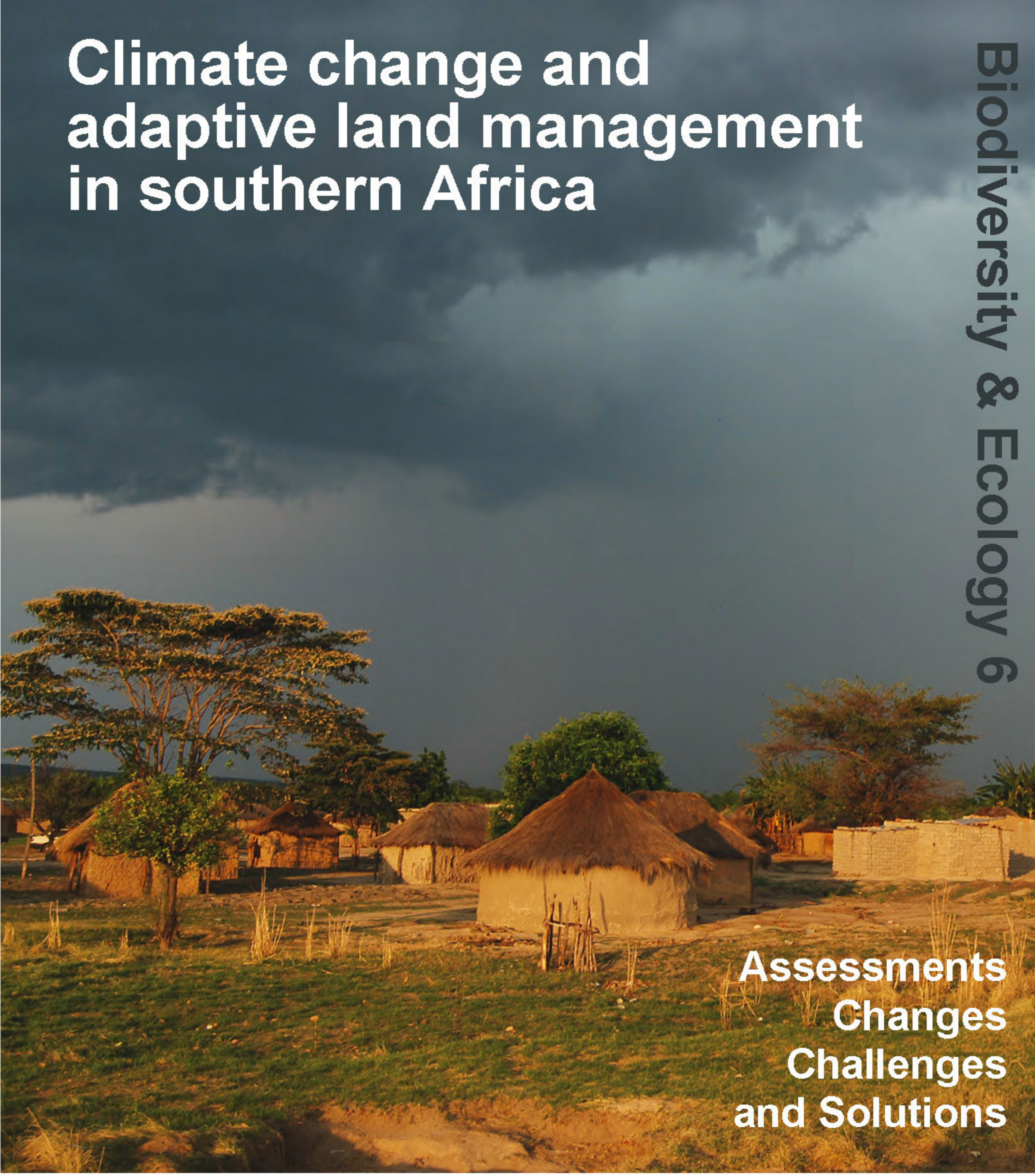
Climate change and adaptive land management in southern Africa

Biodiversity & Ecology 6



Assessments
Changes
Challenges
and Solutions

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Climate change and adaptive land management in southern Africa

Assessments, changes, challenges, and solutions

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Impacts of fire history in a semi-arid woodland savanna

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Rangelands

Abstract: Fire is known to be an important element shaping semi-arid ecosystems. Within SASSCAL we conducted several projects in the woodland savanna of the Waterberg Plateau Park to gain a better understanding of the impact of fire on ecosystem properties and processes (soil characteristics, species composition and structure of the vegetation, changes in plant forage quality, insect biodiversity, and the utilization of habitat and plants by large herbivores). Four adjacent areas of around 2,000 ha–2,500 ha each with different times since last burn were studied (in 2014, when most of the measurements were done, the areas had been burnt 2, 3, 14, and 24 years prior to the study). We found inconsistent effects of different fire histories on soil nutrients, soil organic carbon, and soil respiration, which suggests that soil resources return rapidly (within a year or two) to pre-fire conditions at our sites. We also assume (based on the standing biomass of the four areas during the study) that the fires were likely to have not been sufficiently intense to cause long-term detrimental impacts and impair the recovery of soil resources at our sites. Furthermore, fire positively affected the grass component by increasing grass density and enhancing productivity. Fire maintained open savannas through the top-kill of woody plants but did not alter plant species composition. The influence of burning on the quality of grasses was relatively short-lived (two years after burning, grass quality in burnt sites was comparable with that of unburnt sites). However, trees, whose leaves are generally higher in protein, remained at a higher quality for longer periods after fire and thus served as supplementary food not only for browsers and mixed feeders but also for herbivores generally considered to be 'pure' grazers (e.g., red hartebeest, buffalo). Fire had a negative impact on small ground-nesting bees, whereas bigger and above-ground-nesting bees seemed to be favoured by fire. Ground-dwelling invertebrate communities differed with time since last burn, the main driver of the differences being litter cover. Our findings in relation to fire illustrate that heterogeneous habitats, as a result of pyrodiversity, are of great benefit for the habitat utilization and plant utilization of large herbivores as well as increasing the overall diversity of invertebrates. Managers can maximise biodiversity and diversity in resource and habitat utilization by maximising the diversity of fire histories in the managed areas (commonly termed patch-mosaic burning).

