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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 twenty-eight 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 >3cm) 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 if 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.

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.

SECOND ABSTRACT

1. Le réchauffement climatique globale pourrait permettre l'expansion des savanes ligneuses sur les écosystèmes forestiers et ainsi augmenté les surfaces de propagation des feux à l'intérieur des forets. Les mosaïque forets savanes sont caractérisés par une frontière, ou écotone, démarquant ces deux compartiments. Cet écotone particulier peut alors mitiger ou amplifier les effets de ce réchauffement planétaire. Néanmoins, l'écologie de cet écotone de transition foret-savane est jusqu'alors peut étudier. Dans cette étude, nous avons déterminer l'assemblage des espèces ligneuses qui forment une communié végétale distincte, spécifique à cet écotone. Nous avons ensuite évalué et tester les propriétés de cette communauté dans le ralentissement ou la propagation des feux de savane en forêt ; son impact sur la dynamique de cette mosaïque foret-savane, avec soit une colonisation de la forêt vers la savane ou une stabilisation de ces deux composantes paysagères.

2. Nous avons échantillonné vingt-huit transects à travers ce type d'écotones de transition dans une mosaïque forêt-savane d'Afrique centrale. Nous avons recueilli des données sur la taille et les espèces de tous les arbres de plus de trois centimètres de diamètre recensé le long de chaque transects. Notre analyse de "Split moving window dissimilarity" le long de ces transects nous a permis de détecté les limites précise délimitant la communauté végétale de savane, celle propre à l' écotone et celle de la forêt. Pour observer si la communauté végétale spécifique à l'écotone de transition était susceptible de faciliter la propagation du feu dans la forêt, nous avons provoqués des feux expérimentaux et évalué l'ombre et la biomasse d'herbe le long des transects. Pour déterminer si l'écotone était susceptible de faciliter l'avancement de la foret sur la savane, nous avons évalué si les espèces d'arbres formant la communauté végétale spécifique à l'écotone de transition étaient des espèces pionnières ou colonisatrice.

3. Notre étude met en lumière l'existence d'un assemblage d'espèces ligneuses formant une communauté spécifique à cet écotone de transition foret-savane. Cette communauté n'a pas favorisé la propagation du feu en forêt et a au contraire agi comme un coupe-feu grâce à l'ombre qu'elle projette

sur la biomasse d'herbe potentiellement inflammable du sous-bois. Dans notre étude, l'écotone testé a protégé la foret de 95% des feux de savane expérimentaux. Cet écotone permet de stabiliser la dynamique de la mosaïque foret savane ; en permettant à la savane de se régénérer par brulis et en protégeant la forêt des incendies et des températures létales pour les arbres.

4. La communauté d'espèces végétales de l'écotone était composée de nombreuses espèces pionnières forestières qui favorisent l'avancement de la forêt sur la savane, surtout si la fréquence des feux est diminuée.

SYNTHÈSE : Dans ce paysage mosaïqué forêt-savane, une communauté d'espèces végétales distincte propre à l'écotone de transition existe qui tamponnent l'impact du feux sur la forêt. Notre étude démontre alors que les feux de savane sont peu susceptibles de compromettre l'intégrité de la forêt. Inversement, la suppression des incendies dans ce paysage entraînera alors une perte de l'écosystème de savane car l'écotone permet le recrutement d'espèces ligneuses colonisatrices, favorisant l'expansion de la forêt. Un brûlage régulier semble donc être requis pour la préservation de cette mosaïque forêt-savane.

