1.5 mm between corners, included in involucre; *perianth* 3-lobed or pentagonal, fleshy, margin irregularly dentate, ± 2mm diam.; female flower rudimentary in male cyathium; *styles* 3, horizontally spreading, recurved at apex, ± equal to apex of pedicels, shallowly grooved down inner face, ± 2.6 mm long, united into a column for third to half their length; *stigmas* bifid, papillate. *Capsule* pale green to reddish green when fully developed, glabrous, 3-locular, ± obtusely trigonous or 3-lobed, usually prominently obtusely ribbed in sinuses, 9-13 mm between corners, broadest towards base, 6-9 mm high, apex truncate, base truncate, exserted from involucre on a straight, stout, pedicel, ± 3 mm long, 4–5 mm diam; *perianth* ± triangular or pentagonal, margin irregularly dentate, 7-8 mm diam.; *seed* subglobose, greater diam. 2.8-3.4 mm, lesser diam, 2.4-3.0 mm, pale brown with creamy blotches or *vice versa*, sometimes with dark brown reticulate markings in addition, suture blackish brown, hilum biconvex or ligulate.

Phenology:

Cyathia were recorded from June to September.

Distribution and habitat:

Endemic to Namibia. At present *Euphorbia otavimontana* is only known from the type locality and three other sites in the Otavi Mountains and surroundings: farm Nimitz NE of Outjo, the mining grounds on the outskirts of Tsumeb and at Lake Otjikoto NW of Tsumeb. The new species is found ± 340-470 km from the coast at elevations of 1,350-1,920 m. Annual rainfall of 450-600 mm is received in summer (Mendelsohn et al. 2002). Plants are locally uncommon and grow in isolated colonies in savannah on mountain slopes or level ground on stony-sandy soil or limestone outcrops of the Otavi Group (Mendelsohn et al. 2002). (Figure 9).

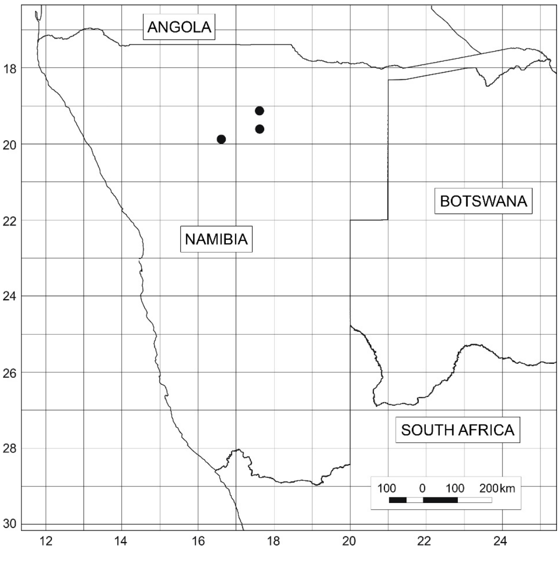

Figure 9: *Known distribution (black dots) of* Euphorbia otavimontana.

Conservation status:

Euphorbia otavimontana is vulnerable, because apart from the population at Lake Otjikoto, plants do not occur in protected areas but on commercial farm land. Potentially the greatest threat to the species is the illegal collecting of plants for the succulent plant trade and for horticultural purposes. It is suspected that due to confusion with the widespread *E. avasmontana*, collecting permits for horticultural purposes were issued in the past. Due to the small known population of less than 250 mature individual plants, an IUCN Red List category of Endangered (EN) is proposed (IUCN 2012; Red List criterion D).

Etymology:

The subspecific epithet refers to the Otavi Mountains in central northern Namibia, to which the new species is endemic.

Additional specimens examined (paratypes):

NAMIBIA. Oshikoto Region: Lake Otjikoto, 12 miles NW of Tsumeb, 1,230 m, 1917BA, *De Winter 3678A* (PRE!, WIND!).
Kunene Region: Farm Nimitz 353, 50 km NE of Outjo, in woodland 500 m north of homestead, 1,354 m, 1916DC, 11 November 2015, *Swanepoel 350* (WIND!).

Notes:

The new species differs from *E. ingenticapsa* in the morphology of the branches, inflorescences, flowers and fruit. Some of the more prominent morphological features to differentiate *E. otavimontana* from *E. ingenticapsa* are compared in Table 1.

Euphorbia otavimontana can be confused with several of the other large spiny species of *Euphorbia* occurring in Namibia, but differs from them in a combination of characters. In *E. avasmontana* the ovary and capsules are far exserted on curved pedicels, *E. otjingandu* Swanepoel (2009: 497) has a short trunk (up to 1 m) terminating in a central stem and in *E. virosa* the flowering eyes produce solitary cymes, the involucres frequently have more than the usual five glands and lobes (up to 10) and the ovary is 3-6-merous.

Euphorbia otavimontana can also be confused with some of the larger members of *Euphorbia* in Angola. It differs from *E. dispersa* Leach (1974: 48) in the peduncles and cyme branches which are always smooth, peduncles and cyme branches which are ± of equal length and by the teeth of the perianth that are

***Table 1**: Prominent morphological differences between* Euphorbia otavimontana *and* E. ingenticapsa.

Character	***E. otavimontana***	***E. ingenticapsa***
Branches		
segments (shape)	Elliptic, narrowly elliptic, ovate, trullate, lanceolate, spathulate or subcircular, rarely oblong	More or less trullate, elliptic or subcircular
margins	Sinuate, dentate, crenate or irregular, rarely wavy, sometimes slightly decurrent, often widened at flowering eyes; not hump-like at base of spines; initially green or maroon becoming greyish white or grey	Sinuate-dentate, often wavy, widened, thickened and hump-like at base of spines; pale brown
Inflorescences		
no. of cymes	1-3(-5) per flowering eye	(1-)3 per flowering eye
Peduncle		
diam. at base	1.2-2.0 mm	± 4 mm
diam. at apex	4.5-5.5 mm	6-7 mm
length	1.5-3.4 mm	5-10 mm
bracts (length)	2.2-3.5 mm	± 8 mm
Involucre		
shape	Obconic	Bowl-shaped
lobes (number of)	4-6	5-7
lobes (length)	1.1-1.5 mm	± 2.5 mm
Glands		
number of	(4)5(6)	5-7
shape	Transversely oblong, elliptic-oblong or reniform	Transversely elliptic
arrangement	Spreading in central initial cyathium, erect or suberect in lateral cyathia	Spreading
texture	Smooth	Rugulose
Male flowers		
number of flowers	16-48 per involucre	± 70 per involucre
pedicels (length)	1.8-3.6 mm	± 5 mm
filaments (length)	1.2-2.0 mm	± 1 mm
fascicular bracts (shape)	Unequally deeply laciniate, irregularly fimbriate	Filiform-fimbriate, laciniate
bracteoles (shape and size)	Filiform or filiform-laciniate; 0.9-2.9 mm long	Filiform-fimbriate; ± 4 mm long
Female flowers		
ovary	Ovoid, trigonous	Subglobose, when developing having an appearance of being 6-lobed when viewed from above
styles (length)	± 2.6 mm	± 5 mm long
stigmas (shape)	Papillate, bifid	Capitate, rugulose, emarginate
perianth	3-lobed or pentagonal	3-lobed
Capsule		
shape and size	± Obtusely trigonous or 3-lobed, usually prominently obtusely ribbed in sinuses, sinuses not turgid when developing; 9-13 × 6-9 mm	3-lobed, almost triangular when seen from above, when developing sinuses turgid, capsule appearing 6-lobed; 26-28 × 11-13 mm
perianth (shape)	3-lobed or pentagonal	3-lobed
pedicel (length)	± 3 mm	5-6 mm
Seed	2.8-3.4 mm (greater diam.), 2.4-3.0 (lesser diam.)	± 4 mm (greater diam.), 3.5 mm (lesser diam.), slightly compressed

not fused to the sinuses of the developing capsule. From *E. faucicola* Leach (1977: 99) it differs in the branches that are 4-8-winged with margins not becoming blackish and corky, prickles which do not become widely separated and positioned above the leaf scar, smooth peduncles and cyme branches, and an ovoid ovary seated on a 3-lobed or pentagonal irregularly dentate perianth.

Smaller plants of *Euphorbia otavimontana* can be confused with *E. atrocarmesina* Leach (1968: 167), *E. cannellii* Leach (1974: 47), *E. semperflorens* Leach (1970: 185) and *E. strangulata* Brown (1913: 1041), small shrubs from western Angola, due to a similar acaulous habit, branches which are variably segmented and straight paired spines which are longest at the widest part of the segments. The new species, however, can be readily distinguished from all of these by its cymose inflorescences and shortly pedicellate capsules instead of single cyathia and sessile capsules.

Dinter (1928) mentions a species of *Euphorbia* from Auros, the type locality of the new species, with similar habit to that of *E. dinteri* Berger (1906: 109), a synonym of *E. virosa* (Leach 1971). Marloth in his description of *E. venenata*, refers to plants of similar shape and flower structure from near Auros (Marloth 1930). White et al. (1941) in their treatment of *E. venenata* also mention the latter as occurring near Auros, in the Tsumeb region and near Lake Otjikoto and include several pictures of plants from the mentioned localities. During the present study, apart from the new species and *E. volkmanniae* Dinter (1928: 124) (sympatric at Auros), no other shrub species of *Euphorbia* was found at or near any of the mentioned localities. It is thus concluded that Dinter, Marloth and White et al. all referred to the new species in their publications.

In his description of *E. ingenticapsa*, Leach (1971) provided a comparative picture of fruiting cymes of the latter and of *E. venenata*. In the caption of the figure it is mentioned that the fruiting cymes of *E. venenata* are from the specimen *Leach & Cannell 14047* from Tsumeb. Since the fruiting cymes in the figure agree with those of the new species and no other species of *Euphorbia* shrub was found in or near Tsumeb, it is concluded that the fruiting cymes depicted in Leach's picture are in fact those of the new species. The distribution records shown for *E. venenata* from the Tsumeb area in Mannheimer and Curtis (2009) most probably also refer to *E. otavimontana*. The close-up picture of a fruiting branch in the latter publication corresponds with that of the new species.

Euphorbia otavimontana is easily grown from cuttings. Porcupines (*Hystrix africaeaustralis*) feed on the branches during periods of drought.

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REFERENCES

Berger A (1906) *Euphorbia dinteri* Berger n. sp. *Monatsschrift für Kakteenkunde* 16: 109, 110.

Brown NE (1913) Addenda. In: Thiselton-Dyer WT (ed) *Flora of Tropical Africa* 6, 1021-1094. Reeve & Co., London.

Bruyns PV, Mapaya RJ, Hedderson T (2006) A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and psbA-trnH sequence data. *Taxon* 55: 397-420.

Bruyns PV (2012) Nomenclature and typification of southern African species of *Euphorbia*. Bothalia 42: 217-245.

Dinter K (1928) Sukkulentenforschung in Südwestafrika, II. Teil: Erlebnisse und Ergebnisse meiner Reise in den Jahren 1923 bis 1925. *Fedde, Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 53: 1-145. Gustav Winter, Herrnhut (Sachsen).

Germishuizen G, Meyer NL (eds; 2003) Plants of southern Africa: an annotated checklist. *Strelitzia* 14: 1-1231.

IUCN (2012) *IUCN red list categories and criteria, version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

Klaassen E, Kwembeya E. (eds; 2013) A Checklist of Namibian Indigenous and Naturalised Plants. *Occasional Contributions of the National Botanical Research Institute* 5: 1-591.

Leach LC (1968) Euphorbiae succulentae Angolenses - I. *Boletim da Sociedade Broteriana* (série 2) 42: 161-179.

Leach LC (1970) Euphorbiae succulentae Angolenses: III. *Boletim da Sociedade Broteriana* (série 2) 44: 185-206.

Leach LC (1971) Euphorbia virosa Willd. with a new synonym and two new taxa from Angola. *Boletim da Sociedade Broteriana* (série 2) 45: 349-368.

Leach LC (1974) Euphorbiae succulentae Angolenses: IV. *Garcia de Orta série de Botânica* 2: 31-54.

Leach LC (1977) Euphorbiae succulentae Angolenses: VI. *Garcia de Orta série de Botânica* 3: 99-102.

Linnaeus C (1753) *Species Plantarum*. Salvii, Holmiae, pp. 1200 (in two volumes).

Mannheimer CA, Curtis BA (2009) *Le Roux and Müller's Field Guide to the Trees and Shrubs of Namibia*. Macmillan Education Namibia, Windhoek.

Marloth R (1930) A Revision of the group *Virosae* of the genus *Euphorbia* as far as represented in South Africa. *South African Journal of Science* 27: 331-340.

Mendelsohn J, Jarvis A, Roberts C & Robertson A (2002) *Atlas of Namibia*. David Philips Publishers, Cape Town, South Africa.

Swanepoel W (2009) *Euphorbia otjingandu* (Euphorbiaceae), a new species from the Kaokoveld, Namibia. *South African Journal of Botany* 75: 497-504.

White A, Dyer RA, Sloane BL (1941) *The succulent Euphorbiae 2 (southern Africa)*. Abbey Garden, Pasadena.

Willdenow CL von (1799) *Species Plantarum* 4th ed. G.C. Nauk, Berlin.

Vegetation of the Thornbush Savanna of central Namibia: Baseline description of the present vegetation at Farm Erichsfelde, Otjozondjupa Region

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ABSTRACT

The Vegetation Survey of Namibia project has been initiated to provide baseline data in support of sustainable land-use planning. The finding of historical data from the Farm Erichsfelde initiated a long-term monitoring programme. This study serves as a baseline description of the vegetation associations. Regular Braun-Blanquet type sampling was done in April 1999, and additional relevés were obtained from the BIOTA project from 2002 and 2005. The entire data set comprised 232 relevés with 379 species. The data were classified using the modified TWINSPAN procedure. Eleven associations, grouped into five habitat types, were identified from the classification. These habitat types are linked to landscape facets, being wetlands, rocky habitats, plains, soils on calcretes as well as riverine and related habitats. The associations are described in terms of their composition, general position in the landscape and structure. The relevé data were subjected to an NMS ordination. The main environmental gradients identified were the topography, the soil pH and the slope of the landscape. It is, however, very clear from the ordination that the various associations identified are closely related, and in many respects ecotonal to each other. The vegetation associations were mapped using aerial images as well as the GPS position of the relevés as baseline. In addition, a Livestock Farming Suitability Index was calculated for each association, based on its habitat, composition and structure. Only the *Ziziphus mucronata–Dichanthium annulatum* association was rated highly suitable for livestock farming. The two plains associations, *Ondetia linearis–Acacia mellifera* and *Aristida congesta–Acacia mellifera* were rated moderately suitable, whilst all other associations were rated with a low suitability for livestock farming. The main reason for these fairly low ratings is a high degree of bush encroachment and low perennial grass cover.

Keywords: Acacietea; Livestock Farming Suitability Index; Modified TWINSPAN; Nonmetric Multidimensional Scaling; Phytosociology; Veld degradation

INTRODUCTION

Land use planning in Namibia, and specifically grazing planning, has for many years been based on a ‘grazing capacity map’ based on ‘expert opinion’ and dating from the 1970s (Departement Landbou Tegniese Dienste 1979). Changes in vegetation composition and structure, specifically through bush encroachment (Bester 1998, De Klerk 2004), have however also changed the productivity, specifically in terms of grazing capacity, of the semi-arid savannas of central Namibia. Although this has been realised as a problem for sustainable planning and management in the past (Lubbe 2005), few attempts have been undertaken to rectify this (Bester 1988, Espach 2006, Espach et al. 2009). One of the major drawbacks experienced is the lack of suitable baseline information. Presently available sources provide only broad overviews (cf. Giess 1998, Irish 1994, Mendelsohn et al. 2002), whilst more detailed descriptions are often limited to National Parks (Burke & Strohbach 2000).

The Vegetation Survey Project of Namibia has been initiated to provide some of the baseline information needed (in addition to soil and climatic descriptors) for land use planning (Strohbach 2001, 2014). Next to large-scale regional overview descriptions, an emphasis is placed on describing vegetation in greater detail in more localised, small-scale studies. This local detail serves also as seeding studies for the larger scale studies. The selection of Erichsfelde for such a localised, smaller-scale vegetation description came about with the availability of historic data collected in 1956 by Prof. H. Volk (Glen & Perold 2000) during a visit to the farm (Volk 1956). This study thus also serves as a baseline for a long-term monitoring programme to study vegetation changes.

METHODS

Study Area

The farm Erichsfelde is situated in the Okahandja District, Otjozondjupa Region in central Namibia, straddling the B6 trunk road between Okahandja and Otjiwarongo (Figure 1). The farm is 13,907.4 ha in size. The topography is an undulating plain as part of the agro-ecological zones CPL 2 (fringe plains) and CPL 3-4 (inselberg plains). The topography is generally flat, incised only by the major rivers (De Pauw et al. 1998, Petersen 2008). One dominating feature is the Ombotozo Mountain on the western border of the farm, which gives rise to several geological features on the western side of the farm. The mountain itself is based on mudstone of the Omingonde formation and topped by a gabbro sill, as part of the Karoo intrusive dolerite sills and dykes. The footslope of the Ombotozo, which reaches into Erichsfelde, consists of a talus slope of mixed weathered gabbro and weathered mudstones (Geological Survey 1980, South African Committee for Stratigraphy 1980, Schneider 2004). The plains to the east of this are formed by a sequence of syn- and post tectonic granites of the Salem Suite, undifferentiated schists and marbles of the Damara formation and undifferentiated granites of the Damara formation (Figure 1) (Geological Survey 1980). The Salem Suite granites are known to be alkaline (compared to the generally more acidic nature of granites) (Barnes & Sawyer 1980). This has important implications to soil characteristics in especially the western part of the farm.

The climate of Erichsfelde is a typical subtropical steppe climate following Köppen (1936). Rain occurs during the summer months between December and April (Figure 2) (Jürgens et al. 2010). Frost can occur during the winter months (June to August), but is generally restricted to between 5 and 10 days a year (Mendelsohn et al. 2002). The vegetation forms part of the Thornbush Savanna *sensu* Giess (1998).

Field surveys

Surveying followed the general method employed for the Vegetation Survey of Namibia project (Strohbach 2001, 2014). At each survey plot of 20 x 50 m, a Braun-Blanquet type relevé was compiled. All vascular plant species occurring were noted as well as their typical growth forms and estimated percentage crown cover. Habitat descriptors included the position using a GPS, the landscape, local topography, slope and aspect, lithology, degradation indicators, as well as a photograph. Unknown species and reference specimens were collected, identified and deposited at the National Herbarium of Namibia

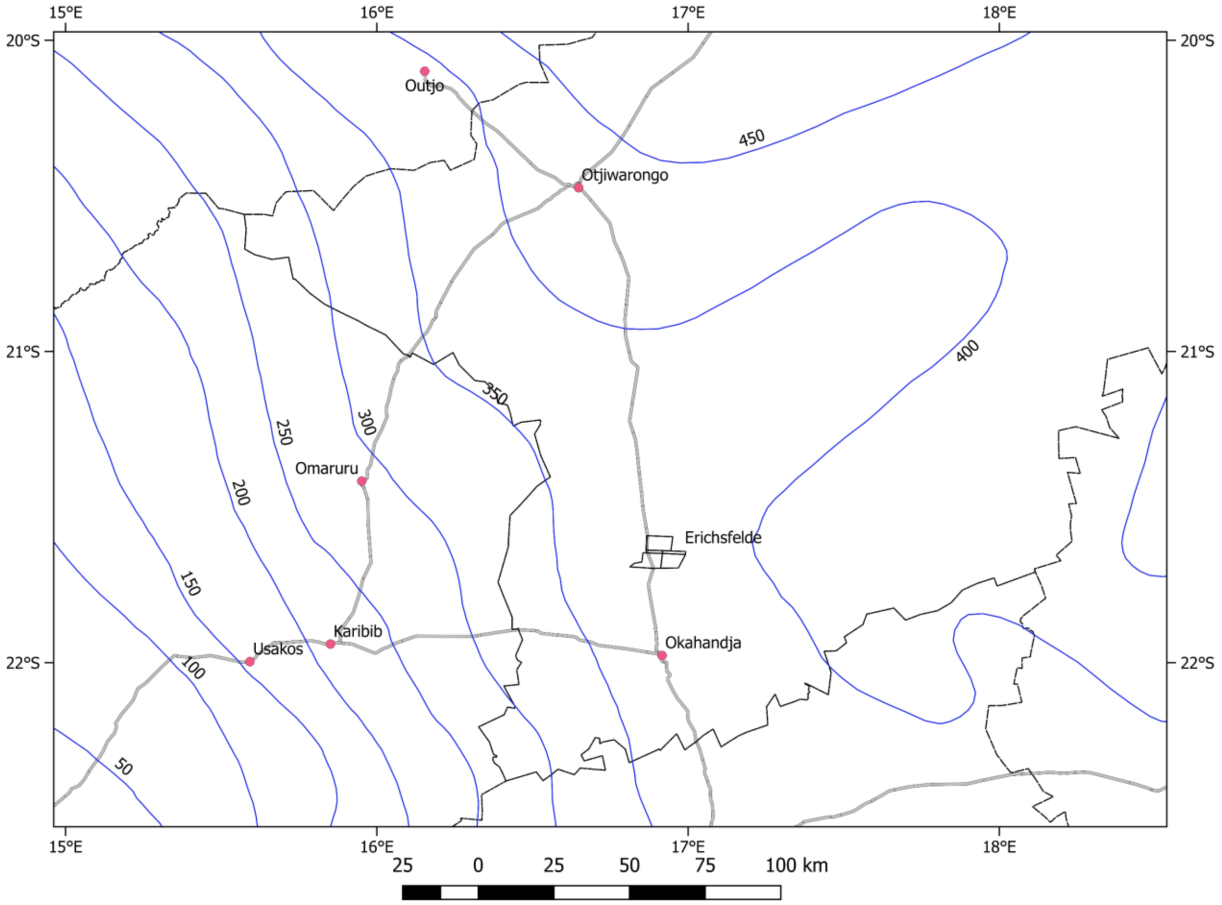

Figure 1*: (a) Overview map to show the position of Erichsfelde between Okahandja and Otjiwarongo in the Otjozondjupa Region. Long-term average annual rainfall isohyets are indicated in blue on the map.*

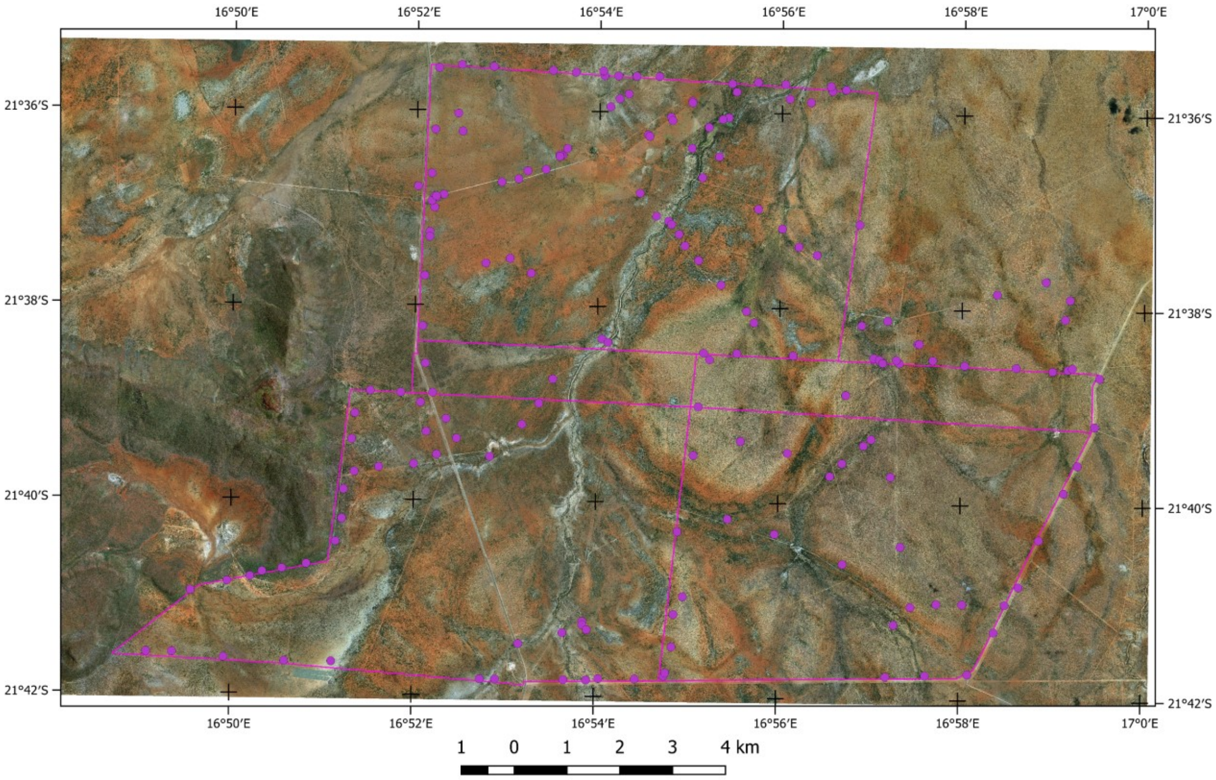

Figure 1: *(b) Aerial view of Erichsfelde, indicating the distribution of survey plots on the farm.*

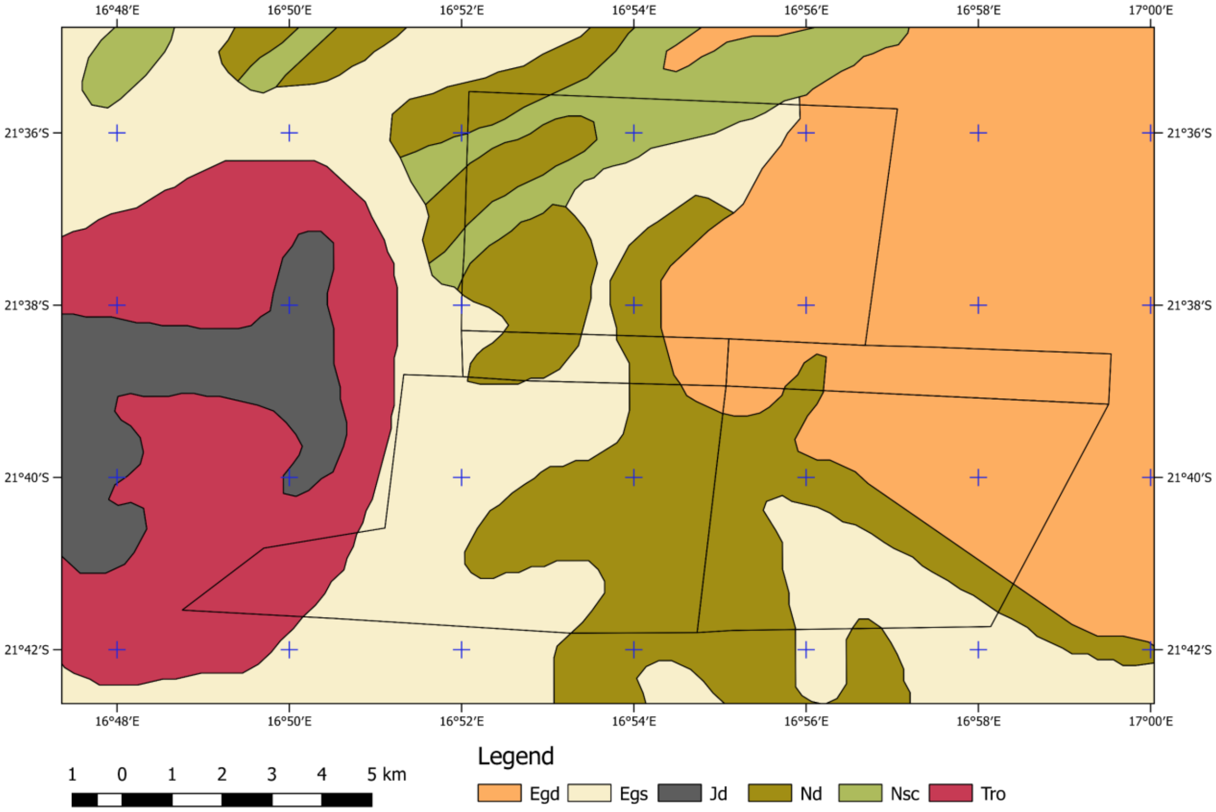

Figure 1: *(c) Geological map of Erichsfelde. Egd: Undifferentiated granites, Damara Sequence; Egs: Syn- and post tectonic granites of the Salem Suite; Jd: Intrusive dolerite sills and dykes; Nd: undifferentiated schists and marbles of the Nosib- and Swakop Groups, Damara Sequence; Nsc: marbles and schists of the Swakop Group, Damara Sequence; Tro: red mudstones and siltstones of the Omingonde Formation, Karoo Sequence. Data sources: Aerial images from Microsoft Bing Maps (undated), others: Geological Survey (1980) as well as NARIS (2001).*

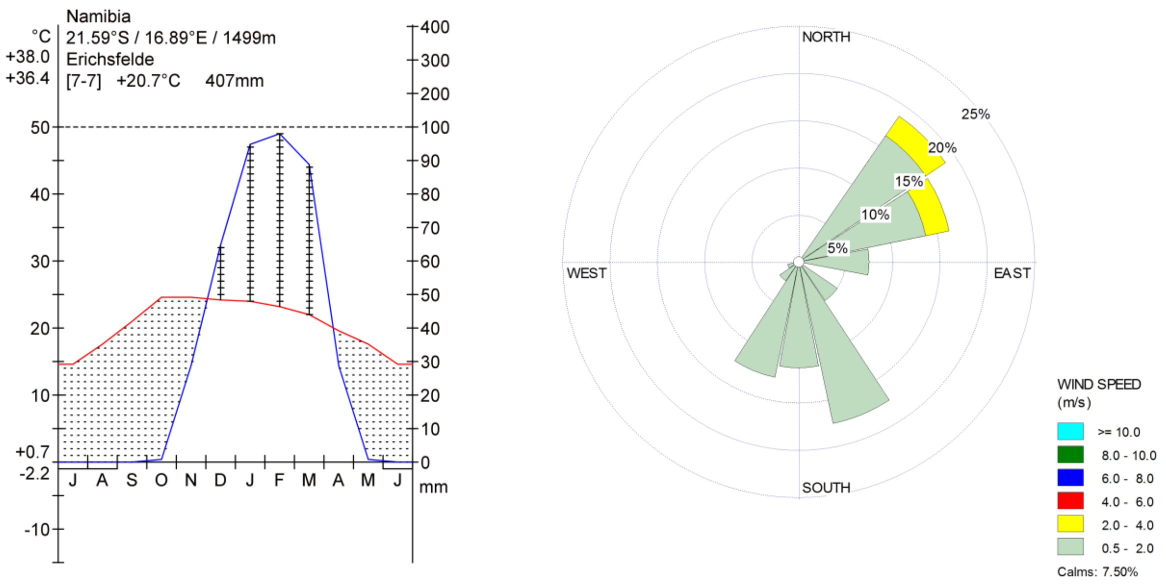

Figure 2: *(a) (left) Climate diagram for Erichsfelde. (b) (right) Wind rose of the prevailing wind directions and strengths at Erichsfelde. Source data: SASSCAL (2014).*

(WIND). The relevé data were captured on TurboVeg (Hennekens & Schaminée 2001). Nomenclature follows Klaassen & Kwembeya (2013).

The data were partially collected for the Vegetation Survey of Namibia Project, partially for the Biodiversity Transect Analysis in southern Africa (BIOTA) project (Jürgens et al. 2010, 2012). Specifically the relevés of Austermühle were collected at the Erichsfelde biodiversity observatory. The data collection follows the general survey scheme of the Vegetation Survey project, but due to the rigid layout of the biodiversity observatory, some of the relevés could span adjacent habitats. Austermühle also sampled several specific habitats outside the biodiversity observatory for general description purposes. A detailed overview of data sources and collectors is given in Table 1. All data form part of GIVD AF-NA-001 (Dengler et al. 2011, Strohbach & Kangombe 2012). The final, extended data set consisted of 232 relevés, with 379 species after cleanup procedures as described by Strohbach (2014).

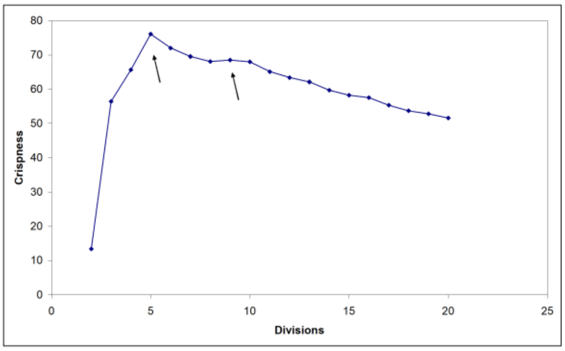

Figure 3: *Crispness values of the levels of subdivisions, indicating a clear peak at five subdivisions (at habitat level), and a lesser peak at nine subdivisions (vegetation association level). The peaks have been indicated by arrows.*

Data analysis

Data analysis followed methods commonly applied for the Vegetation Survey of Namibia project (Strohbach 2001, 2014, Strohbach & Jürgens 2010; see also Strohbach 2013a, b, 2017, Strohbach & Jankowitz 2012). As considerable observer bias, combined with seasonal bias (see seasonal rainfall figures in Table 1), was expected, it was decided to reduce the matrix for classification to phanerophytes, chamaephytes and graminoids only (i.e. the main components of a savanna ecosystem). Non-graminoid forbs, especially ephemeral forbs, were removed. The number of species was thus reduced to 132 species. This corresponds to the synusial approach of vegetation classification developed by Gillet & Julve (2018).

The classification was done with modified TWINSPAN (Roleček et al. 2009), using Total Inertia (Ter Braak 1986) as diversity measure. No pseudospecies were used for this classification. Crispness values (Botta-Dukát et al. 2005) for this classification indicated a highly reliable division into five clusters, and a less strong subdivision at nine clusters (Figure 3). The tenth subdivision (in crispness close to, but slightly lower than subdivision 9) would have resulted in splitting association 3.2 into two variants based on veld condition, and was thus ignored for this work.

Table 1: *Data sources used for this study. Rainfall data were made available by the farm manager of Erichsfelde. The quality of the season was determined according to criteria of Botha (1998) using long-term data from the farm.*

Surveyor	No of relevés (relevé sequence no)	Date of surveying	Rainfall for season (September to August)	Quality of rain season
B. Strohbach	145 (757 – 902)	April 1999	205 mm	Dry
T. Sheuyange	35 (903 – 938)	April 1999	205 mm	Dry
R. Austermühle	26 (50201 – 50226)	March to May 2002	233 mm	Dry
D. Wesuls	26 (10166 – 10191)	April 2005	357 mm	Normal

Upon inspection, it was found that Clusters 1 and 2 each represented two associations each, as observed during fieldwork. In the case of Cluster 2, it would have been split only with further divisions (16 divisions or more). This split was thus done manually. In the case of Cluster 1, a split was achieved using Cocktail (Bruelheide 2000), based on the presence/absence of *Dichanthium annulatum*, *Aerva leucura* and *Ziziphus mucronata* which were found to dominating an ephemeral riverine system. Once a stable classification was achieved, the previously removed forbs were again added to the data set for interpretation of the results and creation of the phytosociological and synoptic tables.

From the final classification, a synoptic table and a phytosociological table were created. Diagnostic species were determined using the phi co-efficient of association (Chytrý et al. 2002). For this calculation the numbers of relevés were standardised following Tichý & Chytrý (2006). Species with phi ≥40 were considered as diagnostic and with phi ≥60 as highly diagnostic; however, species with a non-significant fidelity at α=0.05 using Fisher's exact test were omitted. Species occurring with at least a 60% frequency were regarded as constant and with at least an 80% frequency as highly constant.

For each association an estimated number of species (as indicator of potential species richness) was calculated, using a first-order Jackknife procedure (Heltshe & Forrester 1983, Palmer 1990). This estimator is a function of the number of species occurring in only one relevé, and performed well in the estimation of species richness within forest environments in the USA (Palmer 1990).

Box-and-Whisker plots were constructed to illustrate the structure for each grouping (i.e. tree, shrub, dwarf shrub, perennial grass, annual grass and herb cover), using available growth form data (excluding the data from Wesuls, as these did not contain any growth form information). Description of the vegetation structure follows Edwards (1983). Two diversity indices, the Shannon Index (as an index of evenness) ($H'=-\Sigma\ p_i \ln p_i$) and Simpson's Index (as an index of dominance) ($D=\Sigma(n/N)^2$) (Peet 1974) were calculated for each relevé using Juice (Tichý et al. 2011).

Environmental gradients

A Nonmetric Multidimensional Scaling ordination (NMS) (Kruskal 1964) was calculated with PC-ORD version 7.02 (McCune & Mefford 2016). The data set was reduced by removing the relevé data from associations 1.1 and 1.2, as these would act as outliers due to their unique composition. For the species data, again only the reduced matrix with phanerophytes, chamaephytes and grasses was used in the NMS (as used during the initial classification).

Two secondary matrices were created: one for the physical environmental factors, the second for vegetation-related parameters. As categorical factors the association, the landscape type, and local topography, the lithology as well as the GIS-derived stratigraphy (based on Geological Survey 1980) were included. The available quantitative environmental factors were limited to the slope class. As no soil samples were taken during field work, no information on soil physical and chemical properties was available. However, with the presence of calcretes in several soils, and several wetland/riverine features, both the soil pH and the position in the landscape, relating to water flow patterns (cf. Pringle & Tinley 2003) were considered to be of importance in explaining the environmental gradients. Therefore, two proxy environmental factors were created as follows: Soils were classed as 'acidic' (6), 'neutral' (7) and 'basic' (8) based on the observed lithology, augmented by the stratigraphy. Granitic lithologies derived from the Damara formation were classed as 'acidic'; all schists, shales, mudstones as well as all fluvial system were classed as 'neutral', whilst all calcareous soils (including soils derived from the Salem Suite) were classed as 'basic'. This scheme broadly follows the lithological groupings of SOTER (FAO 1993). A second quantitative environmental factor was created from the landscape and local topography data associated with the relevé data. The observed local topography was sorted in a catena sequence (i.e. a reverse sequence of water flow/water accumulation in the landscape) and numbered, as listed in Table 2.