Resumo: O fogo é conhecido por ser um importante factor na modelação dos ecossistemas semi-áridos. No contexto do SASSCAL, realizámos vários projectos na savana arborizada do Parque Nacional de Waterberg, de modo a obter uma melhor compreensão do impacto do fogo nas propriedades e processos do ecossistema (características do solo, composição e estrutura da vegetação, alterações na qualidade de forragem, biodiversidade de insectos e utilização do habitat e das plantas pelos grandes herbívoros). Foram estudadas quatro áreas adjacentes, de cerca de 2000 a 2500 ha, com diferentes tempos desde o último incêndio (em 2014, altura em que a maioria das medições foi realizada, as áreas haviam sido queimados há 2, 3, 14 e 24 anos). Encontrámos efeitos inconsistentes de diferentes historiais de fogo nos nutrientes, carbono orgânico e respiração do solo, o que sugere que os recursos pedológicos retornam rapidamente (dentro de um ano ou dois) a condições de pré-fogo

nos nossos locais. Assumimos também (com base na biomassa existente nas quatro áreas durante o estudo) que os fogos não deverão ter sido suficientemente intensos para causar impactos negativos de longa duração e comprometer a recuperação dos recursos pedológicos nos nossos locais. Além disso, o fogo afectou positivamente as gramíneas ao aumentar a densidade de ervas e intensificou a produtividade. O fogo manteve as savanas abertas através da morte de plantas lenhosas, mas não alterou a composição específica de plantas. A influência da queima na qualidade de gramíneas foi relativamente breve (dois anos após o incêndio, a qualidade das gramíneas era comparável à dos locais não queimados). No entanto, as árvores cujas folhas têm geralmente um maior conteúdo de proteína permaneceram com maior qualidade por períodos maiores após o fogo e, assim, serviram como alimento suplementar a *browsers* e animais de dieta mista, mas também a herbívoros geralmente considerados como herbívoros "puros" (e.x.: caama; bufalo). O fogo teve um impacto negativo em pequenas abelhas que nidificam no solo, enquanto que abelhas maiores que nidificam acima do solo pareceram ser favorecidas pelo fogo. Comunidades de invertebrados no solo variaram com o tempo desde o último incêndio, sendo o principal factor das diferenças a cobertura de detritos. As nossas descobertas em relação ao fogo ilustram que habitats heterogéneos, como resultado da pirodiversidade, são de grande benefício para a utilização do habitat e das plantas pelos grandes herbívoros, e aumentam também a diversidade geral de invertebrados. Os gestores podem maximizar a biodiversidade e diversidade da utilização dos recursos e do habitat ao maximixar a variedade de historiais de fogos em áreas geridas (comumente denominadas de *patch-mosaic burning*).

General introduction

It is well known that fires shape ecosystems, but our understanding of the directions and extent of this shaping as well as the interactions between fires and other ecosystem components is limited. In African savannas, fire management approaches have changed from attempts to completely exclude fire, to rigid fire regimes with little variability, to flexible fire regimes based on utility (woody biomass; woody mortality; grass quantity and quality; soil fertility; and less commonly biodiversity) (van Wilgen, 2009). The current paradigm is to manage fire for heterogeneity and biodiversity (van Wilgen, 2009). Despite the purported objective of parks to conserve biodiversity, that goal is often not practically considered much by park managers, particularly in Namibian parks, where finances and knowledge transfer are extremely limited. Here we investigated the effects of fire on soil properties, vegetation species composition and structure, plant quality, biodiversity of insects, and habitat and plant utilization by large herbivores. Each component of the study is outlined below, followed by a synthesis and management conclusion.

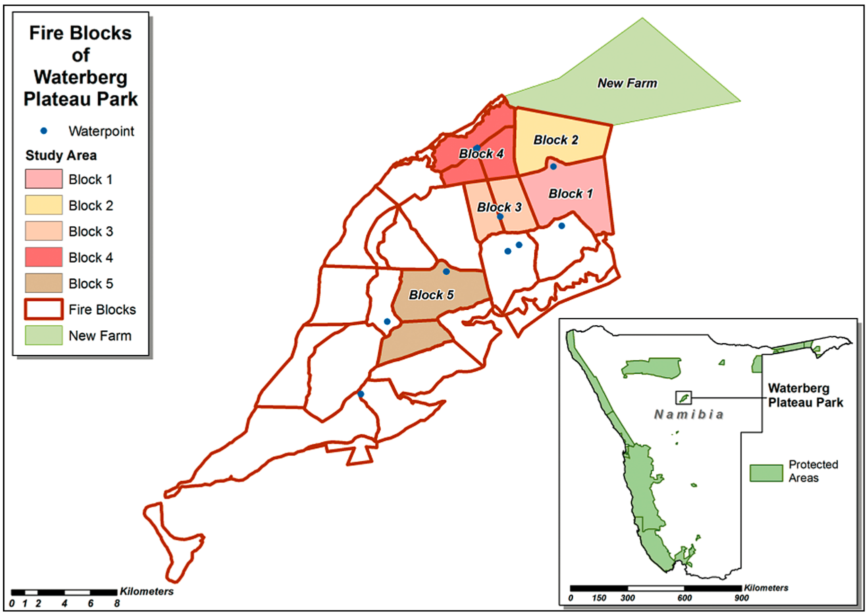


Figure 1: The location of Waterberg Plateau Park in Namibia, and the location of the different fire blocks 1-4 (used for this study), as well as the study area used to investigate frost effects, 5. "New farm" is a portion purchased from a neighbouring farmer that is being incorporated into the park.

The Waterberg Plateau Park (WPP) — our study area

The WPP is a relatively small park of about 47,000 ha in central Namibia, about 280 km northeast of Windhoek and about 60 km east of Otjiwarongo (Fig. 1). The primary aim of the park since its proclamation in 1972 has been to breed up rare, high-value species of antelope and other herbivores. The sandstone plateau rises up to 300 m above the surrounding plain and is on average between 1,550 m and 1,850 m above sea level (Mukaru, 2009). It extends about 50 km in length and 16 km in width. The park lies on aeolian dystrophic Kalahari sands from the Kalahari basin (Erb, 1993), which are heavily leached (Mukaru, 2009). The plateau experiences warm summers with temperatures reaching up to 40 ^{0}C in the hottest months, while winter temperatures can drop to below –10 ^{0}C (www.sasscal-weathernet.org). The mean annual rainfall recorded for the period 1981 to 2001 was 425.5 mm ± 129 mm, with February being the wettest month (Erckie, 2007). The vegetation of the WPP is dominated by typical broadleaf woodland savanna species such as *Terminalia sericea*,

Table 1: Different treatments (blocks) with their mean fire return intervals since 1976 and time since last burn (at 2016) based on interviews with rangers. The last fire was in September 2013, in block 1. Time since last burn depends on the year (2014–2016) when the measurements were taken.

Treatment (block)	Mean fire return interval (years)	Time since last burn (years) – at 2016	Year of last burn
1	6.2	3	2013
2	9.3	4	2012
3	9.3	16	2000
4	18.5	26	1990

Burkea africana, *Ochna pulchra*, *Combretum collinum*, *Combretum psidioides*, *Grewia flavescens,* and *Bauhinia petersiana* as well as *Acacia ataxacantha* and *Acacia fleckii.* Species such as *Pterocarpus angolensis* and *Baikea plurijuga* are absent as a result of the low rainfall and very cold temperatures occasionally experienced in winter. Grass species include *Eragrostis pallens*, *Eragrostis jeffreysii*, *Brachiaria nigropedata*, *Digitaria seriata*, *Panicum kalaharense, Stipagrostis uniplumis, and Aristida stipitata* (Erb, 1993; Schneider, 1993).

