Multidecadal effects of fire in a grassland biodiversity hotspot: Does pyrodiversity enhance plant diversity?

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Abstract. Native grasslands have been vastly transformed with the expansion of human activities. Applied fire regimes offer conservation-based management an opportunity to enhance remaining grassland biodiversity and secure its persistence into the future. Fire regimes have complex interactions with abiotic and biotic ecosystem components that influence environmental heterogeneity and biodiversity. We examined the pyrodiversity–biodiversity hypothesis, which suggests that more species are supported where pyrodiversity, that is, the level of environmental heterogeneity associated with different fire regimes, is greater. A mesocosm-type field experiment, maintained for 38 yr, was used to determine the response of plant diversity to 1-, 2-, 5- and 12-yr fire-return interval treatments, with early-dormant, middormant and early–growing season burns. Our sampling regime was designed to assess the influence of fire treatments and combinations thereof, over spatial scale, on plant diversity. Pyrodiversity was maximized where fire regime diversity, simulated by varying the size of patches with different fire treatments, was greatest. Species richness was predicted to be reduced at short and long extremes of fire-return interval, as suggested by the intermediate-disturbance hypothesis. The influence of fire treatments on alpha and beta diversity, and plant functional groups, were tested using multivariate and Bayesian models. Multilevel models of plant height and growth form, with fire-return interval, reflected the strong indirect influence of fire-return interval on sward structure and the plant environment. The pyrodiversity–biodiversity and intermediate-disturbance hypotheses were only partially supported and depended on the plant group and spatial scale of assessment. Although both frequent and infrequent burns made important contributions to overall species richness, richness peaked where 20–40% of the area was protected from frequent fires. The larger contribution of frequent burning to diversity was due to an interaction with scale and forb turnover over the trial area. Extremes in fire-return intervals reduced forb richness, supporting the predictions of the intermediate-disturbance hypothesis. Spring burns had a weak negative influence on forb alpha diversity, but only at small scales. For a meaningful contribution of management to plant diversity, traditional fixed biennial burns need to be supplemented with smaller patches burned with longer fire-return intervals, and extremes in fire-return intervals avoided.

Key words: burn season; fire-return interval; functional groups; grassland plant diversity; long-term experiment; pyrodiversity.

INTRODUCTION

Fire is a powerful ecological driver, affecting ecosystem functioning and biodiversity, and has been increasingly manipulated across landscapes to serve social and economic objectives (Archibald et al. 2012, Bowman et al. 2016). Concern has been raised that fire regimes, rigidly manipulated for these different objectives, do not maintain grassland biodiversity (Fuhlendorf et al. 2006, Gordijn et al. 2018). Fire-prone grasslands have their origins set deep in geological time and are characterized by exceptional levels of biodiversity and endemism (He and Lamont 2018). This biodiversity evolved under historic fire regimes that are arguably unknowable (Pausas and Keeley 2009), and even if known, their application in transformed landscapes may be inappropriate or impossible to replicate. In the Anthropocene, with the increasing demise of natural systems across the globe, many of these biodiversity-rich grasslands have been lost (Hoekstra et al. 2005), so that appropriate fire management has become critical for maintaining the biodiversity of remaining grassland.

Environmental heterogeneity is a key ecosystem attribute that ecologists have promoted for landscape functioning and biodiversity by manipulating fire and herbivory (Fuhlendorf et al. 2006, Fuhlendorf et al. 2017). Underlying the concept of heterogeneity is an understanding that, within a landscape, there are...
generalist species adapted to a wide range of environmental conditions, and specialist species adapted to a limited range of environmental conditions. Therefore, to maintain overall species richness, sufficient levels of habitat diversity and associated environmental heterogeneity should be conserved (Stein et al. 2014). For a range of taxa with different niche requirements, landscape spatial properties, such as extent, connectivity, and shape of different habitat patches over time, is important (Pickett and White 2013, Fuhlendorf et al. 2017).

Fire regimes strongly influence environmental heterogeneity, and are typically described for a given area by their main components, the average fire-return interval, fire intensity, and seasonality (He et al. 2019). All components of a fire regime are influenced by vegetation structure and composition, soils and topography, weather during each fire event, and the source of ignition. The consequent patch-specific fire regime selects for adapted biota, and influences vegetation structure and soil properties. Within a landscape, the differences in patch-specific fire regimes and associated fire-related heterogeneity shapes environmental heterogeneity (Bond 2019, He et al. 2019). The “level of fire-caused heterogeneity (diversity of patches) in a given area at a stated time” is known as pyrodiversity (He et al. 2019). Following the tenet that increased environmental heterogeneity supports greater biodiversity (Stein et al. 2014), the pyrodiversity–biodiversity hypothesis suggests that more species are supported where fire-caused environmental heterogeneity, that is, pyrodiversity, is greatest (He et al. 2019). The potential of pyrodiversity to enhance ecosystem biodiversity and functioning cannot be ignored (Fuhlendorf et al. 2017, He et al. 2019), especially in the face of the environmental uncertainty associated with global change (Pollock et al. 2017).

Prompted by the concern for biodiversity under rigid human-altered fire regimes, the pyrodiversity–biodiversity hypothesis has been widely accepted, and patch mosaic burning has been used as a conservation-based management strategy for enhancing biodiversity, in order to secure its persistence into the future (Brockett et al. 2001, Parr and Andersen 2006). However, support for the pyrodiversity–biodiversity hypothesis has been mixed, both within and across groups of taxa (Davies et al. 2012, Maravalhas and Vasconcelos 2014), and some management efforts to create pyrodiverse fire regimes have not increased biodiversity (Andersen et al. 2014, Farnsworth et al. 2014), whereas in others pyrodiversity has been associated with greater species richness (Maravalhas and Vasconcelos 2014, Tingley et al. 2016). Differences in how pyrodiversity is measured and range of pyrodiversity considered have also contributed to equivocal support of the pyrodiversity–biodiversity hypothesis (Farnsworth et al. 2014, He et al. 2019). Complications with scale also arise where the reference area in which pyrodiversity is measured is not limited. If a reference area is limited, a greater diversity of patch types can only be accommodated at the expense of patch size (Davies et al. 2018, He et al. 2019). As patch size declines, increased patchiness favors species adapted to patch edges, but rare species that require larger patch scales may be filtered out, and consequently species richness may be reduced (Hortal et al. 2009, Gil-López et al. 2017). Clearly, the potential value of pyrodiversity for enhancing biodiversity requires context-specific evaluation.

A simple measure to evaluate the response of biodiversity to pyrodiversity is species richness (He et al. 2019), but insight from this diversity metric is limited and confounded by scale (Fleishman et al. 2006). The variable relation between species richness and scale has resulted in mixed support for the intermediate-disturbance hypothesis (Mackey and Currie 2001) that suggests the number of species supported is reduced in patches where extremes of a disturbance are maintained (Connell 1978). Species-area curves have been used to evaluate relationships between scale and species richness (Turner and Tjørve 2005). Steeper species-area curves, where new species accumulate rapidly with area, represent patches where differences in composition are increased, and vice versa for gentle slopes. A curve’s steepness reflects beta diversity, which is defined as point-to-point variation in composition (Koleff et al. 2003). Species-area relationships have been successful in assessing the influence of scale on the number of species supported within a specific patch type, but where multiple patch types within a landscape are considered, environmental heterogeneity confounds the species-area relationship (Turner and Tjørve 2005). Measures of beta diversity, such as Bray–Curtis dissimilarity (Bray and Curtis 1957), have become a standard by which the response of composition to multiple environmental drivers is assessed (McCune and Grace 2002).

Increased levels of beta diversity have also been the goal of pyrodiversity management, where differences in composition have been promoted and increased support of species numbers is presumed (Maravalhas and Vasconcelos 2014, He et al. 2019). This assumption is misleading, and management for beta diversity should be approached carefully (Baselga 2010). Beta diversity is made up of two antithetic components—nestedness and turnover—and their respective contributions are related to patterns in species richness. Variation in the nestedness component results from filtering of species from the available pool of species. Conversely, turnover describes differences in beta diversity due to variation in unique species assemblages across space. Pyrodiverse fire regimes should recognize both nestedness and turnover so that the appropriate range of fire-regime components is applied for associated species (Baselga 2010).

Predicting the complex response of biodiversity to fire disturbance also depends on the taxa and functional groups of interest (Farnsworth et al. 2014). This study was interested in the response of vascular plant diversity to pyrodiverse fire regimes. To understand the response of overall plant species diversity to pyrodiversity, the
response of plant communities to specific fire regime treatments was also explored. Fire severity describes the consumption of organic matter by fire, and is typically quantified by ash deposition, phytomass scorching, or mortality rates (Keeley 2009). Fire severity is generally correlated with fire intensity, that is, the heat energy from fire (Keeley 2009). Burn season influences fire intensity and severity. In the dry or dormant compared with the wet or growing season, increased phytomass curing produces burns with greater intensity and scorching (Everson et al. 1985). Despite scorching, perennial grassland plants may regrow from protected or underground meristems but, even with weak-intensity fires in the growing or flowering season, species that rely on aerial meristematic tissues for growth and reproduction may be negatively affected (Howe 1995).

