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A distinct ecotonal tree community exists at central African forest–savanna transitions

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Abstract

1. Global change is expected to increase savanna woody encroachment as well as fire spreading into forest. Forest–savanna ecotones are the frontier of these processes and can thus either mitigate or enhance the effects of global change. However, the ecology of the forest–savanna ecotone is poorly understood. In this study, we determined whether a distinct ecotonal tree community existed between forest and savanna. We then evaluated whether the ecotonal tree community was more likely to facilitate fire spreading into the forest, woody encroachment of the savanna or the stabilisation of both forest and savanna parts of the landscape.

2. We sampled 28 vegetation transects across forest–savanna ecotones in a central African forest–savanna mosaic. We collected data on the size and species of all established (basal diameter >3 cm) trees in each transect. Split moving window dissimilarity analysis detected the location of borders delineating savanna, ecotone and forest tree communities. We assessed whether the ecotonal tree community was likely to facilitate fire spreading into the forest by burning experimental fires and evaluating shade and grass biomass along the transects. To decide whether the ecotone was likely to facilitate woody encroachment of the savanna, we evaluated if ecotonal tree species were forest pioneers.

3. A compositionally distinct and spatially extensive ecotonal tree community existed between forest and savanna. The ecotonal tree community did not promote fire spreading into forest and instead acted as a fire buffer, shading out flammable grass biomass from the understorey and protecting the forest from 95% of savanna fires. The ecotone helped stabilise the forest–savanna mosaic by allowing the fire-dependant savanna to burn without exposing the fire-sensitive forest to lethal temperatures.

4. The ecotonal tree community was comprised of many forest pioneer species that will promote woody encroachment in the savanna, especially if fire frequency is decreased.

5. *Synthesis*. A distinct fire-buffering ecotonal tree community in this forest–savanna mosaic landscape illustrated that savanna fires are unlikely to compromise forest integrity. Conversely, suppression of fire in this landscape will likely lead to loss of savanna as the ecotone becomes the frontier of woody encroachment. Regular burning is essential for the preservation of this forest–savanna mosaic.

KEYWORDS

alternative stable states, ecological threshold, ecotone, edge effects, fire, forest–savanna mosaic, functional traits, transition

1 | INTRODUCTION

In Africa, forest and savanna cover approximately half of the continent's land surface (11% and 34%, respectively) and provide invaluable ecosystem services at local and global scales to millions of people (Grace et al., 2006; Lewis et al., 2009; Moore et al., 2017; Olsson & Ouattara, 2013; Parr et al., 2014). Global change threatens the provision of these ecosystem services by eroding forest and savanna ecosystem function through changes to the natural fire regime (Heubes et al., 2011; Scheiter et al., 2019; Seddon et al., 2016; Willis et al., 2013; van Nes et al., 2014). When fire-sensitive forests burn more regularly, they are invaded by grasses and become more 'savanna-like', and when fire-dependant savannas burn less regularly they are invaded by trees and become more 'forest-like'. Neither a grass-invaded forest nor a woody-encroached savanna possess the extensive biodiversity or ecological functionality of their intact counterparts (Balch et al., 2008, 2015; Bond & Parr, 2010; Brando et al., 2014; McCleery et al., 2018; Parr et al., 2014; Ratnam et al., 2011; Silvério et al., 2013; Veldman, 2016; Veldman et al., 2015; Veldman & Putz, 2011). The forest–savanna ecotone is the most vulnerable part of each biome. The ecotone is where forest is closest to savanna fires and savanna is closest to a pool of potentially invasive tree species (Aleman & Staver, 2018; Balch et al., 2008; Barlow et al., 2019; Favier, De Namur, et al., 2004). The ecology of the forest–savanna ecotone dictates whether this landscape feature mitigates or enhances the negative effects of global change. The forest–savanna ecotone is therefore a critical, yet poorly understood, component of tropical landscape dynamics.

Ecotones are 'zones of tension' (Odum, 1959) between adjacent communities. In the case of forest–savanna ecotones, this 'tension' arises, to a large extent, from the opposing fire- and light-driven feedbacks that maintain forest and savanna (Hoffmann, Geiger, et al., 2012; Oliveras & Malhi, 2016). The closed canopy of the forest reduces light levels in the understorey, creating a fire suppressing microclimate, shading out flammable grasses, and keeping the forest virtually fire-free (Biddulph & Kellman, 1998; Charles-Dominique et al., 2018; Hennenberg et al., 2008; Hoffmann, Jaconis, et al., 2012). In contrast, the open canopy of the savanna allows ample light to reach the understorey, promoting a drier microclimate, the accumulation of flammable grasses and frequent burning

(Biddulph & Kellman, 1998; Bond & Van Wilgen, 1996; Hoffmann, Jaconis, et al., 2012; Scholes & Archer, 1997). When fire-dependant savannas border fire-sensitive forests, there is a risk that fire burns from the savanna into the forest and destroys the forest's functionality (Balch et al., 2015; Silvério et al., 2013). Conversely, without regular burning savannas become invaded by trees and can no longer provide their full suite of ecosystem services (Parr et al., 2014; Pausas & Bond, 2020; Veldman, 2016; Veldman et al., 2015). For a forest–savanna mosaic to remain stable and not become dominated by only forest or savanna, there must be a mechanism within the forest–savanna ecotone that allows savannas to burn while keeping forests fire-free. We therefore expect the ecotone to experience a distinct fire and light regimes which is intermediate to that of forest and savanna (Charles-Dominique et al., 2018), and we expect a distinct ecotonal tree community to have filled this niche (Odum, 1959). Previous work on forest–savanna ecotones in Africa has noted the presence of potential 'margin specialist tree species' (Abiem et al., 2020; Charles-Dominique et al., 2018; White & Abernethy, 1997) but empirical study, quantitative description and ecological exploration of the hypothetical ecotonal community are lacking.

When the fire- and light-driven stabilising feedback loops that enable forest and savanna coexistence become weakened by anthropogenic global change, both forest and savanna become degraded ecosystems (Brando, Paolucci, et al., 2019; Parr et al., 2014). Forests become drier, more flammable and more likely to transform into grass-invaded systems with increases in temperature, the frequency of drought conditions, deforestation and fragmentation (Balch et al., 2008, 2015; Barlow et al., 2019; Brando et al., 2014; Fonseca et al., 2019; IPCC, 2007; James & Washington, 2013; Silvério et al., 2013; Veldman & Putz, 2011). Conversely, savannas have reduced fire frequency and become invaded by trees as increases in atmospheric carbon dioxide favour the growth of trees over grasses and when changes in local land use and management decrease burned area (Andela et al., 2017; Andela & Van Der Werf, 2014; Bond & Midgley, 2012; Buitenwerf et al., 2012; Durigan & Ratter, 2016; Kgope et al., 2009; Mitchard et al., 2011; Stevens et al., 2016, 2017). The forest–savanna ecotone can increase forest's vulnerability to being burned if it is comprised of tree species whose canopies have a high level of light penetration and allow flammable fine fuel to accumulate at the forest edge (Balch et al., 2015;

Charles-Dominique et al., 2018; Hoffmann, Jaconis, et al., 2012). The forest–savanna ecotone can accelerate savanna woody encroachment if it is comprised of forest pioneer species and acts as a source of new tree recruits into the savanna during periods of fire suppression (Favier, Chave, et al., 2004; Favier, De Namur, et al., 2004; Parr et al., 2012). It is also possible that the forest–savanna ecotone is comprised of species that neither facilitate fire spread into forest nor invade savannas. In this case, the ecotone would mitigate against the negative effects of global change by effectively separating the fire and light regimes of forest and savanna and thus facilitating coexistence by strengthening the resilience of both systems.

