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Fire regimes and management options in mixed grassland-fynbos vegetation, South Africa

Izak P. J. Smit^{1,2} , Johan A. Baard¹ and Brian W. van Wilgen^{3*}

Abstract

Background Fire regimes in South African fynbos shrublands have been quantified in the western (winter rainfall) and central (aseasonal rainfall) parts. They have not been quantified at their eastern extremity (summer rainfall), where fynbos transitions to grassland and is embedded in other fire-resistant vegetation types. We assessed fire regimes at the eastern extremity of the fynbos biome and discussed the ecological and management implications of our findings.

Results Using remote sensing, we assessed fires over 21 years in a 350,000-ha study area at the eastern edge of the fynbos biome. Only 9% of the study area burned, almost exclusively in mixed grassland-fynbos vegetation. The largest proportion (44% of the total area burnt) burnt in late winter and early spring, but fires occurred throughout the year. Fires only occurred in 39% of the mixed grassland-fynbos vegetation. Of the mixed grassland-fynbos vegetation that did burn, 44%, 11%, 26%, and 19% experienced one, two, three, and four fires, respectively. Areas with multiple fires had return intervals ranging from 3 to 15 years, with 76% of the area with multiple fires burning every 4 to 6 years. Most large fires were preceded by two relatively dry months, when fuels were drier and more flammable.

Conclusions The mixed grassland-fynbos vegetation at the eastern extremity of the fynbos biome is surrounded by fire-resistant vegetation and exhibits a varied fire regime, with different parts experiencing frequent, infrequent, or no fire over 21 years. Fires were largely aseasonal, occurring throughout the year, although data over more years may reveal that a greater proportion of fires will occur in winter, when grasses are cured and rainfall is low, as well as after relatively long (> 2 months) periods of below-average rainfall. As most fires would burn out safely against fire-resistant vegetation, we conclude that lightning-ignited fires should be allowed to spread unhindered to approximate a natural and heterogeneous fire regime, provided that no neighboring properties or infrastructure are threatened. The response of the biota to fires is not well understood for this transition area, and further research is needed.

Keywords Addo Elephant National Park, Aseasonal fires, Fire-resistant vegetation, MODIS fire scar mapping

Resumen

Antecedentes Los regímenes de fuego en los matorrales finos (i.e. Fynbos) de Sud África han sido cuantificados en dos áreas: en el oeste (con precipitaciones invernales) y en los centrales (sin estación lluviosa definida). No fueron cuantificados en su extremo este (con precipitaciones estivales), donde la transición de estos hacia pastizales

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se ensambla con otros tipos de vegetación resistente a los incendios. Determinamos los regímenes de fuego en el extremo Este del bioma de los Fynbos, y debatimos sobre las implicancias ecológicas y de manejo de nuestros resultados.

Resultados Usando sensores remotos, determinamos fuegos por un período de 21 años en un área de estudios de 350 mil ha en el borde Este del bioma de Fynbos. Sólo el 9% del área de estudios se quemó, y casi exclusivamente lo hizo sobre vegetación mixta de Fynbos y pastizales. La proporción mayor de estas quemadas (el 44% del total quemado) se produjo en el invierno tardío y principios de primavera, aunque los incendios ocurrieron durante todo el año. Los incendios ocurrieron sólo en el 39% de la vegetación mixta de Fynbos y pastizales. De esta vegetación mixta que se quemó, el 44%, 11%, 26%, y 19% experimentaron uno, dos, tres, y cuatro incendios, respectivamente. Áreas con múltiples incendios tuvieron intervalos de retorno del fuego que oscilaron entre 3 a 15 años, con el 76% del área con múltiples incendios que quemaron cada cuatro a seis años. La mayoría de los grandes incendios fueron precedidos por 2 meses relativamente secos, cuando los combustibles estaban más secos e inflamables.

Conclusiones La vegetación mixta de pastizales y Fynbos en el extremo este del bioma de Fynbos está rodeado de vegetación resistente a los incendios y exhibe una variedad de regímenes de fuegos, con áreas diferentes que experimentaron fuegos frecuentes, infrecuentes o sin fuegos en los 21 años de estudio. Los incendios fueron mayoritariamente no estacionales, ocurriendo durante todo el año, aunque más años de datos podrían revelar que una gran proporción de estos incendios ocurrirían en invierno, cuando los pastos están secos y la precipitación es baja, o también luego de un período (> 2 meses) de precipitaciones por debajo de la media. Dado que la mayoría de los fuegos quemarán de manera segura en la vegetación que es resistente al fuego, concluimos que los fuegos iniciados por rayos deberían ser dejados que se propaguen sin obstáculos para aproximar a un régimen de fuegos natural y heterogéneo, teniendo en cuenta que no se ponga en riesgo infraestructura o propiedades vecinas. La respuesta de la biota a los incendios no es aún del todo comprendida, y por lo tanto necesitan aún de más investigaciones.

Background

Fire is an important landscape-scale process that plays a major role in determining the composition and structure of many of the world's ecosystems (Bond et al. 2005). Managers of protected areas are expected to ensure that such processes continue to play their role in maintaining ecosystem health and ensuring the persistence of biodiversity. In the case of fire, this is usually interpreted as promoting a regime that mimics the frequency, season, and intensity of fires under which the ecosystem evolved and to which its component species are adapted or even dependent. Fires are widely used to manage fire-prone landscapes, for example, in North America (Twidwell et al. 2013), Europe (Fernandes et al. 2013; Valkó et al. 2014), Australia (Russell-Smith et al. 2020), and Africa (Nieman et al. 2021).

South African fynbos (shrubland) vegetation is one of Earth's 25 recognized hotspots of biodiversity, with high levels of plant endemism (5700 out of 8200 plant species are endemic, Myers et al. 2000). Fynbos, which extends along the southern coast of Africa for ~750 km from west to east, is an example of a fire-prone and fire-adapted vegetation type (van Wilgen 2013). The climate in the west is strongly seasonal, with wet winters and dry summers, resulting in a regime of fires in summer at intervals of 10–15 years (van Wilgen et al. 2010; Seydack et al. 2007). As one moves eastward in the fynbos, rainfall occurs more evenly throughout the year, and fires

are less seasonal and more frequent (Kraaij et al. 2013a). Together, these studies provided a picture of a gradient of changing fire regimes over about 600 km from the west towards the east (Kraaij and van Wilgen 2014). However, fynbos vegetation occurs further east for at least another 150 km from where previous studies focused (Kraaij et al. 2013a; Kraaij and van Wilgen 2014) into an area where most of the rainfall occurs in summer and where fynbos is juxtaposed with a diversity of other vegetation types. Fire regimes at this eastern extremity have yet to be quantified.