Biota are also indirectly influenced by ecosystem responses to fire events. For example, selection for a group of plants adapted to a specific fire regime may influence vegetation structure, and therefore, the plant environment and overall plant diversity (Keeley 2009). Interactions between fire-regime components and ecosystem responses usually have cascading effects. For example, when unlimited by herbivory under longer fire-return intervals, phytomass accumulates, producing a greater fire intensity and severity for vulnerable woody species through scorching (Keeley 2009). An ecosystem response of increased phytomass may “shade out” prostrate or shorter forbs, whereas cauline species, with their leaves borne on stems, may emerge through the grass canopy and retain vigor (Morgan and Lunt 1999, McCain et al. 2010, Gordijn et al. 2018).

Montane Drakensberg grassland is the most extensive remaining tract of native grassland in southern Africa (Carbutt and Martindale 2014), and is a recognized center of plant endemism (Mucina et al. 2006). This diversity evolved long before human settlement intensified c. 3000–200 BP, and influenced the naturally heterogeneous fire regime driven by lightning ignition (Manry and Knight 1986, Wright and Mazel 2007). The timing of burns in the Drakensberg prior to marked human influence would have been directly dependent on lightning strikes, which occur frequently throughout the growing season (Manry and Knight 1986). Successful ignition and spread of fires would have depended on the amount and spatial extent of accumulated fuel. In the wet season, lightning-ignited fires were likely patchy, because of variable fuel moisture and because the fires could be extinguished by rain associated with thunderstorms (Ramos-Neto and Pivello 2000). Repeat burning in the mid to late growing season may have been limited by decreased fuel for consecutive burns because of reduced grass vigor associated with the removal of live phytomass (Scotcher and Clarke 1981, Biondini et al. 1989, Ramos-Neto and Pivello 2000). Patchy burns in the wet season may have limited the spread of dry-season fires ignited by aborigines, whose acute occupation was periodic from c. 3000 to 600 BP, and agropastoralist farmers who settled in the region c. 600 BP (Wright and Mazel 2007). With the arrival of farmers, fire frequency (Wright and Mazel 2007) and probably the occurrence of extensive dry-season burning increased (e.g., Archibald et al. [2012]). Before these farmers, most herbaceous biomass in the Drakensberg was consumed by fire, owing to a light herbivore biomass as a consequence of the poor nutritional quality of grasses (Rowe-Rowe and Scotcher 1986). In the absence of heavy grazing, herbaceous biomass continues to be consumed primarily by fire (Scotcher and Clarke 1981).

In contrast to the pyrodiversity associated with lightning-driven fire regimes, formal management has advocated rigorously implemented short, 1- and 2-yr fire-return intervals, commonly set in both dormant and early growing seasons since c. 1950, to maintain the cover of a few grasses associated with rangeland production or hydrological functioning (Nänni 1969). Since c. 2000, heterogeneity has been increasingly promoted for diversity, of which >70% is contributed by perennial forbs (Gordijn et al. 2018). Using a landscape-scale approach Gordijn et al. (2018), found that forb richness, as predicted by the intermediate-disturbance hypothesis (Connell 1978), was reduced in patches where extreme fire-return intervals were maintained (shorter than 2 yr and longer than 5 yr), but an undetermined level of pyrodiversity, defined by a range of fire-return intervals within patches across the landscape, was required to maintain unique species assemblages. The important influence of burn season (Howe 1995, Fynn et al. 2004) was, however, not tested (Gordijn et al. 2018). The potential influence of common herbivorous mole rats (Cryptomys natalensis Roberts, 1913), that feed on underground plant parts, on grassland composition is largely unexplored (Reichman and Jarvis 1989); similar animals elsewhere (e.g., pocket gophers) are known to influence vegetation composition (Reichman and Seabloom 2002).

Mesocosm-type field experiments have provided a depth of conceptual and mechanistic insight into the influence of important drivers such as rainfall variability (Knapp et al. 2002), warming, and elevated CO₂ (Zelikova et al. 2014) on grassland biodiversity. Long-term trials of this nature have been invaluable for understanding the impact of fire on grassland diversity (Fynn et al. 2004, Wragg et al. 2018). By controlling for environmental variables, the potential influence of these drivers is revealed, and may inform conservation management, plus supplement landscape-scale experimentation.

Rigid human-altered fire regimes are a concern for Drakensberg plant diversity (Gordijn et al. 2018). If the response of grassland plant diversity to pyrodiverse regimes can be understood, this understanding may guide conservation-based fire management to enhance biodiversity under rigid human-altered fire regimes, and secure the persistence of grassland biodiversity into the future. The aim of this study was to determine whether conservation-based fire management could justify the
use of pyrodiverse regimes to enhance grassland plant diversity. This required a long-term field experiment with both fire-return interval and burn-season treatments. We used the 38-yr, Brotherton burning trial (Manson et al. 2007), serving as a mesocosm, to test the impacts of different fire-return interval and season of burn treatments on plant diversity. Our sampling regime was designed to examine the influence of specific fire treatments and combinations thereof, over spatial scale, on plant diversity. Pyrodiversity was maximal where fire-regime diversity, simulated by varying the area contributed by different fire treatments, was greatest (He et al. 2019). Based on the pyrodiversity–biodiversity hypothesis, the number of species supported was predicted to be greater as pyrodiversity was increased (He et al. 2019). To gain insight into the overall response of plant species diversity to pyrodiversity, we assessed the responses of plant species richness, beta diversity, and functional groups, to specific fire-return interval and season of burn treatments. Species richness was predicted to be reduced at extremes of the fire-return interval gradient as predicted by the intermediate-disturbance hypothesis (Connell 1978). Species richness was also expected to be reduced in dormant-season burns because lightning frequencies would have been lowest during the dormant season prior to human modification of the fire regime (Archibald et al. 2012). The potential influence of mole rats on grassland composition and beta diversity was also examined.

**Methods**

**Study area**

The Brotherton burning trail (29°15'43" S, 29°58'13" E) covers 400 × 200 m (8 ha), and was established in 1980 (Appendix S1: Fig. S1). It is located in the uKhahlamba Drakensberg Park in KwaZulu-Natal, South Africa, on a south–north orientated, flat to gently sloping plateau of approximately 1.25 km² at 1,900 m above sea level. The grassland at the trail represents the major vegetation type in the Drakensberg mountains, known as uKhahlamba Drakensberg Basalt grassland (Mucina et al. 2006), dominated by *Themeda triandra*. Grasses form >90% of this vegetation’s biomass contribution (Mucina et al. 2006) but forbs make up >75% of species richness (Gordijn et al. 2018). These grasslands support a low density of mammalian ungulates of one animal unit (455 kg steer) per 55 ha (Rowe-Rowe and Scotcher 1976). The potential influence of mole rats on grassland composition and beta diversity was also examined.

**Experimental design**

The burning treatments manipulated fire-return interval and season of burn. A randomized block design was used to control for spatial heterogeneity across the trial (Manson et al. 2007). Seven treatments were established, each with a single-plot replicate in each of the trial’s three blocks (n = 7 × 3 = 21 plots). Plots were 25 × 25 m with 5-m walkways separating each plot (Appendix S1: Fig. S1). Treatments included a range of fire-return intervals from 1, 2, and 5 yr, plus an attempted no-burn treatment with a fire-return interval of 12-yr, because of arson and runaway “controlled” fires in the winters of 2000, 2007, 2016, and 2017. The effect of season of burn was only tested where autumn, winter, and spring burns were replicated, which was the case for a return interval of 2 yr (n = 3 × 3 = 9 plots). For analysis of fire-return interval, burn season was not balanced across return interval treatments, but bias was limited. There were two 1-yr fire-return interval treatments burned in autumn and spring (n = 2 × 3 = 6 plots), the 5-yr fire-return interval treatment was alternately burned in autumn or spring every 5 yr (n = 1 × 3 = 3 plots), whereas the infrequent burning of the 12-yr interval treatment (n = 1 × 3 = 3 plots) limited any effect of season.

To reflect the influence of fire at the landscape scale, the size of plots at Brotherton was designed to allow representative burn behavior. Across burn treatments fire intensities have been relatively consistent, being set as head burns with calm winds (<0.5 m/s). Under these conditions, the largest difference in fire intensity was across burn seasons where early wet-season burns may have been less than half (1,000 kJ s⁻¹·m⁻¹) the intensity of winter burns (3,000 kJ s⁻¹·m⁻¹) because of increased fuel moisture and reduced curing during this wetter period (Everson et al. 1985).