Grass invasion and woody encroachment are especially likely to occur in bi-stable landscapes where both forest and savanna are climatically possible ecosystem states (Hirota et al., 2011; Staver et al., 2011). In bi-stable landscapes, the forest savanna ecotone is abrupt, occurring on the scale of a few metres (Bond & Parr, 2010). Forest–savanna mosaics, which cover 10% of Africa (Parr et al., 2014), are the quintessential example of a bi-stable landscape with abrupt ecotones. While some fluctuation in the balance between forest and savanna is expected in mosaics (Aleman et al., 2018; Maley, 2002), current global change has the potential to cause sudden and irreversible state shifts in both forest and savanna (Hirota et al., 2011). This shift is more likely, at least in the medium term, to decrease functional habitat than it is to increase the functional core area of either forest or savanna (Silvério et al., 2013; Veldman et al., 2015). Forest–savanna mosaics are thus the ideal study system for investigating the ecology of the forest–savanna ecotone.

The few available studies on sharp forest–savanna ecotones in bi-stable landscapes have focused on the compositional and functional differences between forest and savanna (Cardoso et al., 2016; Dantas et al., 2013; Hennenberg et al., 2005; Hoffmann, Geiger, et al., 2012), how the forest edge is moving over time (Favier, De Namur, et al., 2004; Ibanez, Munzinger, et al., 2013) or how far the depth of edge influence of one vegetation type (forest or savanna) extends into the other (Hennenberg et al., 2008; Hoffmann, Jaconis, et al., 2012; Ibanez, Hély, et al., 2013). The only studies that explicitly explore the ecotonal tree community usually do so at forest-derived grassland transitions, for example where forest has been cleared for agriculture. These studies usually find the ecotonal tree community to be an ephemeral successional one (Laurance et al., 2006; Oliveira et al., 2004; Peres et al., 2010; Tabarelli et al., 2008) and associated with negative 'edge influence' effects (Harper et al., 2005; Tabarelli et al., 1999). To our knowledge, no similar studies have been undertaken at 'natural' forest–savanna ecotones which persist over long periods of time. One exception is the Cerradão of Brazil, a transitional dry woodland which is distinct from forest and savanna in composition, structure and function (Coelho et al., 2016; Eiten, 1972; Ratter et al., 1996; Ratter & Dargie, 1992; Reis et al., 2017). The Cerradão has been extensively described, however since this ecosystem occurs in large patches across a gradient of transition from forest to savanna rather than in a narrow band at abrupt forest–savanna ecotones in bi-stable landscapes, we differentiate the Cerradão from the ecotonal tree community that is the focus of this study.

In this study, our objective was to assess whether a distinct ecotonal tree community exists between forest and savanna in a bi-stable landscape, and whether this community is likely to reduce or enhance the resilience of the landscape to global change. We sampled 28 vegetation transects across ecotones in a fire-managed forest–savanna mosaic in Lopé National Park, Gabon. Using tree community composition of the savanna, across the ecotone, and into the forest, we first determined whether a distinct ecotonal tree community could be detected between forest and savanna; or if the ecotone was simply a mixture of forest and savanna species that form no distinct community. If a distinct ecotonal tree community could be detected, we then aimed to determine whether the ecotonal tree community was more likely to facilitate (a) woody encroachment of the savanna (i.e. comprised of forest pioneer species), (b) fire spreading into the forest (i.e. comprised of open-canopied species which facilitated the accumulation of grass biomass in the understorey) or (c) neither, thus facilitating stabilisation of the mosaic.

## 2 | MATERIALS AND METHODS

2.1 | Study site

This study was carried out in the northern forest–savanna mosaic of Lopé National Park (LNP), Gabon (0.2S, 11.6E; Figure 1). The mosaic is characterised by an abundance of abrupt ecotones between Lower Guineo-Congolian rainforest (White, 1983) and Middle Ogooué savannas (van de Weghe, 2011; Figure S1). In LNP, mean daily minimum and maximum temperatures were 22 and 28°C in the forest (1984–2018) and 22 and 32°C in the savanna (2002–2018). Mean relative humidity was 98.2% in the forest and 92.7% in the savanna over the same time period (Bush et al., 2019; Tutin et al., 2019). Mean annual rainfall is 1,466 mm (1984–2018), which falls mainly outside of the dry seasons (Bush et al., 2019; Tutin et al., 2019). There is a short (mid-December to mid-February) and a long (mid-June to mid-September) dry season, with controlled fires occurring in the long dry season as part of LNP's conservation plan (Jeffery et al., 2014). Controlled burning has occurred since 1993 but there is evidence that fire has been a feature of the landscape for at least 5,000 years (White, 2001).