While fynbos is fire-prone, the surrounding forest, thicket, and karroid shrublands in our study area seldom burn. Under suitable conditions, fynbos vegetation is characterized by sufficient dry, dead fuel that can support a spreading fire within 4 years of a previous fire, with fuel loads increasing steadily after that with post-fire age (van Wilgen and van Hensbergen 1992). Forest vegetation seldom burns due to a pronounced separation of fuel between the litter layer (i.e., dead leaves and twigs on the forest floor) and tree canopies (van Wilgen et al. 1990), and thicket vegetation is usually too succulent and with limited herbaceous fuel to carry a fire (Cowling and Holmes 1992). Arid karroid shrublands towards the interior typically have insufficient fuel to carry a fire (Rahlaio et al. 2009).

In this paper, we provide an analysis of the prevailing fire regimes that characterize fynbos vegetation at its

eastern extremity. Here, fire-prone fynbos shrubs and reed-like restios are intermixed with grasses, constituting a unique transitional vegetation type between the fynbos to the west and the grasslands to the east. This intermixed grassland-fynbos vegetation (Rebello et al. 2006) is embedded in a predominantly fire-resistant landscape (i.e., forest, thicket, and karoo). We used well-established remote sensing-derived fire scar products, together with vegetation maps and long-term rainfall data to examine the occurrence of fires in the dominant vegetation types at the eastern extremity of the fynbos biome as delineated by Rebello et al. (2006). We also discuss the appropriate responses with respect to fire management.

Methods

Study area

Our study took place in the Suurberg mountain range, most of which falls within the Addo Elephant National Park (hereafter the park) in the Eastern Cape Province, South Africa ($33^{\circ} 31' S$, $25^{\circ} 45' E$) (Fig. 1). The park was established in 1931 to conserve some of the last remaining wild elephants in the then Cape Province. The park

originally covered 4517 ha in the low-lying thicket vegetation but has subsequently been expanded to cover 172,000 ha (Brett 2019), stretching inland from the coast for 60 km. The mean annual rainfall in the Suurberg mountains ranges from 220 to 820 mm (mean 545 mm), peaking bimodally in October to November and February to March, and lower in winter (Rebello et al. 2006). The Suurberg mountain range was incorporated into the park in 1985, and our study focused on 346,176 ha which included the Nyathi, Kabouga, and Zuurberg sections of the park and surrounding areas (Fig. 1).

The Suurberg occurs at the transitional zone between the fynbos which extends towards the west (winter and aseasonal rainfall) and grasslands towards the east (summer rainfall). The vegetation of the Suurberg includes a mixture of fire-prone grasses and fynbos shrubland plant species at higher altitudes between 600 and 950 m above sea level. It is surrounded at lower altitudes by fire-resistant thicket and small pockets of Afrotropical forest to the south and by thicket and karroid shrublands to the north. The fire-prone vegetation type, which we term mixed grassland-fynbos, consists of three vegetation

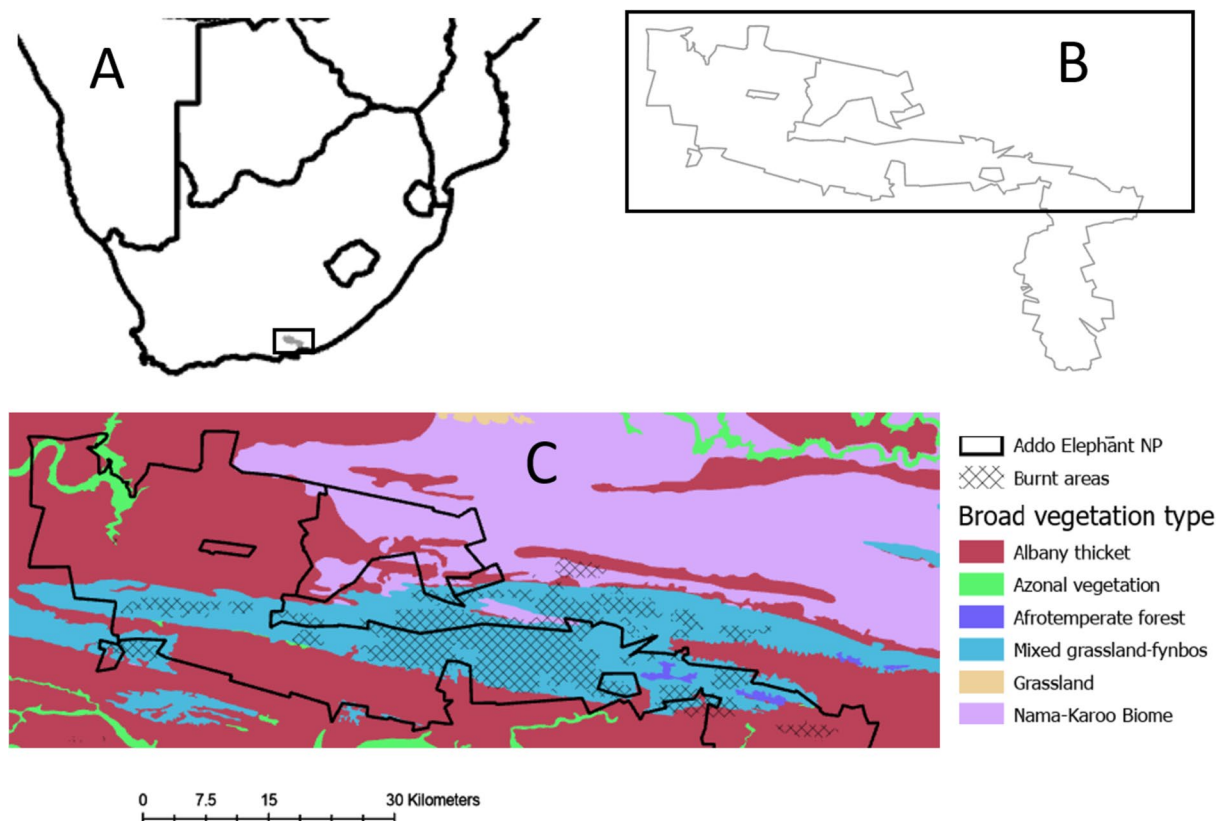


Fig. 1 Location of the Addo Elephant National Park in South Africa (A) and the extent of the study area in relation to the boundary of the Addo Elephant National Park (B). C The broad vegetation types in the study area (Table 1) and the total extent of fires between 2001 and 2021 (hatched shading)

