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RESEARCH ARTICLE

Flora and fire in an old-growth Central African forest-savanna mosaic: a checklist of the Parc National des Plateaux Batéké (Gabon)

Gretchen M. Walters[1,2], Diosdado Nguema[3], Raoul Niangadouma[4]

1 Faculty of Geosciences and the Environment, Institute of Geography and Sustainability, University of Lausanne, Switzerland
2 Department of Anthropology, University College London, United Kingdom
3 Tropic-Forest, BP 4474 Libreville, Gabon
4 Herbier National, Libreville, Gabon

Corresponding author: Gretchen M. Walters (gretchen.walters@unil.ch)

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Abstract

Background and aims – Old-growth savannas in Africa are impacted by fire, have endemic and geoxylic suffrutices, and are understudied. This paper explores the Parc National des Plateaux Batéké (PNPB) in Gabon and the impact of fire on its flora to understand if it is an old-growth savanna. It presents 1) a vascular plant checklist, including endemic species and geoxylic suffrutices and 2) an analysis of the impact of fire on the savanna herbaceous flora, followed by recommendations for fire management to promote plant diversity.
Material and methods – 1,914 botanical collections from 2001–2019 collected by the authors and others were extracted from two herbaria databases in 2021 to create the checklist. The impact of fire was explored through a three season plot-based inventory of plant species (notably forbs and geoxylic suffrutices) in five annually, dry-season burned study areas located at 600 m in elevation. A two-factor ANOVA was conducted across two burn treatments and three season treatments.
Key results – The area has a vascular flora of 615 taxa. Seven species are endemic to the Plateaux Batéké forest-savanna mosaic. Seventeen species are fire-dependent geoxylic suffrutices, attesting to the ancient origins of these savannas. Burning promotes fire-dependent species.
Conclusion – The PNPB aims to create a culturally-adapted fire management plan. The combination of customary fire and fire-adapted species in the savanna creates a unique ancient forest-savanna mosaic in Central Africa that merits protection while recognising the role that the Batéké-Alima people have in shaping and governing this landscape.

Keywords

checklist, Plateaux Batéké, Gabon, fire, forest-savanna mosaic, floristics, Central Africa, national park, ancient grassy biome, old growth savanna, geoxylic suffrutices

INTRODUCTION

In recent years, research on the importance of savanna ecosystems has shown that while major conservation and restoration efforts have focused on forested ecosystems, savannas in some parts of the world have remained understudied and their biodiversity value relatively unknown or undervalued (Veldman et al. 2015a). In many cases, savannas are misunderstood as degraded or deforested ecosystems (Fairhead and Leach 1996), and were at the centre of many colonial era debates about savanna origins, if they were anthropogenic or natural (Pellegrin and Le Testu 1938; Mangenot 1955; Keay 1959; Aubréville 1962; Swift 1996) and how savanna fire policy should favour forest growth (Collin 1951; Perriguey 1951). The use of savanna fire has remained contentious, as fire is often perceived to degrade savannas (Kull 2004; Laris 2004).

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However, recent research on African savannas provides evidence of their ancient origins (Bond 2016). These biomes often have species compositions that are influenced by anthropogenic and natural fire (Maurin et al. 2014; Solofondranohatra et al. 2020; Demichelis et al. 2021). These old-growth savannas, defined as "ancient ecosystems characterized by high herbaceous species richness, high endemism, and unique species compositions" (Veldman et al. 2015a) can be distinguished by the presence of endemic species, geoxylic suffrutices that form underground forests, and/or forbs with underground storage organs or flowering stimulated by fire (Veldman et al. 2015a; Bond and Zaloumis 2016). Geoxylic suffrutices are species with underground, woody stems, owing their structure to regular fires which kill the leaves but not the stems, creating underground forests (White 1976; Maurin et al. 2014). A forb is defined as an herbaceous flowering plant that is not a grass, sedge, or rush (Siebert and Dreber 2019). Savanna species often exhibit fire-related traits such as fire-resistant tree bark, underground storage organs that release leaves post-fire (White 1976; Menaut 1983), and post-fire resprouting (Lamont and Downes 2011). The dominant savanna tree species of the study area, *Hymenocardia acida*, is a post-fire resprouter and its response to fire regimes is explored elsewhere (Walters 2012).

In Central Africa, savanna ecosystems and their floral diversity in relation to fire remain underexplored; studies focus on carbon stocks and biomass (Batsa Mouwembe et al. 2017; Ifo et al. 2018; Nieto-Quintano et al. 2018), forest recovery (Deklerck et al. 2019), or the forest-savanna interface (Cardoso et al. 2018). In general, research on African savanna forb floras in relation to fire constitutes a significant knowledge gap, with most studies focusing on grasses and trees, and dry savannas (Siebert and Dreber 2019). Here, we explore the impact of fire on forbs and geoxylic suffrutices, fostering fire-stimulated flowering (FSF) (Lamont and Downes 2011).

The Plateaux Batéké are covered with a forest-savanna mosaic situated within the Guineo-Congolian centre