We investigated the impacts of time since last burn in the WPP, where fire blocks are generally clearly delineated, with access roads acting as effective fire breaks. The fire history was obtained through interviews with longtime staff members. The study site is located on the northern part of the Park Plateau at the more arid end of Namibia's woodland savanna vegetation type (Giess, 1971).

In the late 1950s the plateau was run as cattle rangeland. The farm owners burned every four years during dry cycles and every three to four years during wet cycles (Jankowitz, 1983). It is perceived that woody vegetation cover has increased in the park since its proclamation and the termination of the regular burning programme by farmers. The reduction in anthropogenic fires and consequent increase in the cover of woody species, such as *T. sericea*, is thought to have caused a reduction in the density of palatable climax perennial grass species such as *B. nigropedata* and *D. seriata*. No vegetation monitoring programmes existed in the WPP prior to our study, and thus the perceived changes have not been tested.

General common methods

The park is divided into six fire zones, which are further subdivided into fire blocks, with roads acting as fire breaks. Each block has a different history (fire frequency, time since last burn [TSLB], year of fire). The studies were done in four fire blocks (treatments) adjacent to one another (Fig. 1.) with different fire histories (Tab. 1). Treatment 1: treatments 2, 3, and 4: burned in 2013, 2012, 2000, and 1990, respectively. A space-for-time substitution approach was applied (Pickett, 1989).

Most of the studies were conducted along randomly located 200 m transects within each block at 40 m (in some cases 20 m) intervals along the transects. This allowed comparisons to be made amongst different parameters within each block (Fig. 2a–d).

A. The impacts of fire history on soils

Introduction

Why is it important? Fire is recognized as an integral part of savanna ecosystems that has shaped those landscapes since the Miocene and continues to do so. The prevalence of fire in this system influences nutrient cycling and soil carbon (C) pools (Holt & Coventry, 1990). Fire may affect ecosystem productivity and biogeochemical processes through nutrient volatilization, altered organic matter quantity, and, indirectly, altered vegetation structure (Satyam & Jayakumar, 2012). Despite the resulting general effects on soil resources, substantial uncertainty about fire history effects exists (Concilio et al., 2006), especially in semi-arid ecosystems. Semi-arid ecosystems are typically much more heterogeneous than mesic systems, with large biotic and abiotic differences among distinct vegetation patch types such as shrubs, grass, and bare ground (de Graaff et al., 2014). Changes in biogeochemical cycles and microbial physiological responses vary among vegetation patch types (Han et al., 2014). We wanted to know whether different fire frequencies in the park had any negative effects on soil properties. We specifically investigated the effects of time since last burn on these properties. Because fire also affects vegetation structure, and thus could indirectly affect soil in this way (Coetsee et al., 2010; Holdo et al., 2012; Khavhagali, 2008), we were also interested in the effects of vegetation patch types (under shrub, under grass, and bare ground) on these parameters. We explored the independent and interactive effects of time since last burn and patch type on soil nutrients, soil organic carbon (SOC), and soil respiration in this semi-arid ecosystem.

Methods

To determine the independent and interactive effects of fire history and vegetation patch types on soil nutrients and SOC, we collected soil samples in four fire blocks with different fire histories (time since last burn ranging from 1 to 25 years and fire intervals ranging from 6.2 to 18.5 years). In each fire block, six transects (200 m) were laid out randomly, and five soil samples were collected at every 40 m along each transect in the 0–10 cm soil layer, amounting to 30 samples per treatment. Chemical analyses for soil nutrients (total N, P, K, Na, Ca, Mg) and SOC were performed at the soil laboratory of the Ministry of Agriculture, Water and Forestry. To determine the effect of fire history on soil respiration and how it responds under different vegetation patch types, we used a LI-6400XT instrument. Eight sampling sites were established in all four fire blocks, with three treatments per site. The treatments represented the vegetation patch types (bare ground, under grass, and under shrub). Additionally, we collected soil cores from each sampling point for the

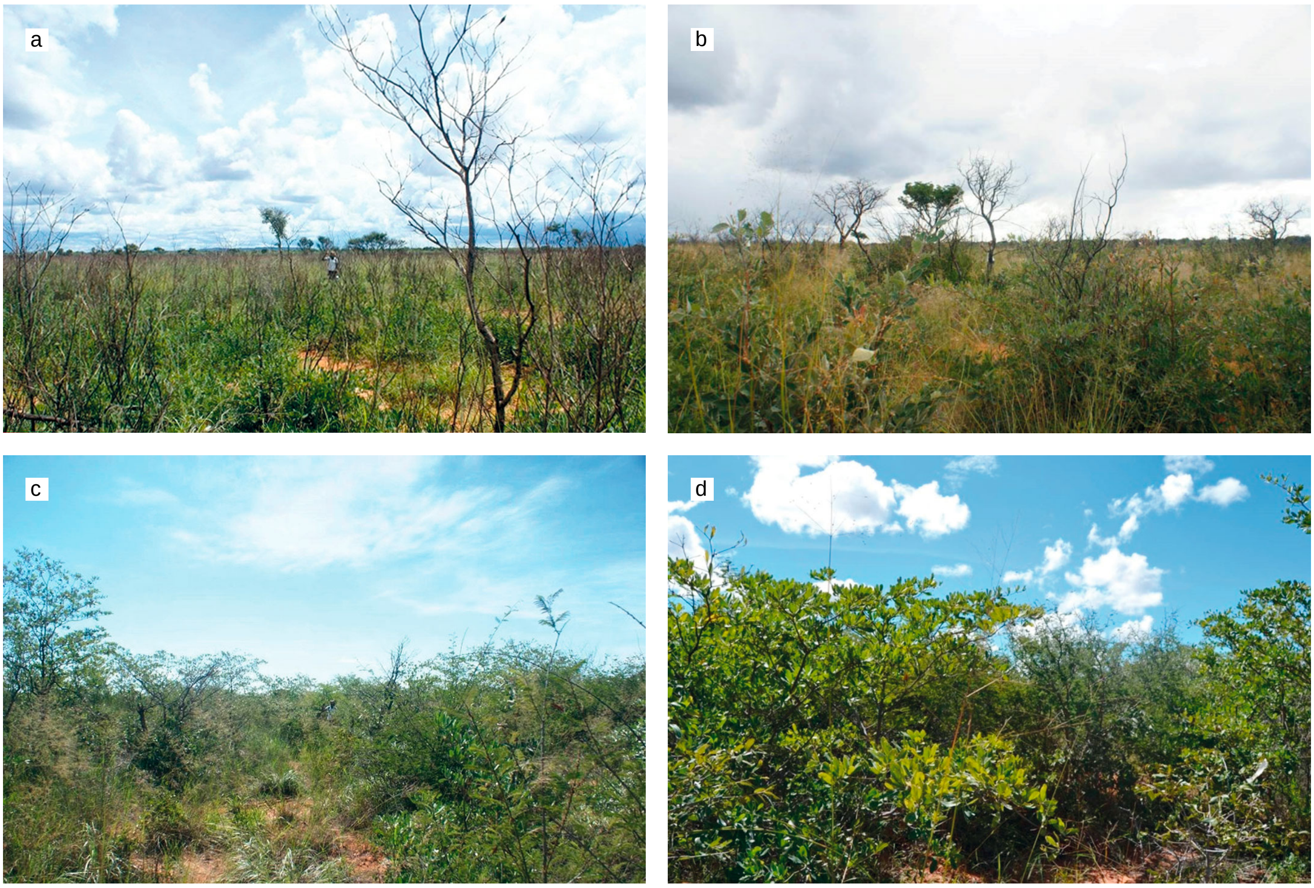


Figure 2: Vegetation structure in (a) Block 1, burned in September 2013, (b) Block 2, burned in 2012, (c) Block 3, last burned in 2000, (d) Block 4, last burned in in 1990.

assessment of gravimetric water content and a laboratory incubation experiment that allowed us to measure potential carbon mineralization under controlled conditions. In the incubation experiment, soil cores were incubated for 3 weeks at 60% water holding capacity, at room temperature. Soil CO_2 efflux was measured for 15 days with an infrared gas analyzer (Licor 6400).