sub-types, namely (i) fynbos (medium–high shrubland), which is more dominant on south-facing slopes; (ii) grasslands, more common on relatively arid north-facing slopes (Rebello et al. 2006; Fig. 2); and (iii) grassy fynbos, an intermediate vegetation type between true fynbos and true grassland, containing elements of both sub-types (Rebello et al. 2006; van Wyk et al. 1988a; Campbell 1983; Fig. 2). Grassy fynbos is distinguished from grassland by the presence of fynbos elements, including proteaceous shrubs (e.g., *Leucadendron salignum* P.J. Bergius and *Leucospermum cuneiforme* (Burm.f.) Rourke) and ericoid shrubs (e.g., *Erica demissa* Klotzsch ex Benth. and *E. simulans* Dulfer) (Fig. 3A, B; van Wyk et al. 1988b). In true fynbos, grasses are rare, and the herbaceous layer is dominated by the families Restionaceae and Cyperaceae. In grassy fynbos, the Restionaceae are less prominent (covering 10–50%), while grasses such as *Themeda triandra* Forssk., *Diheteropogon filifolius* (Nees) Clayton and *Alloteropsis semialata* (R.Br.) Hitchc. cover 30–90% (van Wyk et al. 1988b). To the south, tall dense thickets dominate the landscape, comprising a mixture of trees, shrubs, and succulents, with numerous spinescent species (Fig. 2B). To the north, the mixed grassland-fynbos gives way to open grassy karroid dwarf shrubland with

scattered low trees. The study area also contains smaller areas of tall (15–20 m) multi-layered evergreen forests, grassland, and riparian fringe (“azonal”) vegetation (see Table 1 for the extent of each broad vegetation type in the study area). Three cycad species of conservation concern (*Encephalartos lehmannii* Lehm., *E. longifolius* (Jacq.) Lehm., and *E. caffer* (Thunb.) Lehm.) also occur in the Suurberg (Fig. 3C), but all are able to survive relatively frequent fires (Bezuidenhout 2018). Some parts of the Suurberg mountains are invaded by alien (non-native) plant species, most notably the black wattle (*Acacia mearnsii* De Wild.; Fig. 3D), the Aleppo pine (*Pinus halepensis* Mill.), and jointed cactus (*Opuntia aurantiaca* Lindl.) (van Wilgen and Herbst 2017).

Fires are known to be common in mixed grassland-fynbos at higher elevations in the Suurberg, although there has been no formal assessment of the prevailing fire regime to date (Bezuidenhout and Bissett 2017). Historically, many fires would have been ignited by lightning, as is the case for fynbos vegetation to the west of the Suurberg (Kraaij et al. 2013b). However, fires of human origin are also possible. A pass which traverses the Suurberg from south to north is a public road, and some power lines also cross the range. Finally, some fires may be

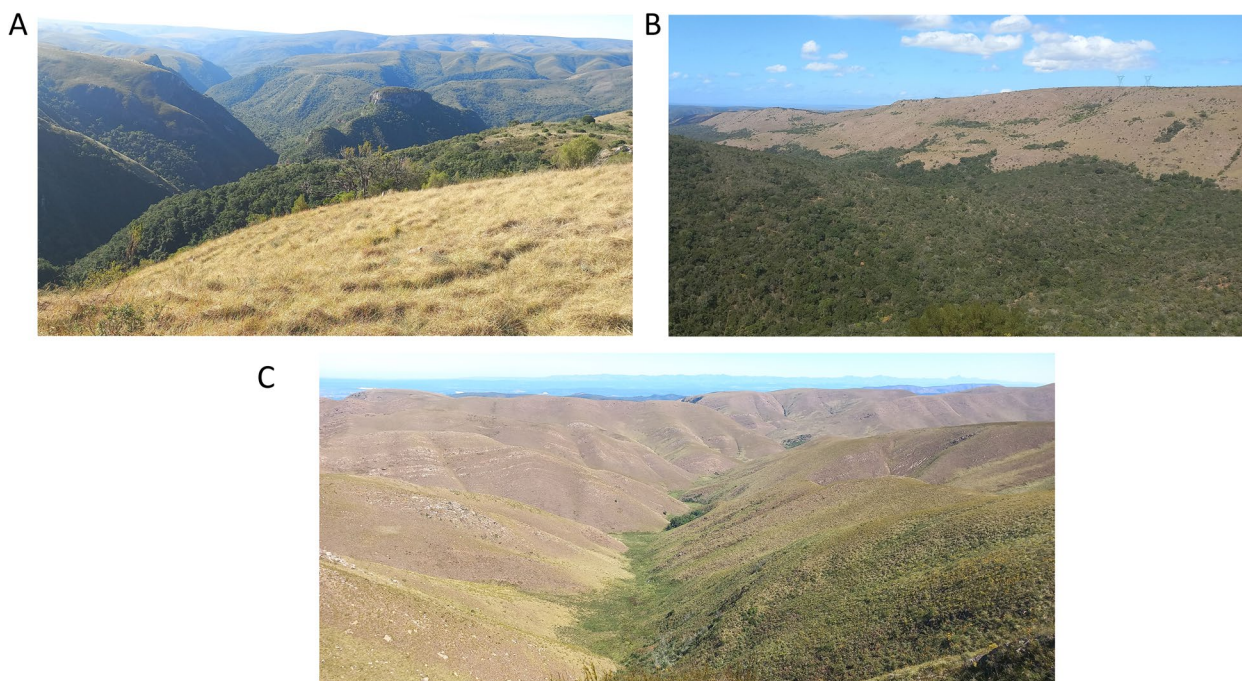


Fig. 2 Landscape features of the Suurberg mountains. **A** General view across the Suurberg range showing dissected topography and a mix of fire-prone and fire-resistant vegetation types. **B** Altitudinal gradient with fire-resistant Afrotemperate forest and thicket on the lower slopes (dark green) and fire-prone mixed grassland-fynbos vegetation on the upper slopes (light brown). **C** The effect of aspect on the composition of the mixed grassland-fynbos vegetation. North-facing slopes (on the left) are dominated by grasses, while south-facing slopes (on the right) have a much higher proportion of fynbos shrubs and non-grass herbaceous plants. Both types have been mapped as a single vegetation type (Suurberg fynbos) and fires seem to spread readily across both fire-prone types