The second environmental matrix prepared contained structural data on the tree, tall shrub (>1 m), dwarf

Table 2: *Catena sequence used to convert categorical landscape and topographical data to numerical landscape data for use in NMS.*

Landscape	Local topography	Catena sequence no
Level land	Ephemeral river	1
	Ephemeral river embankment	2
	Floodplain	3
	Pan	4
	Wash	5
	Plain	6
Sloping land	Medium gradient footslope	7
	Rocky ridges	8
Steep land	Talus slope	9

shrub (<1 m), grass, herb and bare soil cover. These were additionally combined as a categorical structure parameter, i.e. woodlands, thickets, bushlands and shrublands, following Edwards (1983). Also included were the diversity indicators number of species per 1000 m^2, Shannon Index (H') and Simpson's Index (D).

The resulting data set had 226 relevés with 97 species, 13 environmental factors and 15 structural and biodiversity factors. Average Sørensen dissimilarity was used as distance measure, and the ordination was calculated in three dimensions (i.e. three resulting axes), based on an initial scree plot of stress versus dimensions (McCune et al. 2002, Peck 2010). The solutions were calculated with 200 iterations using real and 249 runs using randomised data for a Monte Carlo test. To aid the interpretation of the resulting scatter plots of the ordination results, the environmental, structural and biodiversity parameters were overlain as a joint plot onto a scatter diagram of the plots, with an r^2 cut-off level of 0.180.

Suitability for livestock farming

As the main aim of the Vegetation Survey Project is to support sustainable land use planning, a suitability rating for livestock farming was developed to help with the interpretation of vegetation classifications and descriptions as presented here (Strohbach 2018). This 'Livestock Suitability Index' is calculated based on the habitat, species composition and structure of the vegetation units. Habitat data were derived from the relevé data collected as well as GIS data sources, in particular the AEZ map (De Pauw et al. 1998) and the Namibian Soils Map (ICC et al. 2000). These spatial data however are at a rather course scale (1:1,000,000), but represent the best available habitat data for Namibia at present. For the factor 'Water Holding Capacity' within the Habitat Subindex, data from ICC et al. (2000) were adapted in the sense that only the rocky habitats (habitat cluster 2) was regarded as having extremely low water holding capacity (factor 20), whilst all calcrete habitats (habitat cluster 4) were regarded as having low water holding capacity (factor 40). All other habitats were classed, as per ICC et al. (2000) data, as 'moderate to high' with a factor of 120.

For the compositional data, species attributes were obtained from the following sources: species toxicity data were derived from Mannheimer et al. (2012), whilst grass palpability and ecological status was derived from Müller (2007) and Gibbs Russell et al. (1990). All other required data were derived from the relevé data.

Mapping

A vegetation map was created using Google Earth and Microsoft Satellite (Bing) imagery as baseline. The Google Earth and Microsoft Satellite maps were used complementary to each other, as the Google Earth Map was a wet-season image (2/1/2010) showing vegetation features well, whilst the Microsoft Satellite map was an apparent dry season map (undated), showing soil features well. Using the position of the classified relevés as ground truth points, a map was manually digitized by visual interpretation in QGIS software package (QGIS 2.14.5-Essen 2016).

RESULTS

Classification results

The classification resulted in five higher syntaxonomic groups, and eleven associations. These classification results are depicted in Figure 4 as a dendrogram. The full phytosociological table is presented as downloadable online Appendix 1, the synoptic table as online Appendix 2. As this study covers only a fairly small part of the Thornbush Savanna *sensu* Giess (1998), or the Acacietea *sensu* Volk & Leippert (1971), no attempt has been made to describe the higher syntaxonomic groupings apart from associating them with a particular landscape facet or broad habitat type on the farm.

The associations are not described formally according to the International Code for Phytosociological Nomenclature (ICPN) (Weber et al. 2000), pending further descriptions of the vegetation of the greater Thornbush Savanna *sensu* Giess (1998). Within the synopsis, highly diagnostic species (with phi coefficient >60), highly constant species (occurring in more than 80% of relevés) and dominant species (with on average more than 30% crown cover) are indicated in **bold**. All structural descriptions follow Edwards (1983).

1. Wetlands

1.1. *Ziziphus mucronata–Dichanthium annulatum* association on ephemeral river beds with heavy soils

Synopsis:
Number of relevés: 2
Number of species observed: 44
Estimated number of species: 60
Average species density per 1000 m^2: 32

Diagnostic species: ***Tagetes minuta***, ***Gomphrena celosioides***, ***Aerva leucura***, ***Solanum lichtensteinii***, ***Dichanthium annulatum* var. *papillosum***, ***Eragrostis lehmanniana***, ***Trichodesma angustifolium***, ***Osteospermum muricatum* subsp. *muricatum***, ***Ruelliopsis damarensis***, ***Nicolasia stenoptera* subsp. *stenoptera***, *Xanthium spinosum*, *Tribulus terrestris*, *Hibiscus trionum*, *Platycarphella carlinoides*, *Alternanthera pungens*, *Solanum delagoense*, *Sesbania macowaniana*, *Ziziphus mucronata*, *Setaria verticillata*, *Eragrostis rotifer*, *Oxygonum alatum*, *Panicum coloratum*, *Chloris virgata*, *Schkuhria pinnata*, *Indigofera holubii*
Constant species: ***Urochloa brachyura***, ***Kyphocarpa angustifolia***, ***Cenchrus ciliaris***, ***Acacia tortilis* subsp. *heteracantha Acacia mellifera,* subsp. *detinens***
Dominant species: ***Dichanthium annulatum* var. *papillosum***

This association occurs in a small tributary on the south-western part of the farm draining the mud plains of the *Anthephora schinzii–Leucosphaera bainesii* association (number 5.2 below). The topography is a fairly deeply incised water channel with heavy clay soils as river bed. With *Acacia tortilis*, *Aerva leucura* and *Ziziphus mucronata*, prominent elements of the regular riverine thickets (see 5.3 below) are present, indicating a close relationship to these. The striking feature though is a dense grass sward of *Dichanthium annulatum* and other perennial grass species. The typical structure is thus a tall, closed grassland (Figures 5a and 6a).

1.2. *Marsilea–Leptochloa fusca* association of the vlei areas

Synopsis:
Number of relevés: 4
Number of species observed: 38
Estimated number of species: 55
Average species density per 1000 m^2: 19

Diagnostic species: ***Eragrostis leersiiformis***, ***Marsilea ephippiocarpa***, ***Schoenoplectus muricinux***, ***Sporobolus nebulosus***, ***Leptochloa fusca***, ***Cyperus difformis***, ***Vahlia capensis***, ***Nesaea drummondii***, ***Mollugo nudicaulis***, ***Artemisiopsis villosa***, ***Courtoisina assimilis***, ***Cotula anthemoides***, *Portulaca oleracea*, *Panicum pilgerianum*, *Heliotropium baclei* var. *rostratum*, *Amaranthus thunbergii*, *Listia marlothii*, *Cucumis sagittatus*, *Phyllanthus fraternus*
Constant species: *Eragrostis rotifer*, *Aristida adscensionis*
Dominant species: ***Marsilea ephippiocarpa***, ***Eragrostis leersiiformis***

This association is typical for the vlei areas (shallow depressions with temporary, seasonal standing water). These occur occasionally in the shallow *omiramba* (King 1963) as part of the drainage system crossing the farm. The structure is a short, closed grassland (Figures 5b and 6b), surrounded by a fringe of dense, thicket-like vegetation.

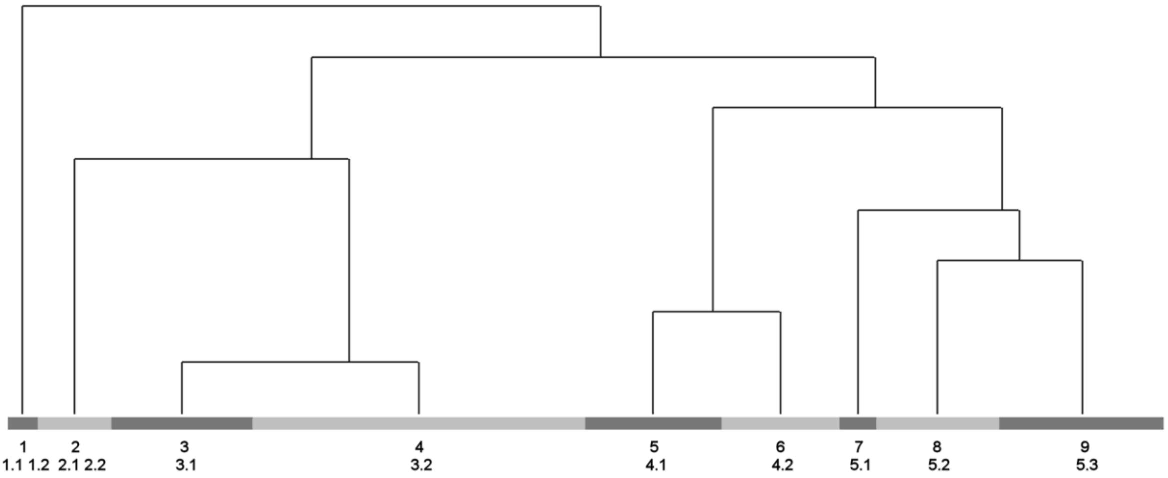

Figure 4: *Dendrograms depicting the classification results. The upper row numbers represent the cluster numbers, the lower row numbers correspond to the numbering of the association descriptions.*

2. Rocky habitats

2.1. *Andropogon gayanus–Combretum apiculatum* association on granitic outcrops

Synopsis:
Number of relevés: 4
Number of species observed: 31
Estimated number of species: 52
Average species density per 1000 m^2: 23

Diagnostic species: ***Triraphis ramosissima***, ***Helichrysum tomentosulum* subsp. *tomentosulum***, ***Combretum apiculatum* subsp. *apiculatum***, ***Tephrosia dregeana* var. *dregeana***, ***Barleria lancifolia***, ***Acacia erubescens***, ***Tephrosia villosa* subsp. *ehrenbergiana* var. *ehrenbergiana***, ***Melinis repens* subsp. *repens***, ***Andropogon gayanus* var. *polycladus***, ***Heteropogon contortus***, *Waltheria indica*, *Searsia marlothii*, *Cleome rubella*, *Grewia bicolor*, *Grewia flavescens*, *Ximenia americana*, *Tavaresia barklyi*, *Maerua parvifolia*, *Hibiscus micranthus*
Constant species: Dichrostachys ***cinerea***, ***Boscia albitrunca***, *Pogonarthria fleckii*
Dominant species: ***Dichrostachys cinerea***

This association is limited to a small granitic outcrop near the entrance gate of Erichsfelde. A similar outcrop was observed ca 250 m west of this on the neighbouring farm Matador. This outcrop is associated with the syn- to post tectonic granites of the Salem suite occurring to the west of the study area (Geological Survey 1980). The slope's steepness is between 10 and 15%, with a high rock cover of over 80%. The outcrop rises barely 3 to 5 m above the surrounding plain. The vegetation structure is a high, semi-open shrubland (Figures 5c and 6c).

2.2. *Maerua parvifolia–Acacia erubescens* association of the mountain slopes

Synopsis:
Number of relevés: 11
Number of species observed: 42
Estimated number of species: 81
Average species density per 1000 m^2: 34

Diagnostic species: ***Acacia senegal***, ***Grewia bicolor***, ***Megalochlamys marlothii***, ***Grewia retinervis***, *Maerua parvifolia*, *Grewia villosa*, *Montinia caryophyllacea*, *Helinus integrifolius*, *Cordia sinensis*, *Acacia erubescens*, *Boscia foetida*, *Albizia anthelmintica*, *Commiphora tenuipetiolata*
Constant species: ***Dichrostachys cinerea***, ***Leucosphaera bainesii***, ***Aristida adscensionis***, ***Enneapogon cenchroides***, ***Boscia albitrunca***, *Monechma genistifolium* subsp. *genistifolium*, *Hibiscus micranthus*, *Lycium eenii*, *Acacia mellifera* subsp. *detinens*
Dominant species: ***Dichrostachys cinerea***, ***Acacia erubescens***, *Leucosphaera bainesii*, *Acacia senegal*, *Acacia mellifera* subsp. *detinens*

This association represents the vegetation of the southern and eastern footslopes of the Ombotozo Mountain. The slopes are moderately steep to steep (15-60%), and consist of a talus with a high stone and rock cover. The main lithology of the bottom slope is mudstones of the Omingonde formation (Ecca Group, Karoo Sequence) (Geological Survey 1980, South African Committee for Stratigraphy 1980) as well as decomposed gabbro (Schneider 2004). The upper slopes of the mountain consist of olivine gabbro as part of wide-spread intrusive sills and dykes of the Karoo Sequence (Geological Survey 1980, South African Committee for Stratigraphy 1980, Schneider 2004). The vegetation structure is a high, closed shrubland (Figures 5d and 6d), not reaching more than 5 to 6 m.

3. Plains habitat

3.1. *Ondetia linearis–Acacia mellifera* association of the omiramba

Synopsis:
Number of relevés: 28
Number of species observed: 130
Estimated number of species: 189
Average species density per 1000 m^2: 45

Diagnostic species: ***Tetragonia calycina***, ***Ondetia linearis***, *Raphionacme lanceolata*, *Aristida congesta* subsp. *congesta*, *Indigofera rautanenii*, *Cucumis anguria*, *Phyllanthus pentandrus*, *Vigna oblongifolia* var. *parviflora*, *Hermannia modesta*, *Persicaria hystricula*, *Commelina livingstonii*, *Helinus spartioides*, *Cyphostemma cirrhosum*, *Ocimum filamentosum*, *Xerophyta humilis*, *Phaeoptilum spinosum*, *Tephrosia burchellii*, *Euphorbia prostrata*, *Coccinia rehmannii*
Constant species: ***Kyphocarpa angustifolia***, ***Geigeria acaulis***, ***Boscia albitrunca***, ***Grewia flava***, ***Urochloa brachyura***, ***Aristida adscensionis***, ***Acacia mellifera* subsp. *detinens***, ***Ptycholobium biflorum* subsp. *angolensis***, ***Lycium eenii***, ***Eragrostis porosa***, ***Dichrostachys cinerea***, ***Barleria lanceolata***, *Pogonarthria fleckii*, *Leucosphaera bainesii*, *Tragus berteronianus*, *Ehretia rigida*, *Pupalia lappacea*, *Melinis repens* subsp. *grandiflora*, *Cleome rubella*, *Aristida rhiniochloa*, *Stipagrostis uniplumis* var. *uniplumis*, *Dicoma tomentosa*, *Catophractes alexandri*, *Albizia anthelmintica*
Dominant species: ***Eragrostis porosa***, ***Acacia mellifera* subsp. *detinens***, ***Dichrostachys cinerea***, *Albizia anthelmintica*, *Stipagrostis uniplumis* var. *uniplumis*, *Ondetia linearis*, *Gisekia africana*, *Catophractes alexandri*, *Boscia albitrunca*, *Aristida*

adscensionis, *Acacia reficiens*, *Acacia hebeclada* subsp. *hebeclada*

This association is typical of the shallow watercourses that form the headwaters of the bigger ephemeral rivers. Typical for *omiramba*, no clear gradient is visible in the landscape (King 1963). These *omiramba* are often only recognisable by a lusher vegetation, generally dominated by *Ondetia linearis*. The vegetation is densely encroached by *Acacia mellifera* subsp. *detinens*, forming a tall, closed shrubland (Figures 5e and 6e).

3.2. *Aristida congesta–Acacia mellifera* association of the sandy plains (Strohbach 2002)

Synopsis:
Number of relevés: 67
Number of species observed: 148
Estimated number of species: 258
Average species density per 1000 m^2: 40

Diagnostic species: *Evolvulus alsinoides*, *Aristida congesta* subsp. *congesta*, *Ipomoea sinensis*, *Felicia smaragdina*, *Gisekia africana*
Constant species: ***Stipagrostis uniplumis* var. *uniplumis***, ***Acacia mellifera* subsp. *detinens***, ***Boscia albitrunca***, ***Pogonarthria fleckii***, ***Eragrostis porosa***, ***Kyphocarpa angustifolia***, ***Urochloa brachyura***, *Aristida adscensionis*, *Tragus berteronianus*, *Talinum arnotii*, *Ptycholobium biflorum* subsp. *angolensis*, *Enneapogon cenchroides*, *Lycium eenii*, *Pupalia lappacea*, *Lycium bosciifolium*, *Dicoma tomentosa*, *Melinis repens* subsp. *grandiflora*, *Geigeria acaulis*
Dominant species: ***Stipagrostis uniplumis* var. *uniplumis***, ***Acacia mellifera* subsp. *detinens***, *Eragrostis porosa*, *Monechma genistifolium* subsp. *genistifolium*, *Dichrostachys cinerea*, *Aristida congesta* subsp. *congesta*, *Aristida adscensionis*, *Lycium eenii*, *Grewia flava*, *Eragrostis lehmanniana*, *Acacia reficiens*

Strohbach (2002) described this association previously (her association 7 - *Acacia mellifera–Aristida congesta* association[1]) as occurring on chromic Cambisols with sandy loam texture in the topsoil. For the Otjiamongombe Observatory (situated near the north-eastern corner of Erichsfelde), haplic Luvisols, with reddish clayey, slightly acidic soils have been described (Jürgens et al. 2010 pp. 195–221). The association occurs on nearly flat to slightly undulating plains (0-5% slope). The structure of the vegetation is a short moderately closed bushland (Figures 5f and 6f). However, it is prone to encroachment, especially by *Acacia mellifera* subsp. *detinens*, turning it into a high, closed shrubland.

4. Shallow soils on calcretes

Especially in the western parts of the farm the subsurface Salem Suite granites form undulating plains with shallow soils on extensive calcrete deposits. The larger ephemeral rivers also eroded into the pediplane, exposing the subsurface calcretes in their floodplains. Depending on the depth of the soil profile, two different associations occur:

4.1. *Acacia mellifera—Monechma genistifolium* association (Strohbach 2002)

Synopsis:
Number of relevés: 27
Number of species observed: 80
Estimated number of species: 204
Average species density per 1000 m^2: 32

Diagnostic species: Enneapogon *desvauxii*
Constant species: ***Acacia mellifera* subsp. *detinens***, ***Enneapogon cenchroides***, ***Leucosphaera bainesii***, ***Acacia tortilis* subsp. *heteracantha***, *Monechma genistifolium* subsp. *genistifolium*, *Cenchrus ciliaris*, *Eragrostis porosa*, *Aristida adscensionis*, *Boscia albitrunca*, *Stipagrostis uniplumis* var. *uniplumis*, *Eragrostis annulata*
Dominant species: ***Monechma genistifolium* subsp. *genistifolium***, ***Leucosphaera bainesii***, ***Acacia mellifera* subsp. *detinens***, ***Acacia reficiens***, ***Stipagrostis uniplumis* var. *uniplumis***, *Cenchrus ciliaris*, *Catophractes alexandri*, *Aristida effusa*, *Anthephora schinzii*, *Acacia tortilis* subsp. *heteracantha*

Within the study area, these bushlands are generally found adjacent to riverine thickets (association 5.1 below) on loamy floodplain deposits, as well as on suboutcropping calcrete banks. Strohbach (2002) describes this association as a transitional association between the *Boscia foetida–Leucosphaera bainesii* association on shallow calcretes, and the deep, sandy-soiled *Aristida congesta–Acacia mellifera* association. The soils are described as chromic Cambisols or leptic-chromic Cambisols by Strohbach (2002), as well as calcic Cambisols and petric Calcisols by Jürgens et al. (2010). Often the underlying calcrete gravels become visible, contributing to the xeric nature of these soils (Figure 6g). The structure is typically a short, semi-open bushland (Figure 5g). There is a distinct resemblance to the *Monechma genistifolium–Acacia tortilis* association (5.3.), which however occurs as an

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[1] The association name has been changed by reversing the two name-giving species, in order to conform to naming concepts of the ICPN (the landscape-dominating species is mentioned last) (Weber et al. 2000).

ecotone (transistion) to the sandy plains of the *Aristida congesta–Acacia mellifera* association.

4.2. *Boscia foetida–Leucosphaera bainesii* association on shallow calcareous soils (Strohbach 2002)

Synopsis:
Number of relevés: 24
Number of species observed: 69
Estimated number of species: 180
Average species density per 1000 m^2: 34

Diagnostic species: ***Eriocephalus luederitzianus***, ***Sericorema sericea***, *Hermannia damarana*, *Enneapogon desvauxii*, *Sida ovata*, *Tragus racemosus*, *Oropetium capense*

Constant species: ***Monechma genistifolium* subsp. *genistifolium***, ***Leucosphaera bainesii***, ***Grewia flava***, ***Acacia mellifera* subsp. *detinens***, ***Cenchrus ciliaris***, ***Stipagrostis uniplumis* var. *uniplumis***, *Eragrostis porosa*, *Enneapogon cenchroides*, *Catophractes alexandri*, *Acacia reficiens*
Dominant species: ***Monechma genistifolium* subsp. *genistifolium***, ***Acacia mellifera* subsp. *detinens***, ***Stipagrostis uniplumis* var. *uniplumis***, ***Enneapogon desvauxii***, ***Acacia reficiens***, *Acacia tortilis* subsp. *heteracantha*, *Leucosphaera bainesii*, *Enneapogon cenchroides*, *Catophractes alexandri*

This association has been previously described by Strohbach (2002) as her association 10. One conspicuous difference is that the name-giving species, *Boscia foetida*, occurs here on only nine of the relevés, on i.e. less than 50%, compared to the

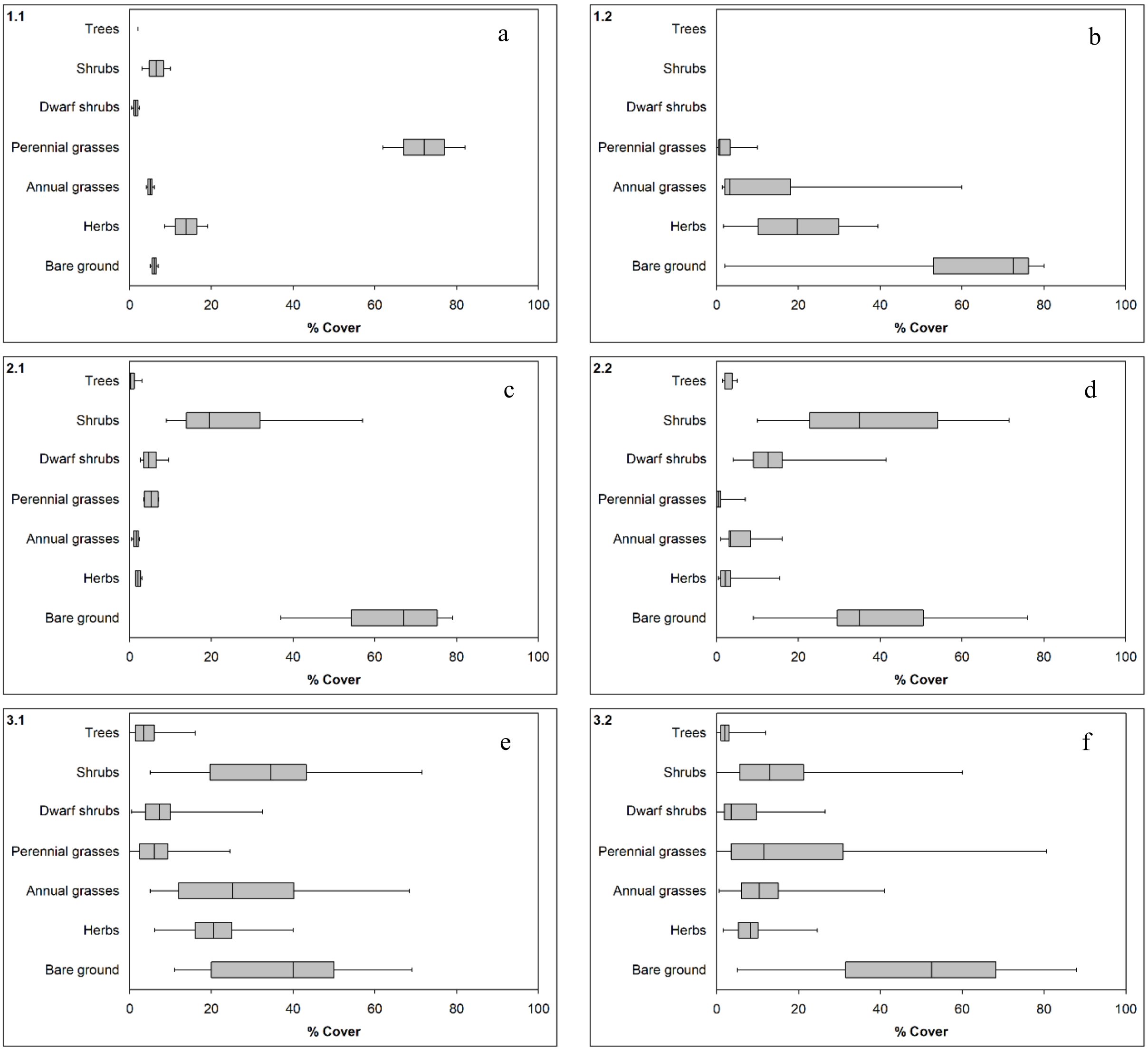

Figure 5: *Box-and-Whisker plots of the average structure of the various associations. (a)* Ziziphus mucronata–Dichanthium annulatum *association; (b)* Marsilea–Leptochloa fusca *association; (c)* Andropogon gayanus–Combretum apiculatum *association; (d)* Maerua parvifolia–Acacia erubescens *association; (e)* Ondetia linearis–Acacia mellifera *association; (f)* Aristida congesta–Acacia mellifera *association.*

70% frequency described by Strohbach (2002). The *Boscia foetida–Leucosphaera bainesii* association occurs on shallow leptic Calcisols (shallow stony soils on calcrete), often associated with suboutcropping rocks of the Damara Sequence (Strohbach 2002, Petersen 2008). Although the dominant structure of the vegetation is a low, semi-open bushland (Figure 5h), it has a dense dwarf-shrub layer associated with the calcretes (Figure 6h).

5. Riverine habitats

5.1. *Ziziphus mucronata–Acacia tortilis* association of the riparian thickets

Synopsis:
Number of relevés: 7
Number of species observed: 95
Estimated number of species: 158
Average species density per 1000 m^2: 31

Diagnostic species: ***Asparagus cooperi***, ***Cymbopogon caesius***, ***Achyranthes aspera* var. *aspera***, *Vernonia fastigiata*, *Searsia ciliata*, *Ziziphus mucronata*, *Eragrostis trichophora*, *Pentarrhinum insipidum*, *Leucas glabrata*, *Tarchonanthus camphoratus*, *Chenopodium murale*, *Eragrostis echinochloidea*, *Brachiaria malacodes*, *Lantana angolensis*
Constant species: ***Pupalia lappacea***, ***Cenchrus ciliaris***, ***Acacia mellifera* subsp. *detinens***, ***Grewia flava***, ***Acacia tortilis* subsp. *heteracantha***, *Setaria verticillata*, *Monechma genistifolium* subsp. *genistifolium*, *Lycium eenii*, *Lycium bosciifolium*, *Eragrostis rotifer*, *Barleria lanceolata*

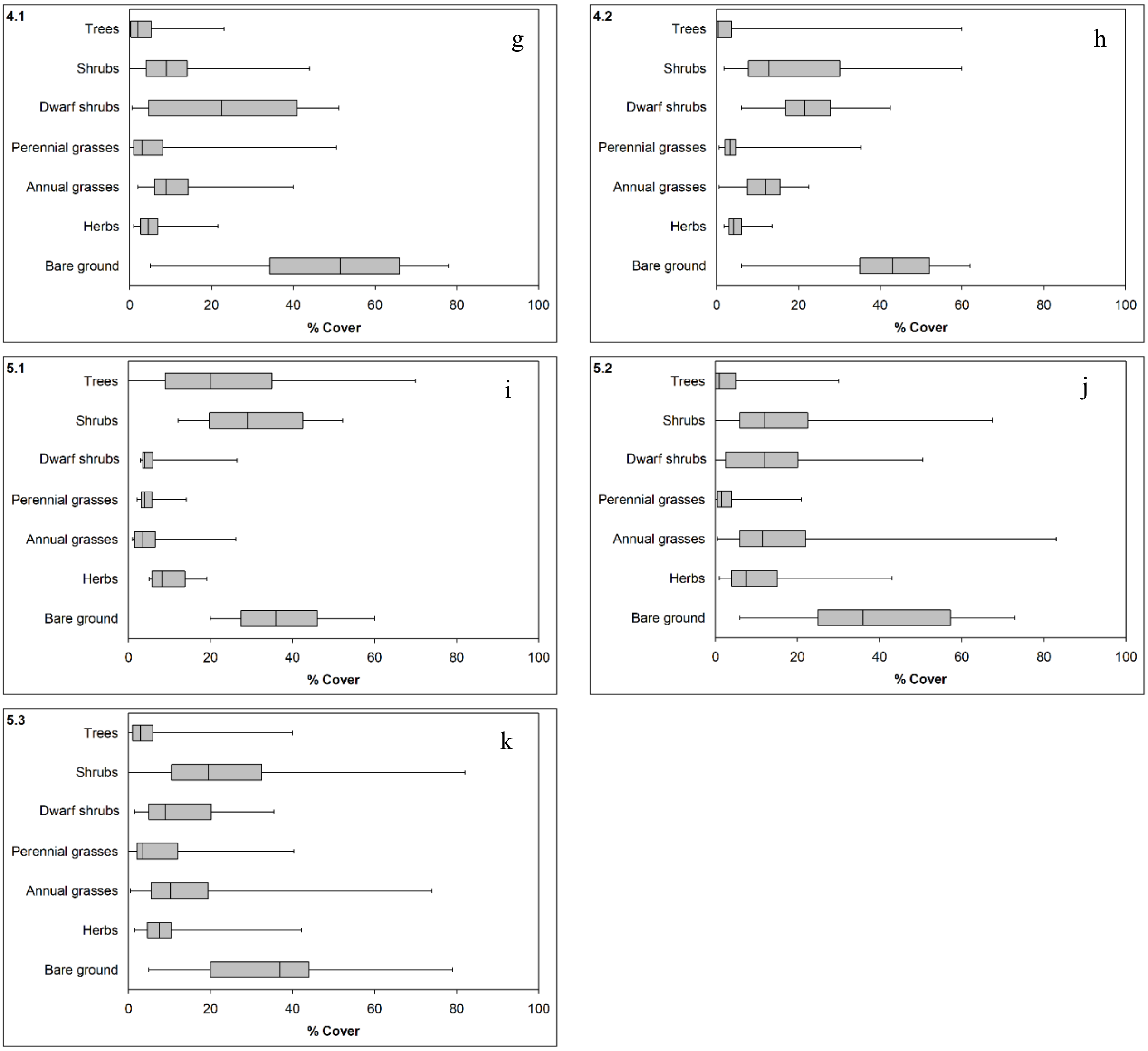

Figure 5 continued: *Box-and-Whisker plots of the average structure of the various associations. (g)* Acacia mellifera–Monechma genistifolium *association; (h)* Boscia foetida–Leucosphaera bainesii *association; (i)* Ziziphus mucronata–Acacia tortilis *association; (j)* Anthephora schinzii–Leucosphaera bainesii *association; (k)* Monechma genistifolium–Acacia tortilis *association.*

Dominant species: ***Acacia mellifera* subsp. *detinens***, ***Acacia tortilis* subsp. *heteracantha***, ***Ziziphus mucronata***, ***Achyranthes aspera* var. *aspera***

A large ephemeral river, with two smaller, but equally incised tributaries, forms the main drainage from south to north through the centre of Erichsfelde. The *Ziziphus mucronata–Acacia tortilis* association forms the ca 5 to 10 m wide embankment to these well-developed, deeply incised rivers. The riparian vegetation forms a short, sub-continous thicket, which is gradually replaced by the bushlands of the *Acacia mellifera—Monechma genistifolium* association (Figures 5i and 6i).

5.2. *Anthephora schinzii–Leucosphaera bainesii* clay soils association

Synopsis:
Number of relevés: 25
Number of species observed: 91
Estimated number of species: 190
Average species density per 1000 m^2: 31

Diagnostic species: *Aristida hordeacea*
Constant species: ***Acacia mellifera* subsp. *detinens***, ***Aristida adscensionis***, *Urochloa brachyura*, *Acacia tortilis* subsp. *heteracantha*, *Lycium eenii*, *Leucosphaera bainesii*, *Setaria verticillata*, *Chloris virgata*, *Cenchrus ciliaris*
Dominant species: ***Acacia mellifera* subsp. *detinens***, ***Leucosphaera bainesii***, ***Aristida adscensionis***, *Eragrostis porosa*, *Acacia tortilis* subsp. *heteracantha*, *Setaria verticillata*, *Enneapogon cenchroides*, *Dichrostachys cinerea*, *Chloris virgata*,

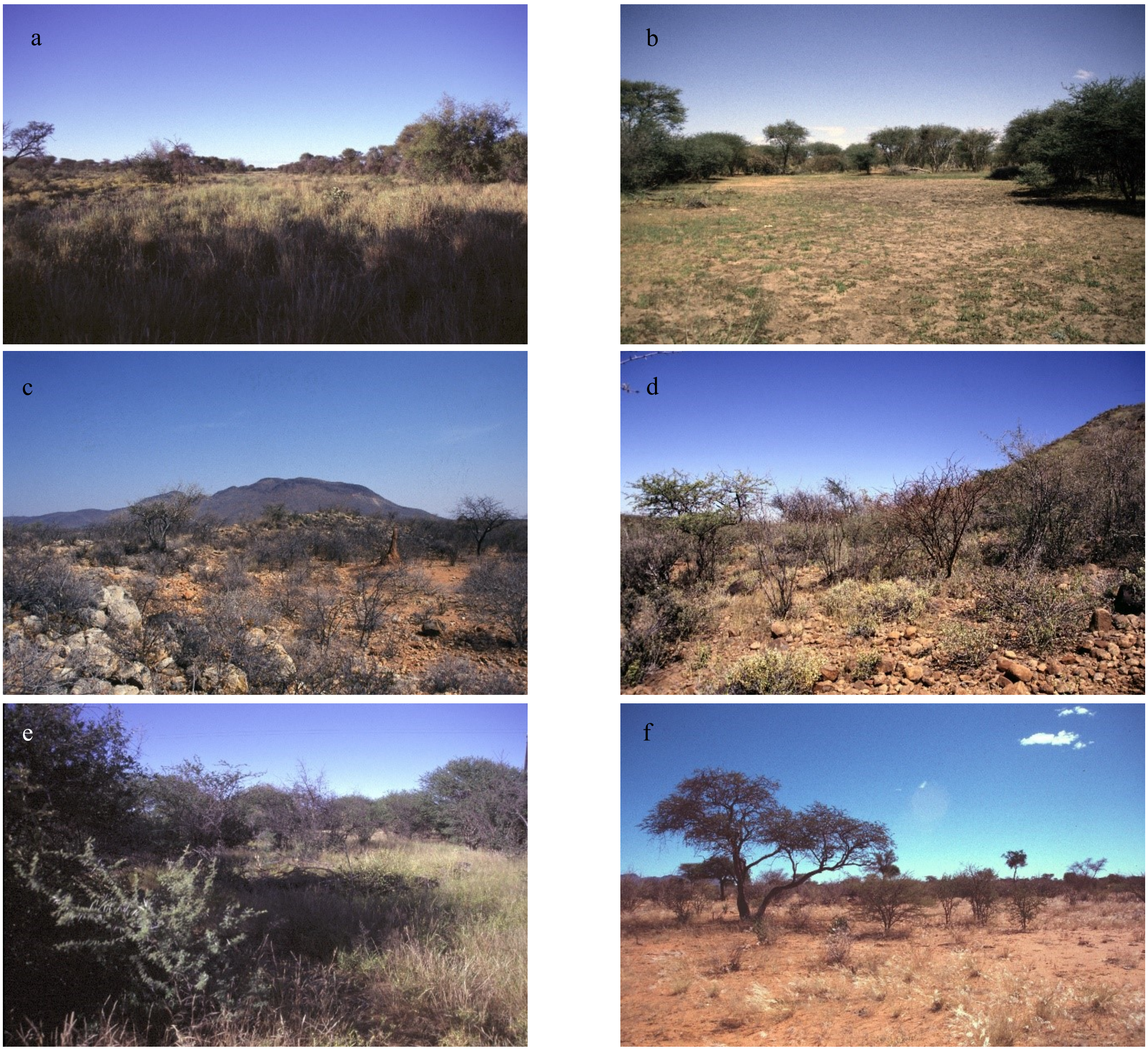

Figure 6: *Typical views of the various associations. (a)* Ziziphus mucronata–Dichanthium annulatum *association (relevé 901); (b)* Marsilea–Leptochloa fusca *association (relevé 770); (c)* Andropogon gayanus–Combretum apiculatum *association (relevé 789); (d)* Maerua parvifolia–Acacia erubescens *association (relevé 887); (e)* Ondetia linearis–Acacia mellifera *association (relevé 909); (f)* Aristida congesta–Acacia mellifera association *(relevé 829)*

Cenchrus ciliaris, *Bidens biternata*, *Anthephora schinzii*

At the base of the Ombotozo Mountain, a series of washes have developed with heavy clay soils as a product of weathering of the mudstones of the Omingonde formation. On these heavy soils the *Anthephora schinzii–Leucosphaera bainesii* association occurs. A few relevés of this association occur also on loamy floodplains in a mosaic with the *Monechma genistifolium–Acacia tortilis* association. Although the structure is a high, open shrubland dominated by *Acacia mellifera*, the actual diagnostic feature of this association is the dwarf shrub understorey dominated by *Leucosphaera bainesii* in association with the annual grass *Anthephora schinzii* (Figures 5j and 6j).