Results

SOC was not significantly different among fire blocks and vegetation patch types. The blocks that burned 2 and 24 years ago (in 2012 and 1990, blocks 2 and 4) had low total N relative to the blocks that burned in 2013 and 2000 (blocks 1 and 3). Block 2, which burned 2 years ago, had the lowest available P relative to other fire blocks. Sodium showed a consistent trend, decreasing with increasing time since last burn. There was no clear trend for other exchangeable cations K, Mg, and Ca; however, their levels were high in the recently burned area (block 1). These cations typically increase after fire because of their presence in the ash as a result of the high threshold temperatures at which these elements volatilize (Satyam & Jayakumar, 2012). These high temperatures might have not been reached during the fire. Soil respiration responded to time since last burn differently under different vegetation patch types, with the under-shrub treatment generally having higher soil CO_2 efflux relative to the under-grass and bare-ground treatments. This suggests that fire may have important indirect effects on soil respiration through its alteration of vegetation cover. In the laboratory experiment, soil CO_2 efflux was higher relative to the field experiment and was not significantly different among vegetation patch types. Based on the field and incubation results, this study concluded that the higher soil respiration observed under shrubs in the field experiment is largely attributable to root respiration, suggesting that fire did not significantly impact soil microbes.

Synthesis and outlook

What can we learn from it? Fire history had a limited and inconsistent effect on soil nutrients, SOC, and soil respiration. This suggests that soil resources return rapidly to pre-fire conditions. In addition, these fires were likely to have not been sufficiently intense to cause long-term detrimental impacts and impair the recovery of soil resources (the standing fuel biomass measurements suggest that fires are generally not very intense). Moreover, site-to-site spatial variation (tree cover, grass cover, microtopography) may have had a stronger controlling influence on soil nutrients, SOC, and soil respiration. Therefore, there should be no concern about using fire within the experienced frequencies (6.2–18.5 years) as a tool to improve positive resource utilization.

B. The impacts of fire history on vegetation

Introduction

Why is it important? Vegetation-fire research is a well-established field in African savannas. Nevertheless, Namibian vegetation-fire studies are very limited, even as fire regimes are being altered in different ways without follow-up research and monitoring. Considering that most of Namibia is arid to semi-arid, Joubert et al. (2012) predicted that fire, although not frequent and generally cooler (low fuel loads) than in wetter savannas, is necessary for keeping savannas in an open grassy state when they occur at the time of seedling establishment. At WPP, the impact of fire history on vegetation structure and species composition was studied in the same fire blocks introduced above.

Methods

At every sample point along the transects, the following three techniques were used: the modified point-centred quarter method (Cottam & Curtis, 1956; Trollope et al., 2013) to determine density and structure, the Bitterlich gauge (Friedel & Chewings, 1988; Zimmermann & Mwazi, 2002) to determine woody cover at different heights, and the visual obstruction reading (VOR) method to estimate standing grass biomass.

The point-centred quarter method used is a version of the Cottam & Curtis (1956) method adapted by Trollope et al. (2013). In each quarter within a 20 m radius (Trollope et al., 2013), the distances to the nearest live perennial grass and to woody species of < 1 m, 1–2 m, 2–3 m, 3–4 m, and > 4 m were measured and recorded (Figure 3). 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.

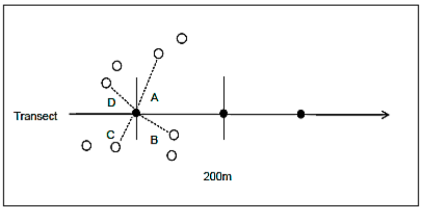


Figure 3: Illustration of how the point-centred quarter method works (Adapted from Mitchell, 2007).

The Bitterlich gauge was used to estimate woody canopy cover (Friedel & Chewings, 1988; 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 crosspiece and pins held horizontally in the direction of a woody canopy. If the woody canopy extends beyond the two tips (Figure 4a), 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 (Figure 4b). This procedure was repeated until a 360^0 turn clockwise had been made at every PCQ point along each transect.

The VOR method was used to estimate standing grass biomass (Robel, et al., 1970; Uresk et al., 2009). This method requires little effort to monitor rangelands and was tested by Joubert et al. (2015) in Namibia, including in the study area, and found moderate to high levels of correlation of grass biomass and VOR. This method requires two people. At each point along the transects, one person stands with a 2 m pole on the soil surface subdivided into 2.5 cm rings with alternating red and white bands. The second person looks towards pole A from pole B with his eye at the 1 m mark. The distance between the poles is 4 m. The lowest visible band obscured by grasses is determined and the number of bands obstructed by grasses counted and recorded. This is repeated so that four VORs are recorded at each designated point (one from each cardinal direction). The readings were calibrated with actual biomass readings from 60 points in the study area. A regression equation between the VOR and dry weight (g) of the grasses was derived to convert all VORs to biomass.

Results

The findings from the study showed that fire in this semi-arid woodland savanna stimulates the regrowth and recruitment of new grass shoots by increasing the grass density and grass biomass in the recently burned areas, without significant changes in grass species composition. Without long periods of fire, perennial grasses accumulate moribund material, which becomes potential fuel load should a fire occur. While fire did not significantly reduce woody density, it caused significant top-kill of woody individuals, reducing the woody cover and thereby maintaining an open savanna. Consequently, in the absence of fire, woody plants grow larger and their individual canopy areas become bigger, resulting in a higher woody cover, and thus a more closed savanna. Woody species composition was not influenced by time since last burn, indicating that there was no plant