2.2 | Vegetation transects

We set up 28 vegetation transects across forest–savanna ecotones. The transects covered a variety of fire frequencies, ranging from the savanna having been burned less than three times in the past 10 years to having been burned up to three times in the past 3 years (Figure 1). The majority of transects were burned between one and three times in the past 3 years, which is considered the optimal fire frequency for a high rainfall African savanna in terms of increasing grass species richness, evenness and diversity (Smith et al., 2013). All transects were at least 100 m apart.
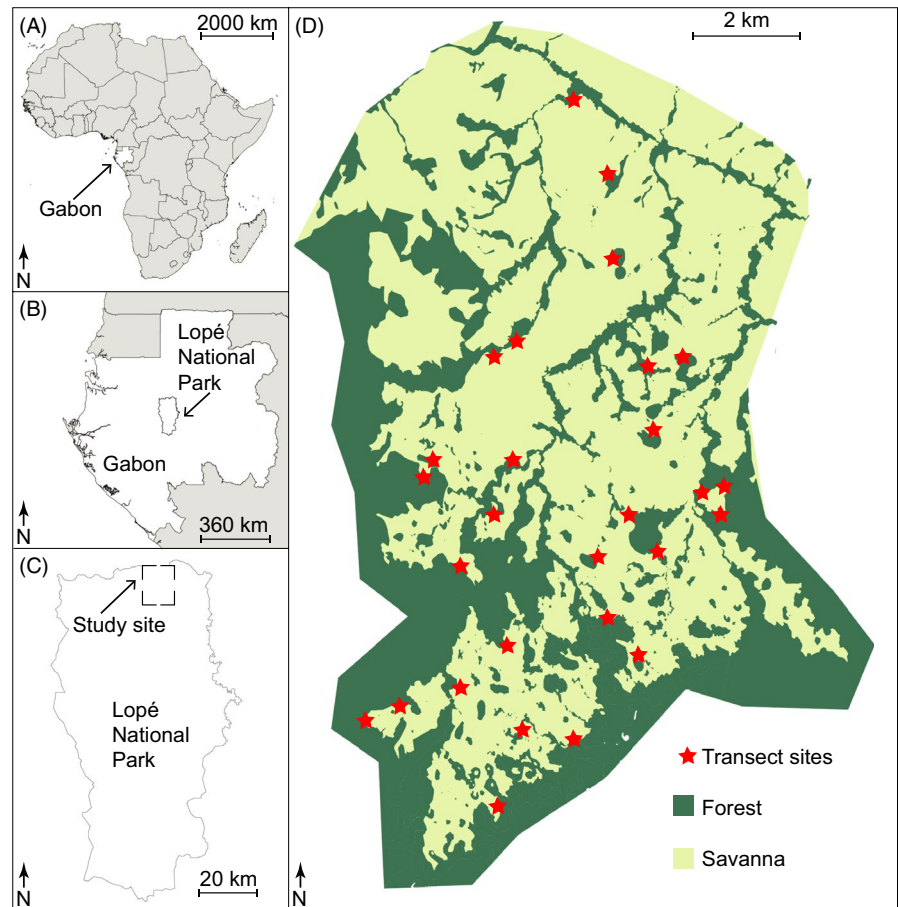
Transects were 2-m wide and varied in length (37–48 m) depending on the sharpness of the ecotone. Transects started by covering 25 m of field-defined savanna, then crossed the entire field-defined ecotone and finally covered 10 m of field-defined forest (Figure S2). Field-defined delineations between savanna, ecotone and forest were used to establish the length of the transect to ensure adequate sampling and were not used in data analyses. In the field, we defined savanna to be where grass cover was continuous, tree canopy cover was discontinuous and visibility at eye level was at least 5 m. The savanna ended and the ecotone began where grass cover became discontinuous and tree canopy cover became continuous. The ecotone was characteristically easy to identify as it was a 'wall of leaves', with visibility at eye level being <5 m and a high level of continuity between the understorey and mid-canopy layers. The ecotone ended and the forest began where the mid-storey became open and visibility increased to more than 5 m, but grass biomass remained low and the tree canopy remained closed. To minimise bias, field-defined vegetation types were delineated based on consensus of at least three researchers.

We sampled transects in adjacent 1-m long blocks, each 2 m wide. In each block, we measured all woody stems with a basal diameter (measured at 10 cm above-ground) >3 cm ('adult stems'), noting their species and basal diameter. Additionally, we measured all woody stems in a nested sampling strip 20 cm wide on the left-hand side of the transect with a basal diameter <3 cm and a height >30 cm ('juvenile stems'), noting their species and basal diameter. All analyses were limited to a focus group of tree and shrub species, hereafter referred to as focus tree species for simplicity, which were those whose adult stems represented 90% of the stems and more than 88% of the basal area sampled across all transects. We tested for spatial autocorrelation of species composition between transect sites using a Mantel test (Sokal & Rohlf, 1995). The Mantel test tested for significant correlation between a Bray–Curtis dissimilarity matrix derived from adult stem counts for each of the focus tree species and a geographical matrix of the distances between transect sites using the nonparametric Spearman correlation method (function *mantel* in R package VEGAN (Oksanen et al., 2019). As the Mantel test was performed on two distance matrices only, our analysis did not violate its assumptions (Guillot & Rousset, 2013; Legendre et al., 2015).

2.3 | Identifying the ecotonal tree community

To assess whether a distinct ecotonal tree community existed between forest and savanna, we looked for evidence of more than one border along the length of the transects. A border is the boundary between two communities at which point the magnitude of change between them is the greatest (Hennenberg et al., 2005). To detect borders between tree communities along the length of the transects,

we used split moving window dissimilarity analysis (SMWDA; Cornelius & Reynolds, 1991; Ludwig & Cornelius, 1987). Using a moving window approach, SMWDA calculated the dissimilarity of adjacent half-windows along a transect and identified borders as locations where significant peaks in dissimilarity occurred (Cornelius & Reynolds, 1991; Ludwig & Cornelius, 1987). Dissimilarities were calculated relative to an expected mean (as determined by a Monte Carlo procedure with 100 replicates), and then normalised (Z-score; Erdős et al., 2014; Hennenberg et al., 2005). Borders along the transect, or significant peaks in dissimilarity, occurred when the Z-score exceeded the one-tailed 95% confidence interval (Z-score > 1.645; Hennenberg et al., 2005). The mean dissimilarity of five half-window sizes (1–5 m) was used to reduce the scale dependency of the results (Cornelius & Reynolds, 1991; Erdős et al., 2014; Hennenberg et al., 2005). The R script upon which our SMWDA was based is published by Erdos et al. (2014).

To determine dissimilarities, we compared squared Euclidean distances calculated using a presence–absence matrix. Presence–absence matrices were produced by merging the transects, since there were too few adult stems in individual transects to detect meaningful differences between tree communities. Merging effectively increased the area, and thus number of stems sampled, in each transect and gave us a better representation of community composition by increasing the probability of sampling rare or large individuals (Staver, 2017). Merging was performed twice to account for the differing lengths of the transects: transects were first aligned at their savanna edge to look for a significant border between savanna and ecotone tree communities, and then they were aligned on their forest edge to look for a significant border between forest and ecotone tree communities (Figure S3). To merge the transects, sampling blocks were numbered sequentially, with block 1 being first in the savanna and then in the forest. Numbered blocks were aligned and merged with one another so that their species composition was a composite of all transects sampled. From this merged transect, a presence–absence matrix was created.

A border will have some length associated with it over which substantial change occurs. Once borders were detected, the length of each border was calculated using moving window regression analysis (MWRA). MWRA calculated the rate of change (i.e. slope) of Z-scores along the transect (Hennenberg et al., 2005; Walker et al., 2003). The slope value for each Z-score was calculated on the Z-score itself and the two Z-scores on either side of it using a moving window approach (Hennenberg et al., 2005; Walker et al., 2003). These slope values were used to verify the location of the borders detected in SMWDA. True borders should be both significant peaks in SMWDA and turning points (slope = 0) in MWRA (Hennenberg et al., 2005). Slope values were also used to determine the length of each border, which was the distance between the maximum and minimum of the slope values either side of the border (Hennenberg et al., 2005; Walker et al., 2003). If two borders were detected and their lengths did not overlap, then three distinct vegetation communities were present. For example, if one border occurred between 25 and 27 m along a transect and a second border occurred between 35

and 37 m along the same transect, then these two borders did not overlap and savanna, ecotone and forest communities were present. Alternatively, if one border occurred between 25 and 35 m and a second border occurred between 27 and 39 m, these two borders overlapped and only one true border was present and separated only two distinct vegetation communities: forest and savanna.