5.3. *Monechma genistifolium–Acacia tortilis* association

Synopsis:
Number of relevés: 33
Number of species observed: 160
Estimated number of species: 323
Average species density per 1000 m^2: 42

Diagnostic species: *Digitaria velutina*
Constant species: ***Aristida adscensionis***, ***Acacia mellifera* subsp. *detinens***, ***Kyphocarpa angustifolia***, ***Urochloa brachyura***, ***Pupalia lappacea***, *Grewia*

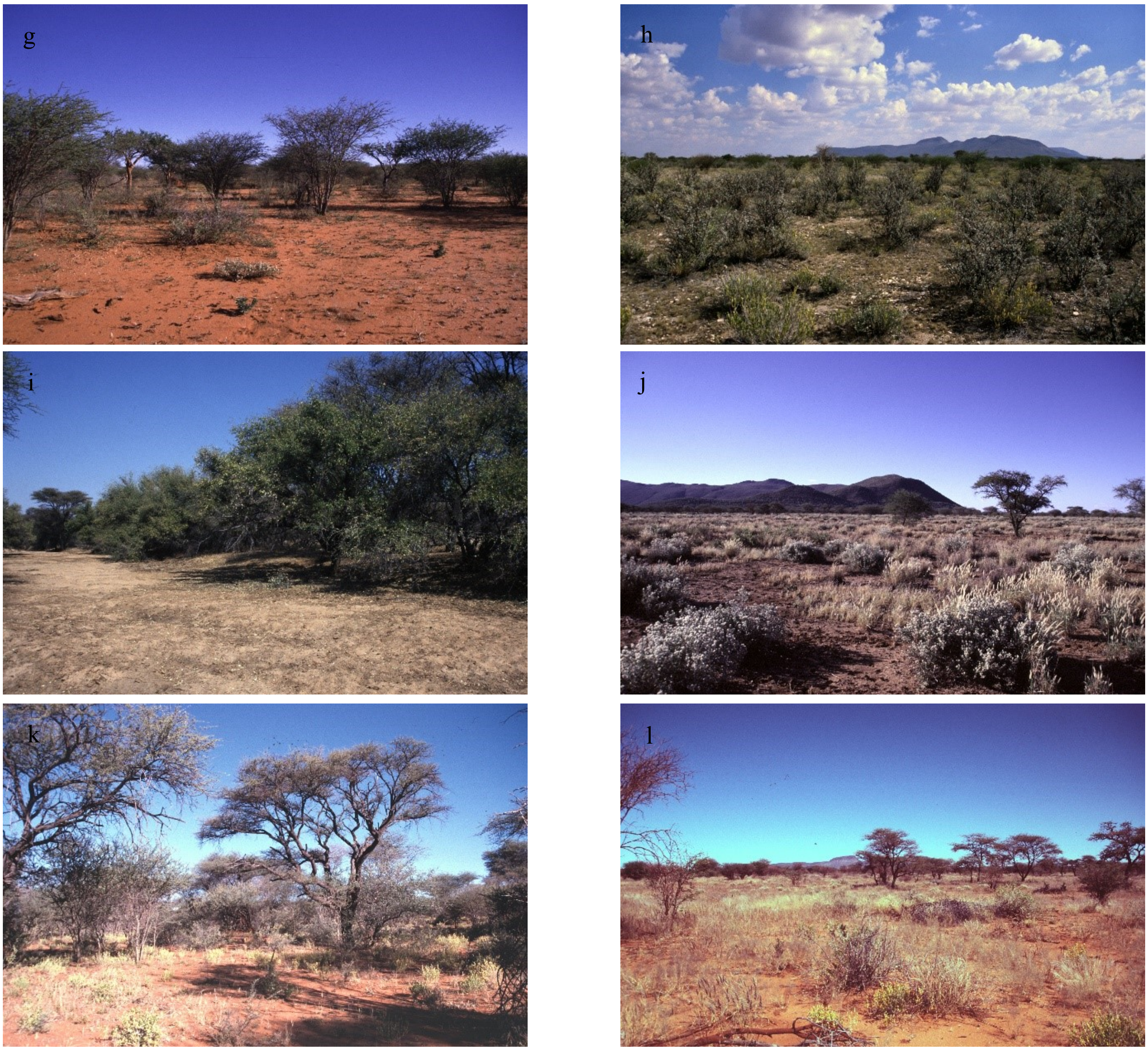

Figure 6 continued: *Typical views of the various associations. (g)* Acacia mellifera–Monechma genistifolium *association (relevé 854); (h)* Boscia foetida–Leucosphaera bainesii *association (relevé 760); (i)* Ziziphus mucronata–Acacia tortilis *association (relevé 782); (j)* Anthephora schinzii–Leucosphaera bainesii *association (relevé 898); (k)* Monechma genistifolium–Acacia tortilis *association in its closed form adjacent to the river floodplains (relevé 833); (l)* Monechma genistifolium–Acacia tortilis *association in its open form, away from the floodplains, transitioning to the plains habitats (relevé 816).*

flava, *Stipagrostis uniplumis* var. *uniplumis*, *Lycium eenii*, *Leucosphaera bainesii*, *Enneapogon cenchroides*, *Boscia albitrunca*, *Dichrostachys cinerea*, *Barleria lanceolata*, *Acacia tortilis* subsp. *heteracantha*, *Lycium bosciifolium*, *Talinum arnotii*, *Monechma genistifolium* subsp. *genistifolium*, *Eragrostis trichophora*

Dominant species: ***Acacia mellifera* subsp. *detinens***, ***Stipagrostis uniplumis* var. *uniplumis***, ***Monechma genistifolium* subsp. *genistifolium***, *Eragrostis porosa*, *Aristida adscensionis*, *Acacia tortilis* subsp. *heteracantha*, *Acacia hebeclada* subsp. *hebeclada*, *Ondetia linearis*, *Leucosphaera bainesii*, *Dichrostachys cinerea*, *Aristida rhiniochloa*, *Albizia anthelmintica*, *Acacia reficiens*

This vegetation forms a transition between the riparian thickets and associated floodplains, and the adjacent plains habitats. It is often an indicator for a degrading *omuramba* eroding to become an ephemeral river. Conspicuous is a gradual increase in trees, especially an increase of *Acacia tortilis* towards the riparian thickets on the riverbanks (Figures 6k and 6l). The structure varies accordingly from a tall, closed woodland to a tall, semi-open to bushland (Figure 5h).

Biodiversity indicators

The species richness per 1000 m^2, Shannon Index (H') and Simpson's Index (D) are depicted in Figure 7.

The narrow range of diversity for associations 1.1 and 1.2, and to a certain extent in 2.1 and 5.1, are likely a result of the low number of relevés sampled within these vegetation associations. The wide range of the lower quartile of Shannon Index as well as Simpson's Index data compared to the fairly compact upper three quartiles in most associations indicates a tendency for these associations to be encroached, dominated by a few phanerophytic species.

Environmental gradients

The NMS produced an ordination in three dimensions, with the final stress for the best solution being 17.920, and a final instability of 0.00000, after 95 iterations. The randomised data in the Monte Carlo test did not result in a stable solution after 249 iterations. The ordination graph is presented in Figure 8.

A great amount of overlap is evident between the various higher order syntaxonomic groupings (habitat types), indicative of the close relationship between the associations and the often ecotonal nature of these associations. There is however a clear split between the plains habitat (association 3.1 and 3.2) and the shallow calcareous soils associations (associations 4.1 and 4.2) visible along Axis 2. The main environmental drivers are the local topography along Axis 1, the soil pH as indicated by the proxy values along Axis 2, and the slope of the landscape along Axis 3. The vegetation reacts to these three main gradients by an increased number of shrubs towards the lower landscape positions (riverine habitats) as represented by Axis 1, a clear increase in dwarf shrubs along the pH gradient along Axis 2, and an increase in number of species and perennial grass cover towards the flatter landscapes, as indicated by Axis 3 (Figure 9).

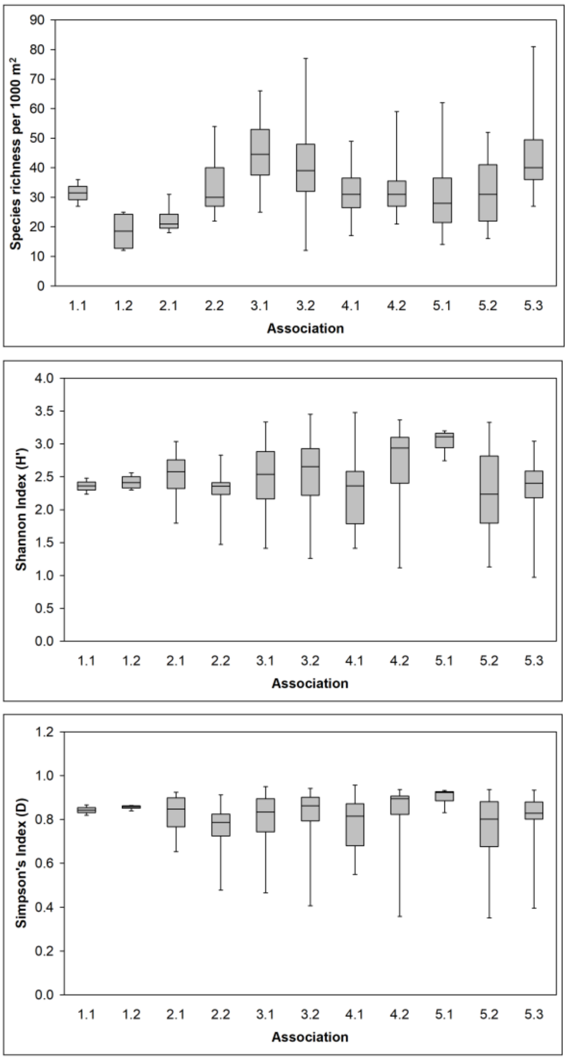

***Figure 7**: Diversity indicators for the various associations described. a) Species density per 1000 m^2; b) Shannon index and c) Simpson's Index*

Livestock Farming Suitability

Results for the Livestock Farming Suitability Index are presented in the graph in Figure 10. Detailed data and index values are presented in Online Appendix 3.

Typically, the suitability index has a maximum value of 2235. The following value-ratings have been set arbitrarily by Strohbach (2018):

- Unsuitable for livestock farming: <400
- Low potential for livestock farming: 400–800
- Moderate potential for livestock farming: 800–1200
- High potential for livestock farming: 1200–1600
- Very high potential for livestock farming: >1600

In all cases, the less a particular factor contributes to the farming suitability (or conversely, the more detrimental it is to livestock husbandry), the smaller is the portion of the bar for that particular factor. In this way the *Ziziphus mucronata–Dichanthium annulatum* association (1.1) scored a 'very high suitability' ranking due to its dense, perennial grass sward (as positive contributors) and little to no bush encroachment (as a detrimental contributor). Only the two plains habitat associations, the *Ondetia linearis–Acacia mellifera* association (3.1) and the *Aristida congesta–Acacia mellifera* association (3.2) are classed as having 'moderate suitability' for livestock farming, whilst all other associations are classed as 'low suitability' for livestock grazing. Key contributing factors are a high degree in bush encroachment (extreme in 2.1 and 5.1) as well as a fairly low grass cover, particular the low perennial grass cover. Only in the *Andropogon gayanus–Combretum apiculatum* association (2.1) no toxic species were found, which added to its potential suitability.

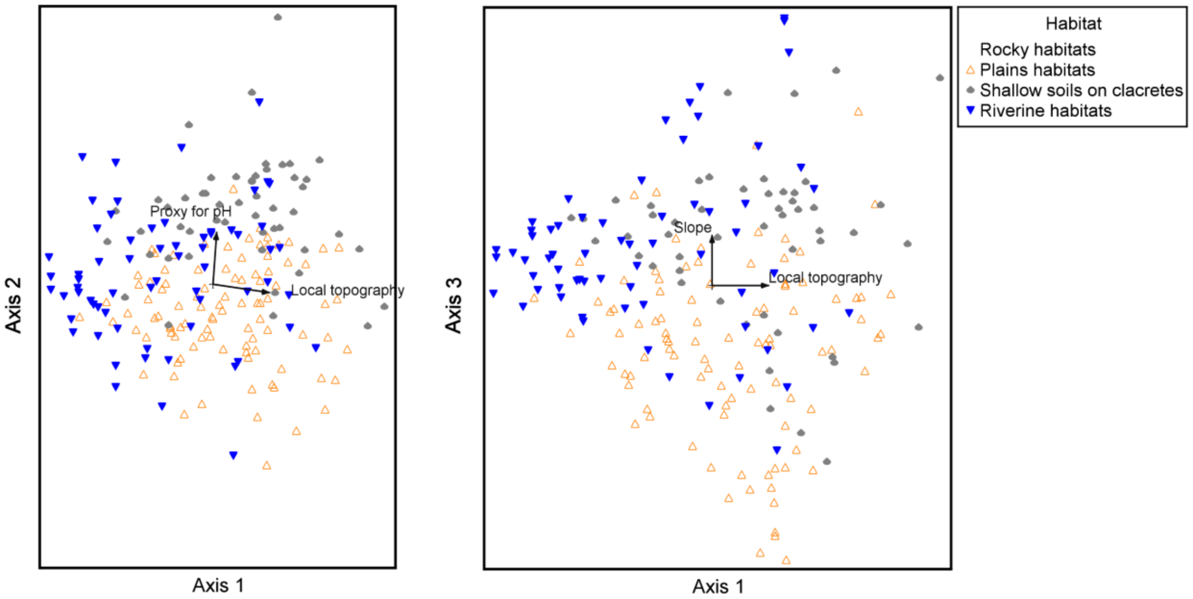

Figure 8: *NMS ordination diagrams, indicating both the identified higher order syntaxonomic groupings (habitat types) and driving habitat gradients.*

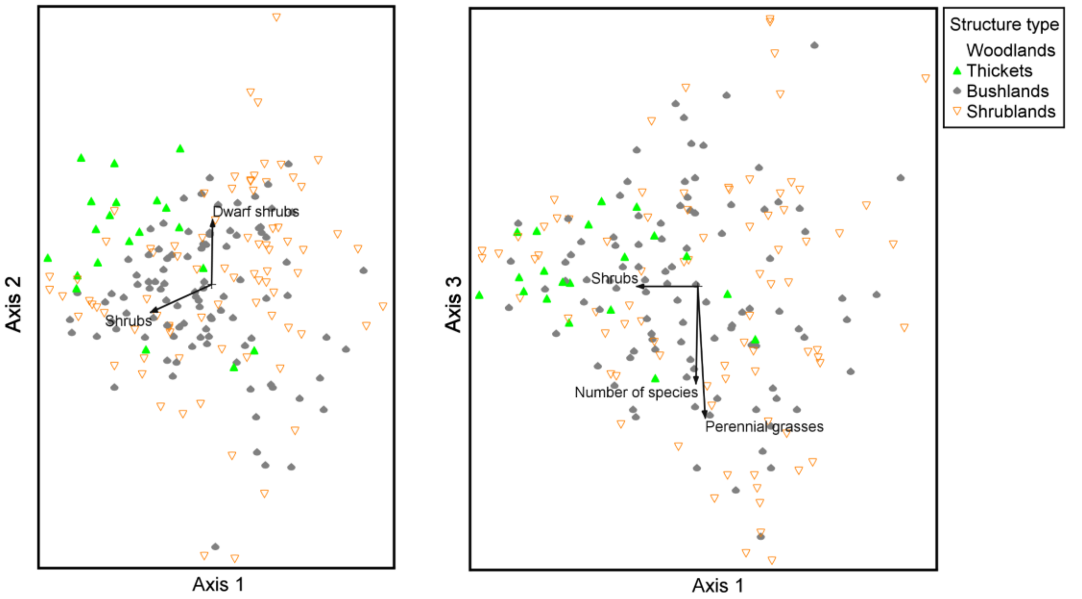

Figure 9: *NMS ordination diagrams, indicating both the vegetation structure types and reaction of growth forms and biodiversity to the environmental gradients indicated in Figure 8.*

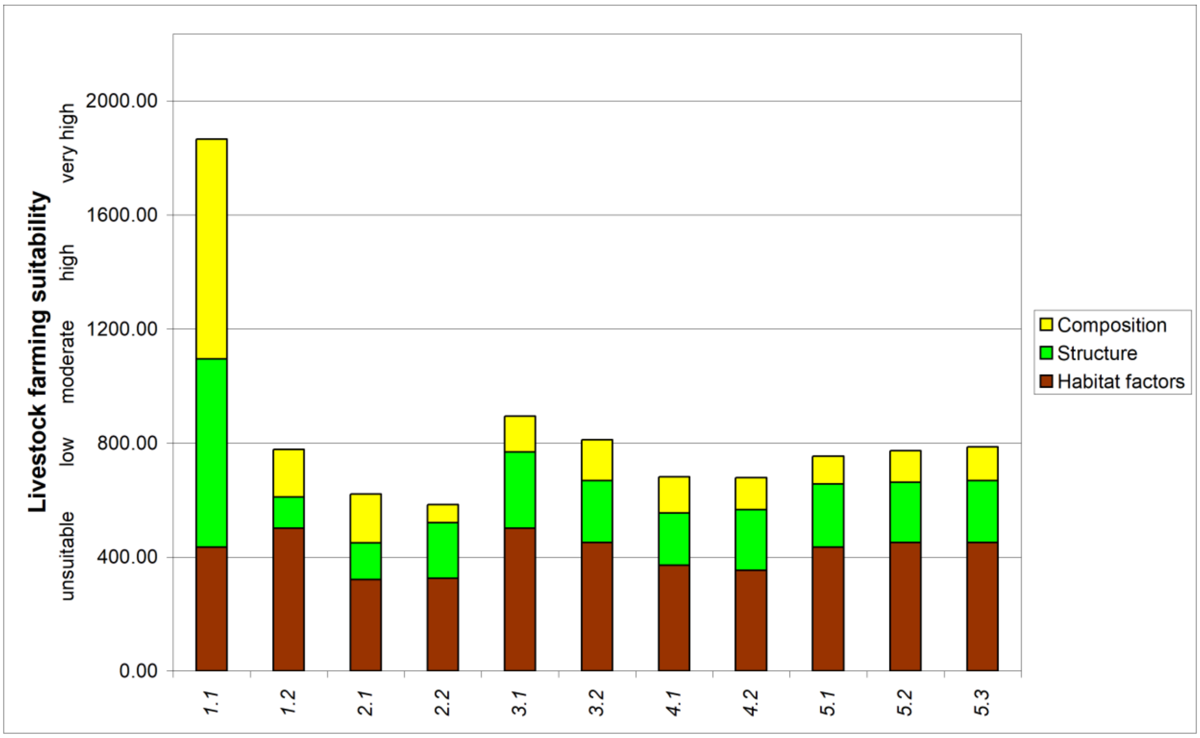

***Figure 10**: Overall Livestock Farming Suitability Index for the vegetation associations of the farm Erichsfelde*

Vegetation map

The vegetation map is displayed in Figure 11, whilst a summary map of the Livestock Suitability Index is displayed in Figure 12. The areas covered by the different vegetation association within the study area are displayed in Table 3.

DISCUSSION AND CONCLUSION

Although five distinct higher order syntaxonomic classifications could be identified, these could only be assigned to broad habitats, but neither ranked nor named, due to the limited spatial nature of the available data set. A comparison to data collected by Strohbach (2002) and other subsequently collected data (as part of the GIVD AF-NA-001 – Strohbach & Kangombe 2012) will provide a better appreciation of the higher-order groupings.

The limitations of the present data set are also evident in the estimated number of species for each association. For most associations, less than half the estimated number of species have been observed, indicating a severe shortcoming in the data set. The observed number of species fall within the range (300 – 399) given by Mendelsohn et al. (2002), as derived from Craven (2001) for the area, whilst the estimated number of 449 species for the entire study area (using

***Table 3:** Areas covered by the various vegetation associations on the Farm Erichsfelde in the Otjozondjupa Region*

Association	Area (m^2)	Area (ha)
1.1 *Ziziphus mucronata–Dichanthium annulatum* association	43,949	4.4
1.2 *Marsilea–Leptochloa fusca* association	25,754	2. 6
2.1 *Andropogon gayanus–Combretum apiculatum* association	3,859	0.4
2.2 *Maerua parvifolia–Acacia erubescens* association	637,263	63.7
3.1 *Ondetia linearis–Acacia mellifera* association	10,273,240	1,027.3
3.2 *Aristida congesta–Acacia mellifera* association	770,39,434	7,703.9
4.1 *Acacia mellifera–Monechma genistifolium* association	12,394,779	1,239.5
4.2 *Boscia foetida–Leucosphaera bainesii* association	6,649,862	665.0
5.1 *Ziziphus mucronata–Acacia tortilis* association	2,091,025	209.1
5.2 *Anthephora schinzii–Leucosphaera bainesii* association	11,383,751	1,138.4
5.3 *Monechma genistifolium–Acacia tortilis* association	7,567,499	756.7
Farm dams	212,089	21.2

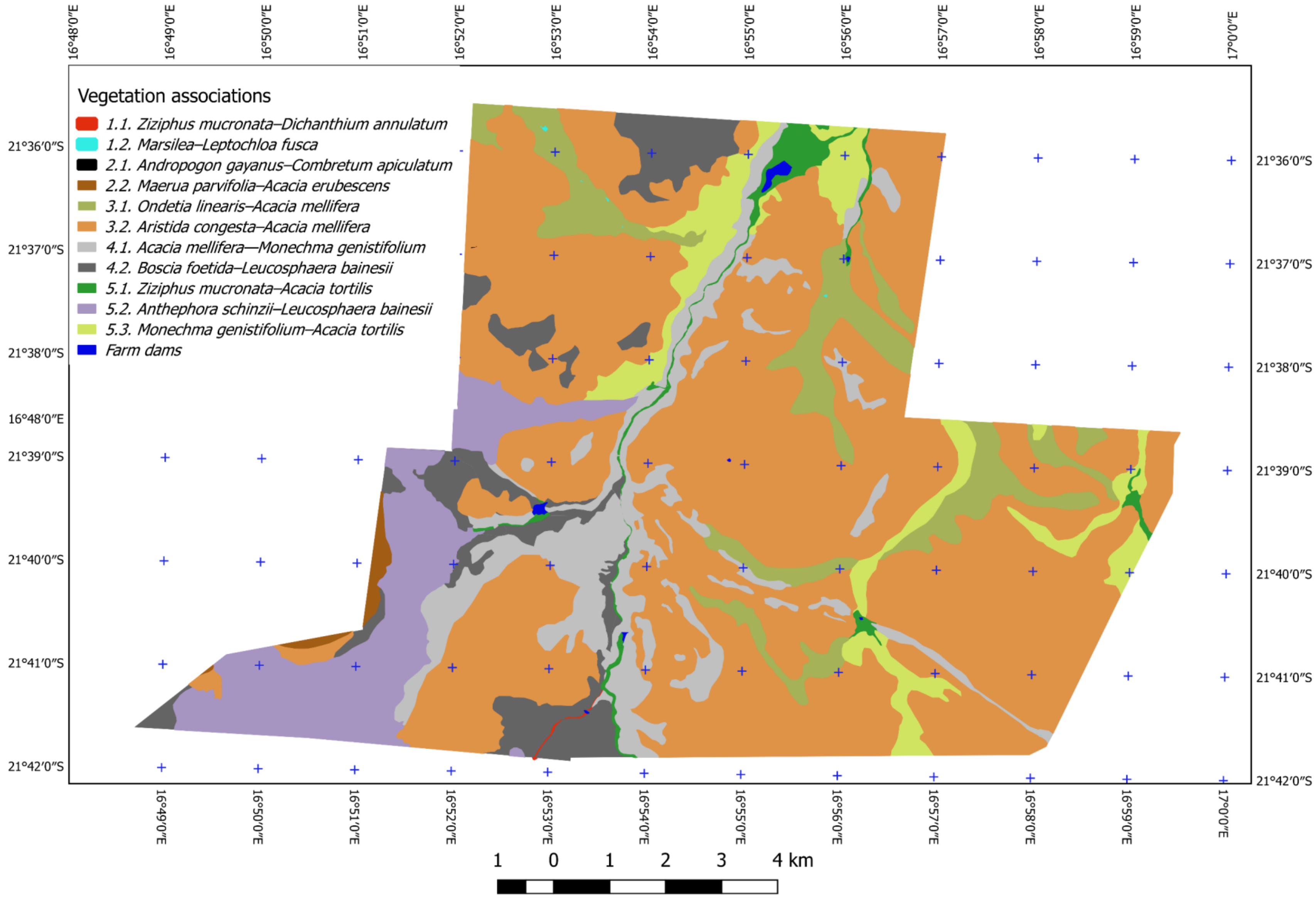

Figure 11: *Map of the vegetation associations described for Farm Erichsfelde.*

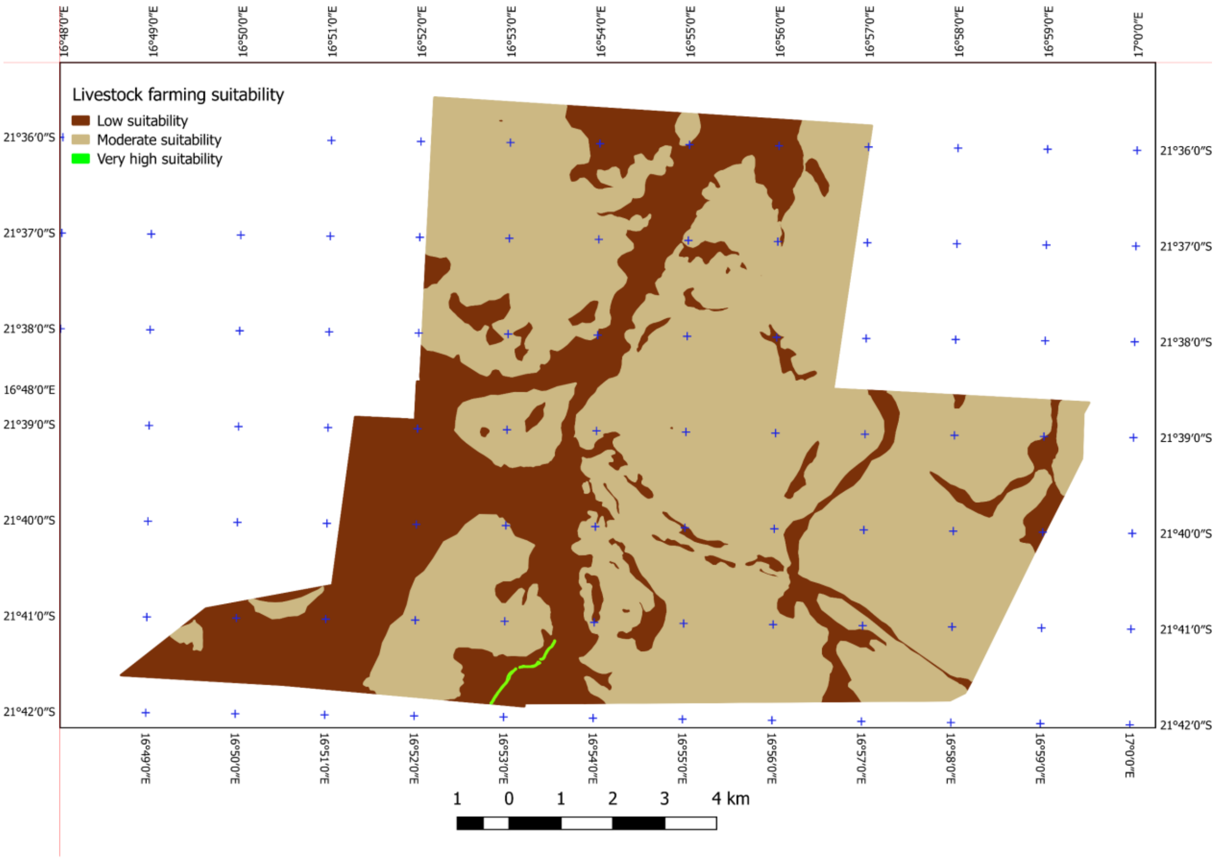

Figure 12: *Livestock farming suitability of the vegetation of Farm Erichsfelde, following the criteria described by Strohbach (2018).*

the first order Jackknife procedure) exceeds this number by far.

Grazing capacity especially for the semi-arid and arid regions, as is the case of central Namibia, is highly dependent on the often fluctuating rainfall. In the case of Erichsfelde, a CV of 44% of the long-term average since 1955 (352 mm) has been calculated (based on data supplied by the farm manager). Because of this high variability, no fixed grazing capacity (as provided e.g. within the Relative Homogenous Farming Areas report (Departement Landbou Tegniese Dienste 1979) can be determined. This problem has been highlighted by various authors before (Bester 1988, Lubbe 2005, Espach et al. 2006). For this reason the Livestock Suitability Index (Strohbach 2018) has been developed. This does not give a grazing capacity, but rather a Suitability Index based on the habitat, composition and structure of the vegetation. The calculated values indicate a reduction in suitability, if one considers that, in 1978, the vicinity of Erichsfelde was rated as the 'second best' farming area countrywide with a carrying capacity of 36 kg/ha. In relation, the highest class for the country was regarded as being able to carry 45 kg of live mass per ha, and the lowest only 4 kg/ha (Departement Landbou Tegniese Dienste 1979).

The main reason for the reduction in this suitability for livestock farming can be attributed to a steady increase in shrub and tree density ('bush encroachment') as well as a reduction in the density and quality of the grass sward (i.e. less high-value, perennial grasses, and a relative increase in low-value, annual grasses). Volk already commented on this in the 1960s (Volk 1966), whilst similar observations were made during recent studies (Jürgens et al. 2010 pp. 220–221). In particular, the *Ondetia linearis–Acacia mellifera* association (*omiramba*) were described by Volk in 1956 as nearly treeless, with a dense, perennial grass sward (Volk 1956), compared to the present-day tall, closed shrublands (Figures 4e and 5e). Similar ecosystems in the Highland Savanna were described as endangered by Volk & Leippert in 1971. This warning was confirmed by a recent study in the Auas-Oanob Conservancy in the Khomas Hochland that found these habitats to be eroded and/or encroached (Strohbach 2017).

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REFERENCES

Barnes S-J, Sawyer EW (1980) An alternative model for the Damara Mobile Belt: Ocean crust subduction and continental convergence. *Precambrian Research* 13: 297–336.

Bester FV (1988) Die bepaling van die grasproduksie van natuurlike veld. *Agricola* 6: 26–30.

Bester FV (1998) Major problem - bush species and densities in Namibia. *Agricola* 10: 1–3.

Botha L (1998) History of drought in Namibia. *Agricola* 10: 5–12.

Botta-Dukát Z, Chytrý M, Hájková P, Havlová M (2005) Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. *Preslia* 77: 89–111.

Bruelheide H (2000) A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science* 11: 167–178.

Burke A, Strohbach BJ (2000) Vegetation studies in Namibia. *Dinteria* 26: 1–24.

Chytrý M, Tichý L, Holt J, Botta- Dukat Z (2002) Determination of diagnostic species with statistic fidelity measures. *Journal of Vegetation Science* 13: 79–90.

Craven P (2001) *Phytogeography of Namibia: A taxon approach to the spermatophyte flora*. M.Sc. thesis, University of Stellenbosch, Stellenbosch, South Africa.

De Klerk JN (2004) *Bush Encroachment in Namibia. Report on Phase 1 of the Bush Encroachment Research, Monitoring and Management Project*. Ministry of Environment and Tourism, Windhoek.

De Pauw E, Coetzee ME, Calitz AJ, Beukes H, Vits C (1998) Production of an Agro-Ecological Zones Map of Namibia (first approximation). Part II: Results. *Agricola* 10: 33–43.

Dengler J, Jansen F, Glöckler F, Peet RK, De Cáceres M, Chytrý M et al. (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22: 582–597.

Departement Landbou Tegniese Dienste (1979) *Die afbakening van redelike homogene boerderygebiede van die noordelike en sentrale substreke van S.W.A. met die heersende knelpunte en beoogde ontwikkleingsprogramme vir die verskillende bedryfstakke*. Departement Landbou Tegniese Dienste, Windhoek.

Edwards D (1983) A broad-scale structural classification of vegetation for practical purposes. *Bothalia* 14: 705–712.

Espach C (2006) Rangeland productivity modelling: Developing and customising methodologies for land cover mapping in Namibia. *Agricola* 16: 20–27.

Espach C, Lubbe LG, Ganzin N (2006) Determining grazing capacity in Namibia: Approaches and methodologies. *Agricola* 16: 28–39.

Espach C, Lubbe LG, Ganzin N (2009) Determining grazing capacity in Namibia with the aid of remote sensing. *African Journal of Range & Forage Science* 26: 133–138.

FAO (1993) *Global and national soils and terrain digital databases (SOTER). Procedures manual*. Land and Water Development Division, Food and Agriculture Organisation of the United Nations, Rome.

Geological Survey (1980) *South West Africa/Namibia: Geological Map 1:1 000 000*. Geological Survey of the Republic of South Africa and South West Africa/Namibia, Windhoek, Namibia.

Gibbs Russell GE, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM, Dallwitz MJ (1990) *Grasses of southern Africa*. National Botanic Gardens/Botanical Research Institute, Pretoria.

Giess W (1998) A Preliminary Vegetation Map of Namibia. *Dinteria* 4: 1–112.

Gillet F, Julve P (2018) The integrated synusial approach to vegetation classification and analysis. *Phytocoenologia* 48: 141–152.

Glen HF, Perold SM (2000) Obituaries: Otto Heinrich Volk (1903-2000). *Bothalia* 30: 215–218.

Heltshe JF, Forrester NE (1983) Estimating Species Richness Using the Jackknife Procedure. *Biometrics* 39: 1–11.

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.

ICC, MAWRD, AECI (2000) *Project to support the Agro-Ecological Zoning Programme (AEZ) in Namibia. Main Report*. Institut Cartogràfic de Catalunya (ICC), Namibian Ministry of Agriculture, Water and Rural Development (MAWRD) and Spanish Agency for International Co-operation (AECI), Windhoek.

Irish J (1994) The biomes of Namibia, as determined by objective categorisation. *Navorsinge van die Nasionale Museum Bloemfontein* 10: 549–592.

Jürgens N, Haarmeyer DH, Luther-Mosebach J, Dengler J, Finckh M, Schmiedel U (eds) (2010) *Patterns at Local Scale: The BIOTA Observatories*. Klaus Hess Publishers, Göttingen & Windhoek.

Jürgens N, Schmiedel U, Haarmeyer DH, Dengler J, Finckh M, Goetze D et al. (2012) The BIOTA Biodiversity Observatories in Africa — a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment* 184: 655–678.

King LC (1963) *South African Scenery*, 3rd ed. Hafner Publishing Company, New York.

Klaassen ES, Kwembeya EG (eds) (2013) *A Checklist of Namibian Indigenous and Naturalised Plants*. National Botanical Research Institute, Windhoek.

Köppen W (1936) *Das Geographische System der Klimate*. Bornträger Verlag, Berlin.

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115–129.

Lubbe LG (2005) Towards an updated carrying capacity map for Namibia: A review of the methodologies currently used to determine carrying capacity in Namibia. *Agricola* 15: 33–39.

Mannheimer CA, Marais A, Schubert S (2012) *Toxic Plants of Veterinary Importance in Namibia*, 2nd revised. Ministry of Agriculture, Water and Forestry, Windhoek.

McCune B, Grace JB, Urban DL (2002) *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR.

McCune B, Mefford MJ (2016) PC-ORD. *Multivariate Analysis of Ecological Data*. MjM Software, Gleneden Beach, Oregon.

Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) *Atlas of Namibia*. David Phillips Publishers, Cape Town.

Müller MAN (2007) *Grasses of Namibia*, 2nd ed. Ministry of Agriculture, Water and Forestry, Windhoek.

NARIS (2001) *Namibian Agricultural Resources Information System (NARIS)*. Agro-Ecological Zoning Program, Ministry of Agriculture, Water and Rural Development, Windhoek.

Palmer MW (1990) The estimation of species richness by extrapolation. *Ecology* 71: 1195–1198.

Peck JE (2010) *Multivariate Analysis for Community Ecologists: Step-by-Step using PC-ORD*. MjM Software Design, Gleneden Beach, Oregon.

Peet RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* 5: 285–307.

Petersen A (2008) *Pedodiversity of southern African drylands*. Ph.D. thesis, University of Hamburg, Hamburg, Germany.

Pringle H, Tinley K (2003) Are we overlooking critical geomorphic determinants of landscape change in Australian rangelands? *Ecological Management & Restoration* 4: 180–186.

QGIS 2.14.5-Essen (2016) Open Source Geospatial Foundation (OSGeo).

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science* 20: 596–602.

SASSCAL 2014. SASSCAL WeatherNet - *Welcome to the weather stations of Angola, Botswana, Namibia and Zambia* [WWW Document]. SASSCAL WeatherNet - Welcome to the weather stations of Angola, Botswana, Namibia and Zambia. URL http://www.sasscalweathernet.org/index.php (accessed 21.10.17).

Schneider G (2004) *The Roadside Geology of Namibia*. Gebrüder Borntraeger, Berlin, Stuttgart.

South African Committee for Stratigraphy (1980) *Stratigraphy of South Africa Part 1: Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophutatswana, Transkei and Venda*. Dept. of Mineral and Energy Affairs, Pretoria.

Strohbach BJ (2001) Vegetation Survey of Namibia. *Journal of the Namibia Scientific Society* 49: 93–124.

Strohbach BJ (2013a) Vegetation of the Okavango River valley in Kavango West, Namibia. *Biodiversity & Ecology* 5: 321–339.

Strohbach BJ (2014) Vegetation of the Eastern Communal Conservancies in Namibia: I. Phytosociological descriptions. *Koedoe - African Protected Area Conservation and Science* 56: 18.

Strohbach BJ (2014) *Vegetation Survey of Namibia: Conceptualisation and implementation of a nation-wide vegetation survey serving practical land management needs*. Ph.D thesis, Department of Biology, Faculty of Mathematics, Informatics and Natural Sciences, University of Hamburg, Hamburg.

Strohbach BJ (2017) Vegetation of the Auas-Oanob Conservancy in the Khomas Hochland of Namibia. *Namibian Journal of Environment* 1: 19–42.

Strohbach BJ (2018) Making more of vegetation classification results: A Livestock Farming Suitability Index as tool for Land-Use Planning in Namibia. *Phytocoenologia* 48: 7–22.

Strohbach BJ, Jankowitz WJ (2012) Phytosociology of the Farm Haribes in the Nama-Karoo Biome of southern Namibia. *Koedoe - African Protected Area Conservation and Science* 54: 8–20.

Strohbach BJ, Jürgens N (2010) Towards a user-friendly vegetation map of Namibia: ground truthing approach to vegetation mapping. In: Schmiedel U, Jürgens N (eds) *Patterns and Processes at Regional Scale, Biodiversity in southern Africa*, 46–56. Klaus Hess Publishers, Göttingen & Windhoek.

Strohbach BJ, Kangombe F (2012) National Phytosociological Database of Namibia. *Biodiversity & Ecology* 4: 298.

Strohbach MM (2002) *Vegetation description and Mapping along a strip transect in central Namibia with the aid of satellite imagery*. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

Ter Braak CJF (1986) Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* 17: 809–818.

Tichý L, Holt J, Nejezchlebová M (2011) *Juice program for management, analysis and classification of ecological data. Program manual*, 2nd Edition. Vegetation Science Group, Masaryk University Brno, Brno, Czech Republic.