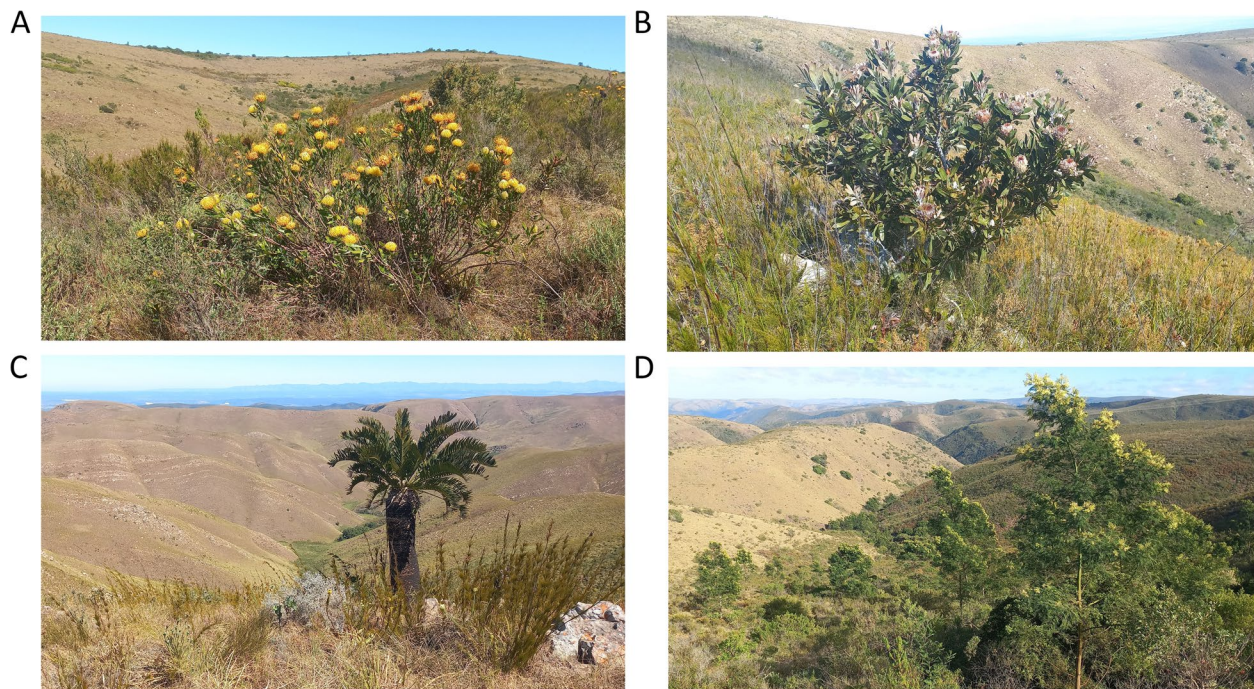


Fig. 3 Examples of species that would be considered in the formulation of fire management guidelines in mixed grassland-fynbos areas in the Suurberg mountains. **A** *Leucospermum cuneiforme* (Burm.f.) Rourke, a slow-maturing species in the family Proteaceae that re-sprouts after fire. **B** *Protea lorifolia* (Salisb. ex Knight) Fourcade, a relatively slow-maturing shrub in the family Proteaceae that does not re-sprout after fire and relies on seeds stored in flowerheads which get released after fire for regeneration (serotiny). **C** *Encephalartos longifolius* (Jacq.) Lehm., a cycad which is able to survive relatively frequent fires in the mixed grassland fynbos. **D** Invasive alien *Acacia mearnsii* De Wild. trees that regenerate after fires from hard-coated seeds stored in the soil and that can influence fuel characteristics

Table 1 Broad vegetation types and component vegetation types (after Mucina and Rutherford 2006) and their extent in the Suurberg study area

Broad vegetation type	Description	Vegetation types included	Area (ha)
Mixed grassland-fynbos	Mixture of grassland, fynbos (medium–high shrubland), and grassy fynbos (intermixing of grasses and fynbos)	Suurberg shale fynbos Suurberg quartzite fynbos	71,351
Afrotropical forest	Tall multi-layered evergreen forests	Southern Mistbelt Forest	1133
Albany thicket	Tall dense thickets dominated by trees, shrubs, and succulent plants	Albany alluvial vegetation Albany coastal belt Groot thicket Kowie thicket Sundays thicket Sundays Noorsveld	162,808
Nama karoo	Dwarf shrubland with scattered low trees	Albany broken veld Lower karoo gwarrieveld	101,096
Grassland	High cover of grasses and herbaceous plants, with trees and shrubs absent	Bedford dry grassland	625
Azonal vegetation	Narrow bands of woodland along perennial or ephemeral river beds	Southern karoo rivers Albany alluvial vegetation	9163

started by commercial cattle farmers whose land is outside of the park, and these could spread into the park. There are, however, very few fire records that note the cause of fires. An examination of fire frequency across most of the fynbos biome found that fires were less frequent in relatively remote areas, compared to areas that

were closer to human habitation (van Wilgen et al. 2010). These authors concluded that human ignitions became more frequent closer to human habitation, increasing the frequency of fires. The Suurberg was not included in their study, but would be considered to fall into the remote category, experiencing less human ignitions. There is also

no wildland-urban interface anywhere along the boundaries of the mixed grassland-fynbos vegetation in the park. Because the fire-prone vegetation is surrounded by fire-resistant vegetation, fires are not suppressed in the Suurberg, but generally allowed to burn out, unless they threaten to spread to neighboring cattle farms, in which case attempts are made to contain them within the park (Bezuidenhout and Bissett 2017).

Mapping of fire scars

Burnt area data for the study area were obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) images between January 2001 and December 2021 using NASA's platform Application for Extracting and Exploring Analysis Ready Samples (AppEEARS, version 3.39) (<https://appears.earthdatacloud.nasa.gov/>). We used the Terra and Aqua combined MCD64A1 Version 6 burnt area data product, which differentiates burnt and unburnt surfaces at a scale of 500×500 m. The product also records the dates on which the relevant pixels burnt. Maps of four large fires that occurred in the Suurberg in 2019 (covering 8987 ha and digitized by the Eastern Cape Umbrella Fire Protection Association) were available at a higher resolution from Sentinel-2 imagery, and we checked the congruence between these maps and the fire scars mapped using the MODIS products. A detailed validation of the MCD64A1 product for the Suurberg was beyond the scope of this study, especially since detailed ground data on fires were not readily available. However, MODIS fire products are widely used in studies to assess fire regimes, especially when field data are lacking and/or if large spatial extents are explored (e.g., Andela et al. 2017; Dwomoh & Wimberly 2017).

Examination of fire regimes

A map of vegetation of South Africa (including our study area) was available from Mucina et al. (2006) at a scale of 1:1,000,000. The South African map was prepared by over 100 contributing authors over a period of 10 years. The map was based on a range of sources, including distribution data for over 10,000 plant species, geology, soil, topography, climate, other existing vegetation maps, and expert knowledge. The methods used are described in full in Mucina et al. (2006). There were 14 vegetation units (as defined by Mucina and Rutherford 2006) in our study area, and we combined them for the purposes of analysis into six broad vegetation types based on the biome in which they occurred (Table 1).

We overlaid burnt pixels to delineate areas of identical fire history (January 2001 to December 2021) and used these to create polygons for further analyses. Areas not covered by fire scars within the study area were mapped as unburnt. We then compared the six broad vegetation

types in terms of the number of times each fire history polygon had burnt to test our assumption that vegetation mapped as fire-prone or fire-resistant was reflected in recent fire history. Except for the analysis of fire extent in the six broad vegetation types described above, all further analyses of fire regimes described below were only examined for fire scars that overlapped with the mixed grassland-fynbos vegetation. All spatial analyses were conducted in ArcGIS Pro 2.5.0 (Esri Inc.).