**Field sampling**

Vegetation was sampled during the main flowering season of these grasslands, the mid-summer of January 2018 (Gordijn 2018). Sampling was confined to the inner 20 × 20 m area of each 25 × 25 m plot in order to avoid possible edge effects. In each 400-m² plot, the presence of species was recorded in 20 2-m²-square quadrats, evenly placed along five 20-m-long transects. Additional species were searched for in the remainder of the 20 × 20 m plot area, and the cover abundance of each species was scored using the 10-point Domin-Krajina scale (Currall 1987). The cover of species in the lowest cover abundance class was transformed by a minimal conversion factor of 0.1, which is equivalent to 0.0025 m² (Currall 1987), a procedure that avoids inflating the cover of smaller, mostly deciduous species whose cover is seasonally variable. This provided a measure of
species presence/absence and cover at the 400-m² plot scale, and by combining particular plot quadrats, the effect of scale could be assessed at scales ≥2 m². Species nomenclature followed “The Plant List” (2013).

To determine whether subterranean mole rats had an influence on grassland plant diversity, their activity was estimated in the spring (October) of 2016. An index of mole rat activity measured was the cumulative distance of mounds intersected along eight evenly spaced 20-m-long transects per plot. Percent basal cover, a component of grassland structure that reflects grassland vigor, was estimated in eight 0.5 × 0.5 m² quadrats, each with 25 subquadrats of 0.05 × 0.05 m², in July 2018.

**Plant groups.**—To develop an understanding of species’ responses to fire treatments, these were classed into functional groups. Groups of plants defined by growth form and height were expected to reflect the effects of shading due to phytomass accumulation under longer fire-return intervals. Three height groups were defined relative to the average height of the grass leaf table at the end of the growing season (approximately 0.3 m): “short” plants were less than half this height; “medium–tall” plants were slightly below the leaf table canopy; and “tall” plants emerged above the canopy. Growth forms expected to respond differently to fire treatments included forbs, graminoids (grasses and sedges) and woody plants. Forbs were further separated into cauline or radical, where leaves are borne along the stem or emerge at ground level, respectively. These two categories were further divided into prostrate or erect, the latter being completely represented by nongraminoid monocotyledons (see illustrations on Fig. 4) (Uys 2006).

To detect a possible influence of burn season, forbs were also classified into phenological groups of winter-to-spring, spring-to-summer, summer only, and summer-to-autumn flowering species (Pooley 2003).

**Data analysis**

To set the contextual background, the analysis begins with a description of grassland botanical composition and structure in relation to fire-return interval, burn season, and mole rat activity using ordination. Then, working towards understanding the response of plant diversity to combinations of different fire treatments, that is, pyrodiversity, the influence of specific fire-return interval and burn-season treatments on plant diversity was examined, at small to larger scales. The primary measure of plant diversity measured was species richness; however, variation in plant species assemblages over space and/or across treatments, that is, beta diversity, was also assessed. Differences in beta diversity and the environmental factors that influence these maintain plant assemblages and overall species richness within a given area. Modeling of other alpha diversity indices (in addition to species richness) and plant functional groups by fire-return interval and burn-season treatments was done to provide insight into how fire regimes drive plant diversity, at the community and functional group levels, respectively. In these analyses, the influence of fire treatments on plant diversity and plant groups was determined by taking advantage of the trial’s block design and controlling for spatial heterogeneity. In the pyrodiversity analysis, quadrats were combined across the study area to simulate small to large patches with contrasting fire regime treatments over the trial area. Because of the neglect of forb diversity by formal management, and the inverse responses of forbs and graminoids to fire treatments (Gordijn et al. 2018), forbs and graminoids were analyzed separately to provide insight for conservation-based management.

**Composition and structure.**—The relation between botanical composition, that is, abundance-based dissimilarity, fire treatments, mole rat activity and basal cover were visualized using nonmetric multidimensional scaling ordinations. Distance was based on species cover using Bray–Curtis dissimilarity (Bray and Curtis 1957). Only species contributing >2.5% cover were included. Separate ordinations for the fire-return interval and season of burn-treatment data subsets were produced using 1,500 and 2,000 iterations to find convergent solutions with four and three dimensions where stress levels were acceptable at 0.010 and 0.023, respectively (McCune and Grace 2002). Fire-regime components for the burn season and fire-return interval ordinations, plus basal cover and mole rat activity, were fitted to nonmetric Multidimensional Scaling ordinations and tested with 999 permutations. Spatial heterogeneity, which reflects the potential variation in plant community organization over space, was controlled by not shuffling plots across the trial’s block structure. However, a reduced sample size (n = 9) for the burn-season ordination using the 2-yr fire-return interval data subset only allowed 199 permutations. Therefore, these tests were also run without block restrictions to allow a full complement of permutations. The analysis was performed using the R Development Core Team (2020) package “vegan” (Oksanen et al. 2019).

**Plant species diversity.**—To assess the contribution of different fire treatments to overall plant diversity, and understand response of plant community organization to fire treatments, alpha and beta diversity were investigated. Alpha diversity components of species richness, Shannon’s diversity (H) and Simpson’s dominance (D) were estimated as $H = - \sum_{i=1}^{S} p_i \ln p_i$ and $D = \sum_{i=1}^{S} p_i^2$, respectively, where $p_i$ is the proportional abundance of the ith species (Hill 1973). Shannon’s diversity reflects the evenness of community organization when compared to Simpson’s dominance, they are generally inversely related, but the strength of this relationship is variable (Hill 1973). When determining the effect of fire treatments on diversity, spatial heterogeneity (represented by the trial’s block structure) was controlled for using Bayesian multilevel models in R Core Team (2020)
“brms” (Bürkner 2017a). Multilevel models account for both group level (e.g., block structure) and population level (e.g., fire treatment) effects. A minimum of 2,000 Hamiltonian Markov iterations times four chains were used to parameterize models (Kruschke 2014).

To compare the influence of fire-regime components across spatial scale on species richness; species-area relationship models were developed for each level of fire-return interval and burn-season treatment. Uncertainty around the mean number of species from small (2-m² quadrats) to larger (40 m²) scales, was modelled from a data set produced by subsampling quadrats without replacement (100 permutations; [Colwell et al. 2012]). To control for spatial heterogeneity, permutations were restricted to within blocks (and plots). The nonlinear accumulation of species with area was represented by the Arrhenius equation, \( S = cX^z \), where \( S \) is the number of species, \( c \) and \( z \) are parameters, and \( X \) is the area. Parameter \( z \), which determines the steepness of the curve (Koleff et al. 2003), was used to estimate within-treatment beta diversity. Informative priors were developed based on population-level parameters. Parameter \( z \) was modeled also by the additive group level effect of the trial’s block structure. The effects of fire-return interval and burn season on Shannon’s diversity and Simpson’s dominance were modeled with linear multilevel models using uninformative priors (Student distribution, identity link [Bürkner 2017a]).

**Partitioning beta diversity.**—Beta diversity can be partitioned into two antithetic components, nestedness and turnover. Differences in nestedness result from filtering of species, such that, all samples consist of a subset of the most species rich sample. Conversely, turnover accounts for variation in unique species assemblages between points (Baselga 2010). The relative importance of the fire treatments, spatial heterogeneity (represented by the experiment’s block design), and mole rat activity for explaining variation in turnover and nestedness was determined through variance partitioning. Variance partitioning using distance-based redundancy analysis allows the determination of the marginal effect of factors on beta diversity. Nestedness and turnover were derived from Sørensen dissimilarity in R Development Core Team (2020) “betapart” (Baselga and Orme 2012). The significance of marginal effects were tested at small (2-m² quadrat samples) and larger scales (400-m² plot samples). Spatial heterogeneity was controlled for by permuting residual variance with restrictions for trial block structure, and quadrats per plot (quadrats were not shuffled). Analyses were run in R Development Core Team (2020) “vegan” (Oksanen et al. 2019) (999 permutations).

**Plant groups.**—The response of plant groups’ richness and cover abundance to fire-return interval and burn season was evaluated with Bayesian multilevel models (Bürkner 2017a). The default family for richness models (count data) was Poisson, and for cover abundance was Gaussian, then Student, then log-normal distribution for skewed responses and finally the Beta distribution for zero or zero-one inflated responses. Models were developed from uninformative priors. Uncertainty around each median response was estimated using posterior fits (Kruschke 2014). Population-level effects for each model were either fire-return interval or burn season, and the trial’s block structure was controlled for as a group-level effect.

**Pyodiversity.**—The response of species richness and the turnover component of beta diversity to pyodiversity was investigated by simulating a continuum of patches of variable size and different fire treatments. Patches with contrasting fire treatments were combined to form a multipatch sample. Patch size was varied by random sampling (199 permutations) and scaling up of 2-m² quadrats in an additive manner. The contribution of contrasting fire treatments to patch size varied from 2 to 60 m² in 29 2-m² increments. Although the area sampled was limited to 60 m², this sample covered the entire 8-ha trial area.