Volk OH (1956) *Vorläufiger Bericht über die Weideverhältnisse der Farm Erichsfelde, Bez. Okahandja*. Botanisches Institut der Universität Würzburg, Erichsfelde.

Volk OH (1966) Einfluß von Mensch und Tier auf die natürliche Vegetation im tropischen Südwest-Afrika. *Beiträge zur Landespflege* 11: 108–131.

Volk OH, Leippert H (1971) Vegetationsverhältnisse im Windhoeker Bergland, Südwestafrika. Journal der SWA *Wissenschaftliche Gesellschaft* XXV: 5–44.

Weber HE, Moravec J, Theurillat JP (2000) International Code of Phytosociological Nomenclature. 3rd edition. *Journal of Vegetation Science* 11: 739–768.

A baseline description of the soils and vegetation of Farm Klein Boesman, Khomas Region, Namibia

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ABSTRACT

The Farm Klein Boesman, south of Dordabis in the Khomas Region of Central Namibia, is situated on the ecotone between the Central Highlands/Central Plateau and the southern Kalahari. Whereas a considerable amount of information is available for the Kalahari Duneveld in South Africa, little is known of the same ecosystem in Namibia, specifically the northern extent of this ecosystem. We stratified the farm according to visible terrain features identified on aerial images, aided by a Shuttle Radar Topography Mission (SRTM) digital terrain model. Based on these initial stratification units, 35 minipits and/or soil augerings were done to sample the typical soil units. From these, soil samples were analysed for soil chemical and physical properties. In addition, 158 relevés were compiled across all initial stratification units. These were classified with modified Two-Way Indicator Species Analysis (TWINSPAN) using a synusial approach. From the results we described and mapped twelve landform and ten soil units, as well as six vegetation associations, of which two were subdivided into two and three subassociations each. We compare these associations with related vegetation types described in the Khomas Hochland as well as in the Kalahari Gemsbok National Park (KGNP) in South Africa. Although several similarities to units described for the KGNP were identified, several discrepancies were also identified, necessitating a thorough revision of the vegetation descriptions for the greater southern Kalahari.

Keywords: Dordabis mountainveld; Kalahari Duneveld; Namibia; phytosociology; soil characterisation; soil and terrain mapping; southern Kalahari; vegetation

INTRODUCTION

The Vegetation Survey of Namibia project as well as the Agro-Ecological Zoning (AEZ) project were initiated to provide much-needed baseline information for land-use planning purposes (De Pauw & Coetzee 1998, Strohbach 2001). Both projects followed an approach of both small-scale (nationwide or regional) overview mapping, as well as large-scale mapping of smaller areas (e.g. at farm level) to highlight specific features. In this sense, the AEZ project produced an initial Agro-ecological Zones (AEZ) and later a soils map for Namibia (De Pauw et al. 1998, ICC et al. 2000), whilst at a local scale the soils of several research stations of the Ministry of Agriculture, Water and Forestry were mapped (Coetzee et al. 1998, Kutuahupira et al. 2001a, b). Likewise, for the Vegetation Survey of Namibia project, regional descriptions and maps were completed for the Omusati and Oshana regions, the Central Namib, the Eastern Communal Areas and Namaland (Kangombe 2010, Jürgens et al. 2013, Strohbach 2014a, Strohbach & Kutuahupira 2014, Mbeeli 2018), whilst several large-scale studies have been published for Alex Muranda Livestock Development Center (Kavango West), Haribes (Hardap), Auas-Oanob Conservancy (Khomas) and Erichsfelde (Otjozondjupa) (Strohbach & Petersen 2007, Strohbach & Jankowitz 2012, Strohbach 2017, Strohbach 2019).

The Farm Klein Boesman south of Dordabis afforded the opportunity for a combined large-scale soil- and vegetation survey. The farm is of interest as it forms a transition between the Central Plateau and the Kalahari basin (in the sense of agro-ecological zones - De Pauw et al. 1998), as well as an ecotone between the Highland Savanna and mixed Tree- and Dwarf shrub savanna/southern Kalahari *sensu* Giess (1998). The mountainveld to the south-east of Windhoek had been described by Volk & Leippert (1971), but we regard the Dordabis Mountainveld as far more arid than the mountains south of the Auas Mountain Range. Likewise, a fair amount of information is available for the Kalahari Duneveld *sensu* Mucina & Rutherford (2006) in South Africa, in particular the Kalahari Gemsbok National Park (Leistner 1959, Leistner & Werger 1973, Van Rooyen et al. 1991a, Van Rooyen & Van Rooyen 1998, Van Rooyen et al. 2008, Van Rooyen 2008). Very little is however known from the same ecosystem in Namibia, in particular the northern extent of this ecosystem.

METHODS

Study area

The farm Klein Boesman (FMM/58/2) is situated south of Dordabis in the Khomas Region in central Namibia, near the M33 road between Dordabis and Uhlenhorst (Figure 1). The farm is 2196 ha in size and was split off the farm Compromise (FMM/58/1 and FMM/58/REM) in the 1990s. It has been used as a cattle farm with extensive rotational grazing.

Klein Boesman lies within agro-ecological zone (AEZ) CPL5 – a ‘flat plain on metamorphic rock, of the Central Plateaux’ (De Pauw et al. 1998). To the south, this is bordered by the Rooirand mountain, part of the Kamtsas formation (Geological Survey 1980), designated as AEZ ‘R’ – ‘undifferentiated rocky hills and inselberg mountains’. South of the Rooirand and Klein Boesman, the AEZ is ‘Kalahari Sand Plateau with longitudinal dunes in Growing Period Zone 2’ (KAL 2-7) (De Pauw et al. 1998). Although Klein Boesman lies outside KAL 2-7, Kalahari sands dominate the plains habitats of the farm (Figure 2).

The climate of Klein Boesman is a typical subtropical steppe climate following Köppen (1936). On average, precipitation is 260 mm per annum, falling as summer rainfall between December and April, with a coefficient of variation of more than 50%. Frost can occur during the winter months (May to August), with between 20 and 30 frost days a year (Mendelsohn et al. 2002). The average growing period is limited to 41 to 60 days, with no dependable growing period (Coetzee 1998, De Pauw et al. 1998). The vegetation forms an ecotone between the Highland Savanna and the Mixed Tree and Shrub Savanna (southern Kalahari) *sensu* Giess (1998).

Initial stratification

Preliminary landform units were mapped with QGIS software (QGIS 3.2.0-Bonn 2018) by visual interpretation, based on colour and texture differences, using Bing Maps – Aerial (Microsoft, 2019) satellite image, and terrain analysis using the Shuttle Radar Topography Mission (SRTM) 1 arc second digital elevation data (NASA JPL 2013). These preliminary units were used for a stratified systematic sampling approach for both soil- and vegetation surveys (Figure 3)

Landform and soil mapping

Visual and augering observations of the landforms and soils of the farm were followed by full site and soil profile descriptions at 35 points (Figure 3), using the FAO Guidelines for Soil Profile Description

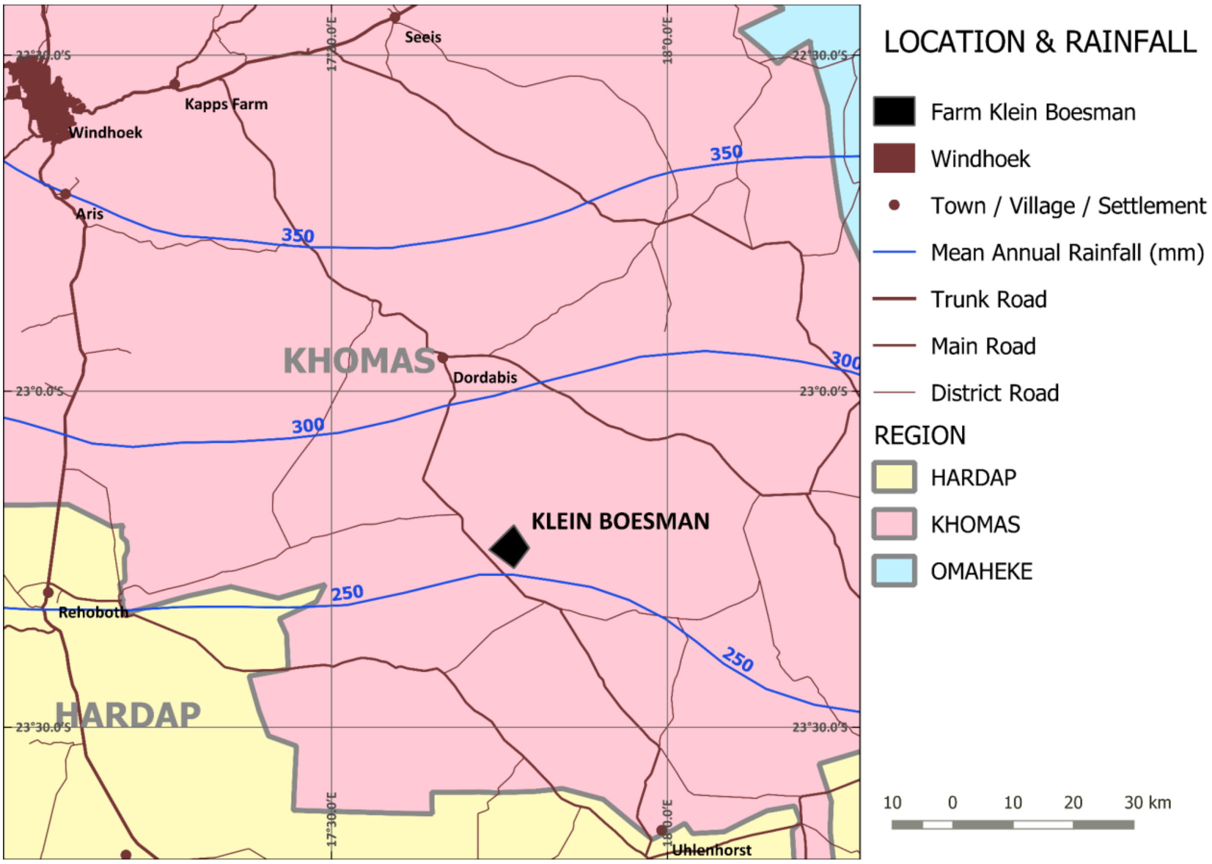

***Figure 1**: Location of farm Klein Boesman in south-eastern Khomas Region, in relation to long-term mean annual rainfall. Data sources: NARIS (2001); Office of the Surveyor General (2019).*

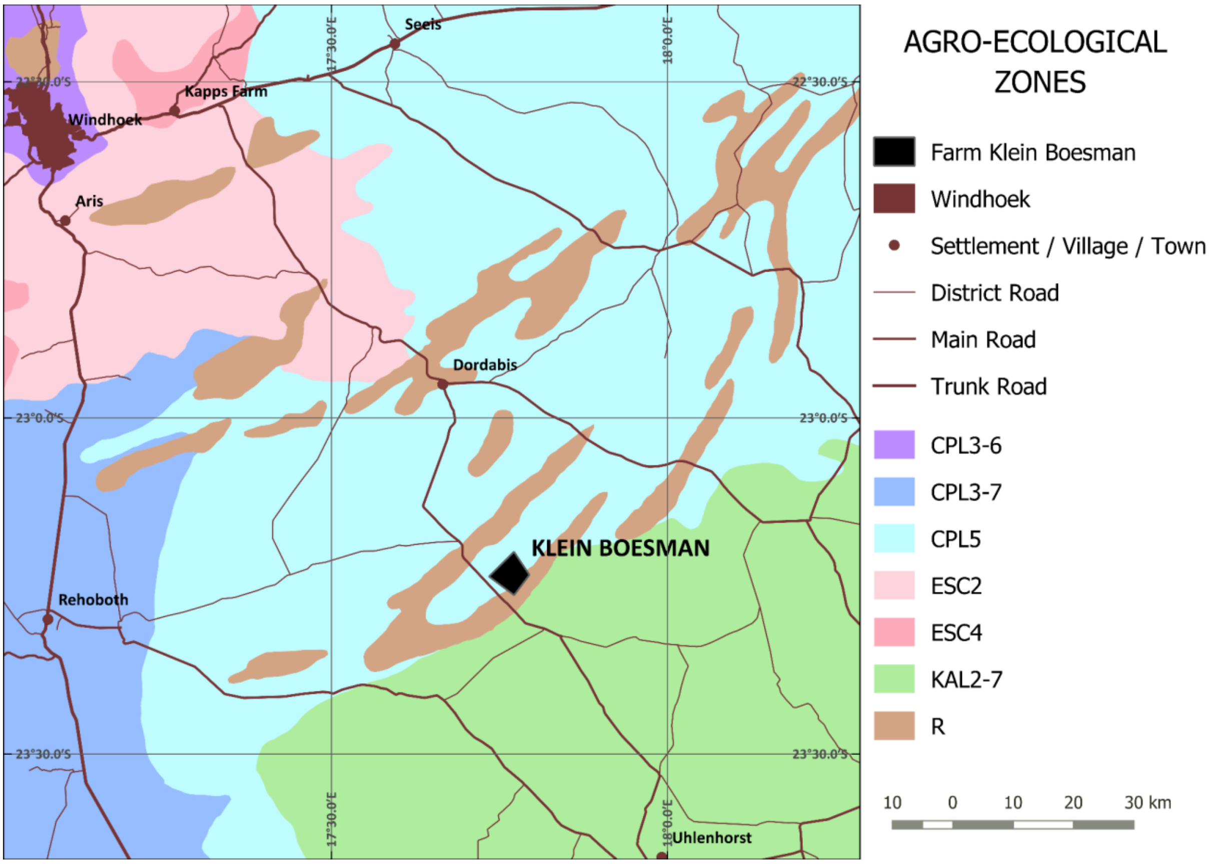

Figure 2*: Location of farm Klein Boesman, in relation to agro-ecological zones. Data sources: De Pauw et al. (1998); NARIS (2001); Office of the Surveyor General (2019).*

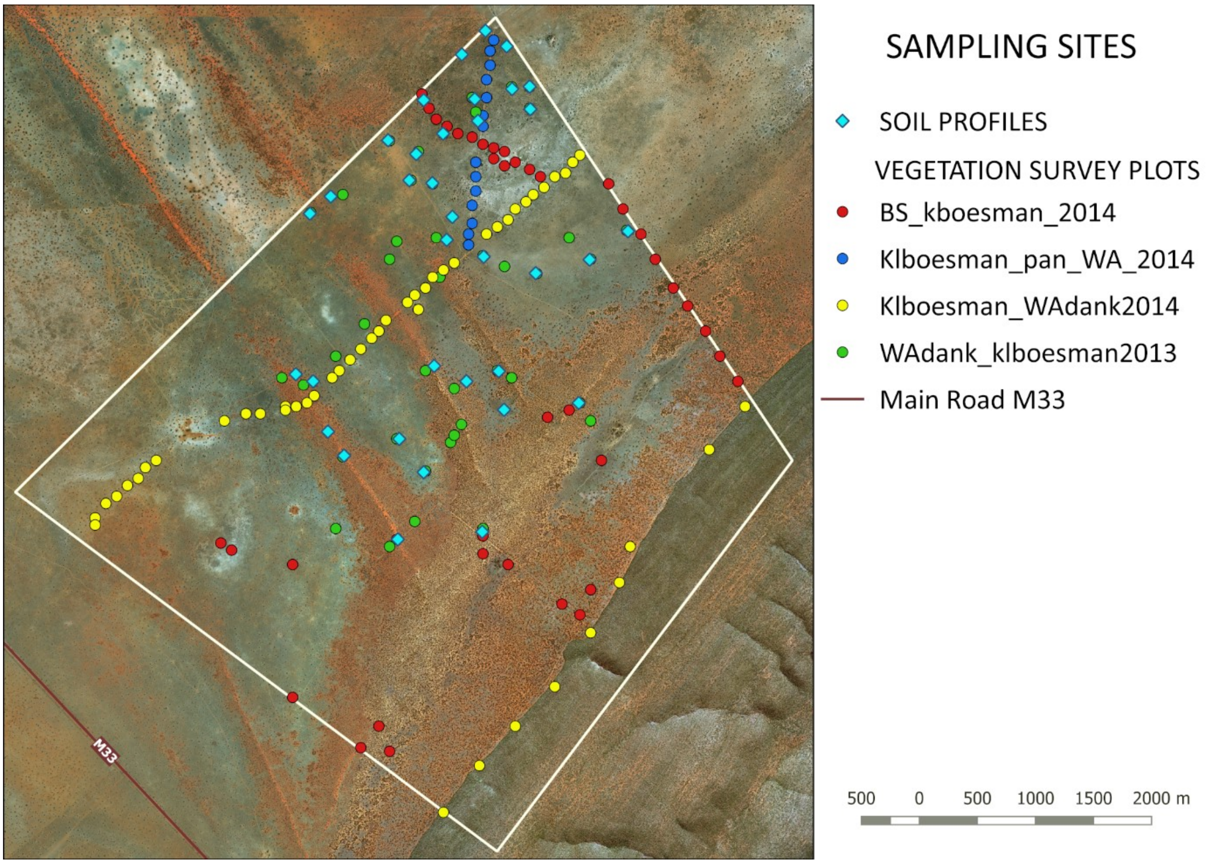

Figure 3*: Location of vegetation and soil sampling sites. Data sources: Microsoft (2019); Office of the Surveyor General (2019).*

(FAO 2006). Soil colour was determined with Munsell Soil Colour Charts (Munsell Color 2010). Chemical and physical analysis of 70 soil samples – 30 from A horizons and 40 from B horizons – were carried out by the Agricultural Laboratory of the Namibian Ministry of Agriculture, Water and Forestry, using their standard operating procedures (MAWF 2000). Samples were analysed for pH(H_2O); electrical conductivity; organic carbon; plant available phosphorus, potassium, calcium, magnesium and sodium; percentages sand, silt and clay; and an estimation of carbonates. Preliminary landform and soil mapping units were verified by ground observation and augerings, and adjustments made to unit boundaries and preliminary classes.

Vegetation surveys

Surveying followed the general method employed for the Vegetation Survey of Namibia project (Strohbach 2001, 2014b). At each survey plot (Figure 3) of 20 m x 50 m, a Braun-Blanquet type relevé was compiled. All vascular plant species occurring were noted down, as well as their typical growth forms and estimated crown cover. Habitat descriptors included the position by way of a GPS-reading, the landforms, local topography, slope and aspect, lithology, degradation indicators, as well as a photograph. Unknown species and reference specimens were collected, identified and deposited at the National Herbarium of Namibia (WIND). Nomenclature follows Klaassen & Kwembeya (2013) throughout. The relevé data were captured on TurboVeg (Hennekens & Schaminée 2001) as four different subsets of GIVD AF-NA-001 (Strohbach & Kangombe 2012) (Table 1). Data was cleaned following procedures described by Strohbach (2014b) prior to classification and mapping.

Data analysis

As considerable observer bias, combined with seasonal bias (see seasonal rainfall in Table 1), was evident, it was decided to reduce the matrix for classification to phanerophytes, chamaephytes and graminoids only (i.e. the main components of a savanna ecosystem). Non-graminoid forbs, specifically ephemeral forbs, were removed. This follows the synusial approach of vegetation classification described by Gillet & Julve (2018) (i.e. a classification using only some (semi-permanent) components of the floristic composition rather than including all species as per classical Braun-Blanquet approach). In addition, the growth form data were ignored (i.e. different growth forms of individual species combined). The matrix used for classification thus consisted of 158 relevés and 75 species. Classification was done with Modified Two-Way Indicator Species Analysis (TWINSPAN) within the Juice package (Tichý 2002, Roleček et al. 2009), using average Sørensen as distance measure without any pseudospecies. Classification was stopped after eight clusters were formed, giving the ecologically best interpretable results.

During analysis, it was found that cluster 3 (the *Acacia mellifera–Acacia erioloba* association) represented two structurally distinct units, on different habitats. These could not be differentiated purely on species composition. Therefore, the relevés for cluster 3 were re-extracted from the database with full growth form data. Again a synusial classification was done using Modified TWINSPAN and average Sørensen as distance measure. However, for this classification, pseudospecies cut levels were set at 0, 5 and 20%. With these pseudespecies levels, the units dominated by *Acacia erioloba* trees could easily be differentiated from units dominated by *Acacia mellifera* shrubs, and thus also differentiating between the two structural types.

Table 1: *Metadata for the GIVD AF-NA-001 data subsets used for this study, as shown in Figure 3.*

Surveyor	Data sets	Relevé sequence numbers	Number of relevés	Survey dates	Rainfall for season (September to August)
Jankowitz & Adank	WAdank_klboesman2013 (initial reconnaissance survey)	11424 – 11434	11	February & May 2012	342 mm
Jankowitz & Adank	WAdank_klboesman2013 (survey of main habitats)	11435 – 11474	40	April & May 2013	56 mm
Jankowitz & Adank	Klboesman_WAdank2014 (cross-section of farm)	11915 – 11968	53	April 2014	246 mm
Strohbach	BS_klboesman_2014 (cross-section of pan and gap-filling survey)	11746 – 11786	40	April 2014	246 mm
Jankowitz & Adank	Klboesman_pan_WA_2014 (cross-section of pan)	2161 – 2174	14	April 2014	246 mm

From the final classification, a phytosociological and a synoptic table were created, using the original full matrix with 240 species (including herbs and forbs). Diagnostic species were determined using the phi coefficient of association (Chytrý et al. 2002). For this calculation the numbers of relevés were standardised following Tichý & Chytrý (2006). Species with phi≥40 were considered as diagnostic and with phi≥60 as highly diagnostic; however, species with a non-significant fidelity at $\alpha=0.05$ using Fisher's exact test were omitted. Species occurring with at least a 60% frequency were regarded as constant and with at least an 80% frequency as highly constant.

Box-and-Whisker plots were constructed to illustrate the structure for each grouping (i.e. tree, shrub, dwarf shrub, perennial grass, annual grass and herb cover), using available growth form data. Description of the vegetation structure follows Edwards (1983). The Shannon Index (as an index of evenness) ($H'=-\Sigma\ p_i \ln p_i$) and Simpson's Index (as an index of dominance) ($D=\Sigma(n/N)^2$) (Peet 1974) were calculated for each relevé using Juice (Tichý et al. 2011).

Vegetation Mapping

The landform and soil maps were used as a baseline for the vegetation map. Soil mapping units were assigned to specific vegetation associations based on the positions of the classified relevé data. In some cases, the mapping units had to be adjusted based on the findings of the vegetation classification results. This was done by visual interpretation of Bing Maps – Aerial (Microsoft 2019) satellite images and adjusting the digitised mapping units.

RESULTS

Landforms and soils

The landscape is dominated by a quarzite ridge (the Rooirand) along the south-eastern border of the farm as part of the Kamtsas formation of the Nosib group (Geological Survey 1980, Killick 1983). This ridge rises to 1605 m above mean sea level at its highest peak on the SE corner of the farm, or 206 m above the lowest point of the surrounding plain (NASA JPL 2013). The plains to the north of this ridge are extensively covered by wind-deposited sands of the adjacent southern Kalahari, forming a series of dunes in the typical NW-SE orientation (Bullard et al. 1995). These rise to between 15 and 33 m (highest is 43 m) above the surrounding plain (NASA JPL 2013). Parallel to the quartzite ridge, a low-angle (3-6% slope) sand ramp has formed (Lancaster & Tchakerian 1996, Rowell et al. 2017). In the far north-eastern corner of the farm, limestones of the Buschmannsklippe Formation of the Kuibis subgroup are covered by a thin soil veneer (Geological Survey 1980, South African Committee for Stratigraphy 1980, Hegenberger 1993). Here, a pan has formed through deflation. The blown-out material had been deposited to the south as a low lunette dune, grading into the more acidic sands of the Kalahari dunes (Hipondoka et al. 2004, Wang et al. 2007, Bhattachan et al. 2015).

Twelve landforms were identified (Figure 4): mountain (quartzite ridge), dune crest; dune slope; dune footslope; interdune valley; plain; sand drift plain; sand ramp; pan; pan rim; depression; lunette dune. Footslopes grade into interdune valleys, locally known as 'streets'. A sand ramp lies between the northwest-southeast trending linear dunes and the north-western flank of the mountain. The large pan in the northeast quadrant grades into a shallow lunette dune to the south. The western corner of the farm is a sandy plain with shallow (<25 cm) to moderately deep (25-50 cm) sand cover and a shallow depression. Two other small depressions occur in one of the interdune valleys.

A detailed listing of soil characteristics is presented in online Appendix 1. These are mapped in Figure 5.

1. Shallow, very stony brown soil of the mountain slope

The **Brunic Skeletic Leptosol (Colluvic)** of the moderately steep (24-30% slope) mountain slope was formed *in situ* from weathering of the quartzitic parent material. The steepness, and surface and subsurface stoniness make this unit less suitable for livestock farming, although game, especially kudu (*Tragelaphus strepsiceros*), were seen on the slopes.

2. Very deep, red sand of the dune crests

Protic Chromic Arenosol (Aeolic) occurs on the convex-sloped dune crests. Slight erosion activity (both raindrop splash and aeolian) is visible over more than 50% of the surface. This soil is very deep (>700 cm), with a red colour (2.5YR4/6 – 2.5YR4/8). There is no significant difference in colour with increasing depth. Moistening results in a slight increase in chroma. Soil horizon development is very poor, with a 40-60% increase in clay content to mark the transition from the thin A horizon (3-8 cm thick) to the deep B horizon. Though the percentage increase in clay seems high, the clay content is actually very low: less than 2% in the A horizon, increasing to 2-6% in the B horizon. Both horizons are sandy, with more than 92% sand content (coarse sand in the topsoil and medium sand in the subsoil) and virtually no silt. This soil is structureless (single grain) with loose consistency of the topsoil in both the wet and moist states, and loose to very soft or friable consistency of the subsoil in the dry and moist states respectively. The low clay content means that it is non-sticky and non-plastic when wet. There are no impediments to root development. Chemical analysis shows that organic carbon (OC<0.25%) and phosphorus (P<2 ppm) contents are very low, on

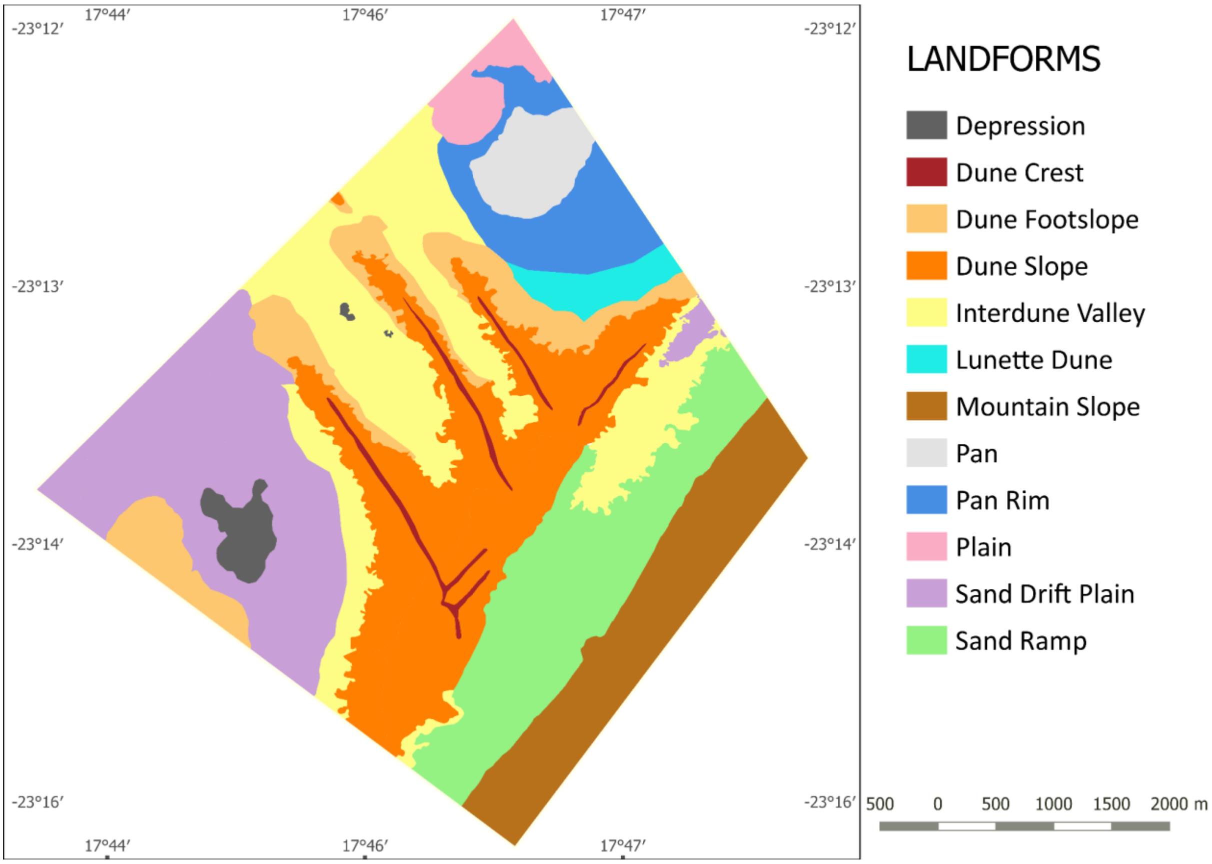

***Figure 4**: Landforms of farm Klein Boesman.*

account of the low vegetation cover on dune crests. Basic cation concentrations are very low, as can be expected from the parent material – single grained quartz of aeolian origin – and the sandy texture: topsoil water-soluble potassium (K) 17-22 parts per million (ppm), calcium (Ca) 99-208 ppm, magnesium (Mg) 28-42 ppm, sodium (Na) 10-14 ppm; subsoil water-soluble potassium (K) 21-35 ppm, Ca 58-134 ppm, Mg 18-46 ppm, Na 4-16 ppm. This also accounts for the slightly acidic nature of the soil (pH 5.2-5.9). There are no primary or secondary carbonates, no mottling or concretions. Quartz grains have a reddish hematite coating, which implies that water infiltration and internal drainage are very rapid and soil aeration very good. [Representative profiles: 4, 31, 32, 34]

3. Deep, reddish sand of the dune slopes, footslopes and sand ramp

Chromic Arenosol (Aeolic) occurs on dune slopes. Slight erosion activity has been observed (both raindrop splash and aeolian) over more than 50% of the surface. This soil is deep (>200 cm on lower slopes) to very deep (>700 cm on upper slopes), with a red to yellowish red colour (hue 2.5YR-5YR, value 3.5-4, chroma 4-6). There is no significant difference in colour with increasing depth. Soil horizon development is poor, with a 30-40% increase in clay content from the thin A horizon (5-10 cm thick) to the B horizon. Topsoil clay content is higher than on dune crests: 2.3-2.6% in the A horizon, increasing to 3.2-4.5% in the B horizon. Both horizons are sandy, with more than 90% sand content and slightly more silt (1-3%) than on dune crests. This soil has weak, fine, subangular blocky to rounded structure and soft (when dry) or very friable (when moist) consistency in the subsoil, while the topsoil is structureless (single grain) with loose consistency in both the wet and moist states. The low clay content means that it is non-sticky and non-plastic when wet. There are no impediments to root development. OC (0.2-0.6%) and P (2-7 ppm) contents are low, but slightly higher than on dune crests. Concentrations of bases are very low, but noticeably higher than on dune crests: topsoil water-soluble K 47-178 ppm, Ca 78-253 ppm, Mg 19-62 ppm, Na 3-23 ppm; subsoil water-soluble K 28-169 ppm, Ca 93-182 ppm, Mg 27-38 ppm, Na 0-26 ppm. The slope soils are less acidic than dune crest soils, with pH 5.9-6.6. There are no primary or secondary carbonates, no mottling or concretions. Quartz grains are mainly coated with reddish hematite, but the somewhat more yellowish red colour of some grains reflects the presence of soil water for longer periods than on dune crests. Water infiltration and internal drainage are still quite rapid and soil aeration good. [Representative profiles: 26, 27, 28, 29].

4. Deep, red to dark reddish brown sand of interdune valleys ('streets')

Chromic Arenosol (Aeolic) is found in sandy interdune valleys, generally with a slope of less than 1%. This soil is deep (>200 cm), with an A horizon of about 7-12 cm thick, and red to dark reddish brown colour (2.5YR4/6 – 2.5YR3.5/5). The entire profile is sandy, though the clay content increases with depth: from about 3.2% in the A horizon to 6-8% in the B2 horizon. This accounts for the subsoil's very weak, fine subangular blocky structure, and soft (when dry) and very friable (when moist) consistency. The low clay content means that this soil is non-sticky and non-plastic when wet. There are no impediments to root development. pH is below normal (5.4-6.5) and similar to that of dune slopes. OC (<0.6%) and P (<8 ppm) contents are low, and concentrations of bases are relatively low: topsoil water-soluble K 60-62 ppm, Ca 278-394 ppm, Mg 66-87 ppm, Na 11-12 ppm; subsoil water-soluble K 51-81 ppm, Ca 272-379 ppm, Mg 67-108 ppm, Na 11-15 ppm. These soils are not calcareous. There are no mottles or mineral concretions. Water infiltration, internal drainage and aeration are very good. Slight raindrop splash and aeolian erosion activity is visible over more than 50% of the surface. [Representative profiles: 30, 35]

5. Moderate to deep brownish to yellowish red soil of the sand drift plains

Brunic Arenosol (Aeolic) occurs on level to very gently sloping (0.2-2% slope) sand drift plains. This soil is moderate to deep (50 cm->100 cm), reddish brown to yellowish red (hue 5YR, value 4, chroma 3-6) when moist, and brown to strong brown (hue 7.5YR-5YR, value 4-5, chroma 4-6) when dry. Soil horizon development is poor, but slightly better than that of the dunes. The soil is sandy throughout the profile, with more than 90% sand, while topsoil clay content is 3.0-3.7%, increasing only slightly with depth. The thin (5 cm thick) topsoil is structureless (single grains), with loose consistency, whether dry or moist. Structure of both B1 and B2 horizons is weak, subangular blocky, with B1 structural elements smaller than that of B2. Consistency of B1 and B2 is soft and slightly hard when dry, and friable and firm when wet, respectively. The low clay content means that it is non-sticky and non-plastic when wet. There are no impediments to root development. OC (0.2-0.4%) and P (1-13 ppm) contents are low, but slightly higher than on dunes. Concentrations of bases are low, but noticeably higher than on dune crests: topsoil water-soluble K 185-224 ppm, Ca 145-180 ppm, Mg 54-86 ppm, Na 5-18 ppm; subsoil water-soluble K 243-274 ppm, Ca 144-212 ppm, Mg 67-86 ppm, Na 7-43 ppm. pH ranges from 6.54 to 7.02. There are no primary or secondary carbonates, no mottling or concretions. The brownish colour is imparted by a mixture of reddish hematite and yellowish goethite coatings on quartz grains, reflecting the presence of soil water for longer periods than on dunes. Water infiltration, internal drainage and aeration are good. Slight raindrop splash and aeolian erosion activity is visible over more than 50% of the surface. [Representative profiles: 5, 10, 11, 21].

6. Shallow brownish to yellowish red soil of the sand drift plains, on calcrete

A smaller unit of virtually identical, but shallower (20-50 cm) **Brunic Arenosol (Aeolic)**, underlain by calcrete, occurs within the sand drift plain.

7. Shallow brownish soil on calcrete, underlain by limestone

Brunic Leptosol occurs in the north-eastern corner of the study area. Despite being underlain by shallow pedogenic calcrete (outcropping on <2% of the surface) and containing calcrete nodules, there is little free calcium carbonate in the profiles. Both field and laboratory tests show that this soil is mildly calcareous. The pH is 7.2-8.3. This soil is generally shallow (<50 cm) and brown to strong brown (hue 7.5YR-5YR, value 4-5, chroma 4-6) when dry. There are clear differences between the thin (1-5 cm thick), sandy, single-grained A and the loamy sand to sandy loam, weak subangular to angular blocky B horizons. Clay content of the B horizon is up to 20% just above the calcrete. This clay enrichment of subsoil can be ascribed to the presence of the calcrete hardpan, which impedes water percolation. While topsoil consistency is loose, the subsoil is slightly hard when dry and friable to very friable when wet. OC (0.2-0.9%) and P (<7 ppm) contents are low. Concentrations of bases show higher calcium than in the rest of the study area: topsoil water-soluble K 129-308 ppm, Ca 371-966 ppm, Mg 34-76 ppm, Na 5-11 ppm; subsoil water-soluble K 102-408 ppm, Ca 345-1243 ppm, Mg 38-114 ppm, Na 5-18 ppm. Slight raindrop splash and aeolian erosion activity is visible over more than 50% of the surface. [Representative profiles: 1, 2, 13]

8. Shallow, clayey soil of the pan

The clay pan soil, **Gleyic Cambisol (Clayic, Takyric)**, is non-saline and only mildly calcareous, though it is shallowly underlain by calcrete. The low position in the landscape accounts for the accumulation of finer material and thus the presence of laminar clay at the surface, that cracks into large blocks when dry. The colour grades from light gray (2.5Y7/2), indicating periodic waterlogged, reducing conditions, to light brown (7.5YR6/3-4).

9. Shallow soil of the pan rim and depressions

The **Eutric Cambisols** of the three depressions and pan rim are shallow, non-saline, non-calcareous, light brown (7.5YR6/3-4) to brown (7.5YR4-5/3-4), with slightly higher silt content than the surrounding plains and shallowly underlain by calcrete.