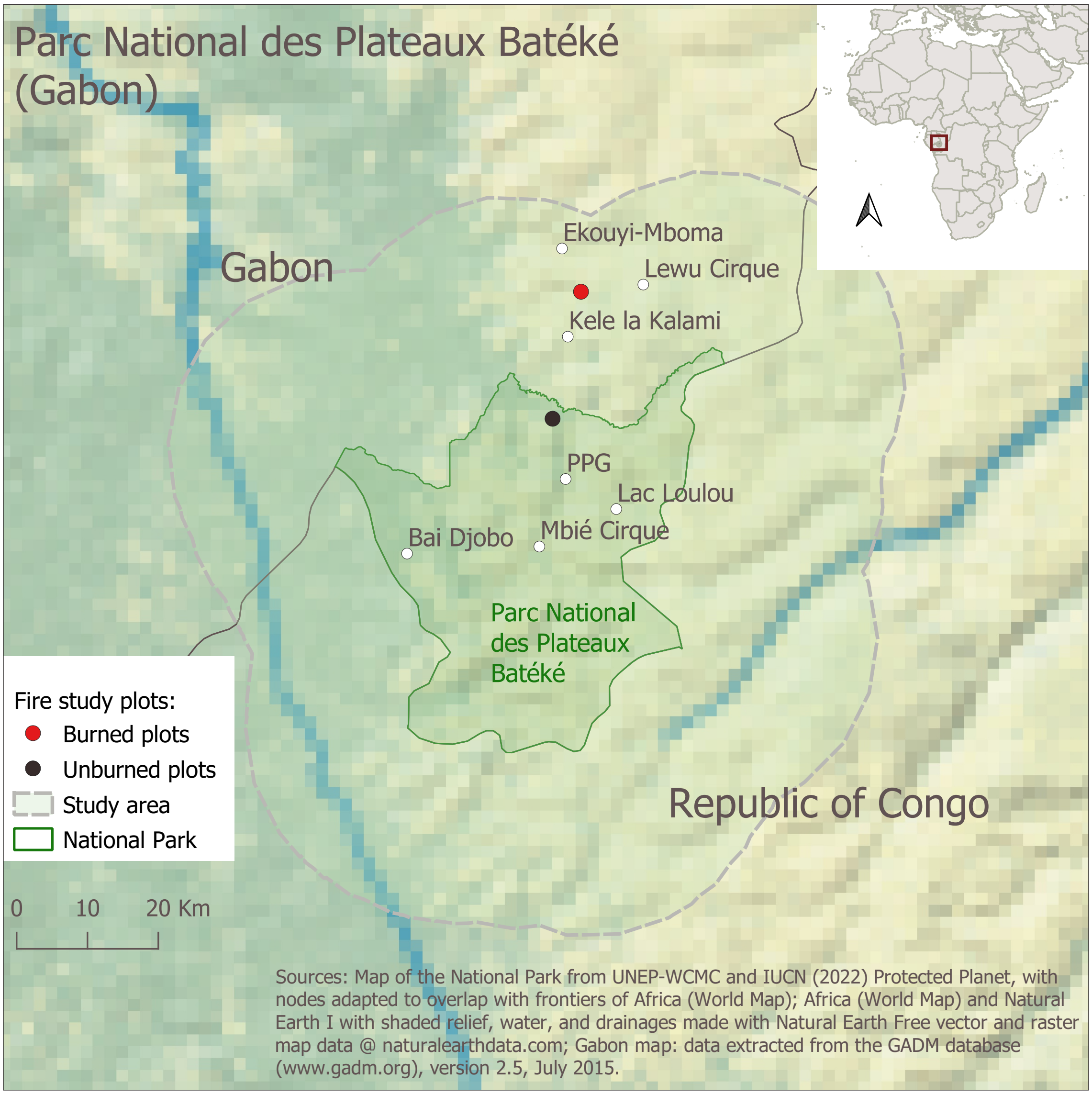

Figure 1. Map of the study area, including the Plateaux Batéké National Park.

of endemism (White 1983) and part of the Guinean savanna flora (Fayolle et al. 2019), stretching 120,000 km^2 from Gabon across the Republic of Congo and into the Democratic Republic of Congo (Dupré and Pinçon 1997). In Gabon, the Plateaux Batéké area comprises the north-eastern portion of these largely Congolese plateaus, straddling the Ogooué and Congo River Basins (Seranne et al. 2008; Flügel et al. 2015). The Parc National des Plateaux Batéké (PNBP) comprises 2,042 km^2 of this area (Fig. 1) and is predominantly covered by savanna (Fig. 2). Rainfall varies from 2,650 mm to 2,890 mm per annum (Walters 2010). A long dry season occurs from June to September, with two short, dry seasons (1–2 weeks each) in January and March. Daytime temperatures range between 24.4–26.8°C (Projet Protection des Gorilles cited in Walters 2010). However, night-time temperatures vary seasonally, being notably colder than daytime temperatures in the dry season.

How old are these savannas? In general, climate fluctuation between arid and moist periods favoured savanna and forest expansion at different times: an arid period favoured savanna formation 40,000–70,000 years BP, followed by a wet period of "forest revival" around 30,000 years BP, followed by an arid period until 18,000 years BP where savanna resurged, followed by a wetter period 3000 years BP (Giresse 1978). The study area is part of the Mega Kalahari, the world's largest sand sea, extending from Gabon and the Republic of Congo to

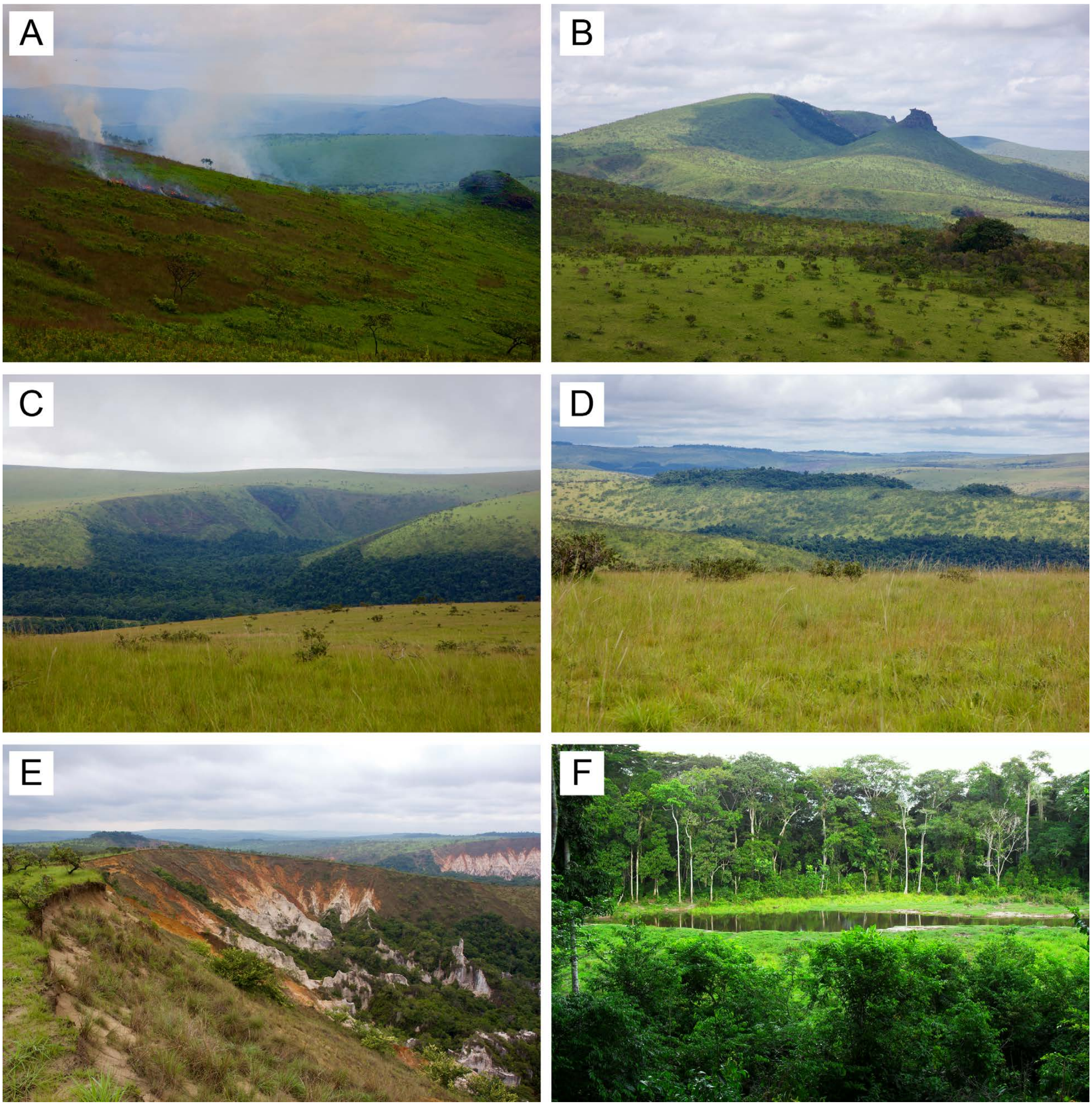

Figure 2. The Plateaux Batéké landscape. **A**. Customary fire in the savanna near Kele la Tsiere. **B**. Kele la Kalami (Mont Kalami), a sacred site and the highest point in the study site at 700 m. **C**. Riparian forest. **D**. Abandoned village forests within the savanna. **E**. Cirque. **F**. Mopia Bai, from the major forest block. All photos were taken by Gretchen Walters.