We examined the distribution of return intervals (in years) experienced in parts of the mixed grassland-fynbos vegetation by calculating the area of all fires burnt at intervals ranging from 1 to 20 years (i.e., the time covered by our data set). This was only possible for those polygons of identical fire history that contained two or more fires, and thus at least one fire interval. Areas that did not burn, or that burnt only once were not included as no interval between fires would be available (see discussion of limitations below). The information was used to create a database of actual fire return intervals in years. For example, if a unique polygon burnt in 2002, 2006, and 2016, there was one interval of 4 years and one of 10 years. The total area burnt at each interval was then summed across all polygons to establish the total area burnt at each return interval.

We explored the relationship between the monthly area burnt and the rainfall for the preceding two months measured at the local ranger station. This analysis was conducted from January 2011 to December 2021 for which rainfall data were available.

We examined the seasonal distribution of fires by totaling the area of all fires over 21 years in each month of the year. We also characterized the phenological patterns in the mixed grassland-fynbos to examine whether this had any influence on the seasonality of fires through grass curing. We used the 500-m resolution 16-day MODIS-derived normalized difference vegetation index (NDVI) data (MOD13A1.061) for the period 1 January 2001 to 31 December 2021, obtained from NASA's AppEEARS platform. We derived a mean value for NDVI by averaging NDVI values for 16-day periods across all 21 years across the mixed grassland-fynbos area of our study site. All mixed grassland-fynbos pixels over all 21 years were included, i.e., recently burnt pixels were not excluded. We then estimated the average and standard error of monthly deviations from this annual mean value (normalized to be at 100%) to derive a phenological pattern for the mixed grassland-fynbos.

Results

Mapping of fire scars

Using the MODIS-derived product, we found that only 9% of the entire study area experienced at least one

fire between 2001 and 2021 (Fig. 4). Of the areas that burnt, we identified 48 polygons that burnt between one and four times where the pixels in each polygon share an identical fire history. We observed both an over- and under-estimation of the MCD64A1 fire scars when compared with the four Sentinel-2-derived fire scars (see Additional file 2: Table S1). Some of this can be explained by the differences in spatial resolution between these two sensors, and future studies would benefit from using higher resolution imagery, especially for detecting smaller scale fire patterns.

Fire return intervals

More than a third (38.5%) of the mixed grassland-fynbos vegetation experienced at least one fire between 2001 and 2021. In contrast, other broad vegetation types remained largely fire-free over the 21 years, with only very small proportions of thicket, Nama karoo, and azonal vegetation (1.2, 1.1 and 0.3% respectively) experiencing at least one fire between 2001 and 2021 (Table 2).

Fires did not occur on 61.5% of the mixed grassland-fynbos between 2001 and 2021, and a further 16.8% burnt only once. The remainder of the area (21.7%) that burnt twice or more was concentrated in the centre of the

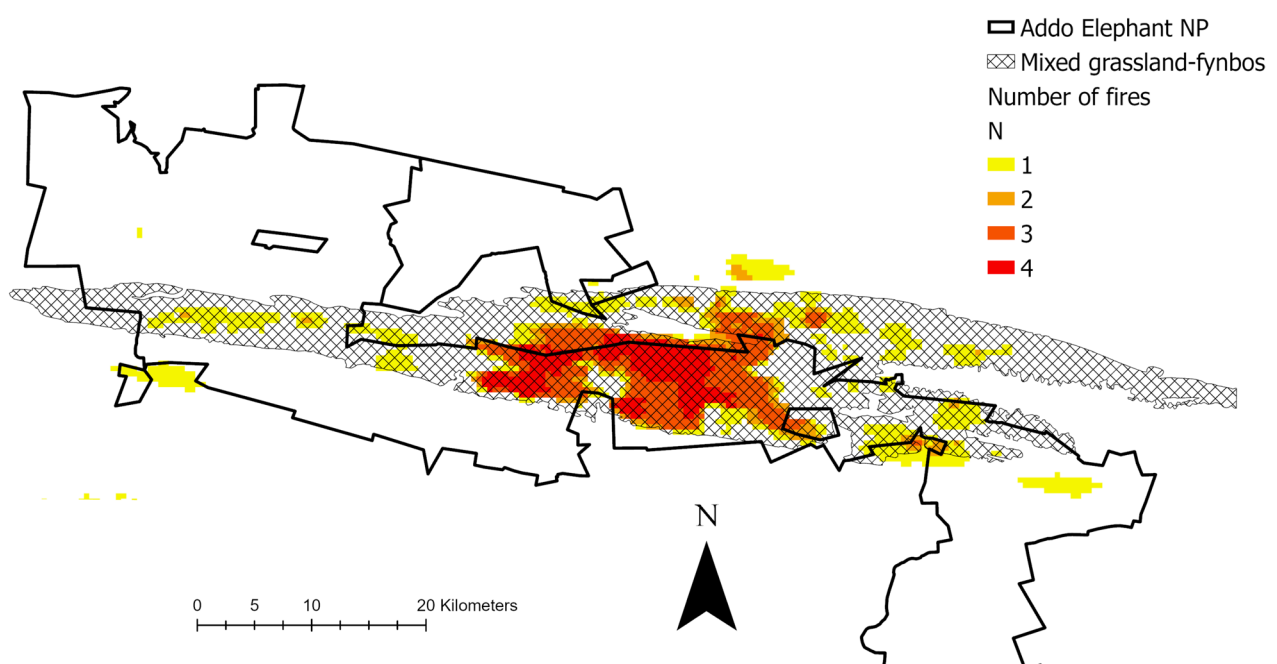


Fig. 4 Extent of fires in the Suurberg mountain range. Shading denotes the number of fires recorded between 2001 and 2021. The solid line shows the boundary of the Addo Elephant National Park, and the hashed area shows the extent of the mixed grassland-fynbos vegetation, illustrating that fires were essentially restricted to mixed grassland-fynbos, with surrounding fire-resistant vegetation remaining predominantly fire-free

Table 2 Proportion of the area in six broad vegetation types in and around the Suurberg mountain range that was burnt once or more between 2001 and 2021

Broad vegetation type	Proportion of area that burnt (%)	Notes
Mixed grassland-fynbos	38.5	Some areas burnt multiple times. Of the areas that burnt, 44%, 11%, 26%, and 19% burnt one, two, three, and four times, respectively
Thicket	1.2	Small proportions mapped as burnt could either be marginal penetration by fire or slight mismatches in the mapping scale
Nama-Karoo	1.1	Small proportions mapped as burnt could either be marginal penetration by fire or slight mismatches in the mapping scale
Forest	0.0	Fire-resistant except under rare severe fire weather conditions
Grassland (dry)	0.3	Only covered 0.2% of the study area, embedded in fire-resistant Nama-Karoo vegetation
Azonal	0.0	Fire-resistant vegetation along ephemeral or perennial rivers, with low fuel loads

mixed grassland-fynbos vegetation (Fig. 4). For areas of the mixed grassland-fynbos vegetation that experienced two or more fires over 21 years, the fire return intervals ranged between 3 and 15 years, with most of the area (76% of area that burnt twice or more) burning at intervals between 4 and 6 years (Fig. 5).