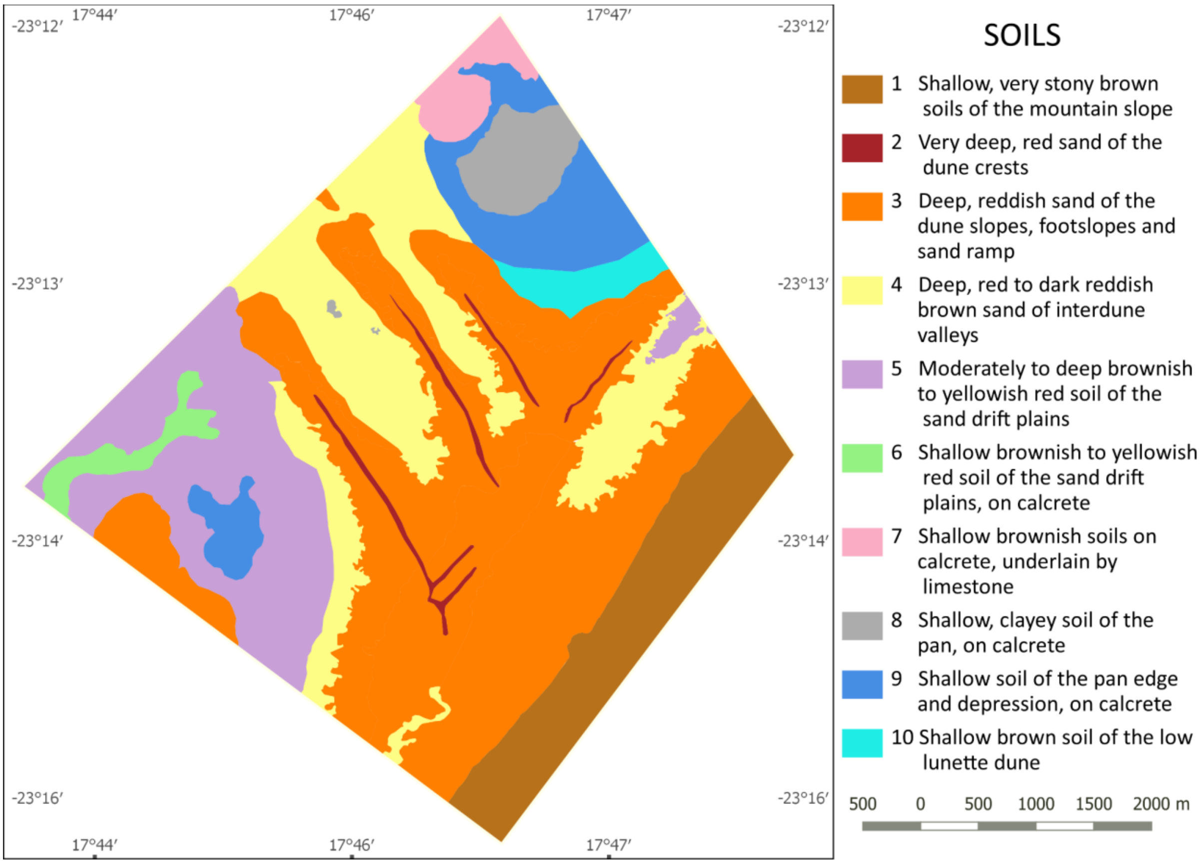

Figure 5: *Soils of farm Klein Boesman.*

10. Shallow brown soil of the low lunette dune

Brunic Arenosol (Aeolic) occurs on the low, very gently sloping (0.2-0.5% slope) lunette dune. This soil is deep (>100 cm), brown to dark brown (hue 7.5YR, value 3-4, chroma 3-4) when moist, and brown to strong brown (hue 7.5YR, value 4-5, chroma 4-6) when dry. The soil surface has a thin (1-2 grain thick) layer of coarse uncoated quartz crystals, which gives the illusion of a much lighter soil when viewed from a distance. Soil horizon development is poor, but slightly better than that of the dunes. The soil is sandy throughout the profile, with around 90% sand and 8-8.6% clay. The thin (6 cm thick) topsoil is structureless (single grains) and consistency is loose, whether dry or moist. Structure of both B1 and B2 horizons is weak to moderate, subangular blocky to blocky. Consistency of B1 and B2 is soft to slightly hard when dry, and very friable when wet. This soil is non-sticky and non-plastic when wet. There is no impediment to root development. OC (0.3%) and P (0-1.4 ppm) contents are low. Concentrations of bases are low: water-soluble K 92-113 ppm, Ca 251-274 ppm, Mg 81-96 ppm, Na 3-4 ppm. pH ranges from 6.88 to 7.12. There are no primary or secondary carbonates, no mottling or concretions. The brownish colour is imparted by a mixture of reddish hematite and yellowish goethite coatings on quartz grains, reflecting the presence of soil water for longer periods than on dunes. Water infiltration, internal drainage and aeration are good. Slight erosion activity was observed (both raindrop splash and aeolian) over more than 50% of the surface. [Representative profiles: 6, 7, 8, 9].

Vegetation Classification

The initial classification based on species composition only, yielded eight clusters, which were found to be ecologically interpretable. The further classification of Cluster 3, based on growth form data and using pseudospecies in the classification procedure, yielded an additional 2 clusters. These classification results are depicted in Figure 6 as a dendrogram. The two subunits of Cluster 3 were interpreted as subassociations of the cluster. Similarly, Clusters 6, 7 and 8 were interpreted as being subassociations of one association due to the similarity in habitat. All other clusters were regarded as being associations.

The full phytosociological table is presented as downloadable online Appendix 2, the synoptic table as online Appendix 3. The associations are not described formally according to the International Code for Phytosociological Nomenclature (ICPN) (Weber et al. 2000), pending a review of vegetation associations described within the southern Kalahari

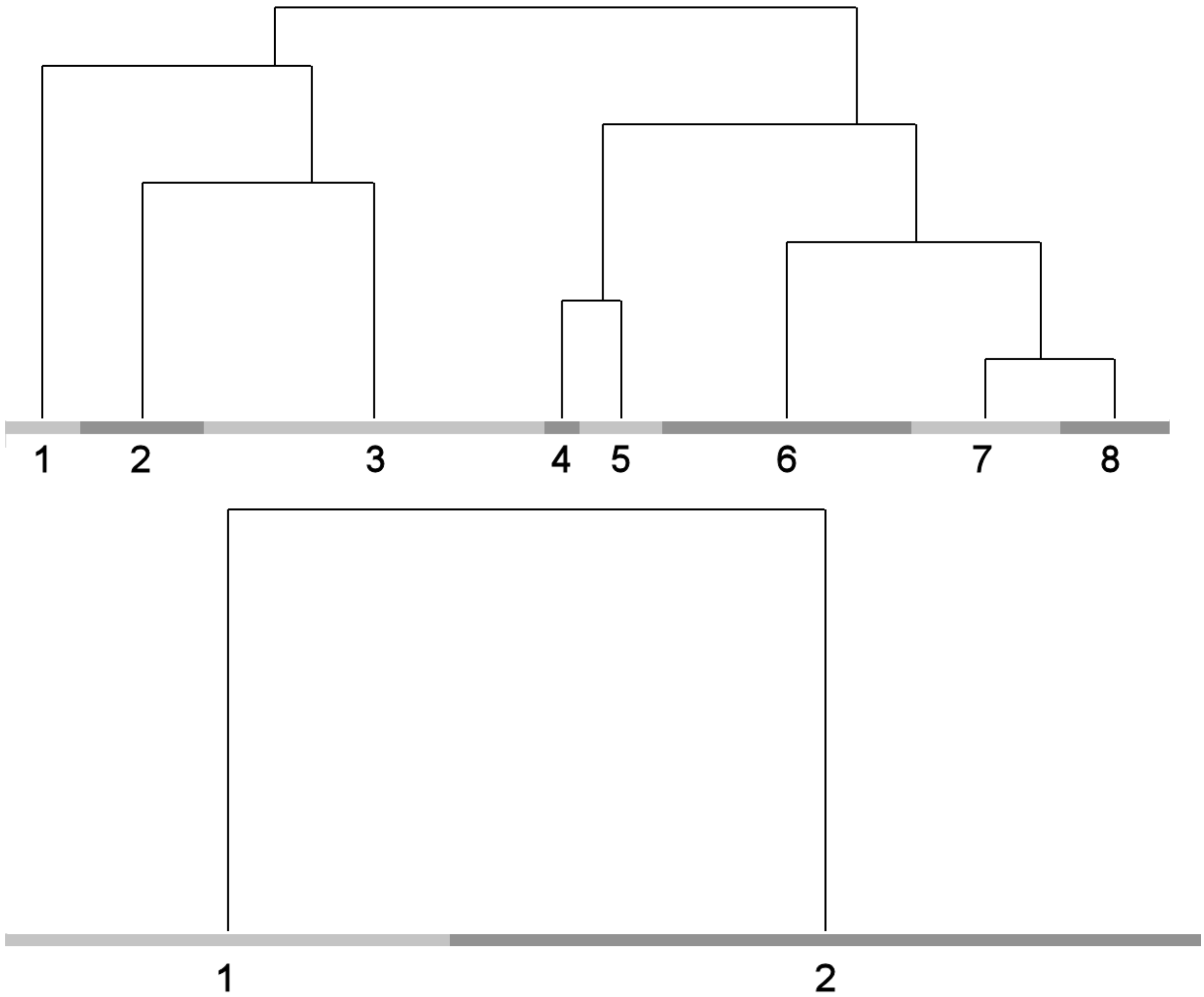

Figure 6: *Dendrogram depicting the classification results. Top: Initial classification of the full synusial dataset (composition only). Clusters 6, 7 and 8 represent sub-associations 6.1, 6.2 and 6.3 respectively. Bottom: Classification of the synusial subset of Cluster 3, using growth form data.*

(*sensu* Giess 1998) and the Kalahari Duneveld Bioregion *(sensu* Mucina & Rutherford 2006). Within this description, highly diagnostic species (with phi coefficient >60), highly constant species (occurring in more than 80% or relevés) as well as strongly dominating species (covering more than 20%) are indicated in **bold**. All structural descriptions follow Edwards (1983).

1. *Triraphis ramosissima–Acacia senegal* association

Synopsis:
Number of relevés: 10
Number of species observed: 47
Estimated number of species: 54
Average species density per 1000 m^2: 19

Diagnostic species: ***Acacia senegal, Nelsia quadrangula, Melinis repens*** **subsp.** ***repens, Combretum apiculatum, Eragrostis nindensis, Crotalaria spartioides, Triraphis ramosissima, Gisekia africana, Cheilanthes dinteri, Tribulus terrestris, Cleome rubella,*** *Elephantorrhiza suffruticosa, Phyllanthus pentandrus, Anthephora schinzii, Phyllanthus parvulus, Hibiscus engleri, Boscia foetida, Aristida effusa*
Constant species: ***Schmidtia kalahariensis, Stipagrostis uniplumis*** **var.** ***uniplumis,*** *Aristida adscensionis*
Dominant species: ***Acacia senegal, Combretum apiculatum,*** *Schmidtia kalahariensis, Melinis repens* subsp. *repens, Triraphis ramosissima*

General description:
The *Triraphis ramosissima–Acacia senegal* association forms a closed, high shrubland on the slopes of the mountain, with their Brunic Skeletic Leptosols, along the south-eastern edge of the farm (Figures 7a and 8a). Indicative for the mountainous habitat are *Combretum apiculatum, Triraphis ramosissima* and *Cheilanthes dinteri*. The association is however dominated by high shrubs of *Acacia senegal*.

2. *Centropodia glauca–Terminalia sericea* association

Synopsis:
Number of relevés: 17
Number of species observed: 75
Estimated number of species: 82
Average species density per 1000 m^2: 23

Diagnostic species: ***Digitaria seriata, Terminalia sericea, Centropodia glauca, Grewia retinervis, Dichrostachys cinerea, Rotheca uncinata,*** *Sida ovata, Calobota linearifolia, Pollichia campestris, Tapinanthus oleifolius, Searsia tenuinervis, Asparagus suaveolens, Boscia albitrunca, Requienia sphaerosperma, Indigofera charlieriana, Commiphora angolensis, Neorautanenia mitis, Commiphora glandulosa*
Constant species: ***Acacia mellifera* subsp. *detinens,*** *Grewia flava, Eragrostis lehmanniana, Acacia erioloba, Stipagrostis uniplumis* var. *uniplumis*
Dominant species: ***Terminalia sericea, Dichrostachys cinerea, Acacia mellifera* subsp. *detinens,*** *Stipagrostis hirtigluma, Schmidtia kalahariensis, Grewia retinervis, Acacia erioloba*

General description:
The *Centropodia glauca–Terminalia sericea* association forms a tall, moderately-closed bushland on the crest of the dunes, with their Protic Chromic Arenosols (Figures 7b and 8b). By the nature of these crests, the association forms a narrow band, often less than 10 m wide. The scattered tall trees of *Terminalia sericea, Acacia erioloba, Boscia albitrunca* and *Albizia anthelmintica* offer shade to animals, which often results in considerable damage to the understorey vegetation, especially the grass sward. Being at the crest of a loose, unconsolidated sand dune, wind erosion is occurring extensively due to the denuded soil surface (Figure 8c).

3. *Acacia mellifera–Acacia erioloba* association (Van Rooyen et al. 2008)

Synopsis:
Number of relevés: 46
Number of species observed: 133
Estimated number of species: 156
Average species density per 1000 m^2: 22

Diagnostic species: *Hermannia tomentosa, Pogonarthria fleckii*
Constant species: ***Acacia erioloba, Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis, Pseudogaltonia clavata,*** *Pollichia campestris, Acrotome inflata, Acacia mellifera* subsp. *detinens, Eragrostis lehmanniana*
Dominant species: ***Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis, Acacia mellifera* subsp. *detinens, Acacia erioloba,*** *Eragrostis lehmanniana, Crotalaria podocarpa, Dichrostachys cinerea, Stipagrostis hirtigluma, Momordica balsamina, Grewia flava*

General description:
The *Acacia mellifera–Acacia erioloba* association has been described for the high parallel duneveld in the Kalahari Gemsbok National Park in South Africa by Van Rooyen et al. (2008). Within the context of the present study, two very distinct forms can be recognised: a shrubland is formed on the slopes of the longitudinal dunes as well as a bushland or woodland dominated by *Acacia erioloba* trees on the sand drift plains. These two forms could not be distinguished based on compositional data, but due to their widely diverging structures, two different subassociations were defined.

3.1 *Acacia mellifera–Acacia erioloba* typical subassociation

Synopsis:
Number of relevés: 17
Number of species observed: 89
Estimated number of species: 106
Average species density per 1000 m^2: 23

Diagnostic species: ***Grewia flava* shrubs, *Dichrostachys cinerea* shrubs,** *Acacia mellifera* subsp. *detinens* shrubs, *Crotalaria spartioides, Boscia albitrunca* trees, *Lycium bosciifolium* shrubs
Constant species: ***Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis, Pollichia campestris, Pseudogaltonia clavata,*** *Acrotome inflata, Acacia erioloba* trees
Dominant species: *Acacia mellifera* subsp. *detinens* shrubs, *Crotalaria podocarpa, Stipagrostis uniplumis* var. *uniplumis, Stipagrostis hirtigluma* subsp. *hirtigluma, Schmidtia kalahariensis, Grewia flava* shrubs, *Dichrostachys cinerea* shrubs, *Dichrostachys cinerea* trees

General description:
The *Acacia mellifera–Acacia erioloba* typical subassociation occurs on dunes slopes with their Chromic Arenosols, the sand ramp at the foot of the Rooirand mountain as well as occasionally on sand drift plains. It forms a tall, moderately closed shrubland dominated by *Acacia mellifera* (Figures 7c and 8d). In many cases, especially along the bases of dunes, the cover of *Acacia mellifera* reaches near continuous proportions and forms an impenetrable thicket.

3.2 *Acacia mellifera–Acacia erioloba–schmidtia kalahariensis* subassociation

Synopsis:
Number of relevés: 29
Number of species observed: 105
Estimated number of species: 125
Average species density per 1000 m^2: 22

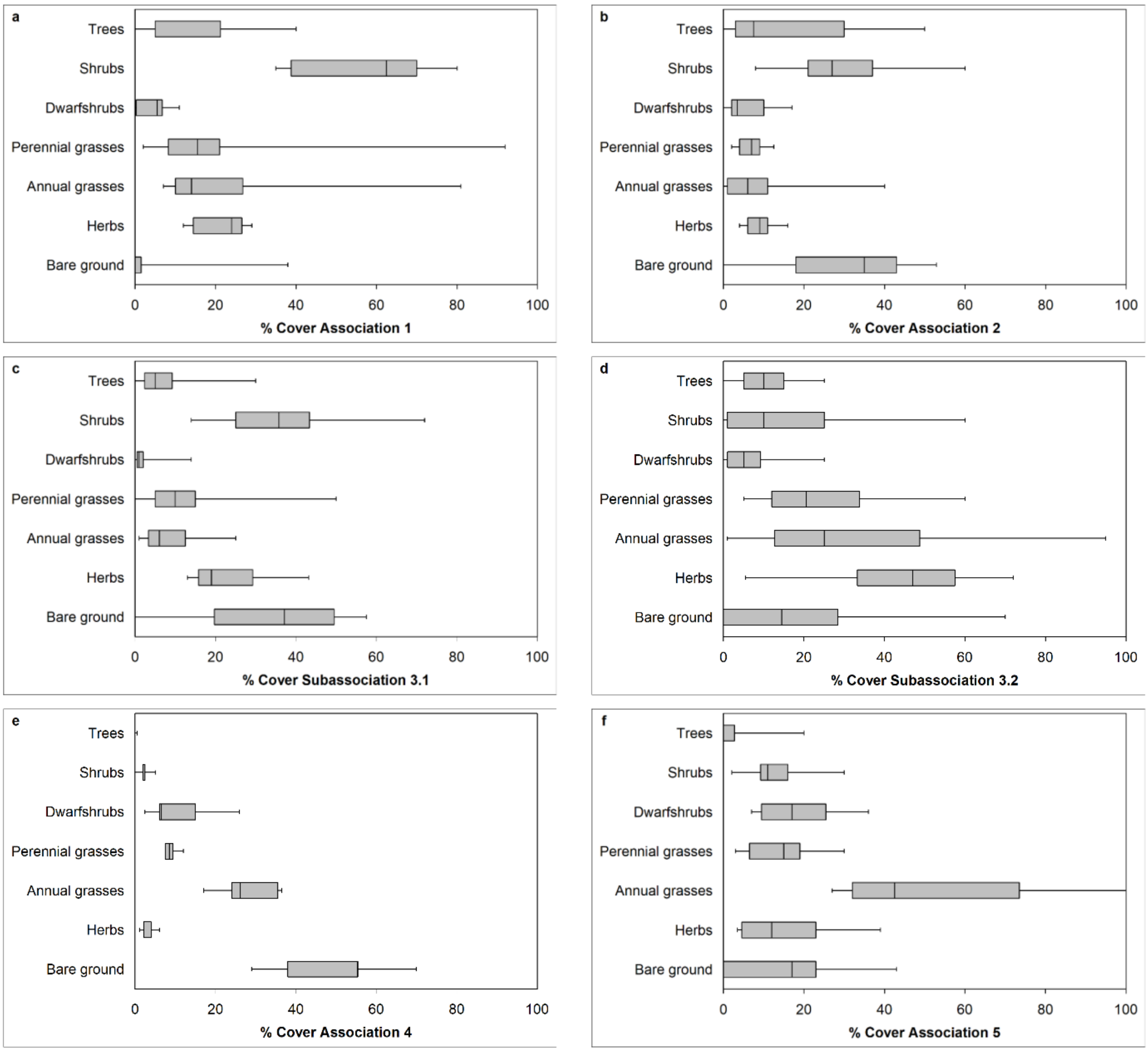

Figure 7: *Structure of the associations. a:* Triraphis ramosissima–Acacia senegal *association; b:* Centropodia glauca–Terminalia sericea *association; c:* Acacia mellifera–Acacia erioloba *typical subassociation; d:* Acacia mellifera–Acacia erioloba–schmidtia kalahariensis *subassociation; e:* Eragrostis truncata–Zygophyllum leucocladum *association; f:* Eragrostis echinochloidea–Leucosphaera bainesii *association.*

Diagnostic species: ***Cleome rubella,*** *Ipomoea obscura* var. *obscura, Indigofera daleoides, Acacia erioloba* trees, *Solanum multiglandulosum, Pentarrhinum insipidum, Grewia flava* shrubs, *Eragrostis lehmanniana*

Constant species: ***Stipagrostis uniplumis*** **var.** ***uniplumis, Schmidtia kalahariensis, Pseudogaltonia clavata, Acrotome inflata,*** *Pollichia campestris, Pogonarthria fleckii, Hermannia tomentosa*

Dominant species: *Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis, Acacia erioloba* trees, *Acacia mellifera* subsp. *detinens* shrubs, *Eragrostis lehmanniana, Momordica balsamina, Dichrostachys cinerea, Acacia erioloba* shrubs

General description:

The *Acacia mellifera–Acacia erioloba–schmidtia kalahariensis* subassociation forms tall, semi-open woodlands or bushlands on the sand drift plains on the western part of the farm, occasionally also in the interdune valleys (Figures 7d and 8e). This subassociation is occurring on Chromic and/or Brunic Arenosols. *Acacia erioloba* trees dominate the landscape, but the presence of *Acacia mellifera*, often at relatively high densities, indicates the susceptibility for encroachment of this subassociation. This, and the compositional high similarity of the two subassociations, indicates that the current typical *Acacia mellifera–Acacia erioloba* subassociation is actually a degraded/bush encroached form of the *Acacia mellifera–Acacia erioloba–schmidtia kalahariensis* woodlands sub-association.

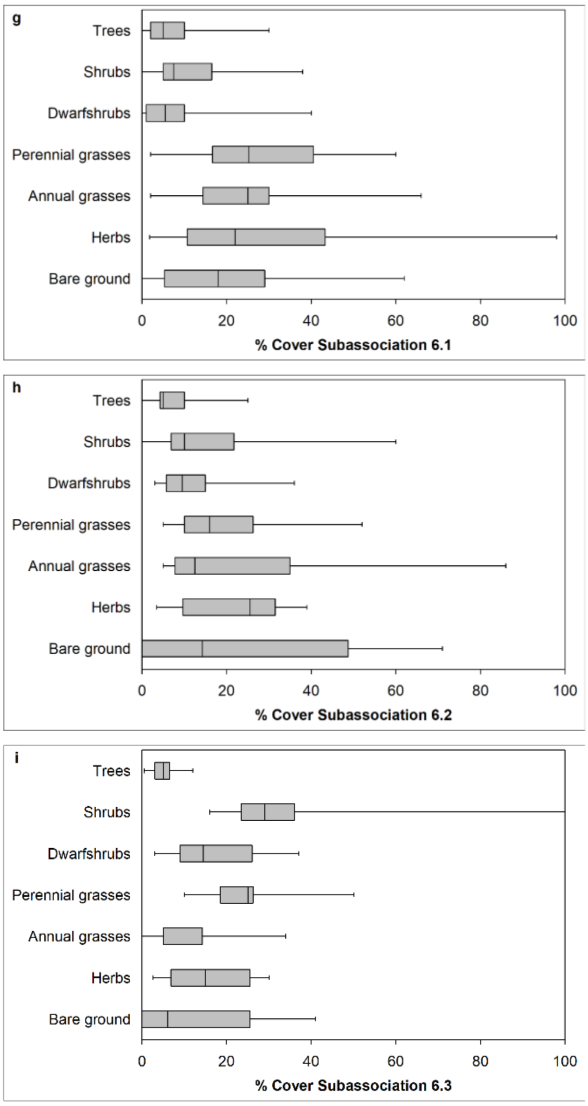

Figure 7 continued: *Structure of the associations. g:* Pseudogaltonia clavata–Rhigozum trichotomum *typical subassociation; h:* Pseudogaltonia clavata–Rhigozum trichotomum–eriocephalus luederitzianus *subassociation; i:* Pseudogaltonia clavata–Rhigozum trichotomum–parkinsonia africana *subassociation*

4. *Eragrostis truncata–Zygophyllum leucocladum* association

Synopsis:
Number of relevés: 5
Number of species observed: 41
Estimated number of species: 41
Average species density per 1000 m^2: 23

Diagnostic species: ***Eragrostis truncata, Zygophyllum leucocladum, Chloris virgata, Tragus racemosus, Platycarphella carlinoides, Heliotropium lineare, Jamesbrittenia canescens, Aizoon schellenbergii, Geigeria pectidea, Eragrostis pilgeriana, Setaria verticillata, Enneapogon desvauxii, Asparagus cooperi, Eragrostis echinochloidea,*** *Schkuhria pinnata, Panicum lanipes, Cyperus amabilis, Aristida adscensionis, Cenchrus ciliaris, Urochloa brachyura, Sporobolus nebulosus, Cyphostemma hereroense, Bidens biternata*
Constant species: *Pseudogaltonia clavata, Eragrostis porosa, Acacia hebeclada* subsp. *hebeclada*
Dominant species: ***Enneapogon desvauxii,*** *Aizoon schellenbergii*

General description:
The *Eragrostis truncata–Zygophyllum leucocladum* association is limited to the clay pan associated with the Boesmanklippe formation in the north-eastern corner of the farm. The structure is a low, semi-open shrubland with a distinct karoid character, both in terms of structure and composition (Figures 7e and 8f). The wetland character is evident from species like *Chloris virgata, Platycarphella carlinoides* and *Sporobolus nebulosus*.

5. *Eragrostis echinochloidea–Leucosphaera bainesii* association

Synopsis:
Number of relevés: 11
Number of species observed: 69
Estimated number of species: 79
Average species density per 1000 m^2: 26

Diagnostic species: ***Limeum argute-carinatum, Leucosphaera bainesii, Stipagrostis obtusa, Rhigozum trichotomum, Eragrostis echinochloidea,*** *Triraphis purpurea, Catophractes alexandri, Eriocephalus luederitzianus, Melolobium candicans, Enneapogon desvauxii, Aptosimum lineare, Gnidia polycephala, Eragrostis porosa, Barleria rigida, Acacia hebeclada* subsp. *hebeclada*
Constant species: ***Pseudogaltonia clavata, Acacia erioloba, Acrotome inflata, Stipagrostis uniplumis*** **var.** ***uniplumis, Melinis repens*** **subsp.** ***grandiflora,*** *Schmidtia kalahariensis, Cenchrus ciliaris*
Dominant species: ***Eragrostis porosa, Rhigozum trichotomum,*** *Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis, Enneapogon desvauxii, Acacia erioloba*

General description:
The *Eragrostis echinochloidea–Leucosphaera bainesii* association forms a short, moderately closed to closed shrubland within a depression in the western side of the farm, as well as fringe vegetation around the *Eragrostis truncata–Zygophyllum leucocladum* pan in the north-eastern corner of the farm (Figures 7f and 8g). The very dense stand of *Rhigozum trichotomum* in the depression forms a near-impenetrable shrubland.

6. *Pseudogaltonia clavata–Rhigozum trichotomum* association

Synopsis:
Number of relevés: 69

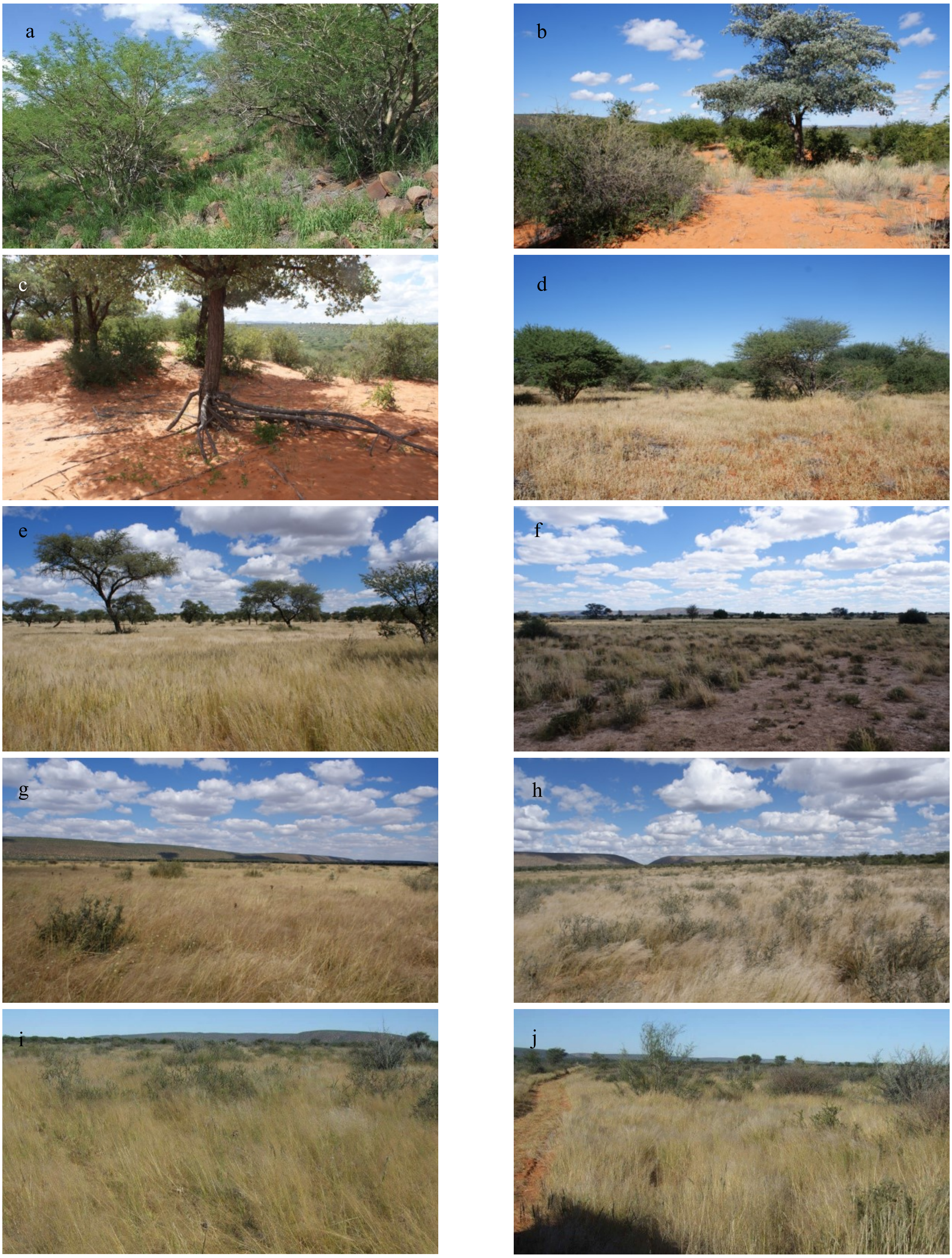

***Figure 8:** Typical examples of the described associations: (a)* Triraphis ramosissima–Acacia senegal *association at relevé 11918; (b)* Centropodia glauca–Terminalia sericea *association in good condition at relevé 11776; (c)* Centropodia glauca–Terminalia sericea *association badly wind-eroded at relevé 11783; (d)* Acacia mellifera–Acacia erioloba *typical subassociation on the dune slopes and dune foots at relevé 11774; (e)* Acacia mellifera–Acacia erioloba–schmidtia kalahariensis *subassociation forming an open woodland in the sand drift plains at relevé 11780; (f)* Eragrostis truncata–Zygophyllum leucocladum *association at relevé 11764; (g)* Eragrostis echinochloidea–Leucosphaera bainesii *association at relevé 11755; (h)* Pseudogaltonia clavata–Rhigozum trichotomum *typical subassociation at relevé 11786; (i)* Pseudogaltonia clavata–Rhigozum trichotomum–eriocephalus luederitzianus *subassociation at relevé 11934; (j)* Pseudogaltonia clavata–Rhigozum trichotomum–parkinsonia africana *subassociation at relevé 2161.*

Number of species observed: 175
Estimated number of species: 190
Average species density per 1000 m^2: 25

Diagnostic species: *Rhigozum trichotomum, Hirpicium gazanioides, Parkinsonia africana, Aristida congesta, Ipomoea sinensis, Catophractes alexandri, Ipomoea bolusiana*
Constant species: ***Acacia erioloba, Stipagrostis uniplumis* var. *uniplumis, Schmidtia kalahariensis,*** *Pseudogaltonia clavata, Acrotome inflata, Acacia hebeclada* subsp. *hebeclada*
Dominant species: ***Stipagrostis uniplumis* var. *uniplumis, Rhigozum trichotomum,*** *Schmidtia kalahariensis, Acacia erioloba, Eragrostis porosa, Eragrostis lehmanniana, Acacia mellifera* subsp. *detinens, Catophractes alexandri, Pogonarthria fleckii, Parkinsonia africana, Lycium bosciifolium, Leucosphaera bainesii, Indigofera alternans*

General description:
This association forms extensive shrublands within the interdune valleys and the plains on the eastern side of the farm. Due to the structural and habitat similarities, three subassociations have been recognised of this association.

6.1. *Pseudogaltonia clavata–Rhigozum trichotomum* typical subassociation

Synopsis:
Number of relevés: 34
Number of species observed: 140
Estimated number of species: 154
Average species density per 1000 m^2: 26

Diagnostic species: *Aristida congesta, Eragrostis lehmanniana, Pogonarthria fleckii, Chascanum pinnatifidum* var. *pinnatifidum*
Constant species: ***Schmidtia kalahariensis, Acacia erioloba, Stipagrostis uniplumis* var. *uniplumis, Pseudogaltonia clavata, Rhigozum trichotomum, Acrotome inflata,*** *Acacia mellifera* subsp. *detinens, Cleome rubella, Geigeria ornativa*
Dominant species: ***Stipagrostis uniplumis* var. *uniplumis, Rhigozum trichotomum, Schmidtia kalahariensis, Eragrostis lehmanniana, Acacia erioloba,*** *Pogonarthria fleckii, Acacia mellifera* subsp. *detinens, Indigofera alternans, Eragrostis porosa*

General description:
The *Pseudogaltonia clavata–Rhigozum trichotomum* typical subassociation forms a short, semi-open bushland, with a moderately-closed understorey of dwarf shrubs dominated by *Rhigozum trichotomum* (Figure 7g and 8h). This subassociation occurs between the dunes in the interdune valleys, mainly on Brunic Arenosols, occasionally underlain by calcretes. The main difference to the sand drift plains towards the west of the farm is the high density of *Rhigozum trichotomum*. The geophyte *Pseudogaltonia clavata* occurs widespread in this association, creating a potential threat to livestock husbandry as it is a known poisonous plant, affecting the heart, nervous systems as well as causing diarrhoea (Mannheimer et al. 2012).

6.2. *Pseudogaltonia clavata–Rhigozum trichotomum–eriocephalus luederitzianus* subassociation

Synopsis:
Number of relevés: 20
Number of species observed: 97
Estimated number of species: 103
Average species density per 1000 m^2: 24

Diagnostic species: *Eriocephalus luederitzianus, Hirpicium gazanioides*
Constant species: ***Stipagrostis uniplumis* var. *uniplumis, Pseudogaltonia clavata, Acacia erioloba, Schmidtia kalahariensis, Rhigozum trichotomum, Acrotome inflata,*** *Acacia hebeclada* subsp. *hebeclada, Pollichia campestris, Melinis repens* subsp. *grandiflora*
Dominant species: ***Stipagrostis uniplumis* var. *uniplumis, Rhigozum trichotomum, Eragrostis porosa,*** *Acacia erioloba, Schmidtia kalahariensis, Catophractes alexandri*

General description:
The *Pseudogaltonia clavata–Rhigozum trichotomum–eriocephalus luederitzianus* subassociation forms a tall, semi-open shrubland (Figures 7h and 8i), occurring on the fringes of the pan and associated lunette dune, with its Brunic Arenosols, south of the pan. The occurrence of *Eriocephalus luederitzianus* indicates edaphically drier conditions due to a finer texture and higher pH of the soils.

6.3. *Pseudogaltonia clavata–Rhigozum trichotomum–parkinsonia africana* subassociation

Synopsis:
Number of relevés: 15
Number of species observed: 78
Estimated number of species: 83
Average species density per 1000 m^2: 26

Diagnostic species: ***Parkinsonia africana, Ocimum americanum* var. *americanum, Ledebouria* species, *Leucas pechuelii, Ziziphus mucronata,*** *Dipcadi viride, Catophractes alexandri, Lycium eenii, Dipcadi platyphyllum, Talinum caffrum, Ipomoea sinensis, Eriospermum roseum*
Constant species: ***Stipagrostis uniplumis* var. *uniplumis, Rhigozum trichotomum, Acacia erioloba, Acacia mellifera* subsp. *detinens, Schmidtia kalahariensis, Lycium bosciifolium,*** *Acacia hebeclada* subsp. *hebeclada*

Dominant species: ***Stipagrostis uniplumis* var. *uniplumis, Rhigozum trichotomum, Catophractes alexandri, Acacia mellifera* subsp. *detinens,*** *Parkinsonia africana, Lycium bosciifolium, Leucosphaera bainesii, Eragrostis porosa*

General description:
The *Pseudogaltonia clavata–Rhigozum trichotomum–parkinsonia africana* subassociation forms a tall, moderately open shrubland (Figures 7i and 8j) with a striking dominance of *Parkinsonia africana.* This subassociation is limited to the Brunic Leptosols associated with the Boesmanklippe formation in the north-eastern corner of the farm.

Biodiversity indicators

The species richness per 1000 m^2, Shannon Index and Simpson's Index are given in Figure 9.

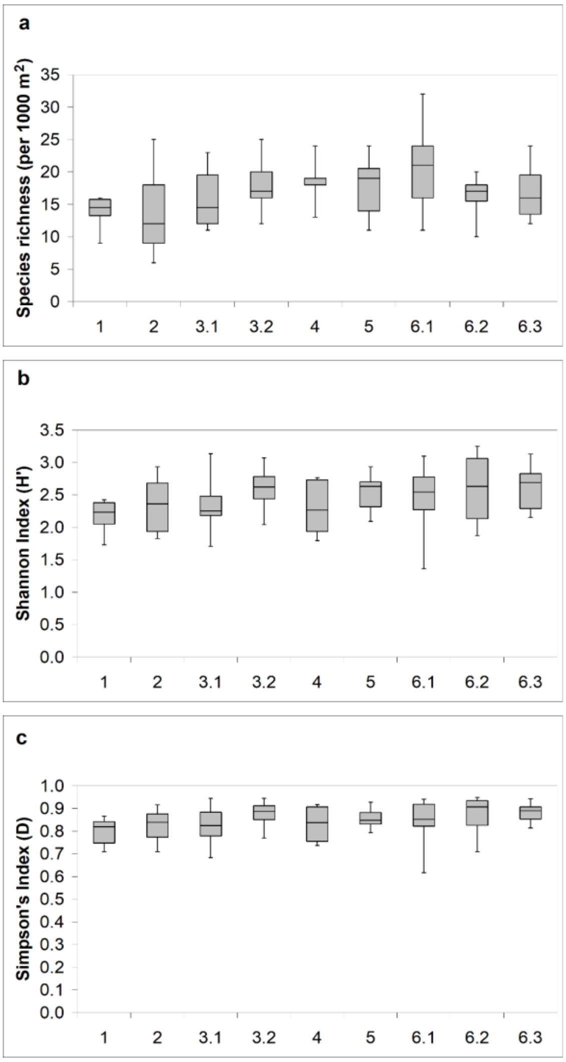

***Figure 9**: Diversity indicators for the various associations described. a) Species richness; b) Shannon index (H') and c) Simpson's Index (D).*

The two diversity indices (H' and D) follow very similar ranges across all associations. Conspicuous is the variability within subassociations 3.1 and 6.1, as indicated by the lower and upper quartiles (whiskers) in Figures 9b and 9c. This is an indication of the variable state of encroachment of these two subassociations. The narrow range of species richness depicted for associations 1 and 4 is likely a result of the limited number of relevés sampled in both associations. This also results in the estimation of species richness for association 4 to be unreliable, as no species were found once only.