South Africa, with sand-depth being at times greater than 300 m (Thomas and Shaw 1991; Haddon 2000). Dune formation occurred several times between 115,000 and 16,000 years BP (Stokes et al. 1997). The plateaus are composed of two sand layers including aeolian deposits from the Tertiary period from the Kalahari Desert and a second layer of ochre sands (Peyrot 1991). The sands have both Aeolian and fluvial origins (Giresse 2005).

Although our study does not aim to date the study site savannas of the Plateaux Batéké, other studies have made several estimations from different sites across the plateaus. In the colonial era, the Plateaux Batéké savannas, like elsewhere in Africa, were thought to be of anthropogenic origin (Aubréville 1949). In Frank White's map of African vegetation, the Guineo-Congolian centre of endemism (White 1983) termed grasslands within this area as "secondary", though considered some small patches to be edaphic. White describes these secondary grasslands as areas that were once forest, then were destroyed by cultivation and hunting fires and now contain fire-resistant trees. Although some researchers in their wider work on past vegetation in the Congo Basin classify the Plateaux Batéké as a "mosaic of rain forest and secondary savanna" yet without study sites in the plateaus (Lebamba et al. 2009), other paleoclimatic studies from the plateaus suggest ancient origins, providing a variety of ages for these savannas based on evidence from different disciplines and from different sites. In the northern plateaus, from 40,000 to 12,000 years BP, based on the analysis of plant fragments in the soil, the forest-savanna mosaic continued to be present despite climatic variation (Dechamps et al. 1988). From the southern plateaus, based on pollen cores, a history of 24,000 years confirms fluctuations with the most recent phase favouring grasslands over the past 3,000 years (Elenga et al. 1994). From lake cores studied throughout Central Africa climatic fluctuations occurred around 2,500 years BP (Giresse et al. 2020), including in the Ngamakala lake in the southern plateaus, where over 10,000 years, forest swamps alternate with savanna swamps, with the current forest swamp phase dating from 930 years BP. In another palynological study from the southern plateaus, over a 2,000-year period, forest transitions to the present-day savanna due to a mixture of drought and fire (Aleman et al. 2019). In a synthetic study across six sites in Central Africa, including Bilanko and Ngamaka in the Plateaux Batéké, 4,000 years BP, all sites experienced a drought, but reacted differently (Vincens et al. 1999) with the two Batéké sites transitioning from woodlands to grassland (Schwartz et al. 1995). The different responses were thought to be driven by local climatic or edaphic conditions (Vincens et al. 1999). In the Bilanko site, 11,000 years BP, an afro-mountainous vegetation was dominant suggesting a much colder climate at that time (Elenga and Vincens 1990). Overall, in the Plateaux Batéké, the savannas of today are thought to be stable since 3,000 years BP (Schwartz et al. 2000), but prior to that, climatic fluctuations in different parts of the plateaus favoured savanna and forest at different times.

No similar studies have been conducted in the Gabonese portion of the plateaus including in the study area and therefore it cannot be confirmed if similar vegetation responses to climate are found there. However, a alternative way to understand if these savannas are ancient is through their vegetation composition. Ancient and old-growth savannas comprise species communities, which require centuries to assemble (Veldman et al. 2015a), including the presence of geoxylic suffrutices. Recent work based on botanical data classifies the Plateaux Batéké as "bistable forest" where rainfall favours forest, and where "other factors" favour the current savanna vegetation (Aleman et al. 2020). Another study classifies the Plateaux Batéké savannas as "unstable", where rainfall favours forest cover, yet fire helps structure the savanna, and in particular its wooded savannas typical of the Kalahari sands (Sankaran et al. 2005). These sands are edaphic factors that likely favoured savanna formation earlier than other areas under the same climate in Central Africa (Schwartz et al. 2000).

Across Gabon, the savannas are of different ages and typically of climatic origin, originating during cooler periods when savannas were expanding. While those of the Plateaux Batéké are estimated to have first formed 30,000 to 70,000 years BP (Schwartz 1988a), other savannas are younger. The savannas in the Mouila-Ndende area are thought to have been present 20,000 years BP, then converted to forest, only to reappear 6,000 years BP (Schwartz and Lanfranchi 1991). Those of Lopé and Mouila-Ndendé likely reformed about 2,500 years BP during a dry climatic period (de Foresta 1990; Maley et al. 2018), but those of Lopé could be as old as 9,000 years (Bremond et al. 2021). Coastal savannas of Gabon originated approximately 3,000 years ago; these are being colonised by *Aucoumea klaineana* and *Sacoglottis gabonensis* over large areas (Delègue et al. 2001). The littoral savannas situated directly behind the beach are also in part formed by changing sea levels, with former beaches now located just inland in long dunes, parallel to the sea (Giresse and Kouyoumontzakis 1990).

Beyond climate, fire is an important factor shaping savannas. Anthropogenic savanna fires in the Plateaux Batéké have occurred since at least 2,100 years BP (Schwartz 1988b), with lightning fires having occurred for much longer. However, evidence of earlier occupation dates to 2,500 years BP in the wider Haut Ogooué province, based on metal-working and plantation burning (Clist 1995). Early large-scale Bantu migrations into the Plateaux Batéké ended around 1,000 AD; smaller migrations continued, influenced by politics and natural resources (Vansina 1990; Dupré and Pinçon 1997). The first written accounts of the Batéké come from Portuguese traders in the 1500s (Pigafetta and Lopes 1883). The Batéké-Alima people who currently live in these savannas have occupied them for hundreds of years, with their cultural practices shaping the present day savanna and forest landscape (Papy 1949; Walters 2012). They moved into the area now called the PNPB in the 1840s (Lotte 1953; Dupré and Pinçon 1997). This area became the site of old villages with areas governed by supreme land chiefs, who used fire largely for communal hunting in the long dry season (Walters et al. 2014). The area was and continues to be governed by family lineages (Ebouli 2001; Walters et al. 2015, 2021). The PNPB was created in 2003 (Quammen 2003), and removed most access to customary hunting and gathering grounds; some of the savannas in the PNPB are still considered to be under the customary authority of present-day land chiefs (Gami 2003; Walters 2010). In the study area, grazing by buffalo and smaller browsers occurs. Domestic animals, largely goats, are only kept near the villages.