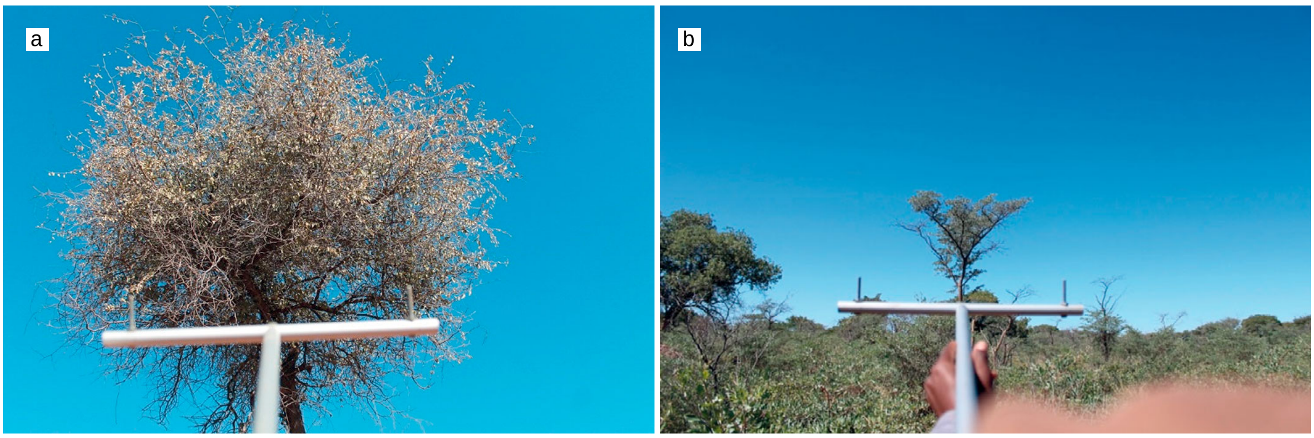


Figure 4: The use of the Bitterlich gauge (a) pointed at a woody canopy to estimate woody cover. In this instance, the overlap of the tree canopy past the pins means this is recorded as cover and (b) pointed at a woody canopy to estimate woody cover. In this instance, there is no overlap and thus this is not recorded as cover (Images: D.F Joubert, J.A.N Kandjai).

species succession occurring in the current time frame, but differences in structure were clearly evident.

Synthesis and Outlook

What can we learn from it? Fire positively affected the grass component by increasing grass density and enhancing productivity through the removal of moribund material and plant cover, but grass biomass was significantly reduced in the first season after fire (recovering a year later). Fire maintains open savannas by causing top-kill of woody plants and not causing total mortality, which is evident as species composition is not altered. Based on these findings, it appears that a modest increase in fire frequency and the burning of areas that have not been burnt in a long time (14–24 years) will have no negative impacts on plant species composition but will only change the structure. Such fires would need to be set after high rainfall seasons to significantly cause top-kill of woody plants (and thus open up closed woodland sites) and improve the grass quantity and quality.

C. Impacts of fire history on the species composition, abundance, species richness, and diversity of ground-dwelling arthropods

Introduction

Why is it important? Fire has been used as a management tool for centuries (Osborne, 2008). Fire effects have been studied in fire-prone ecosystems worldwide, with much focus on vegetation (Joubert et al., 2012), but less effort has been made to understand the response of arthropods to fire (Davies et al., 2010), and thus the response of arthropods (particularly ground-dwelling ones) to fire remains unclear (Hanula & Wade, 2003).

Methods

The study was done along the same transects that were used for soil, vegetation, and resource utilization sampling. At each sampling point, pitfall traps were exposed for 48 hours in April 2016. Data were collected at 40 m intervals along each transect. Each transect had five pitfall traps, and each fire block had 30 pitfall traps. Invertebrates were identified to morphospecies. A morphospecies is defined by its appearance (Work et al., 2002) rather than its taxonomic relations. Morphospecies can be successfully and efficiently used as surrogates for taxonomic species (Oliver & Beattie, 1996). One-way ANOVA was used to test for significant differences in abundance and diversity (Shannon diversity index and species richness) among the different fire treatments. Nonmetric multidimensional scaling (NMDS) ordination techniques in PC-ORD 6 (McCune & Mefford, 2011) were used to determine which variables drove community composition, and whether the communities differed.

Results

The survey collected 1,755 individuals, which represented 99 morphospecies and 13 taxonomic orders. Of this total, 96% were insects, 3% arachnids, and 1% myriapods. The study found inconsistent differences unrelated to time since last burn. There was a statistically significant difference in abundance but no statistically significant difference in diversity between treatments. NMDS revealed that litter, grass density, and woody cover were the strongest variables driving community composition. Litter was the most important variable in the treatments that burned 16 and 26 years ago (in 2000 and 1990; blocks 3 and 4). There was clear separation of the treatments burnt over a decade ago and the treatments burnt recently, with low levels of overlap suggesting that a diversity of fire regimes at WPP increases the beta diversity of ground-dwelling arthropod species. The findings of this study suggest that time since last burn had little effect on ground-dwelling arthropod abundance and species richness and inconsistent effects on Shannon diversity. Variables other than fire (secondary effects such as litter, grass density, and woody cover) seem to be driving the effects.

Synthesis and Outlook

What can we learn from it? As with other taxa and fire effects, resource managers should not be fixated on implementing the 'correct' fire regime. This will reduce beta and gamma diversity. Resource managers can maximise arthropod diversity by maximising the diversity of fire histories in the managed areas. In the study area, this has been achieved unintentionally through a combination of intended fires, natural fires, and accidental fires.

D. Impacts of fire history on bee abundance and species richness

Introduction

Why is it important? Animal pollination is obligatory for the sexual reproduction of roughly 90% of the world's plant species (Potts et al., 2010). Amongst these animal pollinators, bees are assumed to be the most important pollinator in most ecosystems (Michener, 2007). Beside the well-known honeybees, there are numerous species of wild bees (an estimated 20,000 species worldwide), many of them still unknown and undescribed. There is a need for wild pollinator research, especially in certain areas such as sub-Saharan Africa and other parts of the Southern Hemisphere (Potts et al., 2010). The main objective in this study is to investigate how different burning histories influence wild bee diversity at the study sites. Our study is the first to examine wild bee diversity in the Waterberg in Namibia. The results could help us understand what impact the common practice of burning farmlands has on the survival and diversity of wild bees. With this knowledge, the maintenance of pollinator diversity and the associated ecosystem services on private and communal land may be managed and maintained or even improved.

Methods

Pan traps were placed on the same transects outlined in the previous studies to determine bee diversity and abundance. Pan traps are commonly used in pollinator studies (Campbell & Hanula, 2007). The pan traps consisted of plastic bowls that had been sprayed with UV colour in white, blue, and yellow to attract foraging insects. The pan traps were installed

Figure 5: Pan traps fixed to the woody vegetation in block (4) burned in 1990.