Vegetation map

Minor differences between the distribution of vegetation associations and the associated landform- and soil units were found in the western sand drift plain, with the *Acacia mellifera–Acacia erioloba–schmidtia kalahariensis* subassocation not occurring as widely as the mapped sand drift plain, but gradually changing into the *Pseudogaltonia clavata–Rhigozum trichotomum* typical subassociation, with a conspicuous stand of *Acacia erioloba* trees interspersed. Another conspicuous difference is that the mapped pan centre in the north-eastern part of the farm contains two different associations – the *Eragrostis truncata–Zygophyllum leucocladum* association forming a limited area in the absolute centre of the pan, whilst the greater part of the pan centre indicated in the landforms map (Figure 4) is covered by the *Eragrostis echinochloidea–Leucosphaera bainesii* association. This is indicative of changing soil- and soil moisture conditions towards the centre of the pan. The vegetation map is depicted in Figure 10.

DISCUSSION AND CONCLUSION

A fairly close affinity exists between the vegetation types and the described soil types. However, in the transitional habitats (especially along the transition from dune foot to sand drift plain) the alliances are unclear. The vegetation reacts in these sandy environments to the availability of soil moisture, which is a function of the soil texture and the depth of the soil body (Laio et al. 2001a, b, Porporato et al. 2001, 2002, 2003, Strohbach & Kutuahupira 2014). In the north-eastern pan area, our soil sampling was not intensive enough to come to conclusive results regarding soil and vegetation interactions.

A comparison of the presently described associations to other similar associations helps understanding the biogeographical relationships of the vegetation, as well as assisting with the extrapolation about knowledge of the dynamics of the system. In particular, the southern Kalahari ecosystem has been well-studied in South Africa (Van Rooyen et al. 1984, 1990, 1991a, 1991b, Skarpe 1986, Jeltsch et al. 1997a, b, Dougill et al. 1999, 2016, Dreber et al.

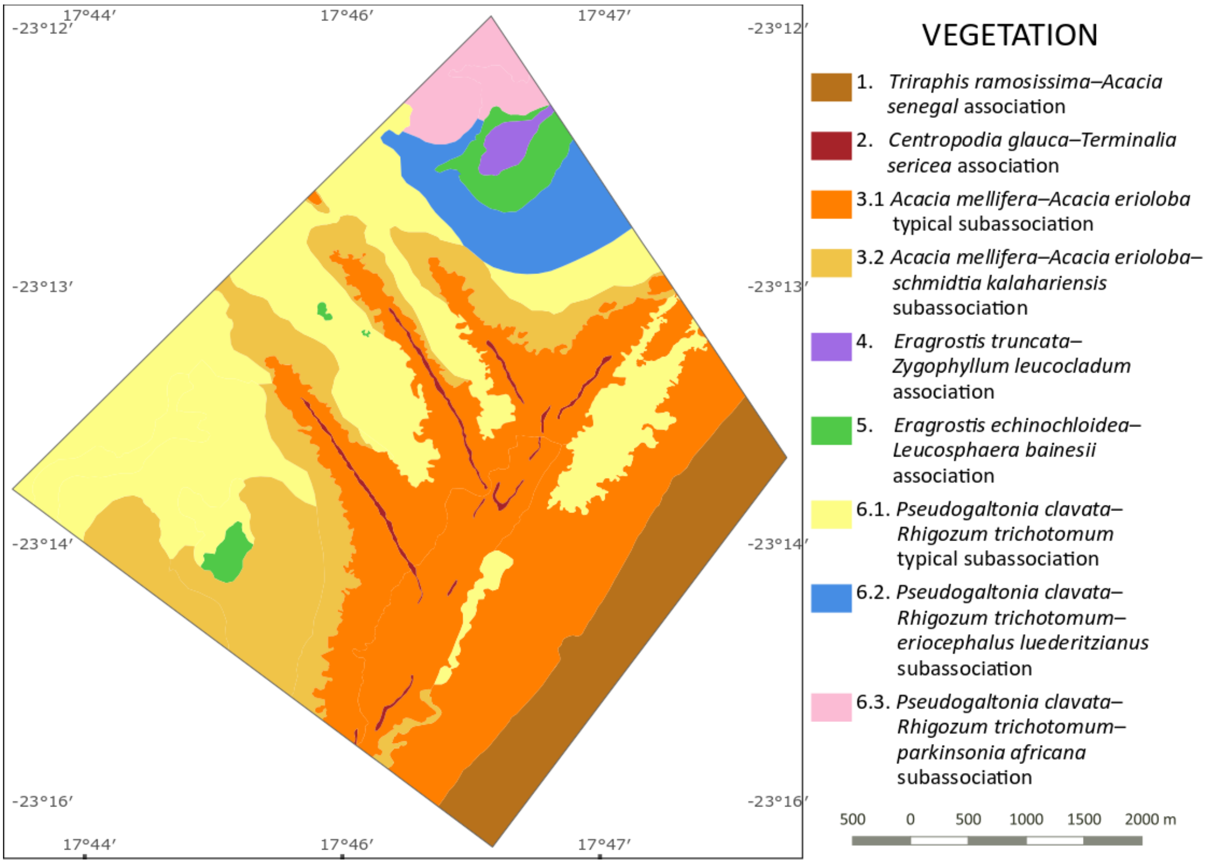

***Figure 10**: Vegetation associations of farm Klein Boesman.*

2017), making it possible to apply the existing knowledge for land use and/or farming management purposes in Namibia.

With the occurrence of *Combretum apiculatum* and *Cheilanthes dinteri*, a clear affinity exists between the *Triraphis ramossisima–Acacia senegal* association and the *Bergdornweide* (mountain thorn pastures) described by Volk & Leippert (1971), or the *Acacia hereroensis* veld described by Strohbach (2017). The dominance of *Acacia senegal* (to the apparent exclusion of all other *Acacia* species) however indicates a separate higher syntaxonomy than the *Acacia hereroensis* veld of the Khomas Hochland.

Leistner & Werger (1973) describe the dune crests as *Stipagrostietum amabilis* (*Stipagrostis amabilis* association), and describe a subassociation *Stipagrostietum amabils–terminalietosum* to this, occurring on some high dunes in the northern part of the Kalahari Gemsbok National Park (KGNP) in the RSA. Van Rooyen et al. (2008) also make mention of stands of *Terminalia sericea* on some of the high dunes in the northern parts of the park. The name-giving *Stipagrostis amabilis* however does not occur at Klein Boesman, but rather the grass *Centropodia glauca*. *Terminalia sericea* is also a remnant from more mesic conditions further north, being the dominant species of the extensive *Combreto collini–Terminalietum sericeae* described for the northern Omaheke and eastern Otjozondjupa regions (Strohbach 2014a).

Leistner & Werger (1973) provide no formal description of the dune slopes. Van Rooyen et al. (2008) describe the dune slope vegetation as the *Acacia erioloba–Acacia mellifera* parallel high Duneveld. The major difference to the presently described *Acacia erioloba–Acacia mellifera* typical subassociation is that here no *Acacia haematoxylon* has been observed. For the KGNP, van Rooyen et al. (2008) describe an *Acacia erioloba–Schmidtia kalahariensis* low duneveld for similar habitats as the *Acacia mellifera–Acacia erioloba–schmidtia kalahariensis* subassociation at Klein Boesman. This subassociation is also very similar to the *Acacia erioloba–Schmidtia kalahariensis* woodlands of the Omeya plains south of Windhoek (Strohbach 2017). It is thus likely that what is presently only recognised as a subassociation, should be elevated to a full association occurring widespread in deep sandy plains habitats from central Namibia to the northern Cape in RSA.

Van Rooyen et al. (2008) describe an *Acacia erioloba–Rhigozum trichotomum–Stipagrostis* *obtusa* as well as an *Acacia mellifera–Rhigozum trichotomum–Stipagrostis obtusa* veld for the interdune valleys and river terraces in the KGNP. The occurrence of these two veld types depends on the depth of the underlying calcrete layers of the soils. The typical arid savanna grasses *Stipagrostis obtusa* and *Stipagrostis ciliata* were not found widespread in the *Pseudogaltonia clavata–Rhigozum trichotomum* association on Klein Boesman, whereas the name-giving geophyte *Pseudogaltonia clavata* is very prominent on Klein Boesman, but rare in the KGNP (Leistner & Werger 1973). Although there is a distinct relationship, the *Pseudogaltonia clavata–Rhigozum trichotomum* association is syntaxonomical different from similar units described for the KGNP.

It is clear that the Kalahari duneveld at Klein Boesman forms the northern extent of the southern Kalahari, and has, due to its higher rainfall regime, clear differences to the more arid environments of the KGNP. A review of the entire southern Kalahari/ Kalahari Duneveld (*sensu* Giess 1998 and Mucina & Rutherford 2006 respectively) is thus needed.

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REFERENCES

Bhattachan A, D'Odorico P, Okin GS (2015) Biogeochemistry of dust sources in Southern Africa. *Journal of Arid Environments* 117: 18–27.

Bullard JE, Thomas DSG, Livingstone I, Wiggs GFS (1995) Analysis of linear sand dune morphological variability, southwestern Kalahari Desert. *Geomorphology* 11: 189–203.

Chytrý M, Tichý L, Holt J, Botta-Dukat Z (2002) Determination of diagnostic species with statistic fidelity measures. *Journal of Vegetation Science* 13: 79–90.

Coetzee ME (1998) Growing Period Zones of Namibia. *Agri-Info*.

Coetzee ME, Beernaert F, Calitz AJ (1998) Soil Survey of Uitkomst Research Station. *Agricola* 10: 17–25.

De Pauw E, Coetzee ME (1998) Production of an Agro-Ecological Zones Map of Namibia (first approximation). Part I: Condensed Methodology. *Agricola* 10: 27–31.

De Pauw E, Coetzee ME, Calitz AJ, Beukes H, Vits C (1998) Production of an Agro-Ecological Zones Map of Namibia (first approximation). Part II: Results. *Agricola* 10: 33–43.

Dougill AJ, Akanyang L, Perkins JS, Eckardt FD, Stringer LC, Favretto N, Atlhopheng J, Mulale K (2016) Land use, rangeland degradation and ecological changes in the southern Kalahari, Botswana. *African Journal of Ecology* 54: 59–67.

Dougill AJ, Thomas DSG, Heathwaite AL (1999) Environmental change in the Kalahari. Integrated land degradation studies for nonequilibrium dryland environments. *Annals of the Association of American Geographers* 89: 420–442.

Dreber N, van Rooyen SE, Kellner K (2017) Relationship of plant diversity and bush cover in rangelands of a semi-arid Kalahari savannah, South Africa. *African Journal of Ecology*: 56: 132-135.

Edwards D (1983) A broad-scale structural classification of vegetation for practical purposes. *Bothalia* 14: 705–712.

FAO (2006) *Guidelines for soil description*, 4th ed. FAO, Rome, Italy.

Geological Survey (1980) South West Africa/Namibia: Geological Map 1:1 000 000.

Giess W (1998) A Preliminary Vegetation Map of Namibia. *Dinteria* 4: 1–112.

Gillet F, Julve P (2018) The integrated synusial approach to vegetation classification and analysis. *Phytocoenologia* 48: 141–152.

Hegenberger W (1993) *Stratigraphy and sedimentology of the Late Precambrian Witvlei and Nama Groups, east of Windhoek*. Geological Survey of Namibia, Ministry of Mines and Energy.

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.

Hipondoka MH, Busche D, Kempf J (2004) Source of Lunette Dune Sediments: A Geomorphic Analysis Approach in Etosha National Park, Namibia (Zur Herkunft von Lunettedünen-Sedimenten im Etoscha-Nationalpark, Namibia). *Erdkunde*: 212–220.

ICC, MAWRD, AECI (2000) *Project to support the Agro-Ecological Zoning Programme (AEZ) in Namibia. Main Report*. Institut Cartogràfic de Catalunya (ICC), Namibian Ministry of Agriculture, Water and Rural Development (MAWRD) and Spanish Agency for International Co-operation (AECI), Windhoek.

Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N (1997a) Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *Journal of Applied Ecology* 34: 1497–1508.

Jeltsch F, Milton SJ, Dean WR, Van Rooyen N (1997b) Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* 8: 177–188.

Jürgens N, Oldeland J, Hachfeld B, Erb E, Schultz C (2013) Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert. *Journal of Arid Environments* 93: 59–79.

Kangombe FN (2010) *The vegetation of Omusati and Oshana regions, central-northern Namibia*, M.Sc. Thesis. University of Pretoria, Pretoria.

Killick AM (1983) A preliminary account of the geology of the Kamtsas Formation of the Damara sequence, eastern Gobabis district, South West Africa/Namibia. *South African Journal of Geology* 86: 11–18.

Klaassen ES, Kwembeya EG (eds) (2013) *A Checklist of Namibian Indigenous and Naturalised Plants*. National Botanical Research Institute, Windhoek.

Köppen W (1936) *Das Geographische System der Klimate*. Bornträger Verlag, Berlin.

Kutuahupira JT, Mouton HD, Coetzee ME (2001a) Soil survey at Sonop Research Station. *Agricola* 12: 67–72.

Kutuahupira JT, Mouton HD, Coetzee ME (2001b) Soil survey at Mahenene Research Station. *Agricola* 12: 59–66.

Laio F, Porporato A, Fernandez-Illescas CP, Rodriguez-Iturbe I (2001a) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. IV. Discussion of real cases. *Advances in Water Resources* 24: 745–762.

Laio F, Porporato A, Ridolfi L, Rodriguez-Iturbe I (2001b) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. II. Probabilistic soil moisture dynamics. *Advances in Water Resources* 24: 707–723.

Lancaster N, Tchakerian VP (1996) Geomorphology and sediments of sand ramps in the Mojave desert. *Response of Aeolian Processes to Global Change* 17: 151–165.

Leistner OA (1959) Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe* 2: 128–151.

Leistner OA, Werger MJA (1973) Southern Kalahari phytosociology. *Vegetatio* 28: 353–399.

Mannheimer CA, Marais A, Schubert S (2012) *Toxic Plants of Veterinary Importance in Namibia*, 2nd revised. Ministry of Agriculture, Water and Forestry, Windhoek.

MAWF (2000) *Quality manual. Standard operating procedures of the Agricultural Laboratory*. Ministry of Agriculture, Water and Forestry, Windhoek, Namibia.

Mbeeli TN (2018) *A vegetation classification of the Nama Karoo Dwarf Shrub Savanna in South Central Namibia*, Master of Natural Resources Management. Namibia University of Science and Technology, Windhoek.

Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) *Atlas of Namibia*. David Phillips Publishers, Cape Town.

Microsoft. (2019). Bing Maps - Aerial. https://www.bing.com/maps/aerial.

Mucina L, Rutherford MC (eds) (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.

Munsell Color (2010) *Munsell soil color charts*. Munsell Color, Grand Rapids, MI.

NARIS (2001) *Namibian Agricultural Resources Information System (NARIS)*. Agro-Ecological Zoning Program, Ministry of Agriculture, Water and Rural Development, Windhoek.

NASA JPL (2013) NASA Shuttle Radar Topography Mission Global 1 arc second [Data set].

Office of the Surveyor General (2019) *GIS Data (unpublished)*. Ministry of Land Reform, Windhoek.

Peet RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* 5: 285–307.

Porporato A, D'Odorico P, Laio F, Ridolfi L, Rodriguez-Iturbe I (2002) Ecohydrology of water-controlled ecosystems. *Advances in Water Resources* 25: 1335–1348.

Porporato A, Laio F, Ridolfi L, Caylor KK, Rodriguez-Iturbe I (2003) Soil moisture and plant stress dynamics along the Kalahari precipitation gradient. *Journal of Geophysical Research: Atmospheres* 108.

Porporato A, Laio F, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. III. Vegetation water stress. *Advances in Water Resources* 24: 725–744.

QGIS 3.2.0-Bonn (2018) Open Source Geospatial Foundation (OSGeo).

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science* 20: 596–602.

Rowell A, Thomas D, Bailey R, Stone A, Garzanti E, Padoan M (2017) Controls on sand ramp formation in southern Namibia. *Earth Surface Processes and Landforms*.

Skarpe C (1986) Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio* 68: 3–18.

South African Committee for Stratigraphy (1980) *Stratigraphy of South Africa Part 1: Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophutatswana, Transkei and Venda*. Dept. of Mineral and Energy Affairs, Pretoria.

Strohbach BJ (2001) Vegetation Survey of Namibia. *Journal of the Namibia Scientific Society* 49: 93–124.

Strohbach BJ (2014a) Vegetation of the Eastern Communal Conservancies in Namibia: I. Phytosociological descriptions. *Koedoe - African Protected Area Conservation and Science* 56: 18.

Strohbach BJ (2014b) *Vegetation Survey of Namibia: Conceptualisation and implementation of a nation-wide vegetation survey serving practical land management needs*. Department of Biology, Faculty of Mathematics, Informatics and Natural Sciences, University of Hamburg, Hamburg.

Strohbach BJ (2017) Vegetation of the Auas-Oanob Conservancy in the Khomas Hochland of Namibia. *Namibian Journal of Environment* 1: 19–42.

Strohbach BJ (2019) Vegetation of the Thornbush Savanna of central Namibia: Baseline description of the present vegetation at Farm Erichsfelde, Otjozondjupa Region. *Namibia Journal of Environment* 3: 17–36.

Strohbach BJ, Jankowitz WJ (2012) Phytosociology of the Farm Haribes in the Nama-Karoo Biome of southern Namibia. *Koedoe - African Protected Area Conservation and Science* 54: 8–20.

Strohbach BJ, Kangombe F (2012) National Phytosociological Database of Namibia. *Biodiversity & Ecology* 4: 298.

Strohbach BJ, Kutuahupira JT (2014) Vegetation of the Eastern Communal Conservancies in Namibia: II. Environmental drivers. *Koedoe - African Protected Area Conservation and Science* 56: 12.

Strohbach BJ, Petersen A (2007) Vegetation of the central Kavango woodlands in Namibia: An example from the Mile 46 Livestock Development Centre. *South African Journal of Botany* 37: 391–401.

Tichý L (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451–453.

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* 17: 809–818.

Tichý L, Holt J, Nejezchlebová M (2011) *Juice program for management, analysis and classification of ecological data. Program manual*, 2nd Edition. Vegetation Science Group, Masaryk University Brno, Brno, Czech Republic.

Van Rooyen TH (2008) The soils of the Kalahari Gemsbok National Park. *Koedoe-African Protected Area Conservation and Science* 27: 45–61.

Van Rooyen N, Bezuidenhout D, Theron GK, Bothma JDUP (1990) Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe* 33: 63–88.

Van Rooyen N, Bredenkamp GJ, Theron GK (1991a) Kalahari vegetation: veld condition trends and ecological status of species. *Koedoe* 34: 61–72.

Van Rooyen N, Theron GK, Bredenkamp GJ (1991b) Long-term vegetation dynamics in the semi-arid Kalahari. *Koedoe* 34: 91–92.

Van Rooyen N, Van Rensburg DJ, Theron GK, Bothma J du P (1984) A preliminary report on the dynamics of the vegetation of the Kalahari Gemsbok National Park. *Supplement to Koedoe*: 83–102.

Van Rooyen N, Van Rooyen MW (1998) Vegetation of the South-Western Arid Kalahari: An Overview. *Transactions of the Royal Society of South Africa* 53: 113–140.

Van Rooyen MW, Van Rooyen N, Bothma J du P, Van Den Berg HM (2008) Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe* 50: 99.

Volk OH, Leippert H (1971) Vegetationsverhältnisse im Windhoeker Bergland, Südwestafrika. *Journal der SWA Wissenschaftliche Gesellschaft* XXV: 5–44.

Wang L, D'Odorico P, Ringrose S, Coetzee S, Macko SA (2007) Biogeochemistry of Kalahari sands. *Journal of Arid Environments* 71: 259–272.

Weber HE, Moravec J, Theurillat JP (2000) International Code of Phytosociological Nomenclature. 3rd edition. *Journal of Vegetation Science* 11: 739–768.

Vegetation secondary succession in response to time since last fire in a broad-leaved savanna in central Namibia

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ABSTRACT

Savanna ecosystems developed as a response to frequent fires, and to date, fire plays an important role in shaping the vegetation structure of these ecosystems. Yet, little research on the effect of fire on Namibian savanna, especially at the more arid end of the rainfall gradient, has been done. This study was conducted at the Waterberg Plateau National Park, which experiences a range of fire frequencies, with the fire return period and time since last fire relatively well-known since 1976. Four fire blocks last burned 1, 2, 14 and 24 years ago prior to the study (2014) were surveyed, with the objective to assess the secondary succession after fire of perennial grasses and woody plants in terms of density, cover and species composition in a broad-leaved savanna on dystrophic sandy soils. Findings revealed that fire positively affects the grass component by increasing grass density and grass productivity ($p<0.05$). On the other hand, as in most southern African savannas, time after fire did not result in a significant change in overall woody plant density ($p>0.05$) but led to a steady increase in woody canopy cover and height ($p<0.05$), thus reducing the amount of browse available for small to medium sized browsers. Overall plant species composition did not significantly change with time after fire, although when grass species were grouped into grazing value categories, species with high grazing value declined with time after fire. Recent fires thus improve grazing and browsing opportunities, without significant plant species successional changes, but rather with significant plant structural succession.

Keywords: Fire occurrence; fuel loads; grazing value; Namibia; space-for-time; vegetation secondary succession; Waterberg Plateau Park

INTRODUCTION

Fire is a megaherbivore that has been burning savanna ecosystems for millennia and has shaped their vegetation structure and floristic composition (Bond & Keeley 2005, Scholes & Walker 1993). This is attributed to the alternation of short wet periods and extended long dry periods in savannas, which make them highly prone to fire due to lightning storms and the highly flammable fuel of dry grass (Trollope 2003, Scholes & Archer 1997, Scholes & Walker 1993). The widespread occurrence of fire in Africa, especially in the savanna and grassland biomes brands it as the “fire continent” (Komarek 1971). Fire is one of many environmental drivers, including rainfall, herbivory and human activities that, in combination, shape African savanna vegetation (Burke 2006).

Fire remains a controversial issue and has seldom been researched in Namibia. There is still a knowledge gap on how fire affects vegetation dynamics, particularly in the more arid woodland savannas found in Namibia. Joubert *et al.* (2012) who focused on the effects of fire on a single encroaching species, *Acacia mellifera*, concluded that, in arid thorn bush savanna, fire had to coincide with seedling establishment to be effective in maintaining an open savanna. In broad-leaved woodland savannas, Sheuyange *et al.* (2005) found that recent fires reduced shrub cover and promoted the herbaceous component (cover, biomass and species richness). Despite little fire research being conducted in the more arid Namibian savannas, fire regimes are being altered in different ways (Joubert *et al.* 2008), without prior and follow-up research and monitoring. For instance, fires occur in the north-eastern woodland savannas on an almost annual basis (Le Roux 2011, Sheuyange *et al.* 2005), while fires are deliberately excluded on commercial farms throughout the country (Joubert *et al.* 2008). In addition, the time of year in which fires occur has been altered in the north-eastern and central savannas from late dry season to late wet to early dry season. It is widely believed that these lower intensity fires will reduce damage to fire sensitive woody species and maximise habitat diversity (patch mosaic effect) (Beatty 2014).

Against this background, the study investigated the secondary succession of vegetation after fire in a broad-leaved savanna occurring on dystrophic sandy soils at the arid end of the rainfall gradient in Namibia, with the aim of reducing the knowledge gap that exists in understanding the impacts of fire on vegetation dynamics.

METHODS

Study site

The study was conducted at the Waterberg Plateau National Park, in central Namibia (study site central coordinates: S 20.39º, E 17.35º) (Figure 1). The national park is an important conservation area with the main aim of protecting and breeding rare, endangered and economically important large herbivores such as African buffalo, black and white rhino, giraffe, roan antelope and sable antelope (Schneider 1993, Eco Impact Consultants 2011).

The study area experiences warm summers with temperatures reaching up to 40ºC in the hottest months, while winter temperatures can drop to below –10ºC (SASSCAL Weather net). The mean annual rainfall recorded at the foot of the plateau for the period 1981 to 2001 was 425.5 (±129) mm, with February being the wettest month (Erckie 2007, Mendelsohn *et al*. 2002). There seems to be no long-term rainfall data for the plateau, with the only available data recorded by the SASSCAL weather station starting from 09 September 2011, which provided the total rainfall amounts for the years 2012, 2013, 2014 and 2015 as 664.1 mm, 395.7 mm, 838.2 mm and 81.6 mm respectively, indicating that although the study site is located between the 400-450 mm rainfall isohyets (Figure 1), actual annual rainfall is highly variable.

The Waterberg Plateau Park forms part of the "Tree Savanna and Kalahari Woodland" vegetation types of Namibia (Giess 1998, Jankowitz 1983). The mostly broad-leaved vegetation occurs on dystrophic (nutrient-poor) sandy red quartzite soils (Mukaru 2009). Common trees in this broad-leaved bushland savanna include *Acacia ataxacantha*, *Acacia fleckii*, *Burkea africana*, *Combretum collinum*, *Combretum psidioides*, *Dichrostachys cinerea*, *Grewia flavescens*, *Grewia retinervis*, *Philenoptera nelsii*, *Ochna pulchra*, *Peltophorum africanum*, *Terminalia sericea* and *Ziziphus mucronata* (Erb 1993). *Terminalia sericea* is the dominant woody species and is even considered to be encroaching the study area (Lutibezi 2016). Perennial grass species commonly occurring are *Brachiaria nigropedata*, *Aristida stipitata*, *Andropogon schirensis*, *Digitaria seriata*, *Eragrostis pallens*, *Eragrostis rigidior*, *Eragrostis jeffreysii*, *Panicum kalaharense*, *Stipagrostis uniplumis*, *Stipagrostis hirtigluma* and *Triraphis schinzii* (Erb 1993). The nomenclature used is as in the latest Namibian plant species list published (Klaassen & Kwembeya 2013).

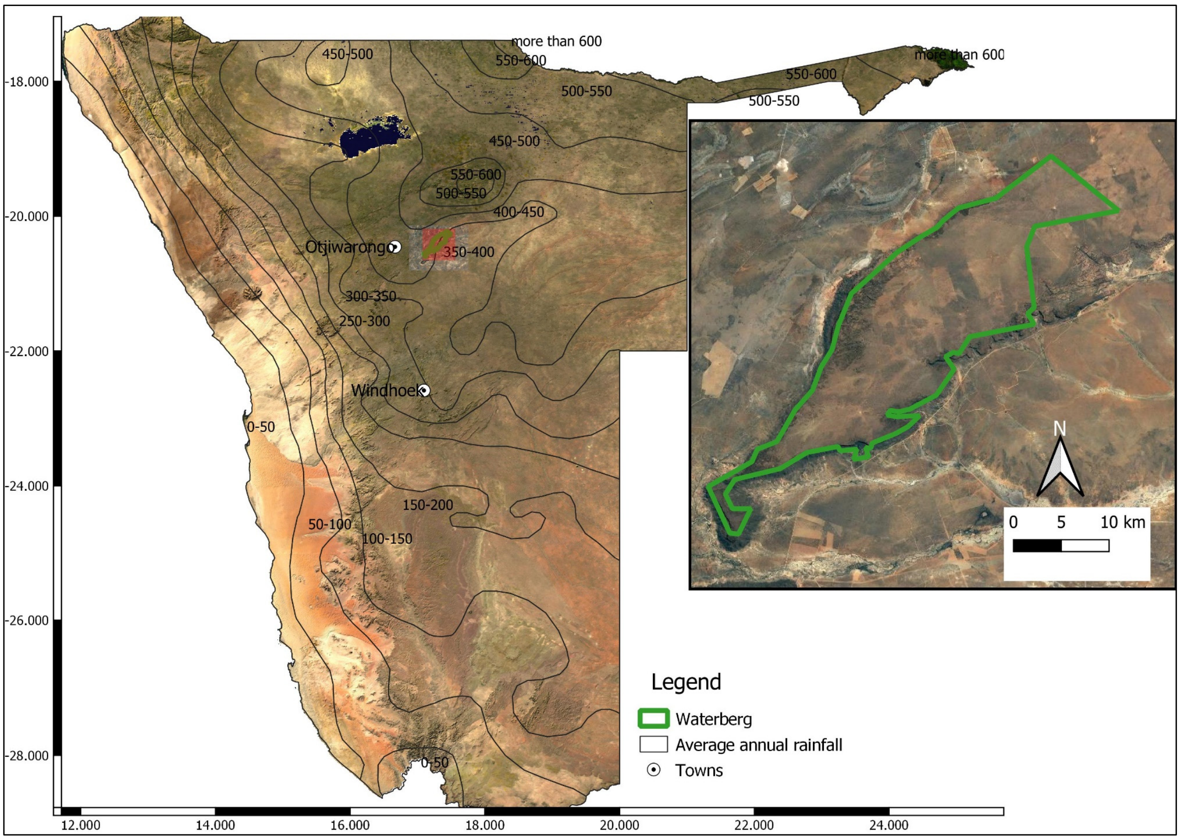

Figure 1: *Location of the Waterberg Plateau Park in central Namibia.*

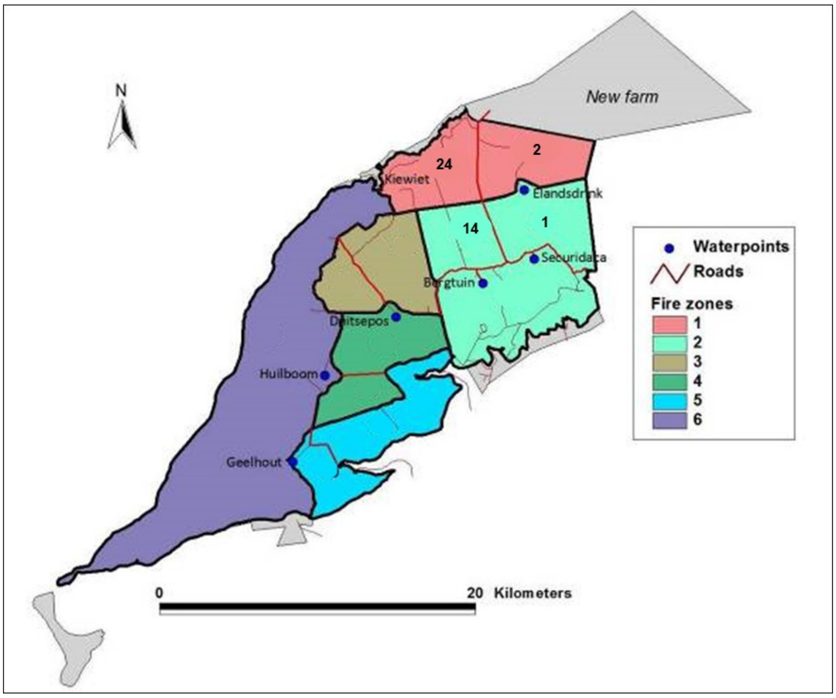

Figure 2: *Location of the surveyed fire blocks, labelled according to time since last fire (1, 2, 14 and 24 years) in the Waterberg Plateau Park (Source: Eco Impact Consultants 2011).*

Study design

A space-for-time (SFT) substitution technique was used for this study since the treatments were adjacent to each other (sharing the same climatic conditions) and showed no or little variation in soil texture (Nghalipo *et al*. 2018). The SFT approach has widely been used for examining vegetation community structure and composition and uses spatial variation to understand temporal dynamics (Likens 1989).

The study was carried out in four adjacent fire blocks, each approximately 2000 ha in size and burned 1 year, 2 years, 14 years and 24 years prior to the study and with mean fire return intervals of 6.2 years, 9.3 years, 9.3 years, and 18.5 years respectively (Figures 2, 13).

This study is inevitably pseudoreplicated (Hurlbert 1984) as there is only one of each fire block in the Waterberg Plateau Park. This pseudoreplication is considered acceptable, as most landscape-scale experiments rely on natural events (Davies & Gray 2015). In each fire block, six 200 m long line transects were randomly placed. Sample points were placed at 40 m intervals along each transect (5 per transect). At every sample point the following three vegetation sampling techniques were used: the modified point-centred quarter (PCQ) method (Cottam & Curtis 1956, Trollope *et al*. 2013), the Bitterlich gauge (Zimmermann *et al*. 2003) and the visual obstruction reading method (VOR) (Smith 2008, Uresk *et al*. 2009).

Data collection

The PCQ method used is an adapted version of Cottam & Curtis (1956) which overcomes the problems linked to the normal PCQ that results in oversampling small, short woody plants and under-sampling taller trees and shrubs (Trollope *et al*. 2013). In each quarter within a 20 m radius the distances to the nearest live perennial grass and woody species of <1 m, 1-2 m, 2-3 m, 3-4 m and >4 m in height were measured and recorded (Trollope *et al*. 2013), instead of just measuring the nearest woody plant in each quarter (Cottam & Curtis 1956). The basal diameter of the perennial grasses and the height of the woody plants in the different height classes were also measured. The different species being measured were also identified and recorded.

The Bitterlich gauge with a percentage factor of 5 based on its dimensions (length=75 cm and breadth=33.5 cm) was used to estimate woody canopy cover (Friedel & Chewings 1988 in Zimmermann & Mwazi 2002). Zimmermann & Mwazi (2002) found it to be an accurate method to estimate woody cover. The tip of the longer rod is held below the eye, with the other tips held horizontally in the direction of a woody canopy. If the woody canopy extends beyond the two tips, the canopy is counted and recorded as 1 (converted to a percentage by multiplying with the percentage factor of 5) and its species identified, if the two tips extend beyond the canopy then it is ignored. This procedure was repeated until a 360^0 turn clockwise was made at every PCQ point along each transect.

The Visual Obstruction Reading (VOR) method was used to estimate standing grass biomass (Smith 2008, Uresk *et al*. 2009). This method requires little effort to monitor rangelands and was tested in Namibia (Joubert *et al*. 2014), including in the study area and found to adequately estimate standing biomass. Calibration in this study was conducted using 60 points in the study area. The VOR and dry weight of the grasses was used to calculate a regression equation used to convert all VORs to biomass (Figure 3).

Data analysis

All vegetation structural (grass & woody density, woody cover, grass biomass and grass tuft size) statistical tests were run with STATISTICA 12 (StatSoft 2002). The Kolmogorov-Smirnov test was used to see if data were normally distributed. The main effects analysis of variance (ANOVA) revealed that time since last fire was the driving variable contributing to significant differences rather than mean fire return interval, and hence time since last fire was considered as the driving variable for all further tests. For normally distributed data the one-way ANOVA was used. If the one-way ANOVA yielded a significant difference, Fisher's less significant difference (LSD) posthoc test was used for multiple comparisons among sites to reveal differences. If the data were not normally distributed, the equivalent non-parametric Kruskal-Wallis test was used to test for significant differences.

For plant species composition, a non-metric multidimensional scaling ordination (NMS) (Kruskal 1964), using the Sorenson distance measure, with the time of day used as the random starting parameter was performed in PC-ORD version 6.08 (McCune & Mefford 2011), separately for perennial grass species (relative density) and woody species (relative woody cover). Based on an initial scree plot of stress versus dimensions, the ordination was done for two dimensions with axis 1 being the most relevant at the final stress of 14.343, with 200 iterations. The following environmental variables were used on the secondary matrix: time since last fire, mean fire return interval, as well as the following soil properties: percentage clay, organic carbon, phosphorus, potassium, calcium, magnesium, sodium, and total nitrogen. The soil data and the description of soil sampling procedures and analysis were obtained from a parallel study conducted in the same area that investigated soil nutrients and soil carbon in relation to time since last fire along the same transects (Nghalipo *et al*. 2018).

RESULTS

Perennial grass component

(a) Perennial grass density

Perennial grass density decreased significantly with time since last fire (F=5.568, df=3, $p<0.05$, n=6). The site burned 1 year ago had about three times higher perennial grass density than those burned 14 and 24 years ago (Figure 4).

(b) Grass biomass and grass tuft size

Grass biomass was significantly different (F=4.611, df=3, $p<0.05$, n=6) between the site burned 1 year ago and that burned 2 years ago, with the latter having about three times higher grass biomass (Figure 5). Perennial grass tuft size was significantly smaller (F=4.017, df=3, $p<0.05$, n=6) in the recently burned site as compared to the other sites (Figure 6).

(c) Perennial grass species composition

The NMS ordination (13.153 at final stress for two axes; 0.00000 final instability and 44 iterations) revealed that percentage nitrogen may be an influential variable for the relative density of different grass species observed in some of the sites (Figure 7).