Although fire and vegetation studies have been the object of many long-term experiments in Africa, dating from colonial times (Collin 1951; Aubréville 1953; Ramsay and Rose-Innes 1963; Louppe et al. 1995), these largely address the woody component of the savanna, given the interest in understanding if and how fire effected the forest edge, which then informed (often erroneously) fire suppression policies (Laris 2004; Laris and Wardell 2006). However, most of these studies did not look at forb diversity, a part of the vegetation typically neglected in savanna studies (Siebert and Dreber 2019). Studies on savanna forb diversity and its relationship to fire are limited; this is perhaps due to a lack of plant surveys or lack of data collection in all seasons, particularly post-fire when many forbs emerge (Bond and Parr 2010). Although fire has been shown to structure the savanna woody vegetation including recurrent fires creating cooler fire regimes which favour increased tree growth (Walters 2012), and the savanna flora is different from other Gabonese savannas (Walters et al. 2012), fire's relation to the floral diversity remains unstudied. Are the savannas of the Plateaux Batéké an old-growth, ancient grassy biome? We seek to understand the role of fire in shaping the plant diversity of the Plateaux Batéké. Until the year 2000, this area had been largely uncollected by botanists (Sosef et al. 2006) and its flora was understudied. Fire is a key factor influencing vegetation, maintaining its open habitat, and the dominant, fire-dependent tree species, *Hymenocardia acida* (Walters 2012) but how does it influence floristic diversity? To understand the relationship of fire and flora, we first present a vascular plant checklist of the area to identify endemic species and geoxylic suffrutices which are indicators of old-growth savannas, we then study the impact of fire and season on a subset of the savanna herbaceous flora. We finish with some recommendations for fire management to promote plant diversity, and suggestions related to the current plans to expand the park.

MATERIAL AND METHODS

The study area comprises the PNPB and a buffer zone of 25 km. This wider zone was included for two reasons: 1) to include botanical collections that had been made in similar habitats, but outside the park, and 2) for the fire study to have access to areas that were regularly burned and accessible to compare with the single area from the park which had not burned for three years. This area was located close to park camps, discouraging the presence of hunters that typically light fires elsewhere in the park, and so the area remained unburned at the time of the study.

Checklist

Botanical specimens have been collected from the PNPB area since 2001 by a variety of collectors, and they are most notably deposited in LBV, MO, and WAG (herbarium acronyms follow Thiers continuously updated). Although the area was traversed by several Europeans during the colonial era, who provided vegetation descriptions and descriptions of fire use in the 1800s (de Brazza 1887; Guiral 1889; de Chavannes 1935), botanical collections from these trips appear to be more localised around cities outside the study area (e.g. Baudon 1929). Botanical collections in Africa were first made from the coasts and rivers starting in the 1780s; the nearby Franceville area was collected by Le Testu late in his career (Raynal 1968). However, some interior areas, including the Plateaux Batéké, have only recently been studied (Sosef et al. 2017), notably by the authors of this paper. Other parts of the Republic of Congo were collected in the 1950–1970s, especially for studying savanna ecology, but these works often did not list their specimens (e.g. Koechlin 1961) and many of their specimens are missing from databases.

The majority of plant collections were identified at BR, LBV, MO, and the National Herbarium of the Netherlands (NHN), and registered in the databases at LBV, MO, and WAG. Database records were obtained in 2016 from the MO and WAG databases and again from MO in 2021 for the area comprising PNPB and including a 25 km limit of the Park. There were no specimens from the Republic of Congo in the circumscribed area. This represented 1,921 collections that have been collected in all seasons, from 2001 to 2019, in part due to residential collection (by the first author) from 2006 to 2008.

Endemic species were determined by their classification in the Checklist of Gabon (Sosef et al. 2006), and research in the botanical literature to understand their distributions, notably in recent treatments of the Flore du Gabon and recent species descriptions.

Collection density was analysed by importing all collection coordinates, where reported, into QGIS v.3.16.4 (QGIS Development Team 2021). A 2.0 km^2 grid was overlaid on the study area, a size that provides a minimum amount of collections per area to be informative; collections densities were given corresponding colours for the following number of specimens per grid: 1–9; 10–26; 27–55; 56–107; 108–238; and 239–379.

Fire and flora

A subset of the savanna flora from the checklist was studied to understand the impact of fire on forb diversity and geoxylic suffrutices, based on the 183 savanna species from a previous study derived from the study area data set (Walters et al. 2012). Our study focused on annually, dry-season burned areas outside the PNPB and comparing it to an area that had not been burned for three years inside the PNPB. Savannas are generally annually burned by local people (Walters 2015); to find an unburned control area, only a single area in the PNPB was available. Three years was the maximum possible time that could be identified for areas that had not been recently burned, in consultation with local people, local resident conservation staff, and Firemapper (University of Maryland 2006), which indicated that the area had last burned in 2004 (three years prior to the field study). In the burned plots, outside of the park, the study areas were burned by local hunters every dry season (June–September). Fire typically stimulates flowering within two years (Lamont and Downes 2011), making this comparison feasible of annually burned versus an area not burned in three years. However, a longer period of no burning would have been preferable.

In each area, five hilltop sites at approximately 600 m in elevation were selected and revisited each season for one year. There is variation in sand type by stratigraphy (Koechlin 1957; Schwartz 1990) and rainfall between hilltops and valleys (Mpounza and Samba-Kimbata 1990; Walters 2010). Hilltop sites were selected to control for these differences. To understand the differences in forb diversity and geoxylic suffrutices in burned and unburned areas, a method sensitive to changes in herbaceous communities was used (Barnett and Stohlgren 2003; see Supplementary file 3). In each of the sites, in each season, plots were selected using a random walk method. Sites were not permanent and each season were established in the same hilltop areas. A random azimuth was ascertained and then followed a random number of steps. In each site, three circular plots of a radius of 7.32 m were established (measurements converted from feet to meters). Each plot consisted of three sub-plots measuring 1 m^2 each and placed at 4.57 m from the centre point at 30°, 150°, and 270°. In each subplot, the percentage of cover per species of forb and geoxylic suffrutex was recorded, and percentage cover by grasses and sedges (all species mixed for these two categories). Finally, all forbs and woody species unrecorded in the three subplots but found in the circular plot were listed. In this study, only the presence of forbs and geoxylic suffrutices was used from the data set. This was done because the focus of this part of the study was to understand how fire influences forb diversity specifically, since forbs, in savanna studies are understudied, and often lumped together, making their contribution to biodiversity or link to management difficult to ascertain (Siebert and Dreber 2019).

Species numbers from the three subplots were grouped together into a single cumulative plot; this became the unit for comparison. Each treatment (burned, unburned) was visited in the long-dry (July 2007), mid-rainy (December 2007), and late-rainy (April 2008) seasons producing two sets of data (burned and unburned sites) across three seasons. Thus, for each of the three seasons, 30 plots could be compared; for each burn treatment, 45 plots could be compared. A total of 90 plots were available for comparison (Table 1).