KEY WORDS

Alternative stable states, Ecotone, Transition, Edge effects, Ecological threshold, Functional traits, Fire, Forest-savanna mosaic

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; Olsson & Ouattara, 2013; Parr *et al.*, 2014; Moore *et al.*, 2017). 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; Willis *et al.*, 2013; van Nes *et al.*, 2014; Seddon *et al.*, 2016; Scheiter *et al.*, 2019). 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; Ratnam *et al.*, 2011; Veldman & Putz, 2011; Silvério *et al.*, 2013; Brando *et al.*, 2014; Parr *et al.*, 2014; Veldman *et al.*, 2015; Veldman, 2016; McCleery *et al.*, 2018). 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 (Favier *et al.*, 2004b; Balch *et al.*, 2008; Aleman & Staver, 2018; Barlow *et al.*, 2019). 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 *et al.*, 2012a; 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; Hennenberg *et al.*, 2008; Hoffmann *et al.*, 2012b; Charles-Dominique *et al.*, 2018). 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 (Bond & Van Wilgen, 1996; Scholes & Archer, 1997; Biddulph & Kellman, 1998; Hoffmann *et al.*, 2012b). 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 (Silvério *et al.*, 2013; Balch *et al.*, 2015). Conversely, without regular burning savannas become invaded by trees and can no longer provide their full suite of ecosystem services (Parr *et al.*, 2014; Veldman *et al.*, 2015; Veldman, 2016; Pausas & Bond, 2020). 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- regime 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" (White & Abernethy, 1997; Charles-Dominique *et al.*, 2018; Abiem *et al.*, 2020) but empirical study, quantitative description, and ecological exploration of the hypothetical ecotonal community is lacking.

When the fire- and light- driven stabilising feedback loops that enable forest and savanna co-existence become weakened by anthropogenic global change both forest and savanna become degraded ecosystems (Parr *et al.*, 2014; Brando *et al.*, 2019a). 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 (IPCC, 2007; Balch *et al.*, 2008, 2015; Veldman & Putz, 2011; James & Washington, 2013; Silvério *et al.*, 2013; Brando *et al.*, 2014; Barlow *et al.*, 2019; Fonseca *et al.*, 2019). 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 (Kgope *et al.*, 2009; Mitchard *et al.*, 2011; Bond & Midgley, 2012; Buitenwerf *et al.*, 2012; Andela & Van Der Werf, 2014; Durigan & Ratter, 2016; Stevens *et al.*, 2016, 2017; Andela *et al.*, 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 (Hoffmann *et al.*, 2012b; Balch *et al.*, 2015; Charles-Dominique *et al.*, 2018). 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 *et al.*, 2004b,a; 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 co-existence 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 (Maley, 2002; Aleman *et al.*, 2018), 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 (Hennenberg *et al.*, 2005; Hoffmann *et al.*, 2012a; Dantas *et al.*, 2013; Cardoso *et al.*, 2016), how the forest edge is moving over time (Favier *et al.*, 2004b; Ibanez *et al.*, 2013b), or how far the depth of edge influence of one vegetation type (forest or savanna) extends into the other (Hennenberg *et al.*, 2008; Hoffmann *et al.*, 2012b; Ibanez *et al.*, 2013a). 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 (Oliveira *et al.*, 2004; Laurance *et al.*, 2006; Tabarelli *et al.*, 2008; Peres *et al.*, 2010) and associated with negative "edge influence" effects (Tabarelli *et al.*, 1999; Harper *et al.*, 2005). 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 (Eiten, 1972; Ratter & Dargie, 1992; Ratter *et al.*, 1996; Coelho *et al.*, 2016; 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 twenty-eight 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 if 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.

MATERIALS AND METHODS

Study site

This study was carried out in the northern forest-savanna mosaic of Lopé National Park (LNP), Gabon (0.2S, 11.6E) (**Fig. 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) (**Fig. S1**). In LNP, mean daily minimum and maximum temperatures were 22 °C and 28 °C in the forest (1984-2018) and 22 °C 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 1466 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 5000 years (White, 2001).

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 ten

years to having been burned up to three times in the past three years (**Fig. 1**). The majority of transects were burned between one and three times in the past three 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 100m apart.