Based on the location and length of the detected borders individual transects were divided into sections of savanna, ecotone and forest. For example, if the border between savanna and ecotone was detected at 25 m along the merged transect, all individual transects were divided into savanna and ecotone at that point. This delineation superseded the field-based delineation of vegetation communities. We then determined whether each of the focus tree species demonstrated a preference for savanna, ecotone or forest by comparing observed and expected frequencies using χ^2 tests (function pchisq in package STATS, R Development Core Team, 2018). Observed frequencies were the counts of each tree species in each vegetation type, and expected frequencies were calculated under the assumption that the stem density of a species was constant across savanna, ecotone and forest parts of the transect. Significant deviation from the expected frequencies was when $p < 0.05$. When χ^2 was significant, we assessed the source of significance by calculating post-hoc the Pearson standardised residual for savanna, ecotone and forest using the formula: $\frac{observed - expected}{\sqrt{expected}}$. A significant residual indicated that the species had a significantly higher than expected density of stems in that vegetation type. Residuals were significant when they were >2.128, and p was adjusted using the Bonferroni correction for multiple comparisons within each species (Sharp, 2015).

2.4 | Investigating the ecology of the forest–savanna ecotone

To determine whether the ecotonal tree community is likely to facilitate woody encroachment of the savanna, we assessed whether it contained forest pioneer species. We considered pioneer species to be those that were a dominant component in colonising and early successional forest types. Colonising forest was where savanna used to occur but fire has been supressed for >20 years and extensive woody encroachment had occurred as a result (Cuni-Sanchez et al., 2016; White, 2001). Tree canopy cover, density and diversity were higher in colonising forest than in savanna, although C4 grasses were still present in the understorey, albeit at a lower biomass than in the savanna (Cuni-Sanchez et al., 2016; White, 2001). Young, or early successional, forest succeeds colonising forest. Young forest encompassed both monodominant forest of *Aucoumea klaineana* in tightly packed even-aged stands, and young Marantaceae forest dominated by *A. klaineana* and *Lophira alata*. Young forest types had a more closed canopy and larger stems than colonising forest, although the dominant species were also present in the colonising forest, specifically *A. klaineana*, *L. alata* and *Sacoglottis gabonensis* (Cuni-Sanchez et al., 2016; White, 2001). The final successional stage sampled was

the 'mature forest', which succeeds young forest (Cuni-Sanchez et al., 2016; White, 2001). Mature forest included mixed mature Marantaceae forest and mature montane forest, both of which had a more closed canopy, larger stems and a higher species diversity than the young forest (Cuni-Sanchez et al., 2016; White, 2001). Increases in tree size, canopy closure and species diversity support that these forest types are successional to one another. The successional classification was supported by the spatial distribution of the forest types within the broader LNP landscape, with younger successional stages occurring closer to the savanna and later successional stages occurring further away, towards the core forest (White, 2001).

We examined tree census data collected in twenty-two 0.08 ha plots in LNP between 2013 and 2017 (original description of plots and sampling methodology can be found in White, 1995). In each census plot, all trees with a diameter at breast height >5 cm had their trunk diameter measured and their species noted. Due to the difference in minimum stem size sampled in the census plots (>5 cm diameter at breast height) and in the transects of this study (>3 cm at 10 cm above-ground level), we compared only stems >5cm from this study to the census plots. However, this still results in slight differences in the minimum cut-off size, and therefore we did not place a strong emphasis on relatively small differences in stem count and basal area.

To assess whether the ecotonal tree community is likely to facilitate regular fire spread into the forest, we estimated how much shade it was casting on the understorey, how much grass biomass was present how often fire spread from the savanna into the ecotone, and whether the structure of the ecotone more closely resembled the forest or the savanna. As a proxy for shading, we estimated canopy leaf area index (LAI, canopy leaf area per unit of ground area), where higher LAI values indicated lower levels of understorey light availability. We calculated canopy LAI from hemispherical photographs taken along the length of each transect (every 5 m in the field-defined savanna and forest and every 1 m in the field-defined ecotone; details available in Cardoso et al., 2018). To estimate grass biomass, we used a disc pasture meter calibrated for the site (details available in Cardoso et al., 2018), taking one reading in each block of each transect. We characterised the fire regime of the ecotone by lighting experimental fires in the savannas of 20 of the 28 transect sites. Fires occurred in July and September 2016 as part of the normal conservation management protocol of LNP (Cardoso et al., 2018; Jeffery et al., 2014). After each fire, we examined the burn scars to determine how far along the length of each transect the fire had burned. From this, we calculated how frequently fire penetrated the ecotone and the forest, relative to the savanna. To assess the structure of the ecotone, we calculated the foliage density index at 0.5, 1, 1.5, 2 and 2.5 m above-ground every 5 m along the transect in the field-defined savanna and forest and every 2.5 m in the field-defined ecotone. The foliage density index is a measure of vegetation density and is calculated as the inverse of the distance at which a white A5 piece of paper is no longer visible to the observer, who is holding their eye at the desired level above-ground (Bond et al., 1980). When vegetation is dense at a certain height above-ground, the foliage density index is higher because the piece of paper becomes obscured by leaves at a closer distance to the observer.

To assess how functionally distinct ecotone tree species were from forest and savanna and to draw additional inferences about ecotone ecology, we measured four key functional traits in each of the focus tree species: relative bark thickness, bark accumulation rate, wood density and leaf mass per area (LMA). Relative bark thickness (mm of bark per mm of trunk diameter) is a measure of a tree's ability to tolerate regular burning, with thicker bark increasing stem insulation from lethal temperatures, and thinner bark increasing the susceptibility of a tree to top-kill during burning (Bova & Dickinson, 2005; Hempson et al., 2014; Hoffmann et al., 2003; Midgley et al., 2011). Bark accumulation rate, or the allometric coefficient of bark, is a measure of the speed of bark production. Rates <1 indicate a disproportionally higher investment in bark at smaller trunk diameters, >1 disproportionally higher at larger trunk diameters, and ≈1 proportional investment in bark with diameter (Jackson et al., 1999). LMA (g/cm^2) and wood density (g of dry wood mass per cm^3 of wood volume) are both indicators of growth rate and longevity, with lower LMA and wood density both associated with pioneer species which have fast growth and shorter life spans (Kunstler et al., 2016; Poorter & Bongers, 2006; Wright et al., 2004).