The fire treatments contrasted were short with longer fire-return interval treatments with alternate burn seasons; the attempted no-burn treatment was excluded. There were four short fire-return interval treatments with variable burn seasons (12 plots with fire-return intervals of 1 and 2 yr and either dormant- or early-growing season burns), and one longer fire-return interval treatment (three plots with 5-yr return intervals and alternating dormant- and early-growing season burns). The bias in sample size with four short and only one longer fire-return interval treatment was controlled by only combining one short with the longer return interval treatment per sample. Doing this for each of the four short fire-return interval treatments with 29 patch sizes each and 199 permutations gave a sample size of 4 × 29 × 199 = 23,084. Spatial autocorrelation, associated with the clustering of quadrats when scaling up over the trial area, was limited by restricting the average distance between quadrats in each patch. Spatial correlation of this type was controlled by taking a narrow data subset to within 0.75 m of the overall mean distance between sample quadrats. This procedure was repeated for the total richness and turnover of forbs and graminoids combined, forbs only, and graminoids only; final sample sizes were 679, 630, and 663, respectively.

The level of pyodiversity was highest where the area contributed by patches with contrasting fire treatments was equal (i.e., where the eveness of fire treatment patches was greatest [He et al. 2019]). Relationships between pyodiversity and species richness and turnover were modeled using Bayesian generalized additive models where the smooth terms are treated as random effects around the linear predictor function. Gaussian process smooths were estimated using five to eight knots and 6,000 chain iterations; default priors were used (Bürkner 2017b).
RESULTS

Composition and structure

Variation in botanical composition along the primary axis of a successful nonmetric multidimensional scaling ordination, was strongly influenced by fire-return interval ($r^2 = 0.94, P = 0.005$), but not by season of burning ($r^2 = 0.1, P = 0.3; Fig. 1$). Basal cover was correlated with variation in botanical composition ($r^2 = 0.66, P = 0.005$), and decreased from vegetation experiencing a short to a long fire-return interval. Mole rat activity did not correspond with compositional variation ($r^2 = 0.09, P = 0.5$).

Plots with long fire-return intervals of 12 yr were dominated by the grass *Harpochloa falx* and the forb *Helichrysum aureonitens*. Other grasses, *Tristachya leucothrix* and *Eragrostis tincta* were more abundant in intermediate fire-return interval treatments of 5 yr. *Themeda triandra* and *Heteropogon contortus* dominated cover under shorter fire-return intervals of 1–2 yr. *Rubus cuneifolius*, a nonnative shrub, had attained an approximate cover of 40% in a 12-yr return interval plot.

Plant species diversity

Forb species richness was threefold greater than graminoid richness over the entire experiment (Appendix S1: Table S1). All species were African or southern African endemics except *Helichrysum drakensbergense*, a Drakensberg near endemic (Carbutt 2019), and three nonnative species, the forbs *Conyza canadiensis* and *Hypochaeris radicata*, and the shrub *R. cuneifolius*. The species-area relationship models were successful ($Rhat \leq 1.02$) and showed that the influence of fire-return interval was four times greater than that of burn season on forb or graminoid richness (Fig. 2). Forb richness was higher under intermediate return intervals, especially at smaller spatial scales. For example, there were four fewer species at the 2-m$^2$ scale for a 12- than a 2-yr return interval. Graminoid richness decreased with longer fire-return intervals across spatial scales. The largest difference in graminoid richness was at the 2-m$^2$ scale, where there was a reduction of four species from the 2- to 12-yr return-interval treatment. The influence of burn season was most strongly evident at small spatial scales. At the 2-m$^2$ scale, spring burns compared with dormant-season burns in autumn or winter reduced the richness of graminoids and forbs by one species.

Successful multilevel models ($Rhat \leq 1.02$) showed that Shannon’s diversity and Simpson’s dominance were generally inversely related (Fig. 3). In response to season of burning, Shannon’s diversity of forbs decreased from autumn, through winter, to spring burns. Shannon’s diversity of graminoids was unresponsive to burn season. At extremes in fire-return intervals Shannon’s diversity of forbs was reduced, and for graminoids Shannon’s diversity decreased under longer fire-return intervals. The level of beta diversity of either forbs or graminoids was not influenced by season of burn, but tended to be reduced at intermediate return intervals (Fig. 2). For example, the respective increase of forb and graminoid beta diversity between fire-return intervals of 2 and 12 yr was 16% (80% Bayesian credible interval [CI]) and 32% (90% CI).
Partitioning beta diversity

Beta diversity was largely composed of turnover with a negligible contribution of nestedness (Appendix S1: Table S1). Therefore, only the turnover component was investigated further. Distance-based redundancy analysis revealed that variance in turnover was mostly explained by fire treatments rather than by spatial heterogeneity (Table 1). Fire-return interval and spatial heterogeneity explained a significant amount of variance in the turnover of forbs and graminoids at small and large scales. The slight influence of burn season on forb turnover was limited to smaller scales. Mole rat activity did not explain variance in beta diversity and was therefore not investigated further.

Plant groups

Successful Bayesian multilevel models (Rhats ≤ 1.02) showed that fire-return interval treatments had a greater influence on the richness and cover of functional groups (Fig. 4) than burn season (Fig. 5). The influence of burn season on the richness of plant groups was not evident, however, the cover of forbs and graminoids was affected (Fig. 5). For example, for winter, compared with autumn and spring burns, forb and graminoid cover was raised by 4% and lowered by 6%, respectively (80% CI). Furthermore, for winter burns compared with autumn and spring burns, cauline prostrate and cauline erect species increased cover by 20 and 30%, respectively (80% CI). Most forb species (88% of the species analyzed) concentrate flowering during the wet season from spring to summer. Forbs flowering from spring into summer followed a similar pattern to cauline erect species (Fig. 5).

Forb cover was not influenced by fire-return interval, and graminoid cover was maintained at approximately 80% in all treatments apart from the 12-yr RI, where its cover was reduced to 67% (95% CI). Woody richness increased with fire-return interval such that from a return interval of 1–12 yr, woody richness increased from one to four species (95% CI) (Fig. 4).
The humped response of forb richness to fire-return interval, with an apex of 32 species at the intermediate return interval of 5 yr, reflected the pattern of the cauline erect species, which was the largest contributor to forb richness (Fig. 4). The richness and abundance of species with leaves restricted to ground level (radical prostrate or radical erect) or short species were limited under the longer fire-return intervals of 5–12 yr. For example, the richness of radical prostrate species was reduced approximately twofold under return intervals of 5 and 12 yr (80% CI). By contrast, taller or woody or cauline prostrate species, able to emerge through the grass canopy, generally had greater species richness and abundance in the longer fire-return interval treatments of 5 and 12 yr (Fig. 4).

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Pyrodiversity

Successful Bayesian smooths (Rhats = 1.00) revealed a significant influence of pyrodiversity on species richness and turnover across the Brotherton trial (Fig. 6). The nonzero model variance parameters justified the use of nonlinear smooths (variance parameters bounded by their 95% CI levels were forb richness 2.3 ≤ 21.1 ≤ 51.0 and turnover 0.3 ≤ 2.1 ≤ 6.9, graminoid richness 3.2 ≤ 8.2 ≤ 19.0 and turnover 1.6 ≤ 5.4 ≤ 13.7, and combined forb and graminoid richness 16.6 ≤ 17.7 ≤ 61.00 and turnover 1.6 ≤ 5.4 ≤ 13.7). The combined richness of forbs and graminoids peaked where pyrodiversity levels were approximately 65%, and between 30% and 40% of the area was burned with longer fire-return intervals. Forb richness was relatively stable throughout the range of pyrodiversity, but increased from 35 to 36 species as the area covered by short fire-return intervals increased from 0 to 60%. Graminoid richness was greatest where between 30 and 60% of the area was under longer fire-return intervals.

The combined forb and graminoid turnover and forb turnover was greatest where 60–80% of the area was burned under shorter fire-return intervals (Fig. 6). Graminoid turnover peaked where 80–100% of the area was under short fire-return intervals. The greater richness over the trial reflected the contribution of turnover to overall species richness (Figs. 2, 6).

DISCUSSION

Contribution of pyrodiversity

The strong influence of fire treatments on grassland structure, plant species composition (Fig. 1), and diversity (Figs. 2, 3, Table 1) observed in this study is supported by evidence from temperate and subtropical grasslands around the world (O’Connor et al. 2010,
Bradstock et al. 2012, Fuhlendorf et al. 2017, Bond 2019). However, although long-term studies have evaluated the effects of fire-return interval on plant diversity, few have tested the additional effect of season of burn (Biondini et al. 1989, Fynn et al. 2005, O’Connor et al. 2010, Gordijn et al. 2018), and less so the interactions between fire regime components and scale, that together shape pyrodiversity (McGranahan et al. 2018, He et al. 2019).