Transects were 2 m wide and varied in length (37m – 48m) depending on the sharpness of the ecotone. Transects started by covering 25m of field-defined savanna, then crossed the entire field-defined ecotone, and finally covered 10m of field-defined forest (**Fig. S2**). Field-defined delineations between savanna, ecotone, and forest were used to establish the length of the transect in order 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 5m. 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 less than 5m and a high level of continuity between the understorey and mid canopy layers. The ecotone ended and the forest began where the midstorey became open and visibility increased to more than 5m, but grass biomass remained low and the tree canopy remained closed. In order to minimise bias, field-defined vegetation types were delineated based on consensus of at least three researchers.

We sampled transects in adjacent 1m long blocks, each 2m wide. In each block, we measured all woody stems with a basal diameter (measured at 10cm above ground) > 3cm ("adult stems"), noting their species and basal diameter. Additionally, we measured all woody stems in a nested sampling strip 20cm wide on the left-hand side of the transect with a basal diameter <3 cm and a height >30cm ("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 geographic matrix of the distances between transect sites using the non-parametric 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).

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) (Ludwig & Cornelius, 1987; Cornelius & Reynolds, 1991). 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 (Ludwig & Cornelius, 1987; Cornelius & Reynolds, 1991). Dissimilarities were calculated relative to an expected mean (as determined by a Monte Carlo procedure with 100 replicates), and then normalised (Z-score) (Hennenberg *et al.*, 2005; Erdős *et al.*, 2014). 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 (1-5m) was used to reduce the scale dependency of the results (Cornelius & Reynolds, 1991; Hennenberg *et al.*, 2005; Erdős *et al.*, 2014). 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 (**Fig. 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 (Walker *et al.*, 2003; Hennenberg *et al.*, 2005). 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 (Walker *et al.*, 2003; Hennenberg *et al.*, 2005). 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 (Walker *et al.*, 2003; Hennenberg *et al.*, 2005). 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 25m and 27m along a transect and a second border occurred between 35m and 37m 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 25m and 35m and a second border occurred between 27m and 39m, 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 25m 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 greater than 2.128, and *p* was adjusted using the Bonferroni correction for multiple comparisons within each species (Sharp, 2015).

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 (White, 2001; Cuni-Sanchez *et al.*, 2016). Tree canopy cover, density, and diversity was 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 (White, 2001; Cuni-Sanchez *et al.*, 2016). 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 *Aucoumea klaineana, Lophira alata*, and *Sacoglottis gabonensis* (White, 2001; Cuni-Sanchez *et al.*, 2016). The final successional stage sampled was the "mature forest", which is succeeds young forest (White, 2001; Cuni-Sanchez *et al.*, 2016). 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 (White, 2001; Cuni-Sanchez *et al.*, 2016). 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 0.08ha 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 >5cm had their trunk diameter measured and their species noted. Due to the difference in minimum stem size sampled in the census plots (>5cm diameter at breast height) and in the transects of this study (>3cm at 10cm 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 (Jeffery *et al.*, 2014; Cardoso *et al.*, 2018). 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 0.5m, 1m, 1.5m, 2m, and 2.5m above ground every 5m along the transect in the field-defined savanna and forest and every 2.5m 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 (Hoffmann *et al.*, 2003; Bova & Dickinson, 2005; Midgley *et al.*, 2011; Hempson *et al.*, 2014). 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 per 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 lifespans (Wright *et al.*, 2004; Poorter & Bongers, 2006; Kunstler *et al.*, 2015).

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 (Lawes *et al.*, 2013; Corrêa Scalon *et al.*, 2019). 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) (Jackson *et al.*, 1999; Hoffmann *et al.*, 2003) (**Fig. 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 5 mature leaves per tree and 3 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.

RESULTS

In the twenty-eight forest-savanna ecotone transects, sixteen 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, Lophira alata, Sarcocephalus latifolius, Cnestis ferruginea, Saccoglottis gabonensis, Xylopia aethiopica, Diospyros zenkeri, Gomphia flava,* and *Aucoumea 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 27m along the transects (**Fig. 2a**) and the border between the ecotone and the forest was located 36m along the transects (**Fig. 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 26m to 36m,

and forest from 36m to 48m. The ecotone was, on average, 10m wide. Using the width of the ecotone and geographical information software, we calculated that the ecotone has a length of 339.6km in the study site, and thus occupies 3.4km^2, or 7% of the area occupied by savanna in the study site (**Fig. S5**).