Fire season

Relatively dry fuel conditions prevailed in winter, arising from below-average rainfall for several months (May to September, Fig. 6A). During this time, grasses cured steadily from May to October (Fig. 6B). Despite this, fires occurred throughout the year, with April being the only month in which no fires were recorded between 2001 and 2021 (Fig. 7). The largest area (44% of total area burnt) was burnt in late winter or early spring (August and September), although the peak in September is largely due to a single very large fire. Fires in our study area usually occurred after 2 months of relatively low rainfall; five of the six largest fires recorded between January 2011 and December 2021 occurred in months recording approximately 50 mm or less in the two preceding months (see Additional file 1: Fig. S1).

Discussion

Factors influencing fire season

Fires occur predominantly in winter in grassland vegetation in South Africa, as a result of low rainfall and low fuel moisture in the cured grasses at that time of the year

(van Wilgen and Scholes 1997). Rainfall in the Suurburg is also relatively seasonal, with above-average rainfall in summer (October to March) and below-average rainfall in winter (May to September, Fig. 6A). The mixed grassland-fynbos vegetation is characterized by a relatively high grass cover, especially on the north-facing slopes (Fig. 2C), and the decline in the NDVI values indicates that grass curing progresses as the dry winter season proceeds (Fig. 6B). Seasonal curing is not typical of plant species which dominate in fynbos to the west of the Suurburg. Kraaij and van Wilgen (2014) reported that weather conditions suitable for fires dominate in the dry summer months in the west of the fynbos biome but become progressively less seasonal towards the east. In the area around 150 to 450 km to the west of the Suurburg in the Outeniqua and Tsitsikamma mountains, fires tended to occur during periods of hot, dry, and windy weather that were not restricted to any particular season, and these allowed fires to occur throughout the year. Due to the shift in rainfall towards dominance in summer (Fig. 6A), and the presence of cured grasses in winter (Fig. 6B), we would have expected that larger areas would have burnt predominantly in late winter in the Suurburg. Although there was a noticeable peak in fire occurrence in late winter (Fig. 7), this was largely due to a single very large fire in September 2008, so the pattern cannot yet be confirmed with confidence, and a longer fire record would be needed to do so. An insightful result, especially for local managers, is that fires in our study area usually

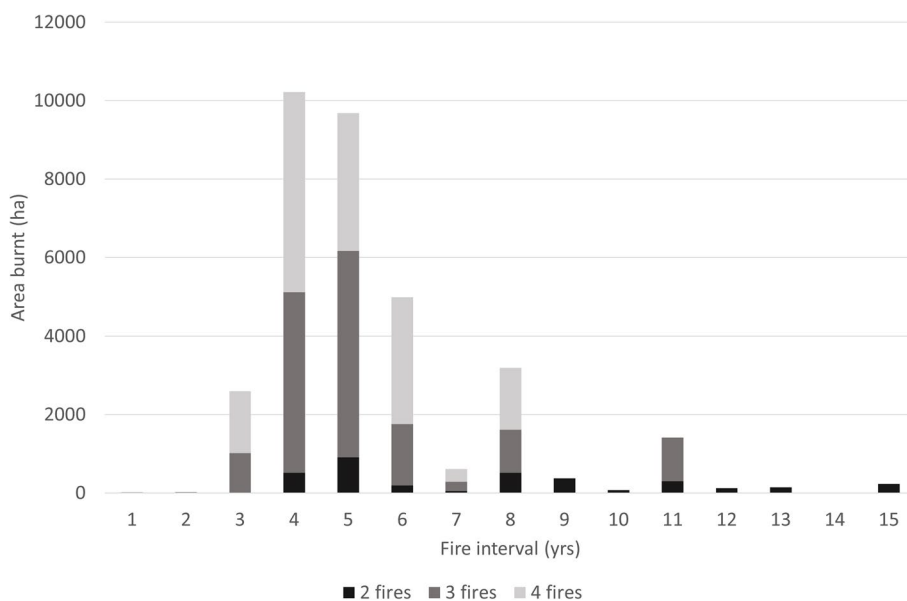


Fig. 5 Fire return intervals in mixed grassland-fynbos vegetation in the Suurburg mountain range. Return intervals were measured as the number of years between each successive fire for each polygon of unique fire history. The data depicted here are from polygons of unique fire history that burnt twice or more over 21 years, i.e., polygons that burnt only once were excluded as return intervals could not be measured in them, while, for example, a polygon with three fires would have two return intervals