Normality of the distribution of species per treatment was tested by calculating the mean and standard deviation per treatment and then determining if 70% of the values fell within this range (Fowler et al. 1998). Variances were homogenous according to both Levene's and Bartlett's tests. A two-factor ANOVA was conducted using Systat v.12.0 (Systat Software Inc. 2007), with two burn treatments (annual and no-burn) and three season treatments (dry, mid-rainy, and late-rainy seasons). Each treatment contained five hilltop blocks, each containing 15 plots for a total of 45 plots (with 44 degrees of freedom per treatment-season). Post-hoc Tukey's tests were conducted amongst the seasons. Species diversity based on individual species was compared using the Jaccard Similarity Index on species lists by season and by burn treatment. The Jaccard Similarity Index is computed as follows:

$$s_{i,j} = \frac{c}{a+b+c}$$

Where c is the number of species in common, a is the number of species only occurring in treatment i and b is the number of species only occurring in treatment j (Gotelli and Ellison 2004).

RESULTS

Checklist

The checklist is the first published checklist of the PNPB and comprises 612 species (615 taxa), representing 105 families (Supplementary file 1). Fabaceae, Rubiaceae, and Poaceae are the top three families, with the top ten families representing 55% of all species (Table 2). The top nine genera comprise *Cyperus*, *Psychotria*, *Campylospermum*, *Vigna*, *Landolphia*, *Dalbergia*, *Vernonia*, *Utricularia*, and *Millettia* (Table 3). The most notable finds are the endemic species and geoxylic suffrutices. Seven species are endemic or near endemic to the Plateaux Batéké forest-savanna mosaic: *Asclepias occidentalis*, *Eriosema batekense*, *Memecylon batekeanum*, *Memecylon sitanum*, *Millettia viridiflora*, *Sorindeia batekeensis*, and *Psychotria callensii*. Seventeen geoxylic suffrutices include *Anisophyllea quangensis*, *Chamaecrista mimosoides*, *Cryptolepis*

Table 1. Plots by burn treatment and season.

		Season			Total plots per burn treatment
		Long-dry	Mid-rainy	Late-rainy	
Burn treatment	Burned plots	15	15	15	45
	Unburned plots	15	15	15	45
Totals plots per season		30	30	30	90

Table 2. Top ten families from the checklist with number of taxa.

Family	Number of taxa
Fabaceae	83
Rubiaceae	77
Poaceae	40
Cyperaceae	30
Apocynaceae	24
Annonaceae	20
Asteraceae	17
Ochnaceae	17
Euphorbiaceae	14
Melastomataceae	13

Table 3. Top nine genera represented in the checklist, with number of taxa.

Genus	Number of taxa
Cyperus	13
Psychotria	12
Campylospermum	10
Vigna	9
Landolphia	7
Dalbergia	6
Vernonia	6
Utricularia	6
Millettia	6

oblongifolia, *Dolichos subcapitatus*, *Eriosema glomeratum*, *Eriosema laurentii*, *Eriosema pellegrinii*, *Eriosema shirense*, *Glossostelma lisianthoides*, *Ipomoea linosepala*, *Kalaharia schaijesii*, *Landolphia owariensis*, *Macrotyloma biflorum*, *Parinari capensis*, *Vernonia daphnifolia*, *Vernonia guineensis*, and *Vernonia potamophila*.

Four species of the checklist have mostly Congolian distributions but reach the edge of their western-most distribution in the gallery forests of the Plateaux Batéké, as confirmed by recent collections: *Dracaena waltersiae* (Damen et al. 2018), *Dewevrella cochliostema* (Leeuwenberg 1985), *Monodora laurentii* (Couvreur 2008), and *Combretum pellegrinianum* (Jongkind 2021).

Of the 1,914 collections from the data set, 1,897 were able to be mapped, with coordinates. Of these, 70% have been collected within the PNPB, and largely in the northern half, with significant collections around the following localities of the park: the "Débarcadère" in the north, Lac Loulou to the east, the Project Protection des Gorilles main camp and Mbié Cirque in the centre, and Bai Djobo in the western forest. The focus on the northern part of the PNPB is due to the difficulty in access: the park is largely bounded by rivers with no bridges, lacks roads, and must be crossed by foot, quad, or boat. The remaining 30% of the collections were made in the proposed area for PNPB to be extended, including around Ekouyi-Mboma village, due to the resident collection by the first author in that area. Collections also include the Kele la Kalami rock outcrop, Lewou Cirque, and the forb-fire study area (see Fig. 1) and additional collections in the Kessala forest area to the west and Boumango area by other collectors (Fig. 3).

Fire, forbs and geoxylic suffrutex diversity

The forbs and geoxylic suffrutices in this part of the study represent a subset of savanna species in the checklist: 49 hilltop species (see Supplementary file 2), comprising 28% of the overall savanna flora, based on the 183 savanna species from a previous study derived from the study area data set (Walters et al. 2012). When comparing species numbers alone, by season and burn treatment, tested in a two-way ANOVA, only season was significantly different. Neither burning alone nor the interaction between burning and season was significant (Table 4).

When Tukey's HSD was used to determine which seasons were most significant, the dry season differed significantly from both rainy season in terms of species numbers, while the rainy seasons were not significantly different from one another (Table 5). Species unique to the dry season were five, mid-rainy season has one unique species, and the late-rainy season had three.

To understand if burning affects species diversity within the burn treatments, species lists from the 90 plots (see Supplementary file 2) of burn treatments were compared using the Jaccard Similarity Index. The dry season is the most divergent, having only 32% species in common with the other seasons (but 45% for mid-rainy season and 50% for the late-rainy season). However, when species lists were pooled by season alone, the dry and late-rainy season were the most dissimilar, with 36% in common (for 44% for dry-mid rainy; 50% for mid- and late-rainy). Overall, whether considering species or season, the species overlap was always 50% or less.

However, it is insufficient to consider only species numbers and seasons. To understand if some species

Table 4. 2-Way ANOVA results showing that only season was a significant factor in affecting species diversity. An asterisk "*" denotes significance.

Source	Type III SS	d.f.	Mean Squares	F-ratio	p value
BURN	6.533	1	6.533	2.378	0.124
SEASON	34.956	2	17.478	6.361	0.002*
BURN x SEASON	8.956	2	4.478	1.630	0.198
Error	725.422	264	2.748		

Table 5. Tukey's HSD determine which seasons were significantly different from each other in terms of species numbers. Here, the p-values are displayed. An asterisk "*" denotes significance.