χ^2 tests were used to classify the focal tree species into ecotone, savanna, and forest communities. χ^2 tests showed thirteen of the sixteen focus tree species to have significantly higher than expected densities in either savanna, ecotone, or forest sections of the transect (**Fig. 3, Table S2**). The ecotone community comprised ten 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 (**Fig. 4, Table S3**). For stems >5cm diameter, *M. versicolor* was the single most dominant species in the ecotone, however 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 (**Fig. 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.

To assess whether the ecotonal tree community was likely to facilitate the spread of savanna fires into the forest, we examined tree canopy leaf area index (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 (**Fig. 5**). Tree canopy LAI was significantly lower and grass biomass significantly higher in the savanna than in the ecotone or the forest (LAI: χ^2=206, p<0.0001, df=2, mean: savanna = 1.7, ecotone = 4.6, forest = 4.8; grass biomass: χ^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 significantly higher than the savanna at all measured heights, and significantly higher than the forest at heights 0.5 m and 1 m. The ecotonal tree community was exposed to fire eight of the twenty 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 (**Fig. 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 possible due to the savanna tree community only comprising one tree species.

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 (10m) 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 (Maley, 2002;

Aleman *et al.*, 2018). 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, quantitively 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 the ecotonal tree community also 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 (Jackson *et al.*, 1999; Hoffmann *et al.*, 2012a). 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; Midgley & Bond, 2011; Hoffmann *et al.*, 2012a). 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 (Adie *et al.*, 2017; Abiem *et al.*, 2020). 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 (Parr *et al.*, 2014; Bond, 2016; Stevens *et al.*, 2017; Pausas & Bond, 2020),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 (Brando *et al.*, 2012, 2019a,b; Balch *et al.*, 2015; Barlow *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 (Kgope *et al.*, 2009; Scheiter & Higgins, 2009; Staver *et al.*, 2011; Bond & Midgley, 2012; Buitenwerf *et al.*, 2012; James & Washington, 2013; Stevens *et al.*, 2016, 2017; Case & Staver, 2018). 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.

DATA AVILABILITY STATEMENT

All data are archived at Oxford University Libraries, DOI: 10.5287/bodleian:VJXGQj09d

AUTHOR'S CONTRIBUTIONS

AWC, IO, KA, YM, WB developed ideas, hypotheses, and the experimental setup; AWC lead the data collection and analysis and KJ, DL, JEN assisted with fieldwork and provided substantial feedback on methodology; LJTW, SG contributed data. AWC lead the writing, and IO, KA, WB and YM made significant contributions to the writing; all authors provided constructive comments on the draft.

FIGURE LEGENDS

Figure 1: Map of a) Gabon within Africa, b) Lopé National Park within Gabon, c) the study site within the broader region of Lopé National Park, and d) and the twenty-eight transect sites within the forest-savanna mosaic of the study site (Agence Nationale des Parcs Nationaux, 2006).

Figure 2: Split Moving Window Dissimilarity Analysis (SMWDA) and Moving Window Regression Analysis (MWRA) for the twenty-eight 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**). *s indicate

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 twenty-eight 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 sixteen 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 twenty-eight 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. (unpublished). Data is only shown for stems that are >5cm diameter at the point of measurement (10cm 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 colonizing forest, which is succeeded by young forest, which is succeeded by mature forest (White, 2001).

Figure 5: a) Mean grass biomass and leaf area index along the length of the twenty-eight forest-savanna transition transects. The limits of each vegetation type are shown by shaded blocks. Mean grass biomass was 3.9 tons/ha in savanna, 0.1 tons/ha in the ecotone, and 0.0 tons/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). 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.