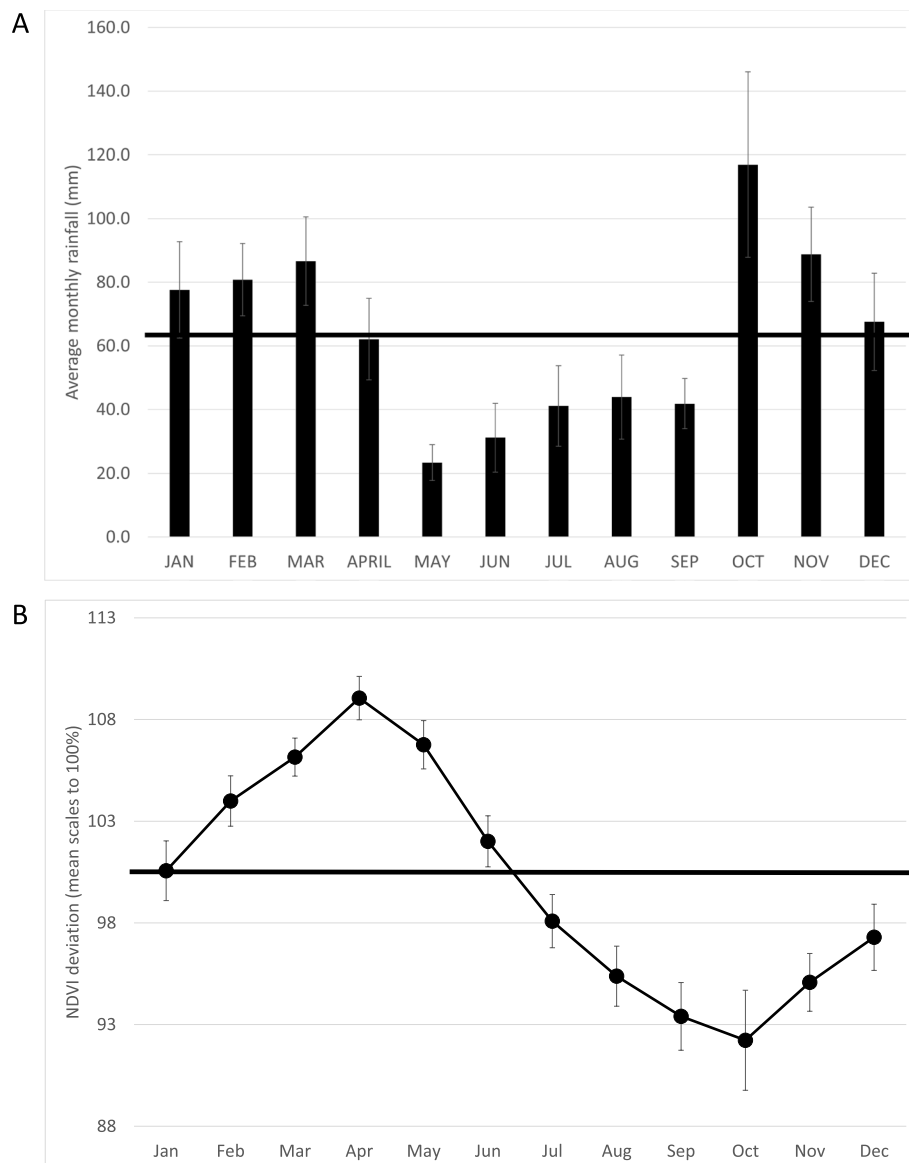


Fig. 6 Seasonal patterns of rainfall and vegetation phenology in the Suurberg mountain range. **A** The mean monthly rainfall at the Suurberg ranger station from 2010 to 2021 (\pm SE). **B** Monthly deviations (\pm SE) from the mean normalized difference vegetation index (NDVI) for mixed grassland-fynbos vegetation (100% representing average annual NDVI). The black parallel lines represent the annual average

occurred after 2 months of relatively low rainfall; five of the six largest fires recorded between January 2011 and December 2021 occurred in months recording approximately 50 mm or less in the two preceding months (see Additional file 1: Fig. S1).

Ecological relevance of fire season and frequency

The seasonality of fires is of considerable concern in the winter rainfall western distribution range of fynbos vegetation, where fires in winter and spring are known to be detrimental to the regeneration of obligate re-seeding

proteaceous shrubs (Bond et al. 1984; van Wilgen and Viviers 1985). However, more recent studies further to the east (where fires are less seasonal) have concluded that the recovery of these shrubs is not adversely affected by the season of burning and that fynbos burning does not have to be restricted to particular seasons in these areas (Heelemann et al. 2008; Kraaij et al. 2017). This would imply that managers could be more flexible with regard to the application or tolerance of fire in different seasons than in western fynbos. Our analysis indicates that fires in the Suurberg are not strongly seasonal

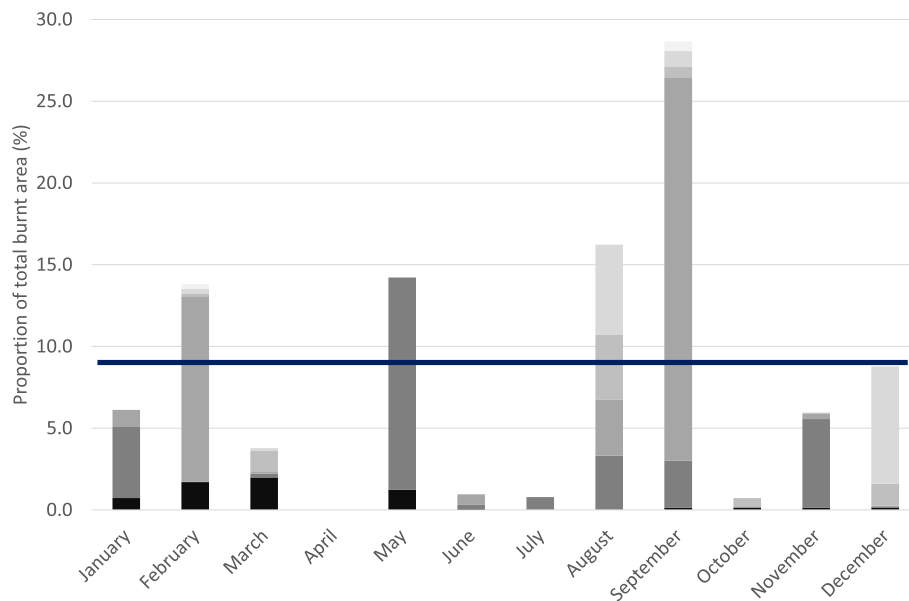


Fig. 7 Monthly distribution of the total area of mixed grassland-fynbos vegetation that burnt between January 2001 and December 2021. The height of the bars indicates the % of all fires burnt within that month. Individual fires are shaded differently to indicate the size of individual fires (the maximum number of fires in a given month was six). The black parallel line represents the expected percentage if each month burnt equally

either, and it can be assumed that regeneration of typical fynbos plants after the fire would similarly not be significantly negatively affected by the season of burn. Lightning strikes occur throughout the year in the fynbos of the Outeniqua and Tsitsikamma mountains that lie to the west of the Suurberg and would have provided an ample source of ignition to start fires in pre-historic times, especially at drier times of the year (Kraaij et al. 2013b). We found that the largest proportion of the area in the Suurberg that burnt, burnt in August and September (late winter and early spring, Fig. 7) when grasses were in a cured state (Fig. 6B), but that some fires occurred in summer (December and February) or autumn (May) (Fig. 7). Fires in summer or autumn could possibly be detrimental for grass cover (as grasses are in an active growing state), while fires in late winter or early spring (when grasses are cured) would be less detrimental for grasses (Cheney and Sullivan 2008). Our understanding of the importance of fire season in mixed grassland-fynbos vegetation would benefit from further research as most of the available literature focuses either on pure fynbos or pure grasslands, which have distinctly different fire requirements in terms of season and frequency (Bond 1997).

Fires that occur frequently [i.e., at intervals less than the juvenile periods of obligate reseeding shrubs like *Protea lorifolia* (Salisb. ex Knight) Fourcade (Fig. 3B) and *P. repens* (L.) L.] are of particular concern in western fynbos, where relatively long juvenile periods suggest that fire return intervals should be 12–15 years (Kruger and

Lamb 1978). However, Kraaij et al. (2013c) indicated that this could be reduced to 9 years between fires further east, where fires are more frequent. Grasslands to the east of the Suurberg typically burn even more frequently (every 2–4 years, van Wilgen and Scholes 1997). The responses of the biota to differences in fire frequency in mixed grassland-fynbos vegetation remains unstudied, and further research would be needed to confidently predict the effects of fire frequency on obligate reseeding fynbos shrubs.