Using a multiscale approach, this study, with nearly four decades of fire-return interval and burn-season treatments, revealed that pyrodiversity can be used to maintain increased levels of plant species richness and turnover. This is particularly significant for biodiversity-rich grasslands with high levels of species endemism, such as the Drakensberg, that require judicious fire management for conserving rare forbs. These inconspicuous forbs only contribute a small portion of total biomass or cover; they have little worth in traditional rangeland production but, they constitute the bulk of plant species diversity (Fig. 1; Appendix S1: Table S1). Support for the pyrodiversity–biodiversity hypothesis, that suggests more species are supported where pyrodiversity levels are highest, was however, only partial (Fig. 6).

Similar to the predictions of Farnsworth et al. (2014), support for the pyrodiversity–biodiversity was dependent on the metric used to quantify diversity. Patterns in diversity also vary with scale (Mackey and Currie 2001) and careful interpretation of trends is needed, especially when scaling up from field experiments to a landscape level. In this study, a greater depth of insight into how pyrodiversity influences plant diversity was obtained through estimation of a range of alpha and beta diversity components (Figs. 2, 3, Table 1), over patches of variable size (Fig. 6). Separation of species into plant groups further aided the interpretation of observed trends. Graminoid and forb plant groups responded differently to the continuum of pyrodiversity evaluated (Fig. 6), affirming that responses to pyrodiversity depend on the taxa and functional groups of interest (Farnsworth et al. 2014, He et al. 2019).

Overall, relatively frequent burning of these grasslands was sustainable, but, in contrast to formal rangeland management, which has advocated rigorously implemented short fire-return intervals for rangeland production and associated palatable grass species, plus water yield, a significant proportion of the landscape requires longer fire-return intervals to maintain plant species richness and turnover (Fig. 6). Although they do not maintain a greater cover of palatable grass species, such as Themeda triandra (Fig. 1) under return intervals longer than 2 yr, these areas are important forage reserves during drought (Fuhlendorf et al. 2017). The fresh regrowth after burns in areas with longer fire-return intervals also provide good-quality forage (Everson and Everson 2016).

The prediction that species richness and turnover would peak where pyrodiversity was greatest, that is, where the area of contrasting fire regimes were evenly represented, was not supported. Plant richness and turnover were maximized where a significant proportion (20–40%) of total area was protected from frequent fires (Fig. 6). This observation aligns with the predictions of He et al. (2019), specifically, that rare species would be lost as patch sizes declined to accommodate increased levels of pyrodiversity within a given area; consequently, diversity would peak at submaximum levels of pyrodiversity. By testing an asymmetric gradient of pyrodiversity, with variable contributions by both short 1- and 2-yr and longer 5-yr fire-return intervals, we determined that a greater proportion of the landscape should be burned frequently (Fig. 6). The longer 5-yr return

### Table 1. Significance of explanatory variables for forb and graminoid fractions of the turnover component of beta diversity at small (2 m²) and larger (400 m²) scales. Reduced sample size at the large scale prevented analysis of mole rat activity on graminoid turnover.

| Fraction component | Life form | Scale (m²) | df | F    | P     | r²adj |
|--------------------|-----------|------------|----|------|-------|-------|
| Return interval    | Forb      | 2          | 1,415 | 101.9 | 0.001 | 17.8  |
|                    |           | 400        | 1,17  | 9.3   | 0.001 | 28.7  |
|                    | Graminoid | 2          | 1,415 | 88.4  | 0.001 | 13.8  |
|                    |           | 400        | 1,17  | 8.3   | 0.001 | 27.7  |
| Burn season        | Forb      | 2          | 2,174 | 10.4  | 0.088 | 8.2   |
|                    |           | 400        | 2,4   | 1.3   | 0.468 | 5.7   |
|                    | Graminoid | 2          | 2,174 | 7.06  | 0.166 | 5.1   |
|                    |           | 400        | 2,4   | 0.4   | 0.700 | 18.7  |
| Spatial            | Forb      | 2          | 2,415 | 18.8  | 0.001 | 6.3   |
|                    |           | 400        | 1,17  | 3.2   | 0.005 | 7.8   |
|                    | Graminoid | 2          | 2,415 | 18.8  | 0.001 | 16.6  |
|                    |           | 400        | 1,17  | 3.2   | 0.006 | 5.1   |
| Mole rat           | Forb      | 2          | 1,415 | 9.2   | 0.154 | 1.4   |
|                    |           | 400        | 1,17  | 1.0   | 0.455 | 0.0   |
|                    | Graminoid | 2          | 1,415 | 4.7   | 0.670 | 1.0   |
Intervals provide an important contribution to plant species richness and turnover levels (Figs. 2, 4), but decades of shading associated with return intervals longer than 5 yr reduces the vigor of shade-sensitive species, and they are filtered from the landscape (Figs. 4, 6).

Interestingly, unlike the reportedly strong influence of subterranean herbivorous mammals (Reichman and Seabloom 2002), mole rat activity had no detectable influence on composition (Fig. 1) or beta diversity (Table 1). This observation does not rule out the possibility of localized influences near mole rat burrows (Reichman and Jarvis 1989), but this influence was not evident at the scales we investigated (2 m² and 40 m²), and this requires further investigation.

**Fig. 4.** Uncertainty around the median of the functional group responses to fire-return interval (dark and white points represent richness and cover, respectively). The total number of species per functional group is appended in brackets to subplot titles. Graminoids are excluded from all but the Graminoid and Short, Medium, and Tall groups. The dark gray, gray, and off-white bars depict the 50, 80, and 95% uncertainty levels (or Bayesian credible intervals). Cauline and radical growth forms are illustrated on adjacent to respective plots.

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Fire-return interval should be of primary importance for conservation-based fire management. Compared with burn season, fire-return interval had a stronger influence on composition (Fig. 1) and alpha (Figs. 2, 3) and beta diversity (Table 1, Fig. 2). Responses of plant diversity to fire-return interval were dependent on scale and the group of taxa examined (Figs. 2, 4). The richness of forbs (Appendix S1: Table S1), as predicted by the intermediate-disturbance hypothesis (Connell 1978), was reduced at extremes of the fire-return interval gradient examined (Figs. 2, 4). Forbs have historically been neglected by formal management in favor of grasses.
associated with rangeland productivity (Parr et al. 2014). However, the more than 75% contribution by forbs to plant richness highlights their importance for biodiversity (Appendix S1: Table S1).

Regarding the short extreme of the fire-return intervals assessed, conservation-based management should avoid annual burning over the landscape. The productivity of dominant grasses is increased under shorter fire-
return intervals (Collins and Smith 2006, Everson and Everson 2016, Ward et al. 2020), but competitive exclusion of species may occur. In these grasslands, annual burns reduced Shannon’s diversity of forbs (Fig. 3) and forb richness (Figs. 2, 4). The negative effect of annual burns is likely to be exacerbated by greater production demands with global change (Parr et al. 2014) and associated heavier grazing (Joubert et al. 2014). Under annual burns, the trend of reduced diversity is not limited to these grasslands, but is emerging as a common trend in subtropical and temperate grasslands across the world (Bradstock 2010, Baer et al. 2016, Ward et al. 2020). Mitigation of these extremes in grazing and fire-return intervals will be necessary under global change, where rangeland production demands and associated grazing pressures are expected to continue to increase (Polley et al. 2017).

The multiscale approach we used in this study revealed that the increased support of species at intermediate, 2- and 5-yr fire-return intervals (Figs. 2, 4) was not equal. At larger scales, which included quadrats dispersed over the trial area, an interaction with the turnover component of beta diversity revealed that shorter rather than longer return intervals supported more species (Fig. 6). This increase in species richness and turnover under shorter return intervals was associated with an increase in uncommon forbs (Fig. 6), such as radical prostrate and erect species, the latter being represented by perennial geophytes or nongraminoid monocotyledons (e.g., Iridaceae and various ground orchid species) (Fig. 4). This increase in uncommon forbs was not reflected in the average species richness of plots (Fig. 2), but due to increased forb turnover of unique species assemblages in frequently burned treatments over the

![Pyrodiversity for Grassland Diversity](image-url)
The attempted no-burn treatment with a fire-return interval of 12 yr had a lowered species richness (Fig. 2) due to shading by moribund material (Fig. 4). This shading effect is similar to a North American prairie, where a dominant grass species reduced species diversity. However, shading by this tall Andropogon species occurred under short fire-return intervals, where it was most productive (Collins and Smith 2006). In Drakensberg grasslands, where the decomposition rate of grassy moribund material is slow (Everson et al. 1985; Everson and Everson 2016) and the dominant grasses adapted to frequent burning are relatively short, the effects of shading are more intense under longer fire-return intervals (Fig. 4). The increased beta diversity associated with intense shading under 12-yr fire-return intervals, was not observed in the North American prairie (Collins and Smith 2006). In this study, the increase in beta diversity under longer return intervals is likely due to colonization-extinction dynamics, which we did not explore. Little is known regarding the establishment of colonization-extinction dynamics, which we did not explore. Little is known regarding the establishment of these species that are largely absent from surrounding frequently burned grasslands (Figs. 1, 4), but variation in their presence and filtering of other species by shading increased beta diversity in grassland burned infrequently (Fig. 2).