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.
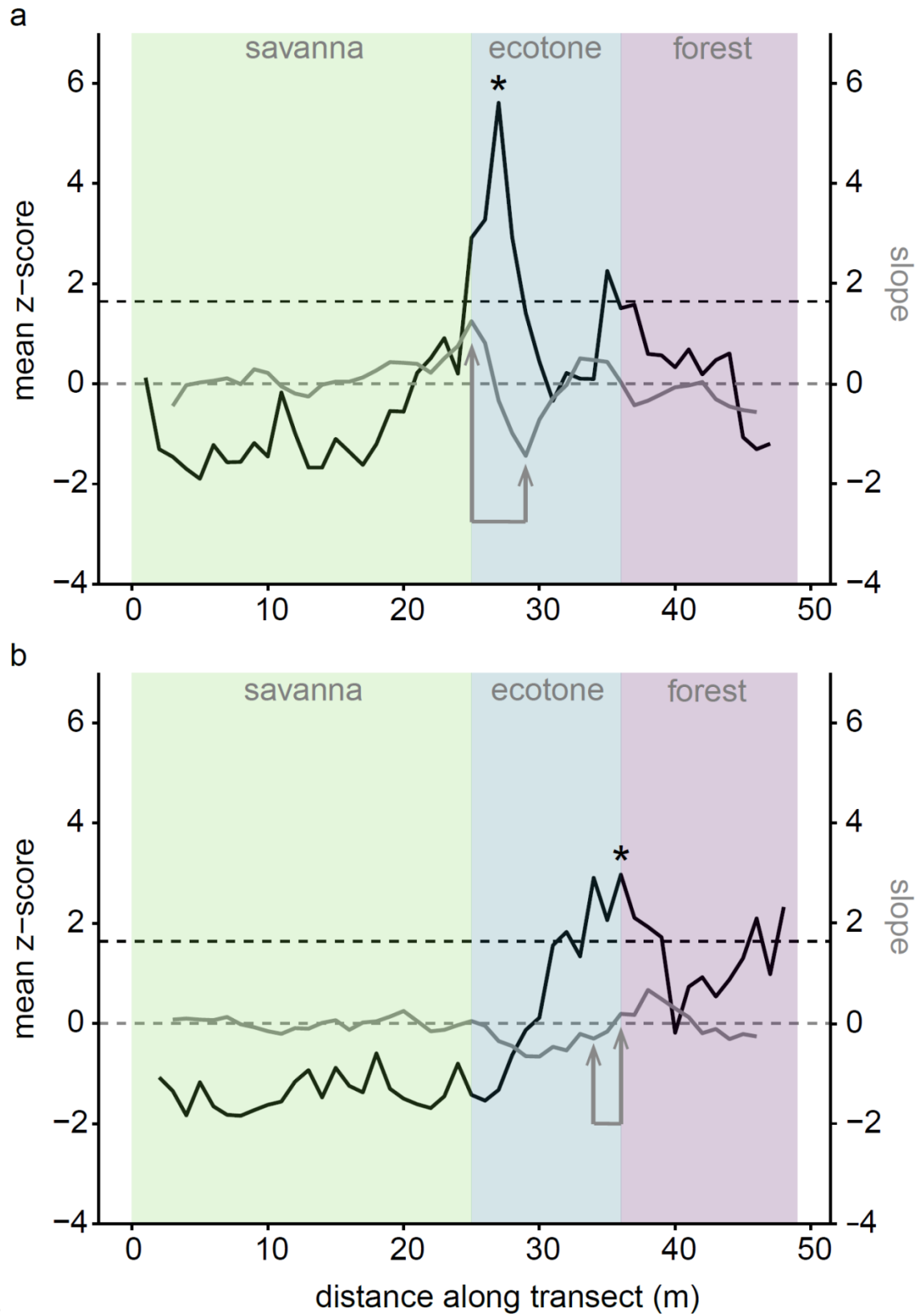