Potential effects of climate change

Climate change is likely to affect the fire regimes of the Suurberg in the future. The absolute minimum temperature, average minimum, and average maximum temperature have already increased in the Suurberg area by 0.8 °C, 1.15 °C, and 1.35 °C, respectively, between 1960 and 2006 (van Wilgen and Herbst 2017). As a result, the number of days per year where the temperature exceeds 35 °C has almost doubled between 1960 and 2006 (from 7 to 13 days per year). Further temperature increases of between 1.1 and 1.9 °C are predicted by 2050, resulting in a further doubling of the number of days experiencing temperatures above 35 °C under the worst-case scenario (van Wilgen and Herbst 2017). An increase in hot and dry conditions would likely provide more opportunities for fires to ignite and to spread, leading to an increase in fire frequency. This could be detrimental to fynbos shrubs that rely on seed production between fires to be able to

persist. In addition, fires in the fire-resistant Afrotropical forest are restricted to very rare conditions of high fire danger. These conditions may become more common in the future, leading to reductions in the extent of these forests (Manders and Richardson 1992).

Limitations

The data that we used for vegetation was developed for use at a national scale, and the remotely-sensed fire pixels were relatively coarse (500×500 m). In addition, previous studies have found that MODIS may underestimate fires in fynbos (Tsela et al. 2014), although we observed some over- and underestimation in the mixed grassland-fynbos area (see Additional file 2: Table S1). A single vegetation type mapped at a scale of 1:1,000,000 sometimes contained more than one vegetation type when examined at a finer scale. For example, mixed grassland-fynbos and thicket were often interdigitated in an area mapped as containing mixed grassland-fynbos only. This would have been interpreted in our analysis as mixed grassland-fynbos that did not burn, and as such, our analyses may have overestimated unburnt areas in the fire-prone vegetation. Without verification on the ground and more detailed mapping tools, there will always be a degree of uncertainty regarding the extent of remotely sensed fires, whether or not all fires were detected, as well as the accuracy of vegetation units linked to the fire patterns.

We did not calculate a single average fire return interval for mixed grassland-fynbos vegetation across our study area. Such a calculation is possible using maximum likelihood survival analysis that employs Weibull distribution functions (Moritz et al. 2009) to account for data censoring (i.e., where neither the date of the last fire prior to the period under examination nor the next future fire is known). However, we felt that calculating a single fire return interval for a dichotomous situation with some areas that burn frequently, and others that did not burn (see Fig. 4) may be misleading and that it would be more useful to present fire return intervals for the 22% of the mixed grassland-fynbos vegetation that burnt frequently. Future refinements to the vegetation map, and ongoing monitoring of fire occurrence over a longer period, will be needed to understand the reasons for this dichotomy.

Finally, we recognize the uncertainty regarding the origin of ignitions (whether caused by lightning or anthropogenic factors). Although field data are limited, management records confirmed that the large fires in 2004 and 2013 were caused by lightning, but records were not available for the large fires of 2008, and the cause was indicated as unknown for the large fires of 2019. Consequently, the fire regimes outlined in this study should not be presumed to be “natural” but rather

understood as potentially resulting from both natural and anthropogenic sources.

Management alternatives

The fire ecology of Suurberg mixed grassland-fynbos vegetation is poorly studied, partly due to its remoteness. An additional challenge arises from the divergent focus in the literature on either fynbos or grassland. This disparity compromises our ability to recommend a fire regime that could effectively accommodate the mixed grassland-fynbos vegetation that comprises elements of both vegetation types, either in their pure forms or as a mixture of both. The grassland components on the north-facing slopes are an extension of highland sourveld grasslands to the east on the summer-rainfall escarpment (R.M. Cowling, Nelson Mandela University, pers. comm.) but have been grouped with the Suurberg fynbos by Mucina and Rutherford (2006). Both aspects support flammable fuels that will burn under suitable weather conditions, and as such it would be impractical (and unnatural) to treat the fynbos, grassland, and grassy-fynbos as separate fire management units. Because fires have continued to occur (including a few deliberate ignitions by park managers in the past), and because they presumably do not pose a threat to an ecosystem that has evolved under such a regime, we propose that fire management should opt for a *laissez-faire* approach. Using this approach, any natural (i.e., lightning-ignited) fire would be allowed to burn freely, while fires of anthropogenic origin would be contained if necessary (Seydack 1992; van Wilgen et al. 1994).

Invasive alien species pose a threat to native biodiversity, *inter alia* through influencing the fuel characteristics and hence ultimately the fire regime (Kraaij et al. 2018). The prospects for gaining control over jointed cactus are reasonably good (due to effective biological control, Paterson et al. 2021). This is not the case for black wattle, *Acacia mearnsii* (Fig. 3D). Australian *Acacia* species (including black wattle) produce copious amounts of long-lived seed, which accumulate in the soil and, importantly, are stimulated to germinate by fire (Richardson and Kluge 2008). Although biological control of black wattle by seed-feeding and flower-galling insects are present in the Suurberg which will substantially reduce seed production and rates of spread (Impson et al. 2021), the ongoing presence of a large seedbank in the soil could present a concern for fire management for some time to come. Managers would need to actively remove emergent seedlings that are stimulated to germinate after a fire if the ongoing invasion is to be prevented.

Conclusion

The mixed grassland-fynbos vegetation at the eastern limit of the fynbos biome remains fire-prone despite being embedded in a landscape of fire-resistant vegetation. The biota within this vegetation type would presumably have evolved under a regime of fires ignited predominantly by lightning (and possibly nomadic cattle herders), and would be adapted to survive such a regime. There is evidence of an aseasonal fire regime, which contrasts strongly with the summer fires that characterize fynbos in the western parts of the fynbos biome. The mixed grassland-fynbos vegetation is surrounded by fire-resistant vegetation but still burns in ways that give rise to a diversity of fire frequencies, suggesting that active fire management (for example, by means of regular prescribed burning) may not be necessary. Interventions in the form of containing fires should only be considered where there are threats to and from commercial cattle farms and infrastructure surrounding the park. The ecosystem should also be monitored to identify any negative conservation outcomes related to fire.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00262-2>.

Additional file 1: Fig. S1. The total area burnt in individual months between January 2011 to December 2021, in relation to cumulative rainfall of past two months, measured at Suurberg ranger station.

Additional file 2: Table S1. Comparison of estimates by MODIS (MCD64A1) and Sentinel-2 of area burnt in four fires in the Suurberg mountain range.

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Authors' contributions

I.P.J.S. conceived and designed the study. Material preparation and data collection were done by I.P.J.S. and J.B. Analysis was performed and figures and maps were drawn by I.P.J.S. The manuscript was written by B.v.W. in collaboration with I.P.J.S. All authors read and approved the final manuscript.

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Availability of data and materials

All of the data used in this study are available from open-access sources.

Declarations

Competing interests

The authors declare that they have no competing interests.

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