Bark thickness was measured (using digital callipers) at three locations on one 4 cm^2 sample of bark removed from the trunk at 30 cm above the ground. Relative bark thickness was determined by dividing the median value of the three thickness measurements by the trunk diameter at the point of sampling (Corrêa Scalon et al., 2020; Lawes et al., 2013). Mean relative bark thickness was calculated on at least nine individuals per species. We determined the bark accumulation rate for each species to be equal to the slope of a linear model fitted to bark thickness as a function of trunk diameter (both variables ln transformed; Hoffmann et al., 2003; Jackson et al., 1999; Figure S4). LMA was calculated by scanning leaves (excluding petioles; using desktop scanner Canon LiDE 120) and converting scans to leaf pixel area via post-hoc image analysis in MatLab (v8.0; Blonder, 2015) before dividing this by leaf mass (determined after oven drying at 70°C to constant weight). LMA was determined for each species on a minimum of five mature leaves per tree and three trees per species. Wood density was calculated on three trees per species. For each tree, the mean oven dry mass of three twigs (±1 – 2 cm diameter) was divided by the volume of each twig (after bark was removed; Marthews et al., 2014). All traits were sampled on trees outside of the transects.

3 | RESULTS

In the 28 forest–savanna ecotone transects, 16 tree species comprised more than 90% of the stems and more than 88% of the basal area sampled. These focus tree species were, in order of decreasing abundance (Table S1): *Crossopteryx febrifuga*, *Millettia versicolor*, *Diospyros dendo*, *Ouratea myrioneura*, *Antidesma vogelianum*, *Psychotria vogeliana*, *Barteria fistulosa*, *Cryptosepalum staudtii*, *L. alata*, *Sarcocephalus latifolius*, *Cnestis ferruginea*, *Saccoglottis gabonensis*, *Xylopia aethiopica*, *Diospyros zenkeri*, *Gomphia flava* and *A. klaineana*.

All analyses presented were performed only with these focus tree species. The transect sites were not spatially autocorrelated in terms of species composition (Mantel test, $R = -0.03$, $p = 0.63$).

To assess whether a distinct ecotonal tree community could be detected between savanna and forest, split moving window dissimilarity analysis (SMWDA) and moving window regression analysis (MWRA) were applied to tree community composition data. SMWDA and MWRA detected two significant borders (where Z-score > 1.96 and a turning point exists) along forest–savanna ecotone transects. The lengths of these borders (i.e. the distance between the maximum and minimum MWRA slope value either side of each border) were non-overlapping, indicating that three distinct tree communities were present: savanna, ecotone and forest. The border between the savanna and ecotone was located 27 m along the transects (Figure 2A) and the border between
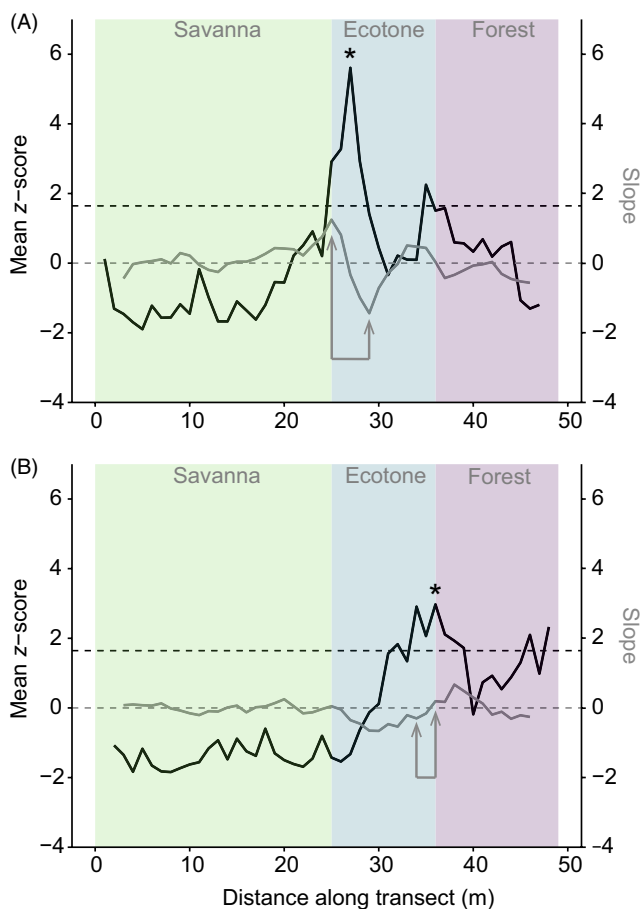
the ecotone and the forest was located 36 m along the transects (Figure 2B). Using the detected border lengths to delineate the tree communities, savanna was found in the first 26 m along the transects, the ecotone from 26 to 36 m, and forest from 36 to 48 m. The ecotone was, on average, 10 m wide. Using the width of the ecotone and geographical information software, we calculated that the ecotone has a length of 339.6 km in the study site, and thus occupies 3.4 km², or 7% of the area occupied by savanna in the study site (Figure S5).

χ^2 tests were used to classify the focal tree species into ecotone, savanna and forest communities. χ^2 tests showed 13 of the 16 focus tree species to have significantly higher than expected densities in either savanna, ecotone or forest sections of the transect (Figure 3; Table S2). The ecotone community comprised 10 tree species: *M. versicolor*, *A. vogelianum*, *P. vogeliana*, *B. fistulosa*, *C. staudtii*, *L. alata*, *C. ferruginea*, *S. gabonensis* and *A. klaineana*. The savanna community comprised one tree species, *C. febrifuga*, while the forest comprised three tree species, *D. dendo*, *D. zenkeri* and *G. flava*. Three species were not able to be classified into any of the three communities: *O. myrioneura*, *X. aethiopica* and *S. latifolius*.

To determine whether the ecotonal tree community was comprised of forest pioneer species, we compared the abundance of each ecotonal tree species in the ecotone section of transects sampled in this study with their abundance in census plots sampled in colonising, young and mature forest types (Figure 4; Table S3). For stems >5 cm diameter, *M. versicolor* was the single most dominant species in the ecotone; however, it was found to contribute negligible proportions (<0.03) to total stem counts and basal area in colonising, young and mature forest types. Similarly, *C. ferruginea*, *P. vogeliana* and *C. staudtii* were also only found to occur only in the ecotone (although *C. ferruginea* did have one stem in the colonising forest plots) types. *A. vogelianum* and *B. fistulosa* were both dominant species in the colonising forest but had low to no presence in young or mature forest plots. The three species contributing the largest proportion to total basal area in the ecotone, *L. alata*, *S. gabonensis* and *A. klaineana* were also dominant species in the colonising forest plots. In fact, *L. alata* contributed nearly a third of all stems and just under 40% of all basal area in the colonising forest while *A. klaineana* was the most dominant species in the young forest, comprising nearly three-quarters of the basal area sampled in these plots. None of the ecotonal tree species dominated in the mature forest, although *L. alata* and *A. klaineana* both contributed a substantial proportion (>0.03) to the total basal area.

All three tree species classified as being part of the forest community in this study contributed proportionally more stems and an approximately equal proportion of basal area to the young and mature forest types as they did to the ecotone, and contributed negligible proportions of stems and basal area to the colonising forest (Figure 4). The tree species classified as being part of the savanna community in this study were absent from young and mature forest, but present in colonising forest.