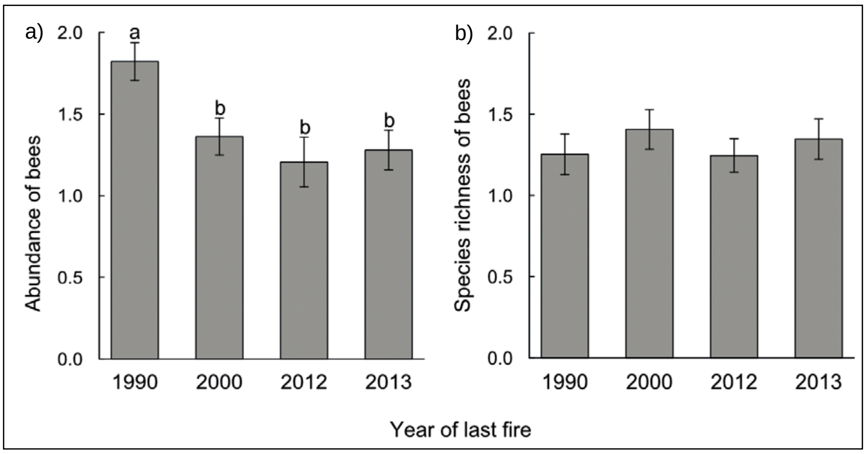


Figure 6: (a) Abundance and (b) species richness of wild bees under the influence of four different burning regimes. The graph is based on model values on the logarithmic scale; whiskers show the standard error of the mean. Different letters indicate significant differences after Tukey HSD *posthoc* comparison (glmer.nb: $F_{4/707}$=19.10, p = <0.001).

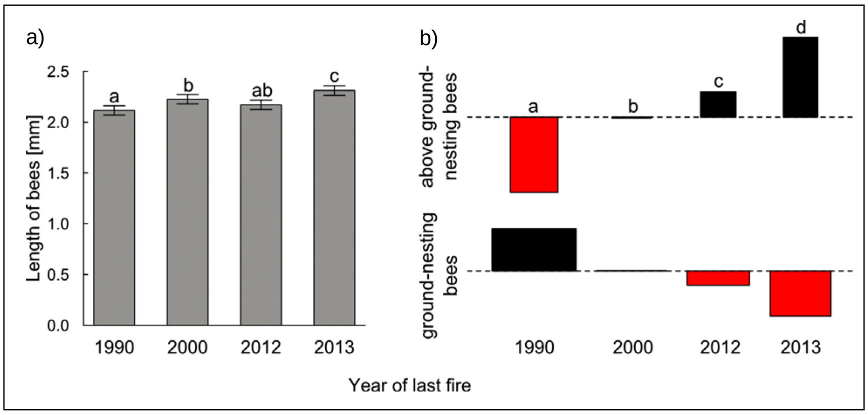


Figure 7: Abundance of bees on the different plot in relation to (a) their body length (in mm) and (b) their nesting-behaviour; (a) The bars show the model estimates for body size after Tukey HSD post-hoc test of the general linear fixed effect model with negative binomial distribution (glmer.nb). Error bars are Standard mean errors (SEM), glm: $F_{3/708}$=8.66, p<0.001; b) the association plot is based on a Chi-square test. If the observed frequency of a cell is greater than the expected one, the box rises above the baseline and is shaded black; otherwise, the box falls below the baseline and is shaded in red. Different letters above the bars show significantly different results.

in vegetation at breast height (Fig. 5) and filled up with water; surface tension was reduced by adding a drop of detergent (Westphal et al., 2008). The pan traps were exposed for 24 hours, repeated four times in October and November 2015 during the onset of the rainy season. Two sets of pan traps, each consisting of three bowls in blue, yellow, and white, were installed 100 m apart, starting from the end line of the transect (between 750 m and 500 m from access roads). After 24 hours the caught insects were collected and preserved with ethanol (Eardley et al., 2010). The collected insects were sorted at a later stage. The collected bees were identified to species level, and morphospecies level where identification to species level was not possible because of gaps in the taxonomic literature. All statistical analyses were calculated using R version 3.2.5 (R Core Team, 2017), except NMDS analyses, which were conducted using PAST software (Hammer et al., 2001).

Results

A total of 3,113 bees were captured in the pan traps. The 3,113 individuals were composed of an estimated 17 different species or morphospecies. Three *Lasioglossum* spp. (65%), *Apis mellifera* (23%) and *Zebramegilla langi* (7%) were the most abundant species. The time since last burn had a significant influence on the overall abundance of bees. Bee abundance was highest on the plot with the oldest vegetation (burnt in 1990) but did not differ between the other fire treatments (Fig. 6a). Total species richness of wild bees was not affected by the time of last burning (Fig. 6b). The nonmetric multidimensional scaling (NMDS) analyses revealed a significant difference between the species composition in the plot that burned in 1990 (block 4), compared to the one that burned most recently (block 1).

The species traits analysis shows that fire seems to be a main driver of bee species composition within the different plots. While ground-nesting bees with a small body size were most abundant on the plot with the oldest vegetation (Fig. 7a), bigger and above-ground-nesting bees were more abundant in recently burned plots (Fig. 7b).

Synthesis and outlook

What can we learn from it? Fire seems to have a negative impact on small ground-nesting bees, which are limited in their dispersal ability because of their small body size. Body size is in most cases linked to the flying ability of bees (Greenleaf et al., 2007). Their nests, which are located not too deep in the ground, appear to be destroyed by fires, which would be in line with findings from a study by Van Nuland et al. (2013) conducted in a savanna biome in Israel. We can conclude, then, that ground-nesting bees with a small body size seem to be mostly restricted to undisturbed areas, while bigger and above-ground-nesting bees seem to prefer foraging on recently burned plots, which may harbor more food resources. This has implications for fire management. Our findings suggest that a patchy burning regime will allow for a highly diverse bee community in a given location. This in turn ensures pollination services to the plant community.

E. The impacts of fire on habitat utilization of large herbivores and changes in their food quality in respect to fire

Introduction

Why is it important? Large herbivores have an enormous impact on ecosystems mainly through their food selection, altering not only the plant community structure but also the chemical composition of plants (e.g., Archibald et al., 2005; McNaughton et al., 1988; Olff & Ritchie, 1998; Stolter, 2008). Different herbivorous feeding strategies have evolved, resulting in differences in food selection and hence in changes in vegetation composition. They also influence fire regimes and, indirectly through their other effects, faunal species composition and diversity.

Fire is another important driver of changes of plant community structure and nutrient composition (e.g., Anderson et al., 2007; Higgins et al., 2007; Roques et al., 2001), which subsequently will affect herbivores and their feeding decisions. Fire is frequently used as a management tool, such as to provide fresh food to herbivores or manage bush encroachment (Anderson et al., 2007; Joubert et al., 2012). Because there is an obvious interaction between fire and herbivores (Archibald et al., 2005; Roques et al., 2001), we investigated the impact of fire on wild large herbivores. Specifically, we investigated habitat and species selection by large herbivores with respect to fire history. Additionally, we investigated the differences in the nutritional quality of the selected species in relation to fire history.