In order to develop fire regimes to conserve vulnerable forb species and facilitate understanding of trends in plant diversity, results from this study demonstrate the usefulness of our broad plant functional groups. The predicted responses of these functional groups to the associated effects of shading by the grass canopy were strong. For example, the humped response of forbs reflected that of cauline erect forbs, whose richness represented more than 60% of the richness of forb life forms (Fig. 4). With their leaves borne on stems, cauline forbs may grow up through a dense grass canopy associated with intermediate to long fire-return intervals, whereas plants of shorter stature that cannot extend through a sward may be shaded out (Fig. 4; McCuin et al. 2010, Bradstock et al. 2012). The monotonic decrease in grass richness at smaller scales (Figs. 2, 4), a pattern similar to lower-altitude grasslands (Fynn et al. 2004), was also associated with grassland structure. Shorter species were limited by increased aboveground phytomass at longer fire-return intervals (Figs. 2, 4).

Interactions between fire and grazing herbivores and their influence on shading by the grass canopy should also be considered. In particular, the size and number of burned patches on which grazing herbivores concentrate on influences the amount of herbaceous biomass removed (McGranahan et al. 2018). Increased removal of herbaceous biomass due to heavier or more concentrated grazing in smaller burn patches would avoid shading out species of shorter stature, similar to the influence of shortening fire-return intervals (Fig. 4). The negative influence of domestic livestock grazing intensities greater than low, on grasslands with a large number of forb geophyte species, should, however, be noted—the associated trampling and direct removal of plant material under these grazing regimes deplete this grassland diversity (O’Connor et al. 2010, Veldman et al. 2015).

Apart from the shading associated with longer fire-return intervals, some other effects associated with grassland structure, particularly intertuf gap gaps, should be noted. Gaps between grass tusfts, and the amount of phytomass that accumulates over these over time, affects the moisture and temperature of the plant environment. Reduced gap size is also associated with increased root competition with surrounding grasses (Morgan 1997, Bradstock et al. 2012). These effects have been noted to have variable consequences for species, depending on their demographic stage (Morgan 1997), but this knowledge is lacking in Drakensberg grasslands.

The limitations of this study’s pyrodiversity assessment needs to be acknowledged. Similar to most studies, the impact of temporal variation of fire regimes on biodiversity was not measured (He et al. 2019). However, with considerable variation (approximately half the mean fire-return interval over a decade) under short, intermediate, and long fire-return interval treatments implemented for over half a century, turnover has been maintained in grasslands nearby (Gordijn et al. 2018). Contrariwise, the presence of rare species, after nearly four decades of rigorously implemented frequent burn treatments in the Brotherton trial, is noteworthy. Temporal variation in fire-return interval and associated differences in gap sizes may, however, be important for the establishment and persistence of some grassland plant diversity (Morgan 1997).

The validity of our multiscale observations at the Brotherton trial complement and are reinforced by a nearby landscape-scale evaluation of plant diversity (Gordijn et al. 2018). The pattern of response in forb diversity, providing support for the intermediate-disturbance hypothesis (Fig. 4), and strong influence of fire-return interval on plant turnover (Table 1) observed in this study, corresponds with patterns over the larger and more environmentally diverse montane landscape (Gordijn et al. 2018). This study, by controlling for environmental heterogeneity, was able to evaluate the effects of fire treatments clinically.

Compared to the Brotherton fire trial, greater environmental heterogeneity at the landscape scale may temporarily delay the response of plant diversity to fire treatments. In a nearby heterogeneous montane environment, Gordijn et al. (2018) noted a delay of two decades in the expected response of grassland diversity to a similar range of fire treatments. Environmental heterogeneity, apart from positively contributing to biodiversity (Stein et al. 2014), also increases the heterogeneity of fire behavior and related severity, as well as promoting variability in fire spread (Meddens et al. 2018).
Heterogeneity in edaphic properties such as rockiness, soil depth, and fertility (Crous et al. 2013), intrinsic vegetation properties such as structure (Maravalhas and Vasconcelos 2014) and flammability (Cardoso et al. 2018), plus hydrology (Schmidt et al. 2017) are some ecosystem properties that contribute to heterogeneity in fire regimes. For example, phytomass accumulation may be retarded on shallow or rocky soils where soil volume is more limited, thereby influencing available fuel for fires and consequential severity (Crous et al. 2013). The influence of environmental heterogeneity and associated differences in grassland structure would have a significant indirect influence on diversity, similar to the influence of fire return on diversity observed in this study. Specifically, the variable accumulation of phytomass over different substrates, plus interactions with grazing herbivores, would provide habitat for shorter or taller species dependent on their sensitivity to shading (Fig. 4).

The task of rangeland and conservation ecologists and managers of developing and implementing fire regimes with such pyrodiversity is not straightforward. The contribution of abiotic factors that influence environmental heterogeneity would be important to consider for developing appropriate fire regimes. Furthermore, in systems where herbivores contribute significantly to the removal of herbaceous biomass, the spread, number, and size of burn patches are important to consider for concentrating or dispersing the impact of herbivores (McGranahan et al. 2018). Rather than a set regime for plant species richness and beta diversity, the trade-offs of different regimes across scales have to be acknowledged, especially in transformed landscapes, where native grassland patches are fragmented and have reduced spatial extents. Where possible, regimes have to be balanced across the landscape for rare species with demographic bottlenecks. The infrequent occurrence of nongraminoid monocotyledons in this study suggests such a bottleneck, similar to that faced by many other perennial grassland geophytes (Veldman et al. 2015). For rare geophytes in Drakensberg grasslands, large patches of relatively frequently burned grassland are important.

Assemblages adapted to longer, 5-yr fire-return intervals require a relatively smaller proportion of the landscape. The ability of species adapted to infrequent burning (fire-return interval of approximately 12 yr) to colonize inconspicuous, rarely burned patches in this frequently burned landscape suggests that these require an even smaller portion of the grassland landscape to survive. The variation in fire-return interval of a frequently burned grassland should not shift towards fire-return intervals longer than 5 yr for multiple decades to prevent the gradual decrease in vigor, then loss, of rare nongraminoid monocotyledons. The nature of this variation is believed to reflect the historic lightning-driven fire regimes, which would have fluctuated with seasonal, decadal, and longer climate phenomena (Tyson and Lindsey 1992). The adaptation of biodiversity to this variation could be taken advantage of to maintain biodiversity and production requirements where appropriate.

Interactions with these patterns in climate, environmental heterogeneity, herbivory plus the fire regime are therefore expected to have provided the appropriate dynamic breadth of niches for grassland biodiversity to survive over evolutionary time scales. A significant challenge remains for maintaining this grassland biodiversity under rapid global climate changes associated with the Anthropocene (Polley et al. 2017). Careful consideration of pyrodiversity will contribute significantly to maintaining grassland biodiversity plus buffer rangeland production.

**Burn season and species diversity**

The influence of burn season on plant species diversity was generally weak, similar to the observations of McGranahan et al. (2018) for a mesic tallgrass–prairie. The expected negative effect of dormant-season burns on species richness, when lightning occurrence is rare, was absent. Instead, burns during spring, the peak season of lightning frequency, had a weak negative effect on species richness, but this was reduced at larger scales with the accrued uncertainty of spatial variation (Fig. 2). The influence of spring burns was not explained by phenological or other traits (Fig. 5). However, on spring burns, dominant species may be excluding some forbs (Tilman 1981, Bradstock et al. 2012) as suggested by a trend of decreased Shannon’s diversity with a concomitant increase in Simpson’s dominance (Fig. 3).

Although there was no opportunity to assess the influence of summer burns in this study, 91% of the forbs in this study are summer bloomers, for which reason they may be poorly adapted to summer burning. In North American tall grass prairie, where the proportion of summer bloomers was roughly equal to that of dormant flowering species (Howe 1994a, 1994b) found differences in plant assemblages burned in midsummer compared with the dormant season. Therefore, in the Drakensberg, with the increased concentration of flowering in the growing season, frequent summer burning would likely have a strong, deleterious effect on diversity. The inferred poor adaptation of diversity to summer burns aligns with the hypothesized historic lightning-driven fire regimes, where the repeat coverage of summer burns is limited (Komarek 1974, Biordini et al. 1989, Ramos-Neto and Pivello 2000).