FIGURE 2 Split Moving Window Dissimilarity Analysis (SMWDA) and Moving Window Regression Analysis (MWRA) for the 28 forest–savanna transition transects. Transects were aligned for the analysis on their savanna side to best detect the border between savanna and ecotone (A) and were aligned on the forest side to best detect the border between ecotone and forest (B). *indicates detected border locations (turning points), ↑ and adjoining lines indicate lengths of borders (maximum and minimum of regression slopes in MWRA). Horizontal dotted lines at $y = 1.645$ and $y = 0$ mark the significance thresholds for SMWDA and turning points in MWRA, respectively. The detected savanna, ecotone and forest tree communities are shown by shaded blocks

FIGURE 3 The mean abundance of each focal tree species along the length of the 28 forest–savanna transition transects. Parts of the line that are solid indicate that the species had significantly higher than expected abundances in that vegetation type (χ^2 p value was significant and residual >2.13). Vegetation types are shown by shaded blocks, savanna is shaded green, ecotone is shaded blue and forest is shaded purple. Species that had significant positive residuals in only one of the three vegetation types were classified into that tree community, with coloured boxes around each species name indicating its community: green boxes are savanna species, blue boxes are ecotonal species, purple boxes are forest species and grey boxes are species which were not classified into any community
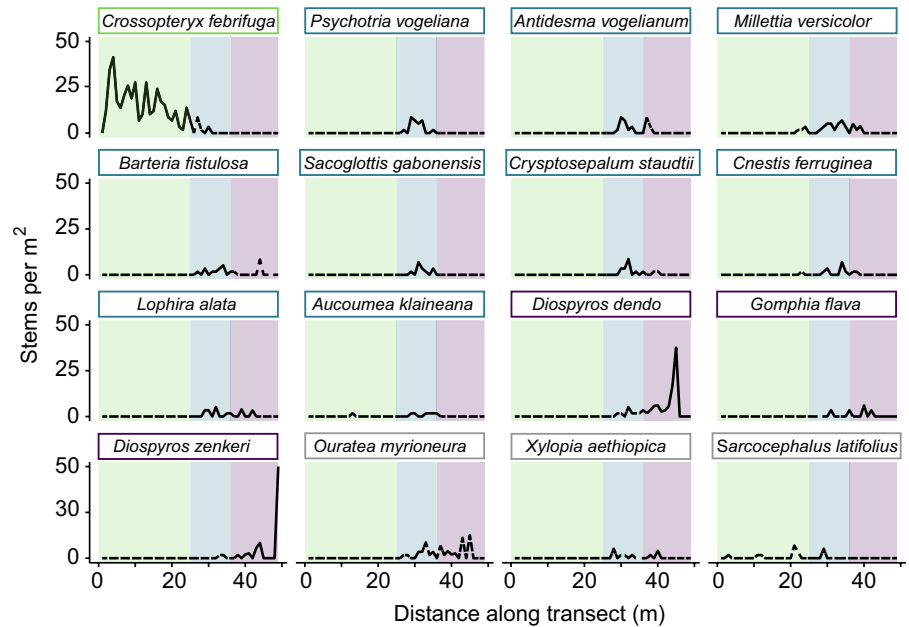

FIGURE 4 The proportion that each of the 16 focal tree species contribute to the (A) sum of basal area and (B) count of stems sampled in each of the forest types. This study sampled 28 forest–savanna transition transects ('ecotone'), while the other forest types ('colonising forest', 'young forest', 'mature forest') were sampled in twenty-two 0.08ha plots by White et al. (L. T. J. White, unpublished). Data are only shown for stems that are >5 cm diameter at the point of measurement (10 cm above the ground for the ecotone, and at breast height for the other three forest types). The pathway for forest expansion into savanna is that fire suppressed savanna becomes colonising forest, which is succeeded by young forest, which is succeeded by mature forest (White, 2001)
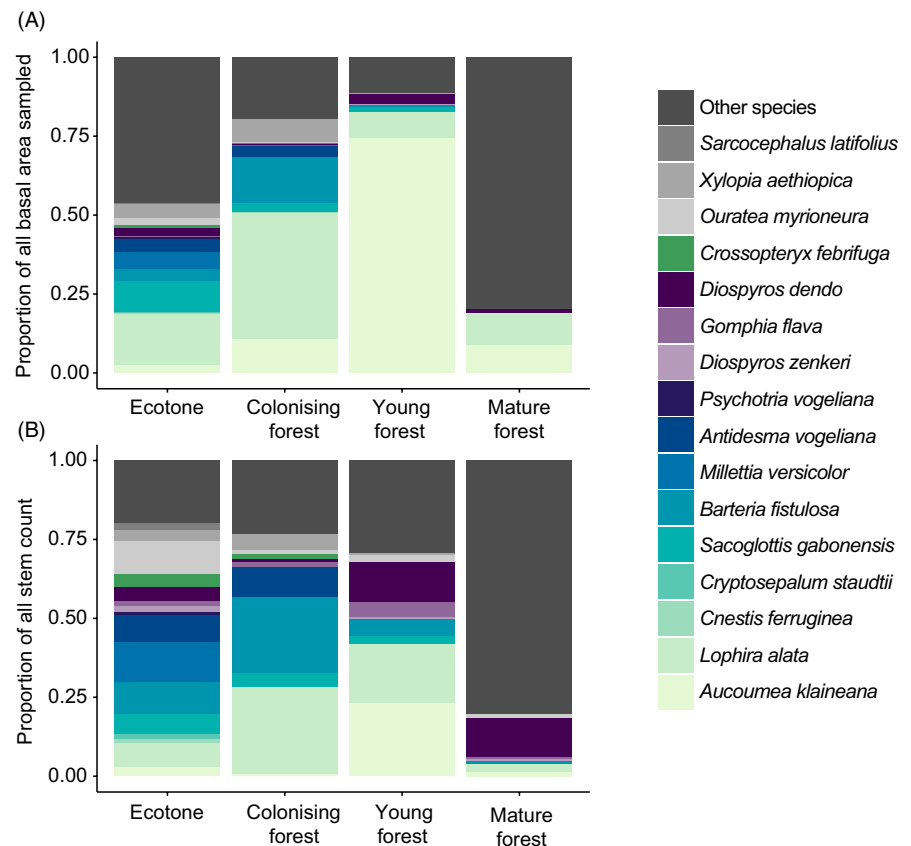
To assess whether the ecotonal tree community was likely to facilitate the spread of savanna fires into the forest, we examined tree canopy LAI, grass biomass, the occurrence of fire along each of the forest–savanna transects and vegetation structure through the foliage density index. We found that the ecotonal tree community was efficient at blocking out light and suppressing grass biomass (Figure 5). Tree canopy LAI was significantly lower and grass biomass significantly higher in the savanna than in the ecotone or