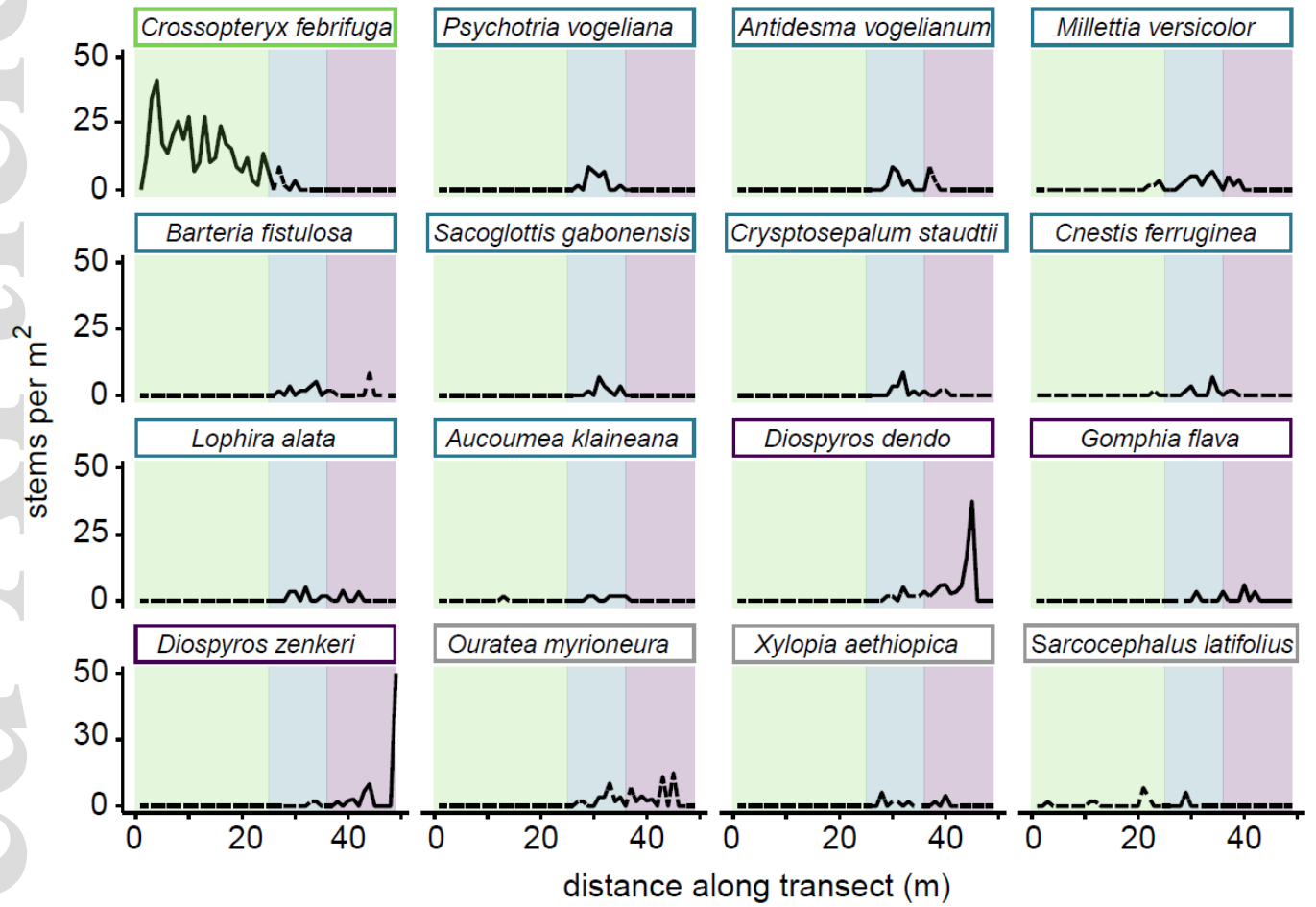