Methods

We investigated differences in the habitat utilization of twelve herbivorous mammals between sites of different fire histories using faecal pellet counts along the transects previously described. This cost-effective method is widely accepted not only for assessing habitat utilization but also for estimating population numbers (Archibald et al., 2005; Barnes & Guenda, 2013; Isaacs et al., 2013; Månsson et al., 2011). It is a particularly useful method in habitats with dense vegetation, such as the treatments that had not burned for many years. Barnes & Guenda (2013) showed that this method is even more accurate than aerial surveys or direct counts. There are some disadvantages, however, as it is not suitable for animals using latrines (e.g., rhino) and there might be a bias if there are large populations of different dung beetle species present, as is the case at WPP (Fig. 8). Dung beetles can be quite selective (with a high preference

Figure 9: Home ranges (red margins) of buffalo herds in relation to recent fire history in the park. The left hand images (a), (c), (e) and (g) right hand images (b), (d), (f) and (h).The dots (yellow for Herd 1 and red for Herd 2) show the locations of the marked animals during the time period.

a) and b) at the time of Fire 1 (lightning fire, September 2013). Herds separate and the fire occurs in the core of Herd 2's home range.

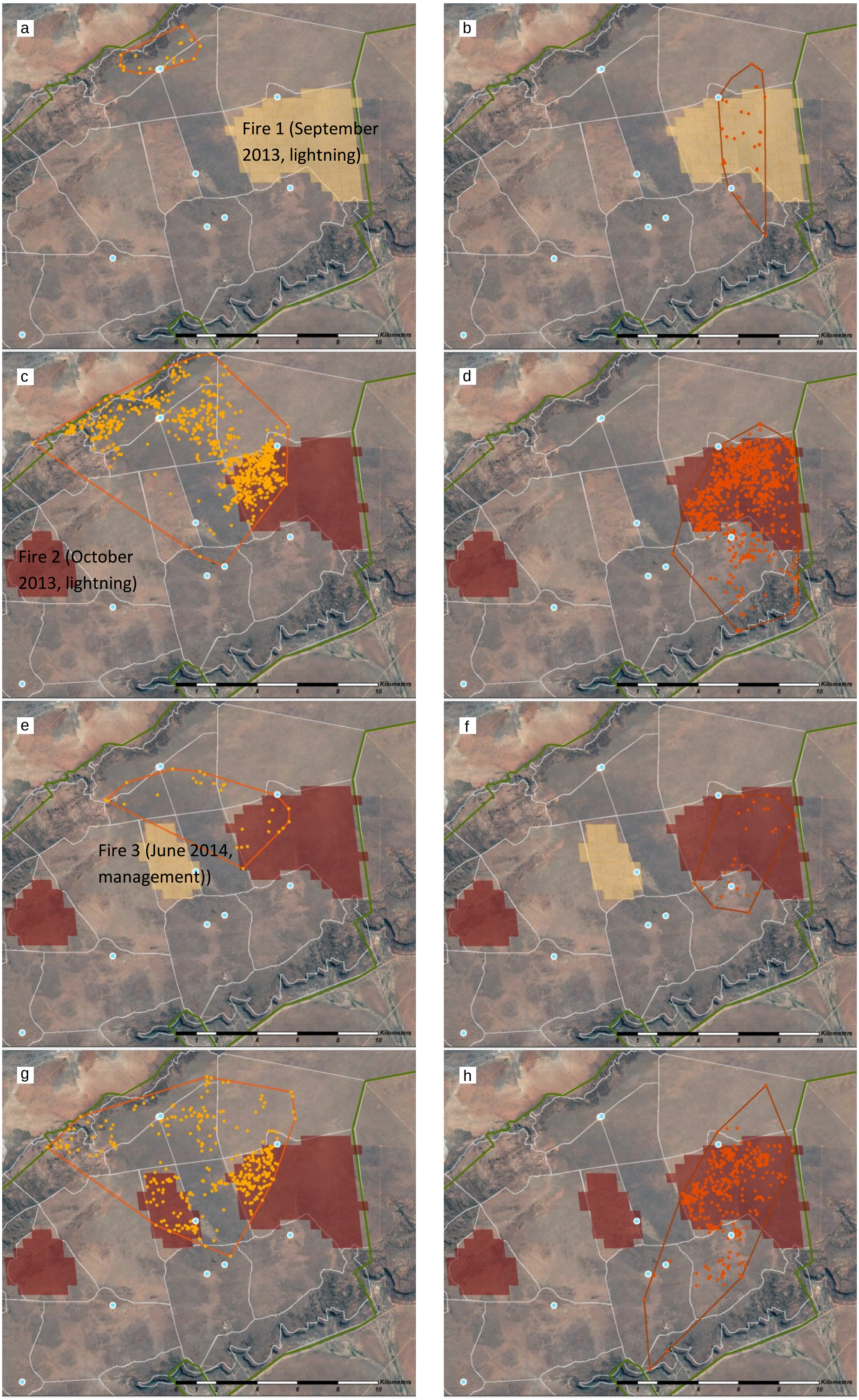
c) and d) during January to March 2014. Herd 1 has shifted its home range to include the Fire 1 patch whilst Herd 2 is strongly focussed on Fire 1 patch. Some spatial overlap between the herds occurs in the burned area. Fire 2 has occurred in October 2013, but the burned patch has not been utilised by either herd.

e) and f) at the time of Fire 3 (a management burn in June 2014). The situation is very similar to the summer grazing shown in c) and d). Fire 2 patch still avoided by both herds.

g) and h) during October to December 2014. Herd 1 now utilises both Fire 1 patch and Fire 3 patch. Herd 2 remains concentrated on Fire 1 patch. The Fire 2 patch is not utilised.

for moist dung such as rhino or buffalo dung), especially during the wet season. During this study, buffalo dung pats were completely removed and covered within a day. To estimate population numbers and compare utilization rates of different herbivore species, which was not part of our study, the accurate defecation rate of a species is required. For example, the

Figure 8: Numerous large dung beetles (*Pachylomerus femoralis*) utilizing rhinoceros dung in the study area.


a
Fire 1 (September 2013, lightning)
b
c
Fire 2 (October 2013, lightning)
d
e
Fire 3 (June 2014, management))
f
g
h
Kilometers
0 1 2 4 6 8 10

defecation rate of buffalo is quite low (5–1 dung heaps per day; Plumptre & Harris, 1995), whereas the rate for kudu is quite high (24 faecal groups per day; Ellis & Bernard, 2005). In this study we were more interested in comparing the relative utilization of different fire treatments by each species, rather than comparing the absolute numbers of each herbivore species. Along each 200 m transect, dung counts were done at every 20 m within a 4 m x 8 m quadrat. Pellet counting was standardized to ten pellets to be counted as an individual animal. Within each 4 m x 8 m quadrant corner, each nearest shrub, weed, and grass was identified, recorded, and observed for grazing and browsing damage (Uunona, 2014). From these data, the total amount of feeding damage per species was assessed, as was preference (the proportion of each species showing feeding damage). Additionally, we installed camera traps to get an understanding of herd size and population structure as well as the occurrence of predators. We also analysed the nutritional quality of known food plants on sites with different fire histories.

Furthermore, we placed GPS collars on collared four African buffalos (*Syncerus caffer*) from three different herds in September 2013 and tracked their utilization of the different fire treatments for close to two years. We were able to track two of the herds that were adjacent to each other and in the study area. From this we were able to visualize their home ranges and different responses to fire history.