the forest (LAI: $\chi^2 = 206$, $p < 0.0001$, $df = 2$, mean: savanna = 1.7, ecotone = 4.6, forest = 4.8; grass biomass: $\chi^2 = 898$, $p < 0.0001$, $df = 2$, mean (tons/ha): savanna = 3.9, ecotone = 0.6, forest = 0). Although LAI was not significantly different between the ecotone and the forest, there were significant differences in vegetation structure between the two communities. The ecotone community had the highest mean foliage density index at all measured heights above-ground level. Notably, the ecotone's foliage density index was
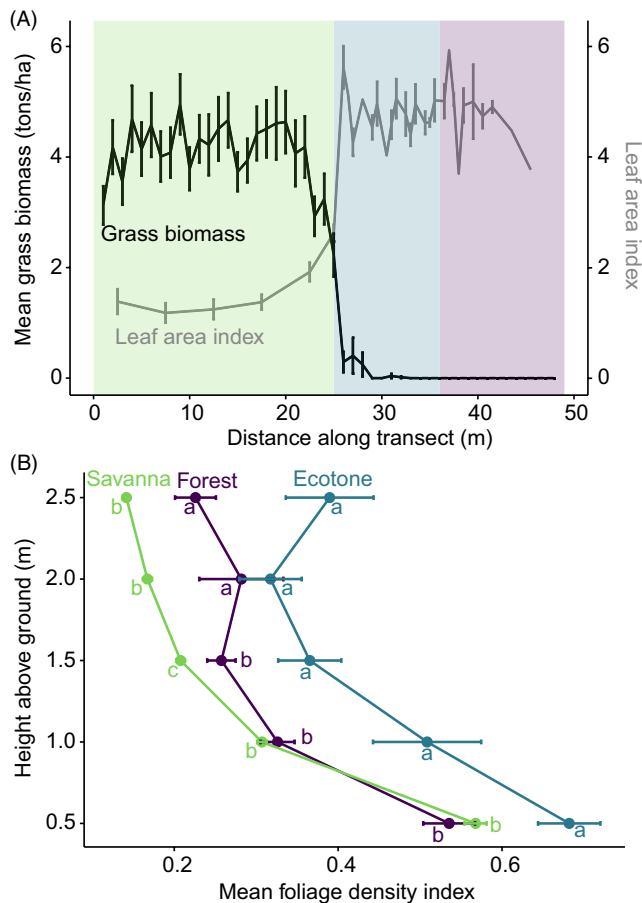
FIGURE 5 (A) Mean grass biomass and leaf area index along the length of the 28 forest–savanna transition transects. The limits of each vegetation type are shown by shaded blocks. Mean grass biomass was 3.9 tonnes/ha in savanna, 0.1 tonnes/ha in the ecotone and 0.0 tonnes/ha in the forest. Mean leaf area index was 1.6 in the savanna, 4.6 in the ecotone and 4.8 in the forest. (B) Mean foliage density index for each vegetation type at increasing heights above-ground level. Different letters indicate significant differences between vegetation types at the height above-ground level according to Kruskal–Wallis tests

significantly higher than the savanna at all measured heights, and significantly higher than the forest at heights 0.5 and 1 m. The ecotonal tree community was exposed to fire 8 of the 20 times that experimental fires were lit in the savanna, while fire reached the forest only once. The ecotonal tree community thus experienced fire at less than half the frequency of the savanna, but eight times the frequency of the forest.

To assess whether the ecotonal tree species were functionally more similar to savanna or to forest tree species, we assessed their functional traits. Ecotonal tree species had a relative bark thickness, bark accumulation rate, wood density and LMA that was intermediate to forest and savanna species (Figure 6; Table S4). Wilcoxon rank sum tests found that ecotonal tree species had significantly higher relative bark thickness ($W = 30$, $p = 0.007$) and bark accumulation rates ($W = 29$, $p = 0.014$) than forest tree species, but did not differ from forest species in terms of LMA or wood density ($p > 0.3$). No statistical comparison between ecotonal and savanna species was
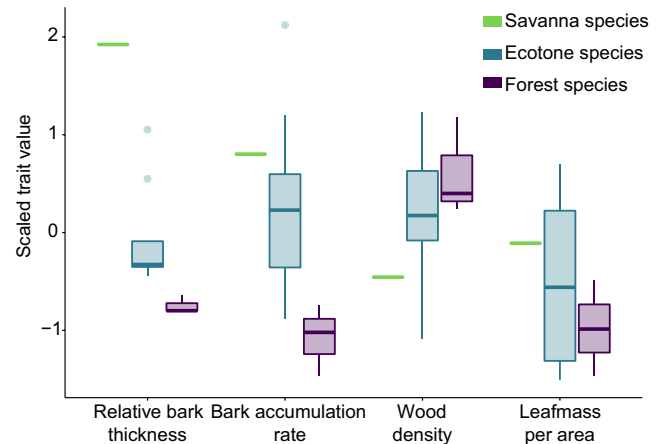

FIGURE 6 The median and interquartile range of the scaled value for each functional trait measured for each group of species. Significant differences between the ecotone and forest groups of species were tested using Wilcoxon rank sum tests, which showed that bark accumulation rate ($W = 29$, $p = 0.014$) and relative bark thickness ($W = 30$, $p = 0.007$) were the only traits that differed significantly between the two groups. The savanna group of species contained only one sampled and therefore could not be statistically compared to the other two groups

possible due to the savanna tree community only comprising one tree species.

4 | DISCUSSION

A compositionally and structurally distinct ecotonal tree community existed in the forest–savanna mosaic of Lopé National Park, Gabon. This community was a significant component of the studied landscape. The ecotonal tree community did not facilitate the savannisation of forest by promoting the spread of fire into the forest. Rather, it stabilised the mosaic by allowing the savanna to burn regularly without exposing the forest to lethal temperatures by acting as a fire buffer between savanna and forest. However, the ecotonal tree community will likely accelerate woody encroachment of the savanna, especially if fire frequency in this landscape was to decrease, because it supported a pool of colonising tree species.

The first aim of this study was to establish whether a distinct ecotonal tree community existed between forest and savanna, or if the forest–savanna ecotone was simply a mixture of forest and savanna tree species. We found strong evidence that the ecotonal tree community was compositionally distinct, as two non-overlapping borders, or discontinuities in tree species composition, were present along transects. The ecotone occupied a relatively narrow (10 m) belt between forest and savanna; however, the fragmented nature of the mosaic gave ecotone significant linear extent. The ecotone was found to occupy a relatively large area (just under a tenth of the amount of area occupied by savanna) and was thus an ecologically relevant component of the forest–savanna mosaic.