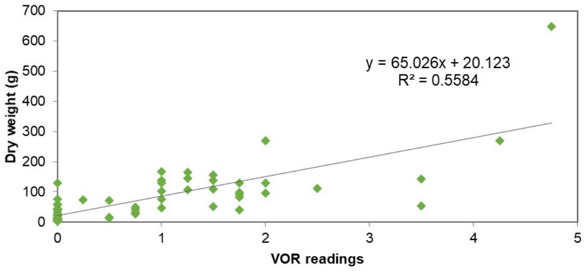

Figure 3: *Regression of VOR readings and dry weight (g) of perennial grasses.*

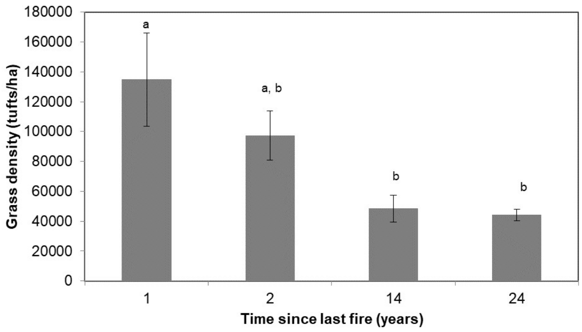

Figure 4: *Perennial grass density (grass tufts/ha) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

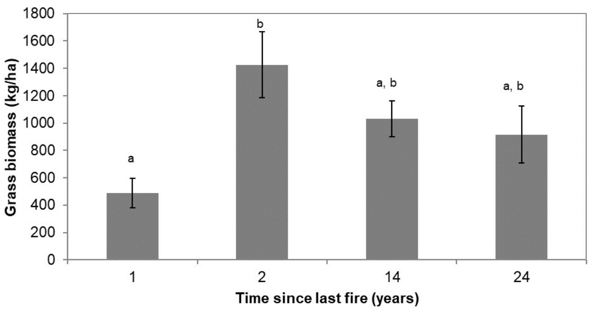

Figure 5: *Grass biomass (kg/ha) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

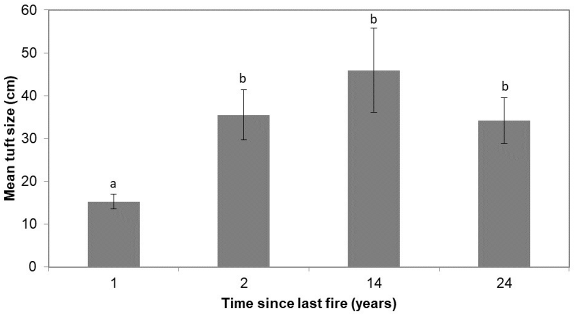

Figure 6: *Perennial grass tuft size (cm) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

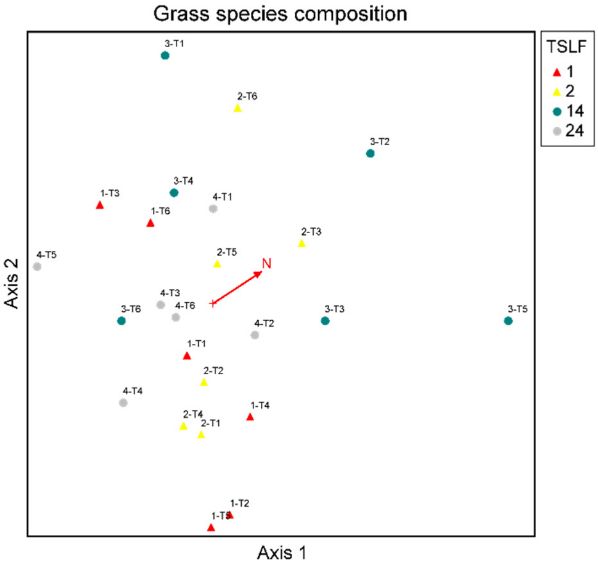

Figure 7: *NMS joint plot for perennial grass species composition in relation to various environmental variables at* r^2 *cut off=0.1. The numbers denote the four fire blocks: 1=1 year, 2=2 years, 3=14 years and 4=24 years, while the letter & number represent the transect numbers, i.e. T1=transect 1*

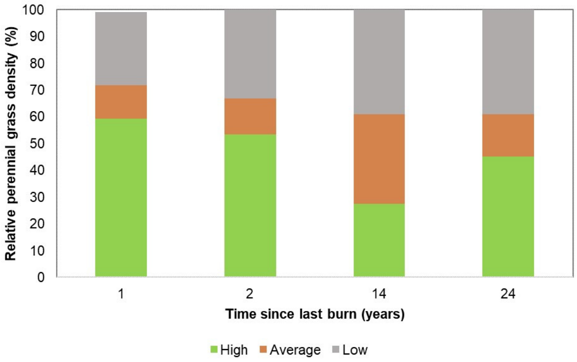

Figure 8: *Proportion of relative grass density in the grazing value categories in relation to time since last fire (years).*

Table 1: *Relative density (%) of perennial grass species with grazing value (van Oudtshoorn 2004) in relation to time since last fire (years).*

		Time after fire (years)			
Perennial grass species	**Grazing value**	**1**	**2**	**14**	**24**
Brachiaria nigropedata	High	0	9.2	0.8	0.8
Digitaria seriata	High	57.5	44.2	26.7	44.2
Panicum maximum	High	1.7	0	0	0
Aristida meridionalis	Average	2.5	0.8	0	0.8
Eragrostis lehmanniana	Average	0.8	0	1.7	0
Melinis repens subspecies *repens*	Average	0.8	0	2.5	1.7
Panicum kalaharense	Average	2.5	7.5	11.7	5
Stipagrostis uniplumis	Average	5	5	14.2	2.5
Triraphis schinzii	Average	0.8	0	3.3	5.8
Aristida stipitata	Low	18.3	23.3	20	22.5
Eragrostis jeffreysii	Low	3.3	2.5	12.5	0.8
Eragrostis pallens	Low	5.8	4.2	2.5	12.5
Stipagrostis hirtigluma	Low	0	3.3	4.2	3.3

(d) Grazing value and relative density of grass species in relation to time since last fire

Three grass species of high grazing value were encountered with *Digitaria seriata* having the highest relative density overall and mostly in the recently burned areas (Table 1). The recently burned areas had higher relative grass density of high grazing value species compared to areas burned more than 14 years ago (Figure 8).

Woody component

(a) Woody density and canopy cover

Total woody density was not significantly different (F=1.004, df=3, p>0.05, n=6) between sites with different time since last fire (Figure 9). There were however significant differences (F=5.416, df=15, p<0.05, n=6) found for woody density of <2 m and >2 m woody plants among the sites (Figures 10a and 10b). Total woody cover significantly (H=19.698, df=15, p<0.05, n=6) increased with time since last fire (Figure 11).

(b) Woody species composition

The NMS ordination (14.254 at final stress for two axes, 0.00000 at final instability and 43 iterations) revealed that time since last fire (TSLF) and mean fire return interval (MFRI) contribute to differences in woody species composition (relative woody cover) in the different sites (Figure 12).

(c) Relative cover of woody species (Table 2)

Table 2: *Relative woody cover (%) of woody species in relation to time since last fire (years)*

	Time since last fire (years)			
Woody species	**1**	**2**	**14**	**24**
Acacia ataxacantha	16.3	13.8	20.9	23.6
Acacia fleckii	0	8.9	0	1.3
Bauhinia petersiana	1	2.9	4.1	11.9
Burkea africana	4	2	4.6	0.5
Combretum apiculatum	0	1.1	0.8	0
Combretum collinum	10.3	11	6.1	5
Combretum psidioides	10.5	7.1	15.2	3
Croton gratissimus	0	0	0	0.7
Grewia avellana	0	1.5	0	0
Grewia flavescens	1	0.8	2	1.6
Grewia retinervis	1.9	0.8	0	1
Ochna pulchra	1.4	2.2	2.2	5.2
Peltophorum africanum	11.2	0.4	2.5	0.7
Philenoptera nelsii	6.8	7	3.3	3.9
Searsia tenuinervis	0	0	1.6	0
Terminalia sericea	34.9	40.5	35.9	41.6
Ziziphus mucronata	0.6	0	0.7	0

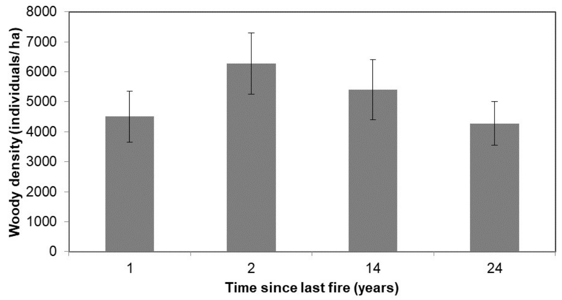

Figure 9: *Total woody density (individuals/ha) in relation to time since last fire (years). The bars show standard errors.*

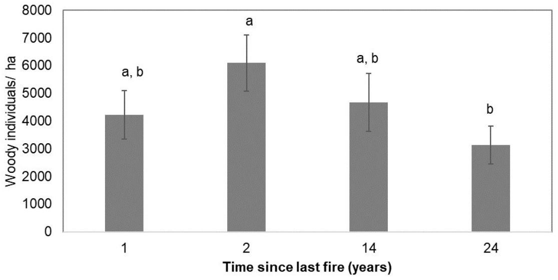

Figure 10a: *Woody density (individuals/ha) of <2 m woody plants in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

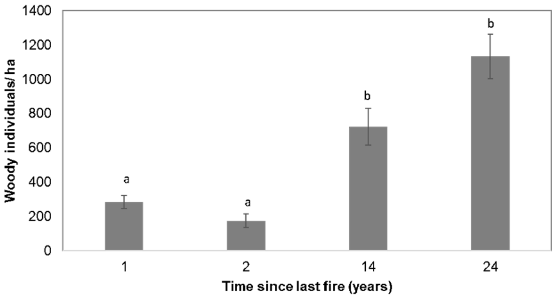

Figure 10b: *Woody density (individuals/ha) of >2 m woody plants in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

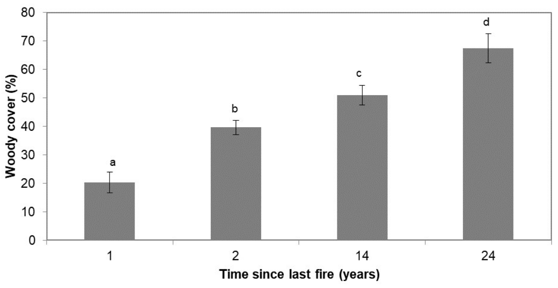

Figure 11: *Total woody cover (%) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.*

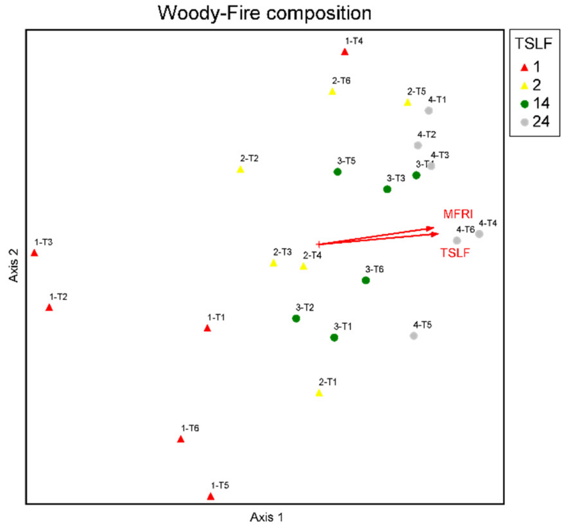

Figure 12: *NMS joint plot for woody species composition in relation to various environmental variables at* r^2 *cut off= 0.1. The numbers denote the four fire blocks: 1=1, 2=2, 3=14 and 4=24, while the letter & number represent the transect numbers, i.e. T1=transect 1.*

DISCUSSION

Perennial grass component

Perennial grass density decreased with time since last fire and was about three times higher in the recently burned site (Figure 4). The removal of moribund grass, reduced plant canopy cover and reduced competition from established plants by fire contributed to this, which supports observations from other studies (Holdo 2005, Mapiye *et al.* 2008, Zimmermann *et al.* 2010, Nepolo & Mapaure 2012, Gul *et al.* 2014). Fire stimulates the recruitment and regrowth of new grass shoots (Menke 1992, van Oudtshoorn, 2004, Gul *et al.* 2014, Roodt 2015). This is especially evident for *Digitaria seriata* where dry stolons were burned by the recent fire, resulting in the production of numerous new tillers.

The recently burned site (488.4 kg/ha) had about three and two times less grass biomass than blocks burned 2 (1425.7 kg/ha) and 14 years (1030.2 kg/ha) ago respectively (Figure 5), as well as significantly smaller grass tufts (Figure 6). The low biomass is to be expected because the recent fire burned away above-ground material of grasses causing a temporary decline in standing biomass and overall productivity and this is supported by other studies conducted in southern African savannas (Scholes & Walker 1993, van Langevelde *et al.* 2003, Goldammer & de Ronde 2004, Mbatha & Ward 2010, Zimmermann *et al.* 2010). In addition, due to the highly nutritious regrowth, herbivores utilised this block about four times more than the other blocks (Uunona 2014), resulting in even less grass biomass. Despite the site burned 2 years ago being much more utilised than the sites burned 14 or more years ago (Uunona 2014) the grass biomass was significantly higher. This suggests that grass production and biomass recover rapidly after fire (du Toit *et al.* 2015). The post-fire regrowth of grasses and woody plants is highly nutritious and attracts herbivores that readily forage on it (Uunona 2014), allowing for other recently burned areas to rest and recover (Archibald *et al.* 2005). Grass tuft size also recovered within two years after fire (Figure 6). This could be due to reduced grazing pressure because herbivores are being attracted away from the area by other more recently burned areas nearby (Scholes & Walker 1993, Zimmermann *et al.* 2010). This is supported by Archibald *et al.* (2005), who showed that burned areas attract animals off unburned grazed patches long enough for patches to recover full grass biomass in one growing season. Besides being available forage for grazers, grass biomass is an important factor that influences fire behaviour, as fire intensity is positively related to the amount of fuel load (Scholes & Walker 1993, Trollope *et al.* 2002, Sah *et al.* 2006). Grass biomass in the study area is generally low, with 1425.7 kg/ha being the highest recorded (Figure 5), despite the above-average rainfall (913.9 mm) recorded for the 2013/2014 period (SASSCAL Weather net), prior to the study. Fuel loads tend to be sparser and more unevenly distributed in bushland savannas as compared to open savannas because of the influence of tree neighbourhoods on grass growth (Holdo 2005). In addition, *Terminalia sericea*, a species considered to be an encroacher species in the study area, is dominant in all fire blocks and is likely to compete intensively with grasses, due to its shallow root system (Hipondoka & Versfeld 2006, Lutibezi 2016).

The steady decline in perennial grass density is partially due to the build-up of competitive pressure between individuals which becomes severe enough to lead to high mortality but also moribundity which increases with time since last fire (Scholes & Walker 1993, Zimmermann *et al.* 2010, van Oudtshoorn 2004, Roodt 2015). Therefore, fire temporarily resets standing grass biomass and competitive pressure (Zimmermann *et al.* 2010). Recent fires tended to result in a higher proportion of high grazing value species (Figure 8) and an improvement in the rangeland for grazing herbivores, but according to the NMS analysis there was no significant grass species composition successional change with time since last fire (Figure 7), but rather a structural change in terms of grass density (Figure 4), grass biomass (Figure 5), and grass tuft size (Figure 6).

Woody component

Time since last fire did not significantly affect total woody density (Figure 9). This suggests that fire in this bushland savanna is not sufficient to reduce woody plant density and maintain an open savanna. However, other factors such as fire intensity should be taken into account. High-intensity fires increase tree mortality in higher rainfall savannas such as the woodland savanna in the Kruger National Park (Govender *et al*. 2006), and thus may reduce woody density in southern African savannas (du Toit *et al*. 2003, Scholes & Walker 1993). These effects are more prevalent in higher rainfall areas such as in the miombo woodlands found in Zimbabwe and Zambia as well as the north-eastern parts of Namibia (Mendelsohn & el Obeid 2005). Therefore, high intensity fires are likely to be rare in the study area due to relatively low fuel loads (Figure 5), that may also be attributed to grazing pressure in the recently burned areas and the high density and cover of woody individuals in the unburned areas (Figure 9**,** 11). As in most savanna systems, fire maintains an open savanna mainly through causing a top-kill of woody stems and branches, decreasing their canopy cover (Figure**s** 11**,** 13) and height to "browsable" heights (Higgins *et al*. 2000, Trollope 2003, Bothma & du Toit 2005, Joubert *et al*. 2012, Nyazika *et al*. 2017); the resulting resprout is more accessible and highly nutritious for small to medium sized browsers (Scholes & Walker 1993).

In the absence of fire woody plants grow larger and their individual canopy areas become bigger resulting in a higher woody cover (Figure 11) (Accatino *et al*. 2010, Smit *et al*. 2010) and a more closed woodland with woody plants mainly >2 m tall (Figure 10b) beyond the fire trap. Thus, the increase in woody cover is due to an increase in the size of individual canopies free of fire, rather than an increase in the density, which also suggests very little recruitment in this bushland savanna.

Woody species composition was influenced by time since last fire and mean fire return interval (Figure 13), indicating that there may be plant species secondary succession occurring in the current time frame, but structural succession is clearly more evident and significant (Figures 10, 11, 12). This supports other studies in southern African savannas (du Toit *et al*. 2015, Trollope 2003, Bond & van Wilgen 1996) who found that the main effect of fire on woody vegetation is that it causes top-kill of above-ground plant material, forcing the plants to coppice from the base of the stem, confining woody plants in the fire trap (Holdo 2007), but fire does not significantly alter plant species composition, which indicates that savanna vegetation is well adapted and resistant to fire. This is further strengthened by a synergistic study of fire and elephant damage in a miombo woodland that revealed a complete shift in woody plant species composition, mainly a drastic reduction in woody species preferred by elephants for browsing (Mapaure & Moe 2009), suggesting that fire alone could not cause significant changes to plant species composition.

CONCLUSIONS AND FIRE MANAGEMENT IMPLICATIONS

For the study area, fire increases the availability and utilisation of the vegetation by increasing perennial grass density and biomass and reducing woody plants through top-kill to browsable heights for small to medium sized herbivores, thus maintaining an open bushland savanna. There appears to be no significant grass and woody species succession after fire, rather

Figure 13: *A series of images illustrating the changing vegetation structure with time since last fire in the bushland savanna.*

there is a dramatic structural change, with a steady increase in woody plant height and canopy cover leading to a more closed savanna in the absence of fire.

Based on the findings of this study, a modest increase in fire frequencies, and the burning of areas that have not been burnt in a long time (14-24 years) will have no detrimental impacts on plant species composition but will rather support grazers and small to medium sized browsers. Such fires would need to be set after high rainfall seasons, to cause a significant top-kill of woody plants and thus open up the more closed woodland sites (Figures 11, 13) and improve grass quantity & quality.

ACKNOWLEDGEMENTS

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REFERENCES

Accatino F, De Michele C, Vezzoli R, Donzelli D, Scholes R (2010) Tree-grass co-existence in savanna: Interactions of rain and fire. *Journal of Theoretical Biology* 267: 235-242.

Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications* 15(1): 96-109.

Beatty R (2014) *Integrated transfrontier fire management for Liuana Partial Reserve (Angola) and Bwabwata National Park (Namibia): A proposed approach*. 321Fire, Namibia.

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20(7): 387-394.

Bond WJ, van Wilgen BW (1996) *Fire and plants.* Chapman and Hall, London.

Bothma JP, du Toit JG (2010) *Game ranch management.* 5th Edition, Van Schaik Publishers, Pretoria.

Burke A (2006) Savanna trees in Namibia: factors controlling their distribution at the arid end of the spectrum. *Flora* 201: 189-201.

Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. *Ecology* 37: 451 460.

Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution* 5(22): 5295-5304.

du Toit JT, Rogers KH, Biggs HC (2003) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington D.C.

du Toit JCO, van den Berg L, O'Connor TG (2015) Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. *African Journal of Range & Forage Science* 32 (1): 13-20.

Eco Impact Consultants (2011) *Waterberg Plateau Park Management and Tourism Development Plan*. Ministry of Environment and Tourism, Windhoek, Namibia.

Erb KP (1993) *The Roan antelope (*Hippotragus equinus*, Desmarest 1804), its ecology in the Waterberg Plateau Park*. M.Sc thesis: University of Stellenbosch. Unpublished.

Erckie JB (2007) *Assessing the effects of grazing intensity by large herbivores on species diversity and abundance of small mammals at Waterberg Plateau Park, Namibia*. MSc. Thesis, University of Namibia, Windhoek. Unpublished.

Giess W (1998) A Preliminary Vegetation Map of Namibia. 3rd edition. *Dinteria* 4: 1-112.

Goldammer JG, de Ronde C (Ed.) (2004) *Wildland fire management handbook for Sub-Sahara Africa*. comPress, Global fire monitoring centre.

Govender N, Trollope WSW, van Wilgen BW (2006) The effect of fire season, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748 758.

Gul B, Islam M, Ahmad S, Gul S (2014) Effects of prescribed fire on forage production and nutritive value of the perennial grass *Saccharum griffithii. International Journal of Experimental Botany* 83: 415-421.

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.

Hipondoka MHT, Versfeld WD (2006) Root system of *Terminalia sericea* shrubs across rainfall gradient in a semi-arid environment of Etosha National Park, Namibia. *Ecological Indicators* 6: 516-524.

Holdo RM (2005) Stem mortality following fire in Kalahari sand vegetation: effects of frost, prior damage, and tree neighbourhoods. *Plant Ecology* 180: 77-86.

Holdo RM (2007) Elephants, fire and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* 17(2): 558-568.

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2): 187-211.

Jankowitz WJ (1983) *Die plantekologie van die Waterberg Platopark*. PhD Thesis. Universiteit van die Oranje Vrystaat. Unpublished.

Joubert DF, Powell LA, Schact WH (2014) Visual obstruction as a method to quantify herbaceous biomass in southern African semi-arid savannas. *African Journal of Range and Forage Science* 32: 1-6.

Joubert DF, Rothauge A, Smit GN (2008) A conceptual model of vegetation dynamics in the semi-arid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera. Journal of Arid Environments* 72: 2201-2210.

Joubert DF, Smit GN, Hoffman MT (2012) The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. *Journal of Arid Environments* 87: 1-7.

Klaassen ES, Kwembeya EG (Ed.) (2013) *A Checklist of Namibian Indigenous and Naturalised Plants*. Occasional Contributions No. 5, National Botanical Research Institute, Windhoek, Namibia.

Komarek EV (1971) Effects of fire on wildlife and range habitats. *Proceedings of the Prescribed Burning Symposium*, pp. 46-52.

Kruskal JB (1964) Nonmetric Multidimensional Scaling: A Numerical Method. *Psychometrika* 29: 115-129.

Le Roux J (2011) *The Effect Of Land Use Practices on the Spatial and Temporal Characteristics of Savanna Fires in Namibia*. PhD. Thesis, University of Erlangen-Nürenburg.

Likens GE (ed.) (1989) *Long term studies in Ecology: Approaches and alternatives*. Springer-Verlag, New York, Inc. Pp 110-135.

Lutibezi SP (2016) *The effect of fire history on the root carbohydrate concentration of encroaching Terminalia sericea at the Waterberg Plateau Park, Central Namibia*. Master thesis, University of Science and Technology. Unpublished.

Mapaure I, Moe SR (2009) Changes in the structure and composition of miombo woodlands mediated by elephants (*Loxodonta africana*) and fire over a 26-year period in north-western Zimbabwe. *African Journal of Ecology* 47: 175-183.

Mapiye C, Mwale M, Chikumba N, Chimonyo M (2008) Fire as a rangeland management tool in the savannas of southern Africa: a review. *Tropical and Subtropical Agroecosystems* 8(2): 115-124.

Mbatha KR, Ward D (2010) The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. *Journal of Arid Environments* 74: 1294-1301.

McCune B, Mefford MJ (2011) PC-ORD. *Multivariate Analysis of Ecological Data*. Version 6.08. MjM Software, Gleneden Beach, Oregon, U.S.A.

Mendelsohn J, el Obeid S (2005) *Forests and woodlands of Namibia*. RAISON, Windhoek.

Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) *Atlas of Namibia*. David Philip, Cape Town. Accessed at: http://www.uni-koeln.de/sfb389/e/e1/download/atlas_ namibia/ 16 October 2017.

Menke JW (1992) Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia Journal of the California Native Plant Society* 20(2): 22-25.

Mukaru WC (2009) *Impacts of large herbivores on vegetation and soils around water points in Waterberg Plateau Park, central Namibia*. M.Sc. Thesis, University of Namibia and Humboldt University in Berlin. Unpublished.

Nepolo E, Mapaure I (2012) Short-term influence of fire on herbaceous composition, diversity and grass biomass production in Savanna woodland in Windhoek, Namibia. *International Journal of Ecosystem* 2(6): 154-160.

Nghalipo E, Joubert D, Throop H, Groengroeft A (2018) The effect of fire history on soil nutrients and soil organic carbon in a semi-arid savanna woodland, central Namibia. *African Journal of Range and Forage Science* 1-8.

Nyazika T, Gandiwa P, Chanyandura A, Muboko N, Gandiwa E (2017) Influence of fire frequency on woody vegetation structure and composition in Lake Chivero Recreational Park, northern Zimbabwe. *Tropical Ecology* 58(3): 583-589.

Roodt V (2015) *Grasses and grazers of Botswana and the surrounding savanna*. Struik Nature, Cape Town.

Sah JP, Ross MS, Snyder JR, Koptur S, Cooley HC (2006) Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests. *International Journal of Wildland fire* 15: 436-478.

SASSCAL (Southern African Science Service Centre for Climate Change and Adaptive Land Management) - weather net: http://www.sasscalweathernet.org. Accessed: 18 October 2016.

Schneider I (1993) *Waterberg Plateau Park, Namibia*. John Meinert, Windhoek.

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annual Review Ecological Systems* 28: 517-544.

Scholes RJ, Walker BH (1993) *An African Savanna*: *Synthesis of the Nylsvley study*. Cambridge University Press, Great Britain.

Sheuyange A, Oba G, Weladji RB (2005). Effects of anthropogenic fire history on savanna vegetation in north eastern Namibia. *Journal of Environmental Management* 75: 189 198.

Smit IPJ, Asner GP, Govender N, Bowdoin TK, Knapp DE, Jacobson J (2010) Effects of fire on woody vegetation structure in African savanna. *Ecological Applications* 20: 1865-1875.

Smith MA (2008) *Robel pole technique and data interpretation*. University of Wyoming, United States of America.

StatSoft Inc (2002) *STATISTICA*. Tulsa, OK.

Trollope WSW (2003) *Fire effects in African grasslands and savannas*. Department Livestock and pasture Science, University of Fort Hare, Eastern Cape, South Africa.

Trollope WSW, Trollope LA, Goode R, de Bruyn P, van den Broeck D (2013) Assessment of veld condition using the adapted point centred quarter method for bush surveys. *Special Report- Research & Development, Working on Fire*, South Africa: 1-20.

Trollope WSW, Trollope LA, Hartnett DC (2002) *Fire behaviour a key factor in the fire ecology of African grasslands and savannas*. Mill press, Rotterdam.

Uunona NM (2014) *Impacts of fire on grazers and browsers utilization at the Waterberg Plateau Park, Central Namibia*. Work Integrated Learning project, Polytechnic of Namibia. Unpublished.

Uresk DW, Mergen DE, Benzon TA (2009) Estimating standing vegetation with a modified Robel pole on meadows and grasslands in the southern black hills of South Dakota. *Proceedings of the South Dakota Academy of Science* 88: 91-97.

van Langevelde F, van De Vijver CADM, Kumar L, van Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84(2): 337-350.

van Oudtshoorn F (2004) *Guide to grasses of southern Africa,* Briza Publications, Pretoria.

Zimmermann I, Joubert DF, Graz FP (2003) Proposed ground monitoring of bush thickening in Namibia. In *Proceedings of the VIIth International Rangelands Congress* 26th July - 1st August, Durban, South Africa, 793-795.

Zimmermann I, Mwazi FN (2002). The effect of a prescribed burn, followed up with browsing pressure on rangeland condition in the Mountain savanna and Karstveld of Namibia. *Dinteria*, 27: 49 57.

Zimmermann J, Higgins SI, Grimm V, Hoffman J, Linstadter A (2010) Grass mortality in semi-arid savanna: The role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 1-8.

Do swing gates prevent black-backed jackal (*Canis mesomelas*) from entering commercial sheep farms?

PL Cunningham

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Abstract

Black-backed jackal (*Canis mesomelas*) are responsible for much loss of small livestock throughout Namibia, but especially so in the predominantly sheep farming regions of southern Namibia. Impermeable fences, colloquially termed jackal-proof fences, are used by small-stock farmers to prevent jackals from accessing their land. Access through jackal-proof fences is mainly facilitated by specialist burrowing species, although black-backed jackal are also capable of burrowing under fences themselves. Installing swing gates and maintaining artificial holes are simple ways to encourage burrowing species to use these thoroughfares while minimising the maintenance of fences. A study to determine the effectiveness of swing gates in excluding black-backed jackal was conducted on a farm in southern Namibia over a 5 month period. Nine other species were confirmed to use burrows fitted with swing gates while black-backed jackal were not found to utilise these swing gates at all, although probably will learn to do so over time. The biggest advantage of using swing gates is the decrease in fence maintenance activities which was reduced by almost 90% during this study.

Keywords: black-backed jackal; fences; Namibia; predator control; swing gates

Introduction

Impermeable fences impact on the dispersal and genetic fitness of wildlife, restrict migration as well as prevent access to resources; therefore innovative alternatives to such barriers need to be considered (Coetzee 2016). Although outer boundary fences of commercial small-stock farms in southern Namibia are made "jackal-proof" – i.e. wire-mesh reinforced, dug into the soil and weighed down with rocks – black-backed jackals (*Canis mesomelas*) continue to access farms via burrows typically dug by species such as aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*) and porcupine (*Hystrix africaeaustralis*). Black-backed jackal are responsible for significant sheep and goat losses (e.g. Drouilly *et al*. 2017) as well as preying on small wild ungulates (Kamler *et al*. 2012). They use holes under/through fences extensively (e.g. 22% of tracks for open holes and 2.5% for open swing gates in north-central Namibia) (Schumann *et al*. 2006) as well as tyre-passages used as wildlife thoroughfares (44% in central Namibia) (Weise *et al*. 2014). Although black-backed jackals are also capable of burrowing under fences if/when required, they typically use existing burrows rather than dig their own (pers. obs.).

The loss of small livestock is a financial burden on farmers (Lucas 2012, Drouilly *et al*. 2017) which is exacerbated by additional fence maintenance costs (i.e. fuel, materials and time). Such added expenses for a marginal business in a drought prone and ever changing economic environment could contribute to farmers targeting, and destroying animals perceived as part of the problem (i.e. burrowing species) with dire long term ecological consequences.

Swing gates, albeit designed for and used successfully to reduce fence damage by warthogs (*Phacochoerus africanus*) while excluding cheetah (*Acinonyx jubatus*) from accessing game farms in north-central Namibia, can also exclude black-backed jackal (Schumann *et al*. 2006). Using vehicle tyres as a wildlife thoroughfare does not prevent black-backed jackal from passing through a fence as these are open structures designed to facilitate the movement of smaller wildlife through barriers such as fences while containing valuable large-bodied mammals (Weise *et al*. 2014).

Installing and maintaining artificial thoroughfares – i.e. swing gates – is a simple way to encourage burrowing species to use existing thoroughfares while minimising fence maintenance otherwise required if animals dig their own burrows under/through fences (Schumann *et al*. 2006, Weise *et al*. 2014). Monitoring and maintenance, however, remain important as burrowing is influenced by environmental factors such as season and soil type, resulting in new holes being opened (Rust *et al*. 2014).

This study investigated whether a practical, cost-effective swing gate mechanism along small-stock farm boundary fences in southern Namibia would a) exclude black-backed jackal, b) facilitate the movement of burrowing species and c) reduce the number of holes dug by burrowing wildlife.

Methods

Study area

This study was conducted on farm Korhaan #254, approximately 70 km south of Grünau in the Karas region (homestead: 28°16'12.7"S, 18°03'44.1"E). The farm is 8,000 ha in size and divided by the B1 highway into two approximately equal parts with this study being conducted on the ca. 4,000 ha east of the highway. The vegetation is classified as typical dwarf shrub savanna (Giess 1971) or Karas dwarf shrubland (Mendelsohn *et al.* 2002) dominated by *Rhigozum trichotomum* shrubs and *Stipagrostis* species grasses. The top soil and rock structure is varied, but dominated by hard shale geology. The mean annual rainfall is between 50-100 mm with a high coefficient of variation of between 60-70% while average minimum and maximum temperatures vary between 6-8°C and >36°C during winter and summer, respectively (Mendelsohn *et al.* 2002). Farm Korhaan is used for small livestock (sheep) farming and the only wild ungulates present are springbok (*Antidorcas marsupialis*) and steenbok (*Raphicerus campestris*).

Boundary fence holes

This study was conducted between 3 May 2015 and 7 October 2015 – a total of 157 days. A total length of 24.7 km of the farm boundary fence was monitored on seven occasions during this period.

All holes encountered during the first fence investigation were documented and closed using rocks only or with a combination of rocks and wire netting and covered with soil. On subsequent visits all holes encountered, whether new or reopened, were documented and closed again with rock/soil or fitted with a swing gate. The placement of swing gates was dependent on the condition of the lowest steel wire strand to which these mechanisms were attached to and the frequency of use – i.e. wildlife activity – through the opening, with more active holes being fitted with swing gates rather than those not viewed as very active.

Burrowing species

Species responsible for the holes dug under the fence were identified from tracks and type of excavation – e.g. aardvark holes are big with tell-tale claw and tail drag marks compared to small scrapes with pug marks left by the African wildcat (*Felis silvestris*).

Swing gates

Custom made swing gates were constructed from scrap metal sheeting and wire (Figure 1). A strip of metal sheet with dimensions of 335 x 55 x 1 mm (length x width x thickness) was used as a 'skirting' through which holes were punched. A

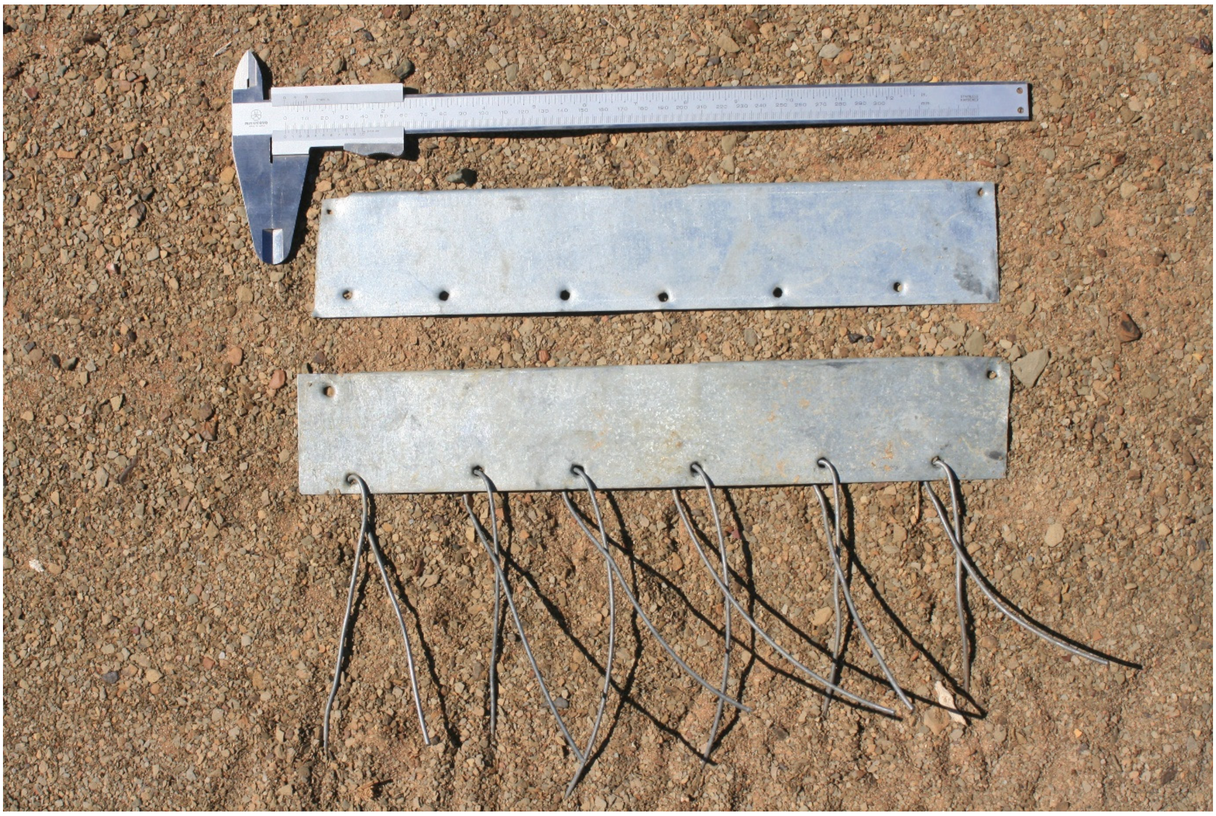

Figure 1: *Custom made swing gate consisting of a metal sheet skirting and wire curtain.*

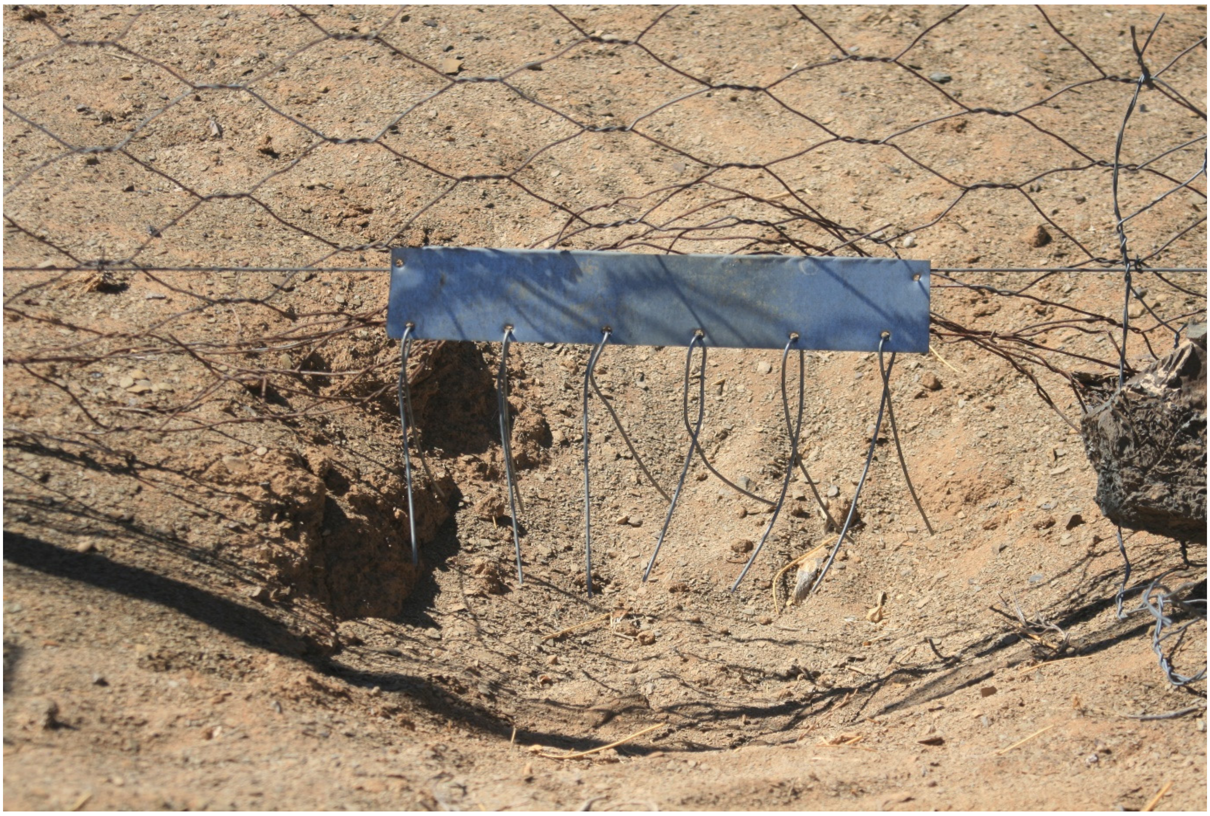

Figure 2: Swing gate attached to the bottom wire strand of the boundary fence.