Results

1. What kind of habitat was used by large herbivores in relation to fire?

As expected, most of the animal species utilized the recently burned site the most (block 1, burned in 2013, investigated in 2014). Warthog and oryx, both low in abundance, were found only in this area. Others, such as giraffe, kudu, sable, and roan, also showed a clear preference for this site. The results were similar for eland and buffalo, but the differences in dung counts were not significant. Utilization by buffalo is most likely underestimated due to the large population of dung beetles in the study area. Dung beetles remove and bury the soft dung pats of buffalo in less than a day (Fig. 8). However, the preference for this area by buffalo is clearly evident in Fig. 9 which show the utilization of burned areas by the GPS-collared buffaloes. Furthermore, our camera traps showed high rates of utilization of the recently burned area by large eland herds (Fig. 10). Both grazers and browsers preferred this recently burned area. Interestingly, the site in the direct neighbourhood of the recently burned site, which was burned 14 years ago (at the time of the measurements, block 3), was the site that was second most strongly utilized and preferred over the site that was burned only two years ago (block 2) for most species, with the exception of warthog and oryx. One can assume that the same individuals were using the recently burned area (block 1) for feeding and the "unburned" area (block 3) for ruminating and resting in the shade, and possibly predator avoidance, as this side had much more canopy and denser vegetation. This kind of dense vegetation was also preferred by small ungulates, such as duiker and steenbok, as well as hares. The overall pattern of high utilization of the burned sites persisted into the next year of our investigation (2015). Importantly, buffalo herds only shifted their home ranges to utilise burned areas adjacent to their pre-fire home ranges (Fig. 9).

2. What has been eaten?

Large herbivores preferred feeding on grasses and trees at the recently burned site, with a higher utilization of trees/shrubs compared to grasses (block 1). The second highest levels of herbivory were found in the area burned a year earlier (block 2). However, these levels were much lower than at the recently burned site. In burned areas, some grass and tree species were 100 % utilized e.g. utilisation of all sampled individuals (e.g., *B. nigropedata*, *P. kalaharense*, *G. flavescens*, and *Philenoptera nelsii*). However, *B. nigropedata* and *P. nelsii* were not abundant despite being preferred, so the most utilized grass species were *D. seriata* (highly palatable), *A. stipitata,* and *S. uniplumis* (relatively unpalatable) and the most utilized tree/shrub species were *T. sericea, Bauhinia petersiana*, and *A. ataxacantha*. Our survey of feeding damage underscores our results from the habitat utilization survey: plants were utilized the most in the burned area (burned recently, block 1). However, we found almost no feeding damage on the neighbouring site (burned long ago, block 3). This supports the suggestion that the neighbouring site is used mainly for resting and ruminating.

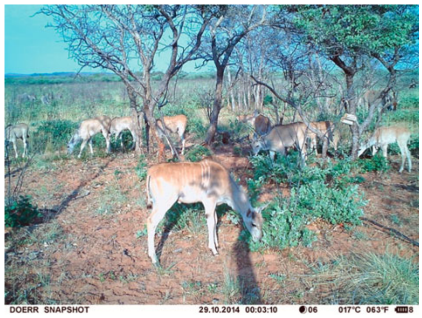


Figure 10: Camera trap image (taken two years after the fire) of eland in the recently burned area (block 1) feeding on resprouting P. nelsi (Image: C.Stolter).

Figure 11: Camera trap image taken two years after the fire) showing a hartebeest (a typical grazer) browsing on tree resprout (Image: C.Stolter).

Figure 12: Heavily browsed resprout of T. sericea (Image: C.Stolter).

3. How does fire affect the nutritional quality of the plant?

We found that the leaves of tree species are generally higher in protein concentration compared to grasses. Looking at the most utilized grasses and trees, we discovered that they are of medium quality. Some heavily utilized species (the grass *B. nigropetata* and the tree *P. nelsii*) had higher protein and hemicellulose concentrations compared to less preferred species. Food selection is further described in the info box about food quality for ruminants and discussed in the chapter on food quality and availability for large herbivores (Stolter et al., 2018).

The nutritional quality of grasses was not different between the recently burned site (block 1, sampled two years after burning in 2015) and the neighbouring site, burned 15 years ago (block 3). In contrast to grasses, almost all tree species showed higher protein concentrations at the recently burned site (block 1, sampled two years after burning in 2015). In dry seasons or periods with restricted grass availability, then, the resprouting of the trees after a fire event might serve as high-quality food not only to browsers but also to grazers (Fig. 11, Fig. 12). However, more investigations of food selection are needed here.

Synthesis and outlook

What can we learn from it? Recently burned sites attract both grazers and browsers. However, neighbouring sites with dense vegetation seem to be important as well. Grazers and browsers use recently burned sites for feeding and the "unburned" neighbouring site for resting (ruminating) and perhaps predator avoidance. Smaller species, however, prefer unburned sites with dense vegetation for feeding and resting. These relatively small herbivores can move easily between the bushes, so the dense vegetation offers them good protection and less competition with larger herbivores. Interestingly, as a result of territorial buffalo behaviour, the two herds show almost no overlap in utilization. Newly burned areas were used by buffaloes only if the areas were part of or close to their pre-fire home range. This was not realised by park managers until these results were shown. This has profound implications for the management of the spatial arrangement of fires in the park.

After burning, grasses and trees/shrubs are heavily utilized by different large herbivores, with a pronounced higher utilization of trees/shrubs. The time since last burning changes the nutritional composition of both plant types (trees and grasses). While grasses did not differ in nutritional composition between sites with different fire histories, tree leaves remained higher in protein concentration for a longer period. Similar plant responses are known from post-herbivory processes on trees (see also the chapter on food quality and availability of large herbivores, Stolter et al., 2018; Stolter, 2008). Hence, they are an important food resource even for grazing animals, which was reflected in their high utilization. At the time of sampling, animal utilization of this site (block 1, two years after burning) was still high. This implies that the most frequently burned site will be the most attractive until another site is burned. Nevertheless, the site has to be situated in the home range or territory of the animal of interest. Concerning the general quality of a burned site compared to unburned sites, one must consider that there are far fewer moribund grasses in a burned area, which might enhance the overall quality.

Why is this interesting? The findings illustrate that heterogeneous habitats, through pyrodiversity, are beneficial for wild ungulates. Even typical grazers utilize neighbouring areas with dense vegetation. Recently burned areas provide higher-quality food, but neighbouring dense vegetation is important for ruminating or resting as well as serving as habitat for species not adapted to open habitats. The most recently burned site will frequently be used for feeding as long as there is no other burned site nearby. The influence of burning on the quality of grasses is relatively short-lived, but the overall quality might be enhanced on the recently burned site because of the presence of a lower proportion of moribund grasses. Trees provide foliage, which is generally higher in protein and serves as a supplementary food source of higher quality after a fire (for at least two years after burning). This might be of special importance in periods of low food supply. In this respect, we need a better understanding of wild herbivores' food selection and plant responses to fire and herbivory. The knowledge gained from this study and future research will enable us to manage livestock and game in coexistence.

Acknowledgements

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