	Dry	Mid-Rainy	Late-Rainy
Dry	0.000	–	–
Mid-Rainy	0.036*	0.000	–
Late-Rainy	0.002*	0.584	0.000

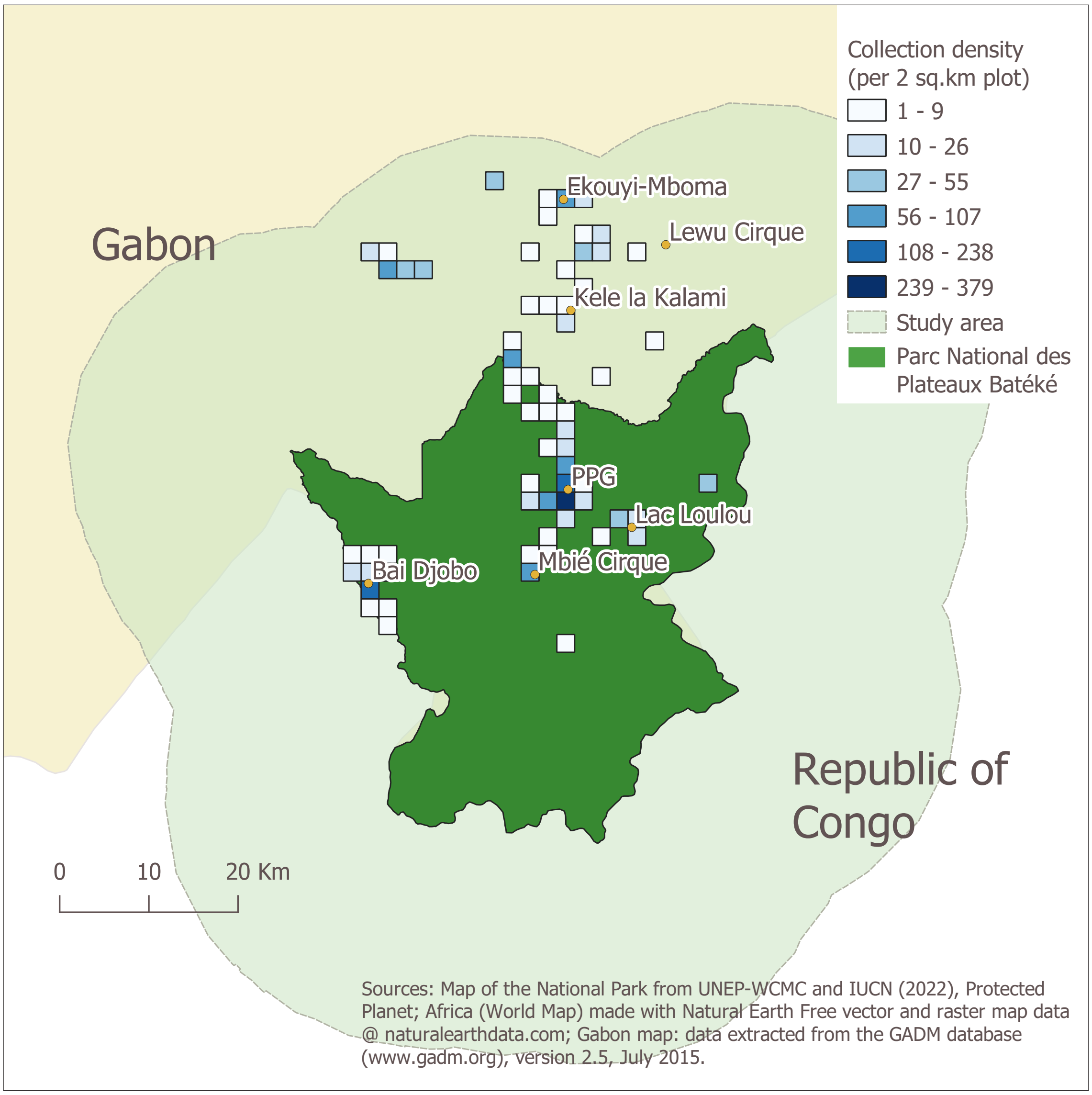

Figure 3. Collection density map of the study area.

Table 6. Species unique to burned plots, with observations on fire-related aspects of species biology.

Family	Species	Observations on fire-dependent species
Apocynaceae	*Glossostelma lisianthoides*	The genus *Glossostelma* has "erect stems coming up after fires from narrow, tuberous, perennial rootstocks…" (Goyder 1995: 528).
Apocynaceae	*Xysmalobium holubii*	Genus noted to comprise "pyrophytic herbs of fire-prone grasslands" (Goyder 2008: 475).
Asparagaceae	*Dipcadi viride*	Bulb (Obone and Sosef 2010: 21). Lifeform likely to emerge after fire.
Asteraceae	*Helichrysum mechowianum* var. *ceres*	Perennial herb. Species noted to be in "regularly burned areas" (Beentje 2000: 361).
Asteraceae	*Vernonia daphnifolia*	Perennial herb with wood rootstock. After fires, the rootstock grows numerous herbaceous stems (Beentje 2021: 128).
Asteraceae	*Vernonia guineensis*	Perennial herb with woody rootstock. Found in burned savannas being the "premier recur" (Beentje 2021: 130).
Asteraceae	*Vernonia potamophila*	Geoxylic suffrutex (Beentje 2021: 133).
Caryophyllaceae	*Polycarpaea eriantha*	Although found in fire-prone habitats, information related to fire was not found.
Fabaceae	*Eriosema glomeratum*	Geoxylic suffrutex. Flowering after fire (van der Maesen and Sosef 2016: 181).
Fabaceae	*Eriosema pellegrini*	Geophytic herb (van der Maesen and Sosef 2016: 183). Although found in fire-prone habitats, information related to fire was not found.
Fabaceae	*Eriosema shirense*	Herb with woody rootstock (van der Maesen and Sosef 2016: 186).
Fabaceae	*Macrotyloma biflorum*	Perennial herb (van der Maesen and Sosef 2016: 242) found in fire-prone habitats.
Fabaceae	*Vigna oblongifolia* var. *oblongifolia*	Annual herb (van der Maesen and Sosef 2016: 372). Although found in fire-prone habitats, the species does not appear to be specifically linked to fire.
Hypoxidaceae	*Curculigo pilosa*	Rhizome. Favoured by fire (Nordal and Iversen 1986: 52). In a fire experiment in Ghana, *C. pilosa* was present in burned and unburned plots, but the presence in burned plots was 10-20 times higher in early and late dry season plots than unburned (Brookman-Amissah et al. 1980).
Lamiaceae	*Kalaharia schaijesii*	Geoxylic suffrutex (Bamps 2013).
Orobanchaceae	*Buchnera paucidentata*	Annual herb, hemiparasitic (Fischer and Ghazanfar 2016: 104). Although found in fire-prone habitats, the species does not appear to be specifically linked to fire.
Orobanchaceae	*Striga asiatica*	Annual herb, hemiparasite (Fischer and Ghazanfar 2016: 126). Although found in fire-prone habitats, the species does not appear to be specifically linked to fire.

were only found in the burned or unburned plots, across the 90 plots, species were compared by burn treatment and season: 17 species are found only in burned areas, representing 35% of the species in the fire study, while three occur only in unburned areas. The dry season has the highest number of unique species, while the late- and the mid-rainy seasons comprise fewer. In order to understand how fire affects these 17 species, the botanical and ecological literature for each species was consulted to understand if the species exhibits Fire Stimulated Flowering (FSF) (Table 6). Several species were present in both burned and unburned plots, in nearly all seasons, including geoxylic suffrutices (e.g. *Anisophyllea quangensis*, *Cryptolepis oblongifolia*, *Chamaecrista mimosoides*, *Kalaharia schaijesii*, *Parinari capensis*) as well as *Dissotis brazzae* and the endemic *Eriosema batekense*.