The second aim of this study was to determine whether the ecotonal tree community was more likely to facilitate woody

encroachment into savanna, fire spreading into forest or the stability of the forest–savanna mosaic by facilitating neither. For a forest–savanna mosaic to be stable, patches of forest and savanna should always exist, even if their spatial arrangement fluctuates through time (Aleman et al., 2018; Maley, 2002). We found strong evidence that the ecotonal tree community facilitated the continued coexistence of forest and savanna in this landscape by buffering the forest from 95% of the fires that burned in the savanna, thus separating forest and savanna disturbance regimes. The ecotone's fire-buffering capacity was likely driven by its distinct structure. The ecotone's foliage density index was higher than the savanna at all measured heights above-ground, quantitatively confirming our field observations that the ecotone can be easily recognised as a 'wall of leaves'. This 'wall of leaves' intercepted light and severely limited the grass biomass in the understorey. The limitation of grassy fuels in a belt between savanna and forest is a crucial component of the fire buffer the ecotonal tree community creates and thus a key driver of mosaic stability.

The ability of the ecotonal tree community to separate the disturbance regimes of forest and savanna is likely resilient through time. Not only does the ecotone limit grassy fuels but also the ecotonal tree community had significantly thicker bark and accumulated bark at a significantly faster rate than forest tree species. A faster bark accumulation rate means that ecotonal tree species will become fire resistant at a small size, and potentially younger age, than forest tree species (Hoffmann, Geiger, et al., 2012; Jackson et al., 1999). Thicker bark also allows the ecotone to maintain buffering capacity over time as thicker bark allows trees to insulate their stems from lethal temperatures and increases their ability to tolerate repeated burning (Bova & Dickinson, 2005; Hoffmann, Geiger, et al., 2012; Midgley & Bond, 2011). These bark traits contribute to the resilience of the buffering capacity of ecotonal tree community through time, which is crucial as recent ground data from the study site confirm warming and drying are at a critical level for forest survival (Bush et al., 2019). Similar patterns have been found in Afromontane forest, where fire-resistant tree species in forest patches buffered the core forest population from the fire in the surrounding grassy matrix (Abiem et al., 2020; Adie et al., 2017). This buffering helped maintain forest function and diversity over long periods of time.

The presence of a resilient, fire-buffering ecotonal tree community suggests that, under current conditions, savanna can be regularly burned without risk to forest. This finding is especially important in places where fire has historically been seen as a 'threat' to forest and suppressed as a result (e.g. Madagascar or Brazil; Alvarado et al., 2018). Fire suppression policies can have disastrous consequences for biodiversity and ecosystem function (Bond, 2016; Parr et al., 2014; Pausas & Bond, 2020; Stevens et al., 2017), as has been the case in the Cerrado of Brazil which has suffered widespread encroachment as a result of fire suppression policies (Durigan & Ratter, 2016; Rosan et al., 2019). It is very important to note that not all fires in open landscapes are safe for forests. If a forest–savanna mosaic lacks a fire-buffering ecotonal community, it may indicate that the 'savanna' is actually degraded grassy patches

that arose within the forest matrix as a result of deforestation and subsequent fires (Ratnam et al., 2011). Under these circumstances, the remaining forested area is vulnerable to further damage and would need to be protected from burning in order to recover (Balch et al., 2015; Barlow et al., 2019; Brando et al., 2012; Brando, Paolucci, et al., 2019; Brando, Coe, et al., 2019; Staver et al., 2019). Assessment of the fire-buffering capacity of the ecotonal tree community is thus essential prior to burning, especially as forests become more flammable under predicted increases in the frequency and severity of drought conditions (IPCC, 2007; Verhegghen et al., 2016).

Although the ecotonal tree community stabilises the forest–savanna mosaic when the savanna is burned regularly, the same community will likely accelerate woody encroachment of the savanna if fire were to be suppressed. The ecotonal tree community contained many forest pioneer species, as evidenced by their high abundances and basal areas in colonising forest census plots as well as by descriptions of their ecology in the literature (Table S1; White & Abernethy, 1997). This pool of pioneer species, while normally largely kept within the ecotone by regular burning, will likely quickly advance into the savanna if fire frequency or intensity is reduced. Evidence of woody encroachment emanating from the ecotone can already be seen in parts of the study site (Jeffery et al., 2014), potentially as a result of fire intensity decreasing nearer to the forest edge (Cardoso et al., 2018). Woody encroachment is a major conservation challenge across tropical Africa and likely to only become worse in the future with increasing global atmospheric carbon dioxide and increasing rainfall in many parts of central Africa expected to favour the growth of trees over grasses (Bond & Midgley, 2012; Buitenwerf et al., 2012; Case & Staver, 2018; James & Washington, 2013; Kgope et al., 2009; Scheiter & Higgins, 2009; Staver et al., 2011; Stevens et al., 2016, 2017). The potential ability of the ecotone to transform into the frontier of woody encroachment emphasises how close forest–savanna mosaics may be to a sudden and practically irreversible state shift, and how important regular burning is for preventing this.

Although beyond the scope of this study, it is also interesting to consider what the ecology of the forest–savanna ecotone might indicate about the evolution and antiquity of forest–savanna mosaics. Forest–savanna ecotones likely first arose 4–8 Mya, when forests contracted and gave way to islands of C4 grassy systems (Osborne, 2008). These ecotones would likely have presented a novel niche in the landscape in which a stable community may have developed. Much like the ecotonal tree community we observed in this study, new communities are more likely to be populated with existing species that already have the necessary adaptations to survive than they are to be filled with newly evolved species (Donoghue, 2008). It is therefore possible that the distinct ecotonal tree community found in this study is as old as the forest–savanna ecotone itself. If this were the case, the ecotonal tree community may hold clues as to how forest tree species were first able to leave the forest and enter the grasslands of Africa to create the savannas we see today.

In conclusion, this study highlighted the unique ecology of the forest–savanna ecotone in a forest–savanna mosaic in central Africa. By acting as a fire buffer between savanna and forest the

forest–savanna ecotone helped stabilise the mosaic. Without this buffer, it would be increasingly difficult to continue to burn savanna without risk to the forest. If fire frequency in this landscape were to be reduced the ecotonal tree community would likely transform from a stabilising buffer to the frontier of woody encroachment. Regular burning of tropical savannas is thus essential to maintain ecosystem function and habitat diversity in forest–savanna mosaics. By describing an ecologically distinct ecotonal tree community, we contribute to an existing body of work that emphasises the high conservation value of forest–savanna mosaics (Parr et al., 2014). Repetition of this study across tropical forest–savanna mosaics to establish under which circumstances similar patterns are found would be a fascinating area for future research.

AUTHORS' CONTRIBUTIONS
A.W.C., I.O., K.A.A., Y.M. and W.J.B. developed the ideas, hypotheses, and the experimental setup; A.W.C. lead the data collection and analysis and K.J.J., D.L. and J.E.N. assisted with fieldwork and provided substantial feedback on methodology; L.J.T.W. and S.G. contributed the data; A.W.C. lead the writing, and I.O., K.A.A., W.J.B. and Y.M. made significant contributions to the writing. All authors provided constructive comments on the draft.

DATA AVAILABILITY STATEMENT
All data are archived at Oxford University Libraries https://doi.org/10.5287/bodleian:VJXGQj09d (Cardoso et al., 2020).

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SUPPORTING INFORMATION

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