The lack of response in forb species richness to dormant-season burns is likely due to the senescence of these species in this season. Therefore, dormant-season burning merely removes their senesced aboveground phytomass without influencing their survival (Figs. 2, 5 [Bredenkamp et al. 2002]). Because of the weak effect of burn season, burning seasons could be alternated to include variation in the fire regime and avoid the dominance of a few graminoid species at the expense of diversity (Fig. 3). The timing of burns could also be manipulated to control resprouting, woody invasive species such as the American bramble *R. cuneifolius* (Fig. 1).
and forest species (Gordijn and Ward 2014) that increase under longer fire-return intervals. For the control of these woody species, scorching of live aboveground phytomass in the early and late growing seasons, to impact carbohydrate reserves and reduce plant vigor should also be considered (Schutz et al. 2011).

Conclusions

Long-term field studies are crucial for identifying the impact of fire regimes on grassland plant diversity, especially in resistant perennial grasslands, where the impacts of fire may only be realized after half a century of treatments (Gordijn et al. 2018). For the remaining patches of protected Drakensberg grassland in a human-transformed landscape, implementation of heterogeneous fire regimes over the long term will prove critical for maintaining diversity. Flexible patch mosaic burning should be used to promote environmental heterogeneity and biodiversity and buffer rangeland production. Monitoring of these fire regimes and herbaceous biomass productivity, the effects of which strongly influence plant diversity, should be done by taking advantage of high-resolution satellite imagery (e.g., Wang et al. [2019]); this should be supplemented by long-term observation of plant communities, so that fire regimes can be adaptively managed under global change.

For application outside of nature preserves or where grazing pressure is greater, consideration of the interactions between grazing and fire regimes would be important. Prolonged heavy grazing should be avoided because sufficient rest from both grazing and fire disturbances is necessary for maintaining grassland health and diversity (O’Connor et al. 2010, Teague et al. 2011). Regarding the effects of fire regimes on grassland functioning across the fire-return interval and burn-season treatments evaluated in this study, soil, water, and nutrient cycling have been shown to function to their potential, only limited by the climate and parent materials (O’Connor et al. 2004, Manson et al. 2007). Observed differences in soil chemistry, nutrient ratios, and infiltration were not large enough to motivate for a shift in grassland management (Manson et al. 2007). Therefore, the recommended pyrodiverse regimes should be considered for securing the persistence of grassland plant diversity into the future.

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Literature Cited

Andersen, A. N., R. R. Ribbons, M. Pettit, and C. L. Parr. 2014. Burning for biodiversity: highly resilient ant communities respond only to strongly contrasting fire regimes in Australia’s seasonal tropics. Journal of Applied Ecology 51:1406–1413.

Archibald, S., A. C. Staver, and S. A. Levin. 2012. Evolution of human-driven fire regimes in Africa. Proceedings of the National Academy of Sciences 109:847–852.

Baer, S. G., J. M. Blair, and S. L. Collins. 2016. Environmental heterogeneity has a weak effect on diversity during community assembly in tallgrass prairie. Ecological Monographs 86:94–106.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Baselga, A., and C. D. L. Orme. 2012. ‘betapart’: an R package for the study of beta diversity. Methods in Ecology and Evolution 3:808–812.

Biondini, M. E., A. A. Steuter, and C. E. Grygier. 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. Vegetatio 85:21–31.

Bond, W. J. 2019. Open ecosystems: ecology and evolution beyond the forest edges. Oxford University Press, Oxford, UK.

Bowman, D. M., G. L. Perry, S. I. Higgins, C. N. Johnson, S. D. Fuhlendorf, and B. P. Murphy. 2016. Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. Philosophical Transactions of the Royal Society B 371:20150169.

Bradstock, R. A. 2010. A biogeographic model of fire regimes in Australia: current and future implications. Global Ecology and Biogeography 19:145–158.

Bradstock, R. A., R. J. Williams, and G. A. Malcolm. 2012. Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world. CSIRO Publishing, Melbourne, Victoria, Australia.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Bredenkamp, G., F. Spada, and E. Kazmierczak. 2002. On the origin of northern and southern hemisphere grasslands. Plant Ecology 163:209–229.

Brockett, B., H. Biggs, and B. W. van Wilgen. 2001. A patch mosaic burning system for conservation areas in southern African savannas. International Journal of Wildland Fire 10:169–183.

Bürkner, P.-C. 2017a. brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80:1–28.

Bürkner, P.-C. 2017b. Advanced Bayesian multilevel modeling with the R package Brms. R Journal 10:1–15.

Carbutt, C. 2019. The Drakensberg Mountain Centre: A necessary revision of southern Africa’s high-elevation centre of plant endemism. South African Journal of Botany 124:508–529.

Carbutt, C., and G. Martindale. 2014. Temperate indigenous grassland gains in South Africa: Lessons being learned in a developing country. Parks 20:101–121.

Cardoso, A. W., I. Oliveras, K. A. Abernethy, K. J. Jeffery, D. Lehmann, J. Edzang Ndong, I. McGregor, C. M. Belcher, W. J. Bond, and Y. S. Malhi. 2018. Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest–savanna transitions. Frontiers in Forests and Global Change 1:1–6.

Collins, S. L., and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87:2058–2067.

Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators
linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Crawley, M. J., A. B. Manry, J. S. Pryke, and D. P. Murphy. 2018. The biodiversity–Pyrodiversity hypothesis: a test with savanna termite assemblages. Journal of Applied Ecology 49:422–430.

Davies, H. F., M. A. McCarthy, W. Rioli, J. Puruntatameri, W. Roberts, C. Kerinauia, V. Kerinauia, K. B. Womatakimi, A. N. Andersen, and B. P. Murphy. 2018. An experimental test of whether pyrodiversity promotes mammal diversity in a northern Australian savanna. Journal of Applied Ecology 55:2124–2134.

Everson, C. S., and T. Everson. 2016. The long-term effects of fire regime on primary production of montane grasslands in South Africa. African Journal of Range & Forage Science 33:33–41.

Everson, T. M., F. Smith, and C. Everson. 1985. Characteristics of fire behaviour in the montane grasslands of Natal. Journal of the Grassland Society of Southern Africa 2:13–21.

Farnsworth, L. M., D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2014. Does pyrodiversity beget alpha, beta or gamma diversity? A case study using reptiles from semi-arid Australia. Diversity and Distributions 20:663–673.

Fleishman, E., R. F. Noss, and B. R. Noon. 2006. Utility and limitations of species richness measures for conservation planning. Ecological Indicators 6:543–553.

Fuhlendorf, S. D., R. W. Fynn, D. A. McGranahan, and D. Twidwell. 2017. Heterogeneity as the basis for rangeland management. Pages 196–196 in D. D. Briske, editor. Range-land systems. Springer, Cham, Switzerland.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Fynn, R. W., C. D. Morris, and T. J. Edwards. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. Applied Vegetation Science 7:1–10.

Fynn, R. W., C. D. Morris, and T. J. Edwards. 2005. Long-term compositional responses of a South African mesic grassland to burning and mowing. Applied Vegetation Science 8:5–12.

Gil-López, M. J., J. G. Segarra-Moragues, and F. Ojeda. 2017. Influence of habitat patchiness on diversity patterns of a habitat specialist plant community. Journal of Vegetation Science 28:436–444.

Gordijn, P. J. 2018. Brotherton higher plant diversity and cover abundance data [Data set]. South African Environmental Observation Network. https://doi.org/10.15493/SAEON.GFW.10000011

Gordijn, P. J., T. M. Everson, and T. G. O’Connor. 2018. Resistance of Drakensberg grasslands to compositional change depends on the influence of fire-return interval and grassland structure on richness and spatial turnover. Perspectives in Plant Ecology, Evolution and Systematics 34:22–36.

Gordijn, P. J., and D. Ward. 2014. Fire can suppress the development of macrophyllous thickets. African Journal of Range & Forage Science 31:147–160.

He, T., and B. B. Lamont. 2018. Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth’s flora. National Science Review 5:237–254.

He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth’s biodiversity. Biological Reviews 94:1983–2010.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432.

Hoeckstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Hortal, J., K. A. Triantis, S. Meiri, E. Thébault, and S. Sfenthourakis. 2009. Island species richness increases with habitat diversity. American Naturalist 174:205–217.

Howe, H. 1994a. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology 8:691–704.

Howe, H. 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. Ecological Applications 4:121–133.

Howe, H. 1995. Succession and fire season in experimental prairie plantings. Ecology 76:1917–1925.

Joubert, L., J. S. Pryke, and M. J. Samways. 2014. Annual burning drives plant communities in remnant grassland ecological networks in an afforested landscape. South African Journal of Botany 92:126–133.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72:367–382.

Kozolziec, E. 1974. Introduction to lighting ecology. Tall Timbers Fire Ecology Conference. Volume 13. Pages 421–427. Tall Timbers Research Station, Tallahassee, Florida, USA.