'curtain' of wire strands hung loosely through these holes formed the swing gate action. Swing gates were then attached with a twist of wire to the lowest steel wire strand of the fence (Figure 2). The length of wire strands was determined by the depth of the burrow. Material costs and time to make and install these swing gates from farm scrap metal was minimal and an important consideration for this study. Swing gates were placed at the most active burrows as it was observed that burrowing species tend to frequent the same burrows, probably related to their foraging routes.

Camera trap monitoring

Two Bushnell Trophy Cam XLT trail cameras were placed adjacent to holes fitted with swing gates to document the movement of wildlife through the fence (Figure 3). The cameras were rotated to monitor various holes fitted with swing gates along the fence during the course of the study period. This was done in an opportune manner as dictated by circumstances and does not allow for formal statistical analysis.

***Figure 3:** Camera trap set adjacent to a burrow fitted with a swing gate to document wildlife movement.*

Results and Discussion

Boundary fence holes

A total of 73 holes, dug by various species but mainly aardvark and aardwolf, were recorded on 3 May 2015 (Table 1). The number of holes under the fence decreased to 8 by 7 October 2015, an 89% decrease over approximately 5 months. This decrease in southern Namibia (Grünau area) is high compared with a 40% decrease in holes in the Otjiwarongo area (Schumann *et al*. 2006) and a 57% reduction in central Namibia (Weise *et al*. 2014) although similar to Piepmeyer's 70% reduction in burrowing holes in the Daan Viljoen Game Park to the west of Windhoek (Piepmeyer pers. com. 1999, in Schumann *et al*. 2006). This can probably be attributed to the substrate as the soils are typically sandy in the Otjiwarongo area while hard to the west of Windhoek and in the Grünau area. This is supported by Rust *et al*. (2014) who noted an increase in holes associated with sandy soils and/or after rains when the soils were softer.

Table 1: *Boundary fence burrow details during this study.*

Hole and swing gate details	Numbers and distances
Total holes: 3 May 2015	73
Total holes: 7 October 2015	8
Total holes reopened: Rock	31
Total holes reopened: Rock and mesh	28
Total new holes	26
Total length of fence	24.7 km
Average distance between holes: Start	338.4 m
Average distance between holes: End	3,087.5 m
Swing gates installed	22

The average number of holes encountered at the start of the study was one hole for every 338.4 m along the fence which decreased to one hole for every 3,087.5 m five months later (Table 1). This indicates that the main burrowing species (i.e. aardvark and aardwolf) made use of the swing gates rather than dig new holes with associated time and energy requirements. My personal observations suggest that aardvark and aardwolf probably have typical foraging routes which include 'favoured holes' and once these holes were not closed, but rather fitted with swing gates, they continued to use these holes, although the study was not designed to provide the data that would support this assumption. The use of swing gates is confirmed for various species such as aardvark, porcupine and warthog (Schumann *et al*. 2006). The use of tyres as a thoroughfare – effectively an open hole – by at least 18 mammal species, including black-backed jackal (Weise *et al*. 2014), makes the latter method futile when attempting to prevent predators accessing farmland.

Although not significantly different (p=0.96) slightly more holes were reopened when using rocks only as compared to holes closed with rocks and wire netting (31 and 28 respectively). Aardvarks are prodigious diggers and using rocks only or a combination of rocks and wire netting does not deter them from reopening such holes (Table 1). The rock and wire netting combination would probably deter most other digging species though and it is thus advisable to determine which species are responsible for the holes before deciding on the technique of closing these holes.

Burrowing species

Four species as identified from tracks and other tell-tale signs were responsible for reopening old holes (69%) or creating new holes (31%) during the course of this study. Aardvark (55%) and aardwolf (39%) were responsible for 94% of these (Figure 4). Aardvark have also been confirmed as prolific burrowers in other studies (e.g. Schumann *et al*. 2006, Rust *et al*. 2014, Weise *et al*. 2014) that also included porcupine and warthog in their data. Porcupine occur on farm Korhaan (albeit at low densities) with no evidence of them creating holes although potentially they could, but they probably make use of aardvark holes. Aardwolf is a known burrowing species and although present in the Otjiwarongo and Windhoek areas they were not deemed to be as active burrowers as warthog (e.g. Schumann *et al*. 2006, Weise *et al*. 2014). Aardwolf probably have higher densities in southern Namibia, consequently making them the second most active fence burrower observed during this study (Figure 4). Warthog do not occur in the Grünau area.

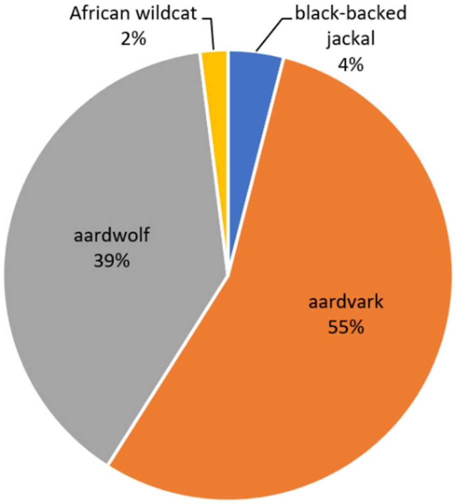

Figure 4: *Species responsible for creating burrows by reopening holes closed with rock and/or rock and mesh under boundary fences between 3 May and 7 October 2015 (n=85).*

Swing gates

A total of 22 swing gates were installed at an average of one swing gate for every 1,122.7 m along the fence (Table 1). The decrease in new holes by almost 90% over five months of investigation suggests that this method is a suitable option to address burrowing activity by indigenous wildlife. Swing gates should however be placed in areas with most or frequent activity for best results and not necessarily evenly spaced along a fence line. This is in accordance with Schumann *et al*.

(2006) who found that fences were damaged more by warthog close to water points. However, aardvark and aardwolf are water independent species (Richardson 1985, Skinner and Chimimba 2005) and the presence of water points is not expected to influence their movements through fences, although this was not tested during the present study.

Camera trap monitoring

Camera traps were only set to identify species using the swing gates and more importantly, to determine whether black-backed jackals made use of these structures. Nine species were confirmed using burrows fitted with swing gates on the farm: aardvark, aardwolf, African wild cat, bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), Cape hare (*Lepus capensis*), porcupine, steenbok and striped polecat (*Ictonyx striatus*) (Figure 5). This is more than the three species (aardvark, porcupine, warthog) confirmed passing through swing gates by Schumann *et al*. (2006), and may be due to the design of the swing gates used on the farm being a lightweight and simple structure mimicking the local fence compared to the formal more robust design used by Schumann *et al*. (2006).

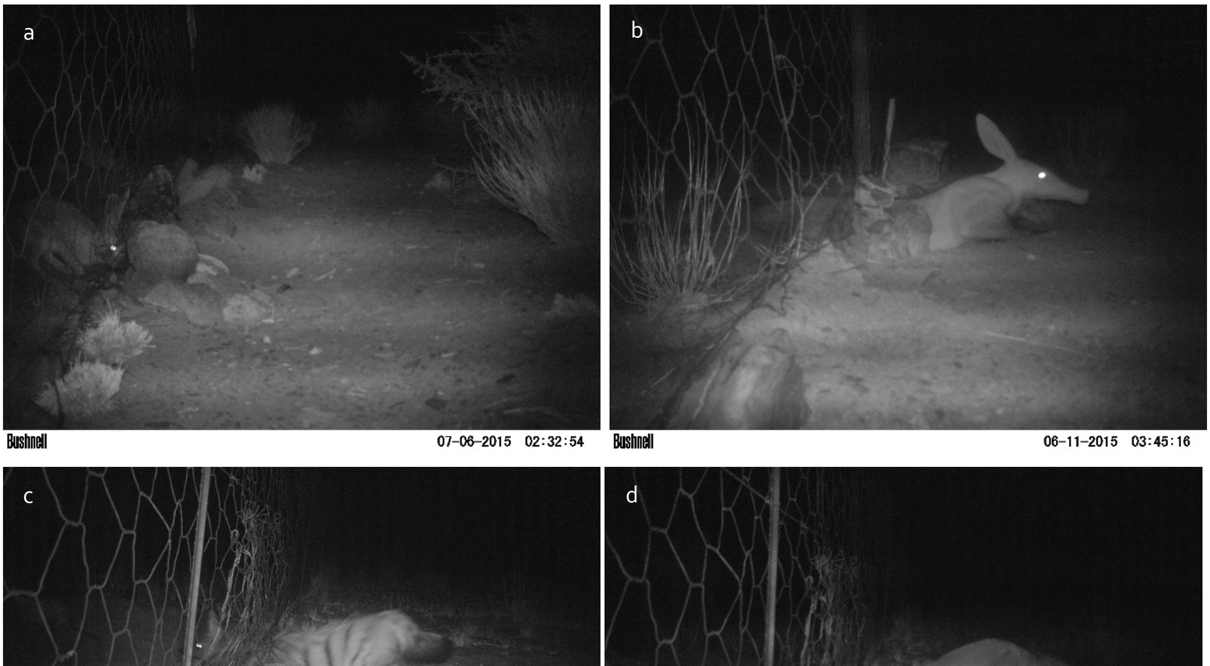

Figure 5: *(a) Cape hare; (b) aardvark; (c) aardwolf; (d) Cape fox; (e) striped polecat; (f) steenbok making use of various swing gates.*

Black-backed jackal are wary of novel items in their environment (Loveridge and Nel 2004). Although black-backed jackals were observed in the vicinity of the swing gates, probably investigating the camera (Figure 6), no images were collected of them using the swing gates. This indicates that during the study period at least, black-backed jackals were wary of the swing gates and consequently avoided those holes.

Figure 6: *Black-backed jackal inspecting a swing gate and camera.*

As black-backed jackal have few absolute dispersal barriers including electrified fences (Kerley *et al*. 2018), the use of swing gates should not be viewed as a panacea to preventing their access to commercial small livestock farms in Namibia. Swing gates have disadvantages as well, for example when the hanging curtain wires become dislodged or stuck in the wire netting, especially when aardvark pass through, the hole is left open. Swing gates do not prevent new holes from being dug by aardvark or aardwolf and allowing access to black-backed jackal; and black-backed jackal will eventually probably learn to use these swing gates as they are a highly flexible predator whose behaviour adapts to its environment (Nattrass *et al*. 2017). Excluding black-backed jackal from commercial farmland, rather than exterminating them along with the burrowing species providing them access to farmland would contribute to biodiversity conservation. Farmland, contrary to popular belief, is viewed as beneficial to some species not found in protected areas (Drouilly & O'Riain 2019). Furthermore, excluding black-backed jackal from farmland would also benefit springbok as their fawns are preyed upon by the species (Klare *et al*. 2010, Kamler *et al*. 2012), and farmers utilise springbok extensively for biltong/venison hunting as an additional source of income (Eloff 2001).

However, the biggest advantage is probably the decrease in fence maintenance activities. Although not quantified during this study, collecting rock, attaching mesh, shovelling in soil, etc. is labour-intensive especially on large farms with extensive boundary fences (pers. obs.). Swing gates also prevent the radical alternative followed by some farmers (pers. obs.) of exterminating aardvark and aardwolf to prevent them from opening holes for black-backed jackal.

It is important to exclude black-backed jackal from livestock farms because once they become resident they exhibit a feeding preference for goats and sheep over similar size wild mammal prey (Drouilly *et al*. 2017). There is no single method of effectively addressing the issue. For best results a combination of techniques, including swing gates but also the active control of these predators once established, should be used to limit black-backed jackal access to farms.

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References

Coetzee K (2016) Practical techniques for habitat & wildlife management. *A guide for game ranches, conservation areas and farmland*. New Voices Publishing Services, Cape Town, South Africa.

Drouilly M, O'Riain MJ (2019) Wildlife winners and losers of extensive small-livestock farming: A case study in the South African Karoo. *Biodiversity and Conservation* (2019): 1-19. https://doi: 10.1007/s10531-019-01738-3.

Drouilly M, Nattrass N, O'Riain MJ (2017) Dietary niche relationships among predators on farmland and a protected area. *Wildlife Management* 82(3): 507-518.

Eloff T (2001) *The economics of the game industry in South Africa*. In: Ebedes H, Reilly B, van Hoven W, Penzhorn B (Eds; 2001) Proceedings of 5th International Wildlife Ranching Symposium, Sustainable Utilization– Conservation in Practice. Pretoria, South Africa. p. 78-86.

Giess W (1971) A preliminary vegetation map of South West Africa. *Dinteria* 4: 1 - 114.

Kamler, JF, Klare, U & Macdonald DW (2012) Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. *African Journal of Ecology* 50: 299-307.

Kerley G, Wilson S, Balfour D (Eds; 2018) *Livestock predation and its management in South Africa: A scientific assessment*. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa.

Klare U, Kamler JF, Stenkewitz U, Macdonald DW (2010) Diet, prey selection and predation impact of black-backed jackals in South Africa. *Journal of Wildlife Management* 74(5): 1030-1042.

Loveridge AJ, Nel JAJ (2004) *Black-backed jackal* Canis mesomelas. In: Sillero-Zubiri C, Hoffman M, Macdonald DW (Eds; 2004) Canids: *Foxes, wolves, jackals and dogs*. IUCN/SSC Canid Specialist Group, Cambridge, United Kingdom, p. 161-166.

Lucas, KJ (2012) *Testing the efficiency of potential deterrents for black-backed jackal*, Canis mesomelas, *both in- and ex situ*. MSc thesis, University of Essex, United Kingdom.

Mendelsohn J, Jarvis A, Roberts A, Robertson T (2002) *Atlas of Namibia. A portrait of the land and its people*. David Philip Publishers, Cape Town, South Africa.

Nattrass N, Conradie B, Drouilly M, O'Riain MJ (2017) *Understanding the black-backed jackal*. CSSR Working Paper No. 399, University of Cape Town, South Africa.

Richardson PRK (1985) *The social behaviour and ecology of the aardwolf,* Proteles cristatus *(Sparrman, 1783) in relation to its food resources*. PhD thesis, University of Oxford, United Kingdom.

Rust NA, Nghikembua MT, Kasser JJW, Marker LL (2014) Environmental factors affect swing gates as a barrier to large carnivores entering game farms. *African Journal of Ecology* 53(3): 339-345.

Schumann M, Schumann B, Dickman A, Watson LH, Marker L (2006) Assessing the use of swing gates in game fences as a potential non-lethal predator exclusion technique. *South African Journal of Wildlife Research* 36(2): 173-181.

Skinner JD, Chimimba CT (2005) *The mammals of the southern African Subregion*. Cambridge University Press, Cambridge, United Kingdom.

Weise FJ, Wessels Q, Munro S, Solberg M (2014) Using artificial passageways to facilitate the movement of wildlife on Namibian farmland. *South African Journal of Wildlife Research* 44(2): 161-166.

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Supplement to “Checklist of the checkered beetles of Namibia” (Coleoptera, Cleridae)

R Gerstmeier

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Abstract

After presenting the first checklist of Cleridae of Namibia, this supplement includes results of the 2019 expedition of the author, data from Hans Mühle, Munich and reports on the genus *Korynetes* (published by Opitz 2018). It includes the label data (locations) from newly collected specimens, distribution maps and colour photos of *Eucymatodera speciosa*, new record for Namibia and *Eucymatodera* sp. 4. Consequently the number of checkered beetle species of Namibia increases to 45 species.

Keywords: Cleridae, checklist, Namibia, distribution maps, colour habitus photo.

Introduction

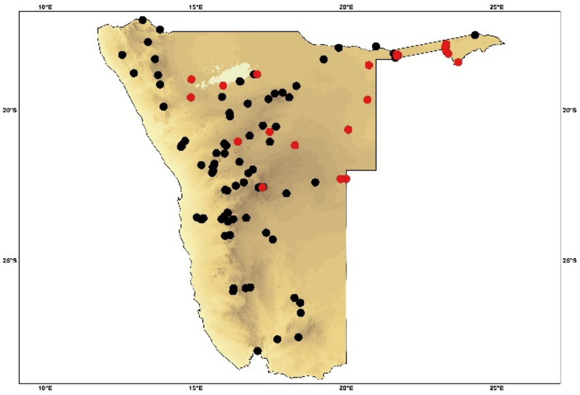
As mentioned in the first publication on Cleridae of Namibia (Gerstmeier 2018), some collecting gaps, especially in the northern and north-eastern parts are striking. An expedition during March 2019 showed some new results for the checkered beetle fauna of Namibia.

Material and Methods

All records are based on UV light-trapping, the light traps installed in trees in about 5-6 m height. The collecting was approved by a research permit (RPIV00012018) of the National Commission on Research, Science and Technology (NCRST). The specimens will be split between the collection of the National Museum of Namibia and the author’s collection. Map 1 shows all cited locations, red dots indicate the new localities.

Abbreviations are:

RGCM	=	Roland Gerstmeier Collection, Munich, Germany
SDEI	=	Senckenberg, Deutsches Entomologisches Institut, Müncheberg, Germany
TMSA	=	Ditsong National Museum of Natural History, Pretoria, South Africa (the former Transvaal Museum of Natural History)
WOPC	=	Weston Opitz Collection, Gainesville, USA



Map 1: *All cited locations: Black circles 2018, red circles 2019.*

Supplement to Checklist

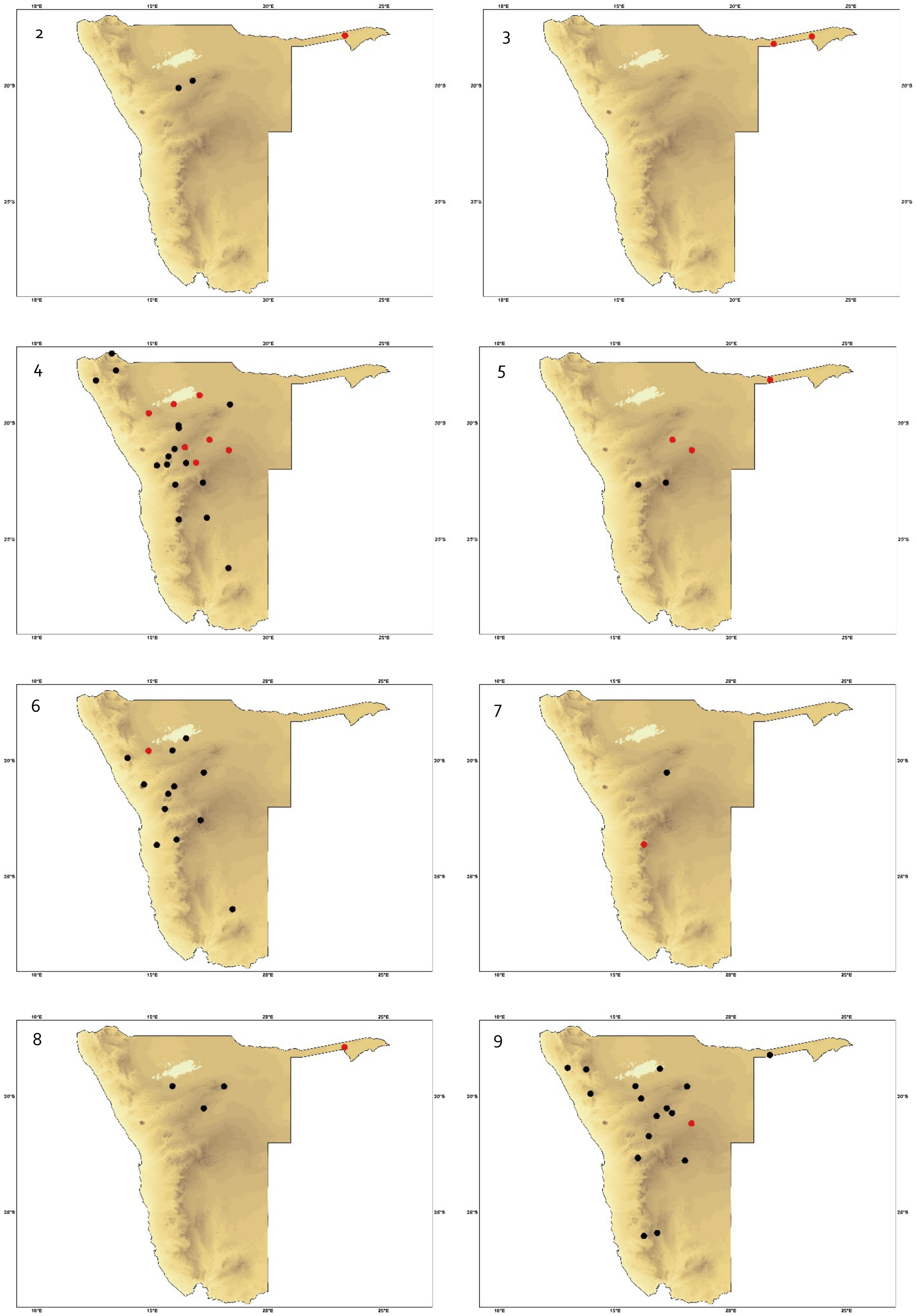
Subfamily TILLINAE

***Diplocladus louvelii* (Spinola, 1844).** Map 2

Namibia, Region Sambesi, Susuwe NP, Nambwa, forest, S17°50.474' E23°18.694', 980 m, 22.03.2019, leg. R. Gerstmeier #17.

***Eucymatodera speciosa* (Gorham, 1883).** Fig. 1, Map 3

Namibia, Region Kavango-East, Mahango NP, Rukange, S18°12.064' E21°40.643', 970 m, 20.03.2019, leg. R. Gerstmeier #15. Namibia, Region Sambesi, Susuwe NP, Nambwa, Campsite, S17°52.623' E23°19.081', 949 m, 23.03.2019, leg. R. Gerstmeier #18.



Maps 2-9: *(2)* Diplocladus louvelii; *(3)* Eucymatodera speciosa; *(4)* Eucymatodera *sp. 1; (5)* Eucymatodera *sp. 4; (6)* Gyponyx *sp. 1; (7)* Menieroclerus nigropiceus; *(8)* Phloiocopus ferreti; *(9)* Phloiocopus *sp. 1.*

Distribution: Namibia (**new country record**), Ethiopia, Tanzania, Kenya, Uganda, Zimbabwe (Gerstmeier 1991).

Eucymatodera sp. 1. (see Gerstmeier 2018), Map 4

Namibia, Region Otjozondjupa, Dinosaur Tracks, 67 km NE Omaruru, S21°02.525' E16°24.092', 1516 m, 01.03.2019, leg. R. Gerstmeier #1 (4 ex.). Namibia, Region Kunene, Kaoko Lodge Campsite, 6 km N Kamanjab, S19°34.514' E14°50.714', 1264 m, 02.03.2019, leg. R. Gerstmeier #2. Namibia, Region Oshana, Etosha NP, Okaukuejo, S19°10.949' E15°55.042', 1139 m, 04.-05.03.2019, leg. R. Gerstmeier #4 (9 ex.). Namibia, Reg. Oshikoto, Etosha NP, Namutoni, 1100 m, S 18°48'26.53", E 16°56'23.64", 07.03.2019, leg. R. Gerstmeier. Namibia, Region Oshikoto, Etosha NP, von Lindequist Gate, S18°48.146' E17°02.552', 1112 m, 07.03.2019, leg. R. Gerstmeier #5 (6 ex.). Namibia, Region Otjozondjupa, Farm Hebron, 14 km S Okakarara, S20°43.128' E17°27.625', 1348 m, 08.-09.03.2019, leg. R. Gerstmeier #6 (3 ex.). Namibia, Region Otjozondjupa, Farm Vergenoeg, 50 km W Otjinene, S21°10.055' E18°18.049', 1498 m, 12.-13.03.2019. leg. R. Gerstmeier #8. Namibia, Otjozondjupa, 25 km N Okahandja, 1500 m, 21°42.552'S/016°53.047'E, 3.2.2019, leg. H. Mühle #426.

Figure 1 Eucymatodera speciosa.

***Eucymatodera* sp. 4.** Fig. 2, Map 5

This species is separated from *Eucymatodera* sp. 1, because the pronotum of *Eucymatodera* sp. 4 is smooth.

Namibia, Region Otjozondjupa, Farm Hebron, 14 km S Okakarara, S20°43.128' E17°27.625', 1348 m, 08.-09.03.2019, leg. R. Gerstmeier #6. Namibia, Region Otjozondjupa, Farm Vergenoeg, 50 km W Otjinene, S21°10.055' E18°18.049', 1498 m, 12.-13.03.2019. leg. R. Gerstmeier #8. Namibia, Region Kavango-East, Mahangu Lodge,outside, S18°08.289' E21°40.684', 1003 m, 18.-20.03.2019, leg. R. Gerstmeier #14.

Figure 2: Eucymatodera *sp. 4*.

Subfamily CLERINAE

***Gyponyx* sp. 1.** (see Gerstmeier 2018), Map 6

Namibia, Region Kunene, Kaoko Lodge Campsite, 6 km N Kamanjab, S19°34.514' E14°50.714', 1264 m, 02.03.2019, leg. R. Gerstmeier #2.

***Menieroclerus nigropiceus* (Kuwert, 1893).** (see Gerstmeier 2018), Map 7

Namibia, Khomas, Namibgrens, 1820 m, 23°36.720'S/016°14.708'E, 11.2.2019, leg. H. Mühle #434.

***Phloiocopus ferreti* (Reiche, 1849).** (see Gerstmeier 2018), Map 8

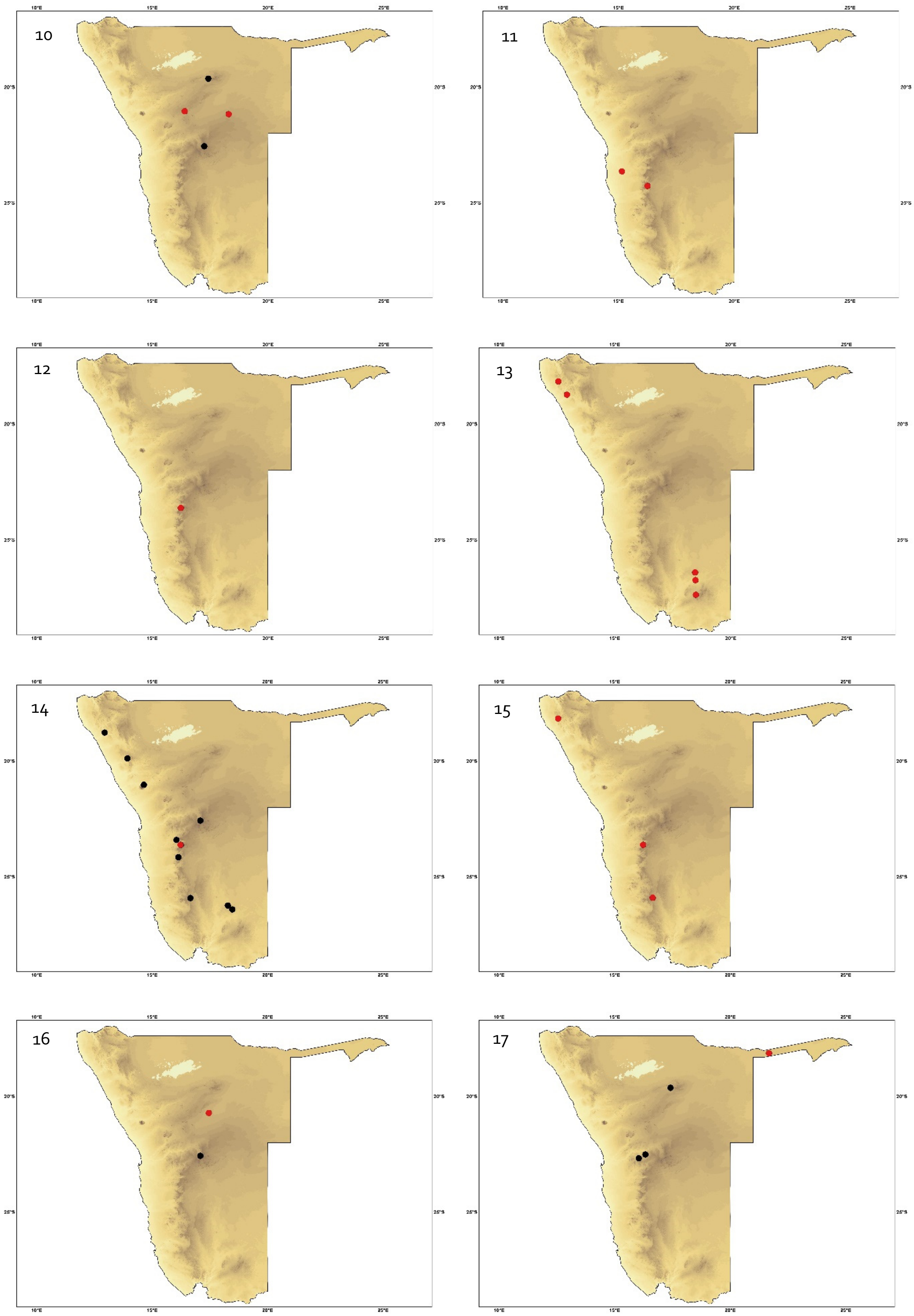
Namibia, Region Sambesi, Susuwe NP, Nambwa, Campsite, S17°52.623' E23°19.081', 949 m, 23.03.2019, leg. R. Gerstmeier #18.

***Phloiocopus* sp. 1.** Map 9

Namibia, Region Otjozondjupa, Farm Vergenoeg, 50 km W Otjinene, S21°10.055' E18°18.049', 1498 m, 12.-13.03.2019. leg. R. Gerstmeier #8 (4 ex.). – Also recorded from Botswana.

***Thanasimodes robustus* (Boheman, 1851).** (see Gerstmeier 2018), Map 10

Namibia, Region Otjozondjupa, Dinosaur Tracks, 67 km NE Omaruru, S21°02.525' E16°24.092', 1516 m, 01.03.2019, leg. R. Gerstmeier #1. Namibia, Region Otjozondjupa, Farm Vergenoeg, 50 km W Otjinene, S21°10.055' E18°18.049', 1498 m, 12.-13.03.2019, leg. R. Gerstmeier #8. – Also recorded from Botswana.



Maps 10-17: *(10)* Thanasimodes robustus; *(11)* Korynetes ligulus; *(12)* Korynetes nigritarsus; *(13)* Korynetes pelidnus; *(14)* Korynetes semistriatus; *(15)* Korynetes ustulatus; *(16)* Necrobia rufipes; *(17)* Prosymnus brevipenis.

Subfamily KORYNETINAE

***Korynetes ligulus* Opitz, 2018.** (see Opitz 2018), Map 11

Naukluft, Naukluft Park, 24°16'S 16°15'E, 26-X-1974, Endrödy-Younga (TMSA, 1 Paratype). Gobabeb, Kuiseb Riverm, ?-XI-1979, B. Wharton & Gray (TMSA, 2 Paratypes).

***Korynetes nigritarsus* Pic, 1948.** (see Opitz 2018), Map 12

Namibgrens Farm, 23°37'S – 16°14E, 4-II-2010, beating, R. Müller (TMSA).

***Korynetes pelidnus* Opitz, 2018.** (see Opitz 2018), Map 13

Namibia, Purros, 300 m, 18°44'S – 12°56'E, 15-4-2005, at light, R. Müller (TMSA). Purros, 18°44'S – 12°56'E, 15-IV-2005, 300 m, at light, R. Müller (TMSA, 1; WOPC, 2). Purros, (Hoaruzsib), 15-16-IV-2005, 300 m, W. Schawaller (TMSA, 4; WOPC, 3). Orupembe, 14-IV-2005, 700 m, W. Schawaller (TMSA, 3; WOPC, 2). Karas, 42 km SE Keetmanshoop, 26°44'.266''S – 18°29'387''E, 25-II-2012, 850 m, H. Mühle (RGCM, 3). Namibia, 40 km NE Keetmanshoop, 26°24'S – 18°28'E, 18-19-II-2010, 850 m, R. Müller (TMSA, 2; WOPC, 1). Namibia, Grünau, 42 km N, 27°22'.951''S – 18°30'936''E, 19-II-2012, 841 m, H. Mühle (WOPC, 2).

***Korynetes semistriatus* Spinola, 1844.** Map 14

Namibia, Khomas, Namibgrens 1820 m, 23°36.720'S/016°14.708'E, 11.2.2019, leg. H. Mühle #434 (RGCM).

***Korynetes ustulatus* Opitz, 2018.** (see Opitz 2018), Map 15

Namibia: 1820 m, Namibgrens farm, 23°37'S – 26°14'E. A second label reads: 4-5.2.2010; E-Y: 3856, at light, leg. Ruth Müller (TMSA). Namibia, Namibgrens farm, 23°37'S – 26°14'E, 4-5-II-2010, 1820 m, at light, Ruth Müller (TMSA, 5; SDEI, 1; WOPC, 2). 15 km E Helm[e]ringhausen, 25°54'S – 16°39'E, 17-II-2010, 1560 m, at light, Ruth Müller (TMSA, 1; WOPC, 1). Oru[m]pembe, 18°11'S – 12°33'E, 14-IV-2005, 677 m, light trap, Ruth Müller (TMSA,1).

***Necrobia rufipes* (Degeer, 1775).** (see Gerstmeier 2018), Map 16

Namibia, Region Otjozondjupa, Farm Hebron, 14 km S Okakarara, S20°43.128' E17°27.625', 1348 m, 08.-09.03.2019, leg. R. Gerstmeier #6.

***Prosymnus brevipenis* Opitz, 2016.** (see Gerstmeier 2018), Map 17

Namibia, Region Kavango-East, Mahangu Lodge, outside, S18°08.289' E21°40.684', 1003 m, 18.-20.03.2019, leg. R. Gerstmeier #14.

With this second checklist, the number of checkered beetle species for Namibia increases to 45 species.

Discussion

The 2019 expedition yielded an equal number of species (10 species) as in 2018, but differed considerably in regards to the species composition. Only four species were recorded in both years (Table 1).

This could either reflect the geographic and hence general ecological situation as the north eastern parts of Namibia are generally wetter and hotter, or be attributed to the better rainy season in 2018, whereas 2019 saw less rainfall in the north western parts of Namibia (nearest BIOTA Observatory Mutompo, S03: March/April 2018: ~110 mm; March/April 2019: ~20 mm). Numerous studies show the effects of rainfall on vegetation and plant communities (Reyer *et al.* 2013) but information on the impact of climate change and rainfall patterns on invertebrates is

Table 1: *Number of species and specimens recorded during 2018- and 2019-expeditions, respectively. 'X' denotes species presence.*

	2018		**2019**	
	Species	**N**	**Species**	**N**
Diplocladus louvelii	X	1	X	1
Eucymatodera sp. 1	X	3	X	25
Eucymatodera sp. 3	X	1	–	–
Eucymatodera sp. 4	–	–	X	3
Eucymatodera speciosa	–	–	X	2
Teloclerus sp.	X	1	–	–
Wittmeridecus sp.n.	X	2	–	–
Gyponyx sp. 1	X	10	X	1
Phloiocopus ferreti	–	–	X	1
Phloiocopus sp. 1	X	3	X	4
Phloiocopus vagedorsatus	X	8	–	–
Thanasimodes robustus	–	–	X	2
Korynetes semistriatus	X	4	–	–
Necrobia rufipes	–	–	X	1
Prosymnus adustus	X	1	–	–
Prosymnus brevipenis	–	–	X	1
∑	**10**	**34**	**10**	**41**

limited (Barnett & Facey 2016). In arid ecosystems, arthropods inhabit a wide range of microhabitats (Doblas-Miranda *et al.* 2009; Hadley & Szarek 1981) and comprise a wide variety of ecosystem functions (e.g. herbivores, predators, pollinators, seed dispersers, decomposers) and are important components of food webs and nutrient cycles (Prather *et al.* 2013). Hence direct and indirect effects (via vegetation) of rainfall on arthropod communities and likewise on the clerid community are likely. A new investigation on ground-dwelling arthropods in an arid savannah showed that the arthropod community composition, as well as activity density, was determined by intermediate term precipitation of 15 to 30 days, not by short- or long-term precipitation (Fischer *et al.*, in review).

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References

Barnett KL, Facey SL (2016) Grasslands, invertebrates, and precipitation: A review of the effects of climate change. Frontiers in Plant Science 7: 1–8.

Doblas-Miranda E, Sánchez-Piñero F, González-Megías A (2009) Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem. *Applied Soil Ecology* 41: 329–335.

Fischer C, Gerstmeier R, Wagner TC. (2019) Long term drought effects on arthropod community composition and implications for food web stability in an arid environment. (in review).

Gerstmeier R (1991) Short communications on systematics of Cleridae. 2. The genus *Eucymatodera* Schenkling, 1899. (Coleoptera, Cleridae, Tillinae). *Mitteilungen der Münchner Entomologischen Gesellschaft* 81: 227–228.

Gerstmeier R (2018) Checklist of the checkered beetles of Namibia (Coleoptera). *Namibian Journal of Environment* 2 A: 7–21.

Hadley NF, Szarek SR (1981) Productivity of Desert Ecosystems. *BioScience* 31: 747–753.

Opitz W (2018) Classification, natural history, and evolution of the Korynetinae (Coleoptera: Cleridae). Part IV. The new genus *Nolafigura* Opitz, and fourteen new species of *Korynetes* Herbst. *Faunitaxys* 6: 1–17.

Prather CM, Pelini SL, Laws A, Rivest E, Woltz M, Bloch CP, Del Toro I, Ho CK, Kominoski J, Newbold TAS, Parsons S, Joern A (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews* 88: 327–348.

Reyer CPO, Leuzinger S, Rammig A, Wolf A, Bartholomeus RP, Bonfante A, de Lorenzi F, Dury M, Gloning P, Abou Jaoudé R, Klein T, Kuster TM, Martins M, Niedrist G, Riccardi M, Wohlfahrt G, de Angelis P, de Dato G, François L, Menzel A, Pereira M. (2013) A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology* 19: 75–89.