The results from this part of the study show that while season heavily influences savanna forb diversity, fire is also important in the life cycle of many forbs and geoxylic suffrutices, and that savanna burning promotes forb species.

DISCUSSION

Floristic diversity

This study shows that the floristic diversity, across 615 species, comprises seven endemic species and 17 geoxylic suffrutices, as well as four Congolian species which reach their limits in the study area. Furthermore, the area, though represented by 1,914 collections, shows a collection bias for the northern part of the PNPB.

Previous analysis of the area's flora showed both a strong element of Lower Guinea species (Walters et al. 2006) and a strong affinity with the Congolian flora (Wieringa and Sosef 2011). Although floristic studies of other national parks in Gabon have been conducted, the savanna component is often understudied, with some notable exceptions such as the case of the Parc National de Loango, where a distinct coastal savanna flora was described (Harris et al. 2012). However, when the species lists from Loango, Pongara (Dauby et al. 2008), and Lopé National Parks were combined, distinct savanna floras emerged, showing the coastal sites to be separate from Lopé and the PNPB; of the 183 known species in Plateaux Batéké savannas, the authors noted that 26% were nationally rare according to the Star Rating (Walters et al. 2012).

Eriosema batekense and *Kalaharia schaijesii* have been described in the past decade or so (van der Maesen and Walters 2011; Bamps 2013), and show that within their limited distribution they are very abundant across vast savanna areas (sensu Rabinowitz et al. 1986), demonstrating a previous lack of attention to herbaceous species and the area in general. *Asclepias occidentalis*, a Plateaux Batéké endemic not in the fire plots, and rarely collected, flowers only after burning (Goyder 2009). Other species where fire stimulates flowering could be additionally found in future collections.

New floristic inventories of the proposed park extension (see next section) have recently begun and it is expected that new species and records will be discovered, especially if new areas are visited. This study presents a baseline from which to work. Future botanical work should focus on the forest, especially its riverine forests, but also the under-collected areas of the southern part of the PNPB. Our checklist shows few forest flora endemic species, however, *Memecylon batekeanum* (Stone et al. 2006) forms part of a monophyletic group with *M. amshoffiae* and *M. diluviorum*, a clade from riverine forests in Cameroon, Gabon, and Angola (Cabinda) (Stone 2014), potentially indicating a unique diversity for these habitats. An additional rare species to consider is *Syngonananthus poggeanus* Ruhland, known from the Haut Ogooué, along the Republic of Congo border, from sandy wetlands, and although it is not currently known from the study area, it could be collected there in the future (Phillips 2016: 18).

The interior savannas of Gabon, such as those of PNPB, continue to be explored, with other floristic studies underway around Franceville and Moanda. Those areas are expected to be floristically distinct from the PNBP. For example, from a Haut Ogooué checklist of ferns, largely collected around Franceville, few of the 84 species reported were found in the PNPB (Mundy 2000). Elsewhere in the Kalahari sands savannas, such as in Angola, recent botanical work notes that the flora of the Kalahari sands is particularly underexplored in the Moxico Province (Goyder and Gonçalves 2019). Future botanical work is also planned for similar areas in the Republic of Congo. Further floristic work in these areas should focus on the endemic herbaceous species, geoxylic suffrutices, and the gallery forests.

Given the age of first savanna formation in the Plateaux Batéké of 30,000–70,000 years ago, and a persistence of savanna in many places in the Plateaux area over time, it is not surprising that they contain endemic species and geoxylic suffrutices. However, beyond climatic origins of the savanna habitat and associated flora, anthropogenic factors also contribute to the floristic diversity: people have created village forests or copses, and initiate fire regimes. The Batéké-Alima have long created copses in open savanna (Aubréville 1949: 318). They were created and abandoned over time (Soret 1973; Guillot 1980); however, this stopped with the implementation of the Regroupement policy (or resettlement), which occurred forced villages to "regroup" in larger settlements near roads. The policy was repeatedly implemented from 1910 to the 1960s (Aubame 1947; Sautter 1966; Coquery-Vidrovitch 1972) and was implemented in the study area in the 1950s–1960s (Walters 2010). These copses remain important components of the PNPB landscape, likely maintaining a specific type of diversity, as found in the Parc National de la Lopé, Gabon, where they harbour 16% of the species (Ukizintambara et al. 2007).

Fire and floristic diversity

In this study, beyond maintaining an open, savanna environment and related diversity, fire appears to be important for floristic diversity in two ways: fire fosters the emergence of some species post-fire and it favours some life forms such as geoxylic suffrutices.

Emergence of forbs in burned areas

Our study shows little connection between forb diversity and fire, when explored by species numbers by burn treatments and season. However, even though fire typically stimulates flowering within two years (Lamont and Downes 2011), other studies report several decades being required to see a difference in species diversity (e.g. Uys et al. 2004). However, when explored further, 17 species only appear in burned areas, with several of these having specific links to fire notably as emerging post fire or being geoxylic suffrutices (Table 6). In a study from southern Africa, Madagascar, and Australia, fire-stimulated flowering (FSF) is found to be more common in monocots than in dicots, and spread across 34 families, representing a variety of growth forms (root tubers, rhizomes, rootstocks, corms, caudex, bunchgrass, woody) with fire being either obligate or facultative for FSF; peak flowering may occur after 1–8 months after fire in southern African savannas (Lamont and Downes 2011). This study thus makes a contribution to understanding fire's impact on forbs because it surveyed several seasons, including post-fire, to understand if some species might emerge after burning.

Early studies from the Plateaux Batéké area described the relationship of fire to the flora. Duvigneaud (1949: 9–10) noted that the dry season flora was the most important one, with a flush of bulbs and forbs coming forth post-fire, and mentioned geoxylic suffrutices in relation to fire. Koechlin (1961: 60) agreed, indicating that grasses flowered at the beginning of the year, with dicotyledons flowering in the dry season. This is supported by our results that shows that, like previous studies, the seasonal change of species composition at a given site is striking, with the highest abundance and diversity of forbs in the dry season.