Kruschke, J. 2014. Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan. Second edition. Academic Press, London, UK.

Mackey, R. L., and D. J. Currie. 2001. The diversity–disturbance relationship: Is it generally strong and peaked? Ecology 82:3479–3492.

Manry, D., and R. Knight. 1986. Lightning density and burning frequency in South African vegetation. Vegetatio 66:67–76.

Manson, A., D. Jewitt, and A. Short. 2007. Effects of season and frequency of burning on soils and landscape functioning in a moist montane grassland. African Journal of Range & Forage Science 24:9–18.

Maravalhas, J., and H. L. Vasconcelos. 2014. Revisiting the pyrodiversity–biodiversity hypothesis: long-term fire regimes and the structure of ant communities in a Neotropical savanna hotspot. Journal of Applied Ecology 51:1661–1668.

McCain, K. N., S. G. Baer, J. M. Blair, and G. W. Wilson. 2010. Invasion of a native grassland by the exotic herbaceous legume Medicago sativa: a biodiversity hot spot. Journal of Applied Ecology 47:959–966.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Second edition. MJM Software, Gleneden Beach, Oregon, USA.

McGranahan, D. A., T. J. Hovick, R. D. Elmore, D. M. Engle, and S. D. Fuhlendorf. 2018. Moderate patchiness optimizes heterogeneity, stability, and beta diversity in mesic grassland. Ecology and Evolution 8:5008–5015.

Meddens, A. J., C. A. Krawchuk. 2018. Fire refugia: What are they, and forage science? A brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Mackey, R. L., and D. J. Currie. 2001. The diversity–disturbance relationship: Is it generally strong and peaked? Ecology 82:3479–3492.

Manson, A., D. Jewitt, and A. Short. 2007. Effects of season and frequency of burning on soils and landscape functioning in a moist montane grassland. African Journal of Range & Forage Science 24:9–18.

Maravalhas, J., and H. L. Vasconcelos. 2014. Revisiting the pyrodiversity–biodiversity hypothesis: long-term fire regimes and the structure of ant communities in a Neotropical savanna hotspot. Journal of Applied Ecology 51:1661–1668.

McCain, K. N., S. G. Baer, J. M. Blair, and G. W. Wilson. 2010. Dominant grasses suppress local diversity in restored tall-grass prairie. Restoration Ecology 18:40–49.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Second edition. MJM Software, Gleneden Beach, Oregon, USA.

McGranahan, D. A., T. J. Hovick, R. D. Elmore, D. M. Engle, and S. D. Fuhlendorf. 2018. Moderate patchiness optimizes heterogeneity, stability, and beta diversity in mesic grassland. Ecology and Evolution 8:5008–5015.

Meddens, A. J., C. A. Krawchuk. 2018. Fire refugia: What are they, and why do they matter for global change? BioScience 68:944–954.
Morgan, J. W. 1997. The effect of grassland gap size on establishment, growth and flowering of the endangered Rutidosis leptorrhynchoidea (Asteraceae). Journal of Applied ecology 34:566–576.

Morgan, J. W., and I. D. Lunt. 1999. Effects of time-since-fire on the successional dynamics of a dominant grass (Themeda triandra) in a temperate Australian grassland. Biological Conservation 88:379–386.

Mucina, L., et al. 2006. Grassland biome. Pages 350–373 in M. Rutherford, editors. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia, Pretoria, South Africa.

Nänni, U. W. 1969. Veld management in the Natal Drakensberg. South African Forestry Journal 68:5–15.

O’Connor, T. G., P. Kuyler, K. Kirkman, and B. Corcoran. 2010. Which grazing management practices are most appropriate for maintaining biodiversity in South African grassland? African Journal of Range & Forage Science 27:67–76.

O’Connor, T. G., R. Uys, and A. Mills. 2004. Ecological effects of fire-breaks in the montane grasslands of the southern Drakensberg, South Africa. African Journal of Range and Forage Science 21:1–9.

Oksanen, J., et al. 2019. vegan: community ecology package. R package version 2.5-6. https://CRAN.R-project.org/packages/vegan

Parr, C. L., and A. N. Andersen. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20:1610–1619.

Parr, C. L., C. E. Lehmann, W. J. Bond, W. A. Hoffmann, and A. N. Andersen. 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. Trends in Ecology & Evolution 29:205–213.

Pausas, J. G., and J. E. Keeley. 2009. A burning story: the role of fire in the history of life. BioScience 59:593–601.

Pickett, S. T., and P. S. White. 2013. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.

Polley, H. W., D. W. Bailey, R. S. Nowak, and M. Stafford-Smith. 2017. Ecological consequences of climate change on rangelands. Pages 229–260 in D. Briske, editor. Rangeland systems: processes, management and challenges. Springer International Publishing, Cham, Switzerland.

Pooley, E. 2003. Mountain flowers: a field guide to the flora of the Drakensberg and Lesotho. Natal Flora Publications Trust, Durban, South Africa.

R Development Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ramos-Neto, M. B., and V. R. Pivello. 2000. Lightning fires in a Brazilian savanna national park: rethinking management strategies. Environmental Management 26:675–684.

Reichman, O., and J. Jarvis. 1989. The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. Journal of Mammalogy 70:763–771.

Reichman, O., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology & Evolution 17:44–49.

Rowe-Rowe, D., and J. Scotcher. 1986. Ecological carrying capacity of the Natal Drakensberg for wild ungulates. South African Journal of Wildlife Research 16:12–16.

Schmidt, I. B., A. Fidelis, H. S. Miranda, and T. Ticktin. 2017. How do the wets burn? Fire behavior and intensity in wet grasslands in the Brazilian savanna. Brazilian Journal of Botany 40:167–175.

Schulze, R. 1976. On the application of trend surfaces of precipitation to mountainous areas. Water SA 2:110–118.

Schutz, A. E., W. J. Bond, and M. D. Cramer. 2011. Defoliation depletes the carbohydrates reserves of resprouting Acacia sappings in an African savanna. Plant Ecology 212:2047–2055.

Scotcher, J., and J. Clarke. 1981. Effects of certain burning treatments on veld condition in Giant’s Castle Game Reserve. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 16:121–127.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Teague, W., S. Dowhower, S. Baker, N. Haile, P. DeLaune, and D. Conover. 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agriculture, Ecosystems & Environment 141:310–322.

The Plant List. 2013. Version 1.1. http://www.thepantlist.org/

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–815.

Tingley, M. W., V. Ruiz-Gutiérrez, R. L. Wilkerson, C. A. Howell, and R. B. Siegel. 2016. Pyrodiversity promotes avian diversity over the decade following forest fire. Proceedings of the Royal Society B 283:1–9.

Turner, W. R., and E. Tjørve. 2005. Scale-dependence in species-area relationships. Ecography 28:721–730.

Tyson, P. D., and J. A. Lindesay. 1992. The climate of the last 2000 years in southern Africa. Holocene 2:271–278.

Tyson, P. D., R. A. Preston-Whyte, and R. E. Schulze. 1976. The climate of the Drakensberg. Volume 31. Town and Regional Planning Commission, Pietermaritzburg, South Africa.

Uys, R. 2006. Patterns of plant diversity and their management across South African Rangelands. Thesis. University of Cape Town, Cape Town, South Africa.

Veldman, J. W., et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment 13:154–162.

Wang, J., X. Xiao, R. Bajgain, P. Starks, J. Steiner, R. B. Doughty, and Q. Chang. 2019. Estimating leaf area index and aboveground biomass of grazing pastures using Sentinel-1, Sentinel-2 and Landsat images. ISPRS Journal of Photogrammetry and Remote Sensing 154:189–201.

Ward, D., K. P. Kirkman, Z. Tsvuura, C. Morris, and R. W. Fynn. 2020. Are there common assembly rules for different grasslands? Comparisons of long-term data from a subtropical grassland with temperate grasslands. Journal of Vegetation Science 31:1–12.

Wragg, P. D., T. Mielke, and D. Tilman. 2018. Forbs, grasses, and grassland fire behaviour. Journal of Ecology 106:1983–2001.

Wright, J. B., and A. D. Mazel. 2007. Tracks in a mountain range: exploring the history of the uKhahlamba-Drakensberg. Witwatersrand University Press, Johannesburg, South Africa.

Zelikova, T. J., D. M. Blumenthal, D. G. Williams, L. Souza, D. R. LeCain, J. Morgan, and E. Pendall. 2014. Long-term exposure to elevated CO2 enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie. Proceedings of the National Academy of Sciences 111:15456–15461.
SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2391/full

OPEN RESEARCH

Data (Gordijn 2018) are available from the South African Environmental Observation Network (SAEON) Open Data Platform (ODP): https://doi.org/10.15493/SAEON.GFW.10000011