However, the annual fire regimes at the time of these observations were disrupted during the colonial and post-colonial periods. In the 1960s, just after Gabon's independence from France, fire regimes changed from annual, dry season fires, to semi-annual fires, with these latter being more frequent, cooler fires, which can be classified as a "frequent, cool, small" regime, which occur on an annual or semi-annual basis (Archibald et al. 2013), resulting in an increase of the savanna tree density (Walters 2012). The fire regime changed due to a reduction in the control of customary chiefs over fire regimes and changes in state laws, rural exodus, and decreased usage of traditional hunting methods (Walters et al. 2014, 2015). Fire continues to be important for local subsistence for hunting and gathering. Near villages, fires are set throughout the year, as a security measure, to reduce flammable, dry grass near villages and plantations; however, further from villages, in hunting areas, fires are set approximately annually (but sometimes after 9 months) (Walters 2010). Unless fire is explicitly stopped (e.g. through an enforced policy, firebreaks), all parts of the study area are burned at least annually.

In studies in other grasslands in Africa, fire does not consistently affect forb diversity. In South Africa, fire regimes had no effect on forb diversity, although there are distinct fire-tolerant and fire-intolerant floras (Uys et al. 2004). In Ghana, forb diversity was similar for all burn regimes tested, though greatest on protected plots (Brookman-Amissah et al. 1980). In Ethiopian grasslands, no connection was found between fire regime and species composition (Jacobs and Schloeder 2008). Other studies report that diversity was increased only when burning was combined with grazing (Fuhlendorf and Engle 2004; Fynn et al. 2005). In Burkina Faso, herbaceous diversity was not significantly impacted by burning, wood cutting, or grazing, but only became significant when burning was combined with one of the other treatments and even then, was site specific (Savadogo et al. 2008); a similar effect was reported in Benin (Biaou 2009). In South Africa, the only treatments to affect forb diversity were wet season fires, annual burning, and fire exclusion in Kruger National Park (van Wilgen et al. 2007). Given this diversity of impacts, Uys et al. (2004: 490) proposes that site-by-site studies are required.

Presence of geoxylic suffrutices

We report seventeen species as geoxylic suffrutices. The presence of this life form is an indicator that the savannas of the PNPB are old-growth, showing a link between the presence of fire in an ecosystem and its adapted flora (Bond and Zaloumis 2016). These life forms are more common in the Zambesian centre of endemism (White 1976, 1979), sometimes covering extensive areas as in Angola (Revermann et al. 2017). Although frost was suggested as a driver of geoxylic suffrutex speciation (Finckh et al. 2016), fire is the main cause for many species (Lamont et al. 2017; Finckh et al. 2021).

Fire management

In Africa, fire is currently used to achieve a variety of park management goals (Nieman et al. 2021). Plans should be based on the understanding of how species respond to fire and the role of fire in maintaining a landscape (He et al. 2019), factoring in customary fire management (Humphrey et al. 2020). Fire management in Gabon's parks has been conducted in some cases for more than 20 years, as is the case of the Parc National de la Lopé (Jeffery et al. 2014). After the PNPB was established, fire management of the savannas became a park management objective, to conserve the forest-savanna mosaic habitat for key species while recognising the cultural heritage of the Batéké-Alima people (ANPN 2008). However, it is not yet practiced due to its large size and long boundary with the Republic of Congo, making it difficult to control fires. It may be possible to develop a full fire management plan, if staffing and resources are made available (Walters et al. 2010). In order to maintain the savanna, including its edge, as well as the copses (Ukizintambara et al. 2007), fire is required, likely in the late dry season, as was found in the Lopé (Jeffery et al. 2014) and suggested by research on fire and savanna woody structure in the study area (Walters 2012). The results from this study show that fire is important for many plant species, and that savanna burning promotes species diversity not found in unburned areas. If promoting species diversity is an objective the fire management plan, burning should be maintained.

Maps of worldwide forest restoration opportunities have misclassified this area (the entire Plateaux Batéké) as one that should be targeted for tree planting (IUCN 2011), fostering the assumption of savannas as places only for afforestation (Veldman et al. 2015b, 2015c; Fagan 2020), a result of "Biome Awareness Disparity" which favours forests over open habitats for restoration interventions (Silveira et al. 2021). Those interested in the conservation of the old-growth savannas of the Plateaux Batéké should be wary of any intervention that only focuses on trees and avoids any fire management, as suppressing fire would result in the degradation of this old-growth savanna (Veldman et al. 2015b, 2015c) and disregard traditional fire and land management practices.

In order to maintain a diversity of plant species, including high forb diversity and species that are fire-dependent, a patch mosaic approach (Parr and Brockett

1999; Parr and Andersen 2006) is suggested, including burning in the late dry season. This will help manage for a variety of objectives, including the needs of ground-nesting birds (Christy 2008), and maintaining a heterogeneous, patchy savanna (Brockett et al. 2001) environment required for grazing areas and the life cycles of species requiring unburned areas (Walters et al. 2010). The long tradition of burning by the Batéké-Alima people can provide cultural ways of conducting patchy burning over such large areas, and contribute to the park's goal of valuing Batéké cultural heritage (Walters et al. 2014).

Potential extension of the PNPB

In terms of protection, the area under consideration for the extension would extend the PNPB by adding 344,460 acres north of the park. This proposed area contains some areas considered to be sacred including Mopia Bai and Kele la Kalami (Mont Kalami), a rock outcrop. The rocky outcrops of the area occur at higher elevations in the savanna, typically at 600–700 m. Their vegetation is distinct, along with unique bird species (e.g. the African River Martin, *Pseudochelidon eurystomina*) and plant species populations including *Polystachya dendrobiiflora* and *Bidens oligoflora*. The area is under customary management with restricted access and constitutes a type of protection similar to a Territory of Life (ICCA Consortium 2021), that could be recognised by the government of Gabon as a category V or VI protected area (Dudley 2008), a formalised hunting territory (Cornelis et al. 2017) or as an "Other effective area-based conservation measure" (Dudley et al. 2018; Gurney et al. 2021). The customary hunting and gathering territories in the proposed extension could also be recognised under these measures, thus permitting the PNPB to expand while recognising the role of the Batéké people in creating this cultural landscape and their continued governance of some of its resources.

CONCLUSION

The savannas of the PNPB are old-growth savannas as demonstrated by their age, the presence of endemic savanna species, and a fire-dependent flora which includes geoxylic suffrutices. The PNPB aims to develop a culturally-adapted fire management plan; this study provides evidence that burning favours some species which flower post fire, or whose life form depends on fire. The combination of customary fire and land traditions which have created unique habitats, and the presence of fire-adapted savanna species create a cultural landscape in Gabon that merits continued protection while recognising how the Batéké-Alima have shaped and continue to govern this landscape.

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SUPPLEMENTARY FILES

Supplementary file 1

Checklist of the Parc National des Plateaux Batéké and a 25 km buffer zone.
Link: https://doi.org/10.5091.plecevo.85954.supp1

Supplementary file 2

List of forb and geoxylic suffrutices species in the burn experiment.
Link: https://doi.org/10.5091.plecevo.85954.supp2

Supplementary file 3

Plot design for the fire study. Figure adapted from Stohlgren et al. (2002).
Link: https://doi.org/10.5091.plecevo.85954.supp3