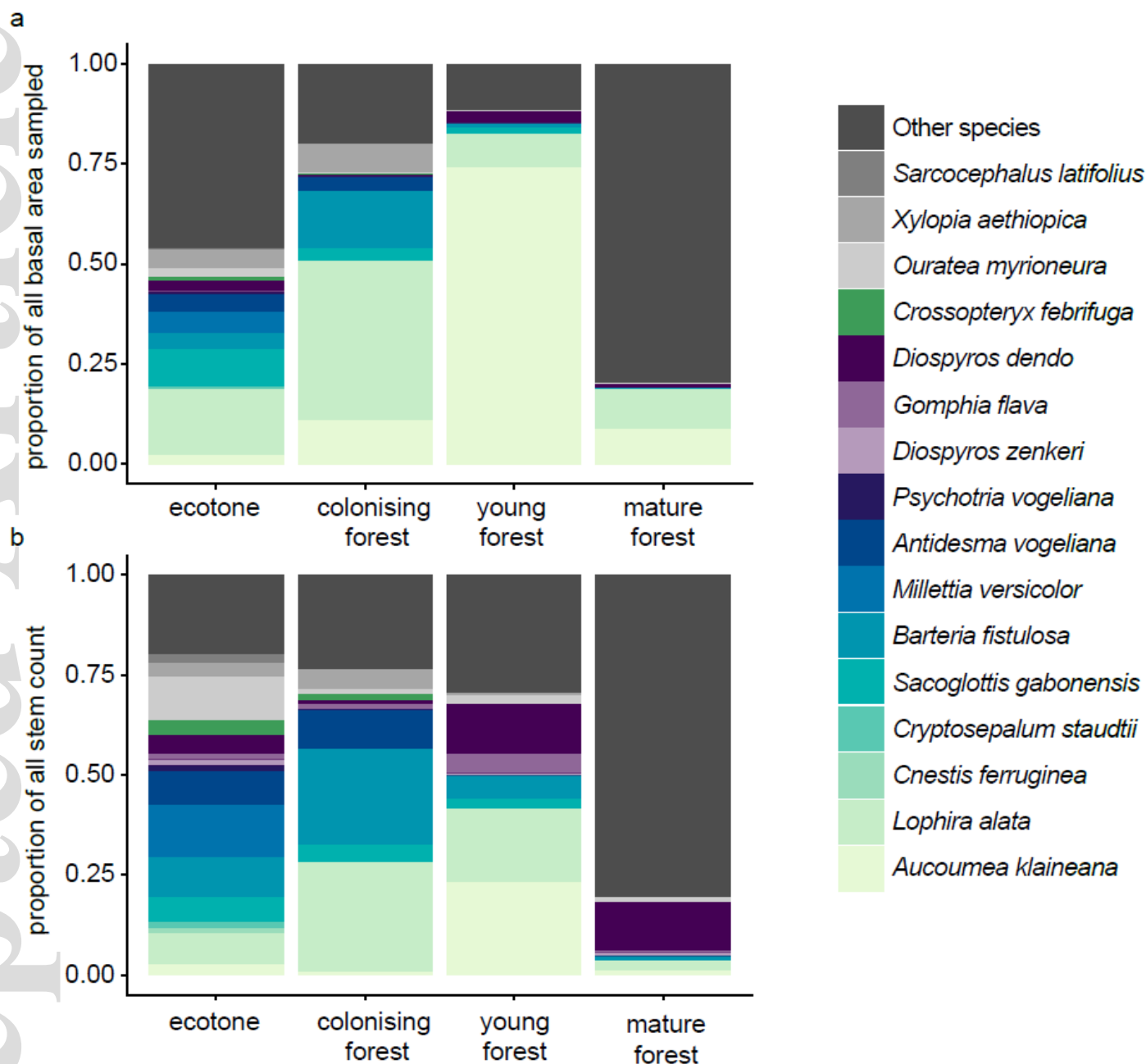
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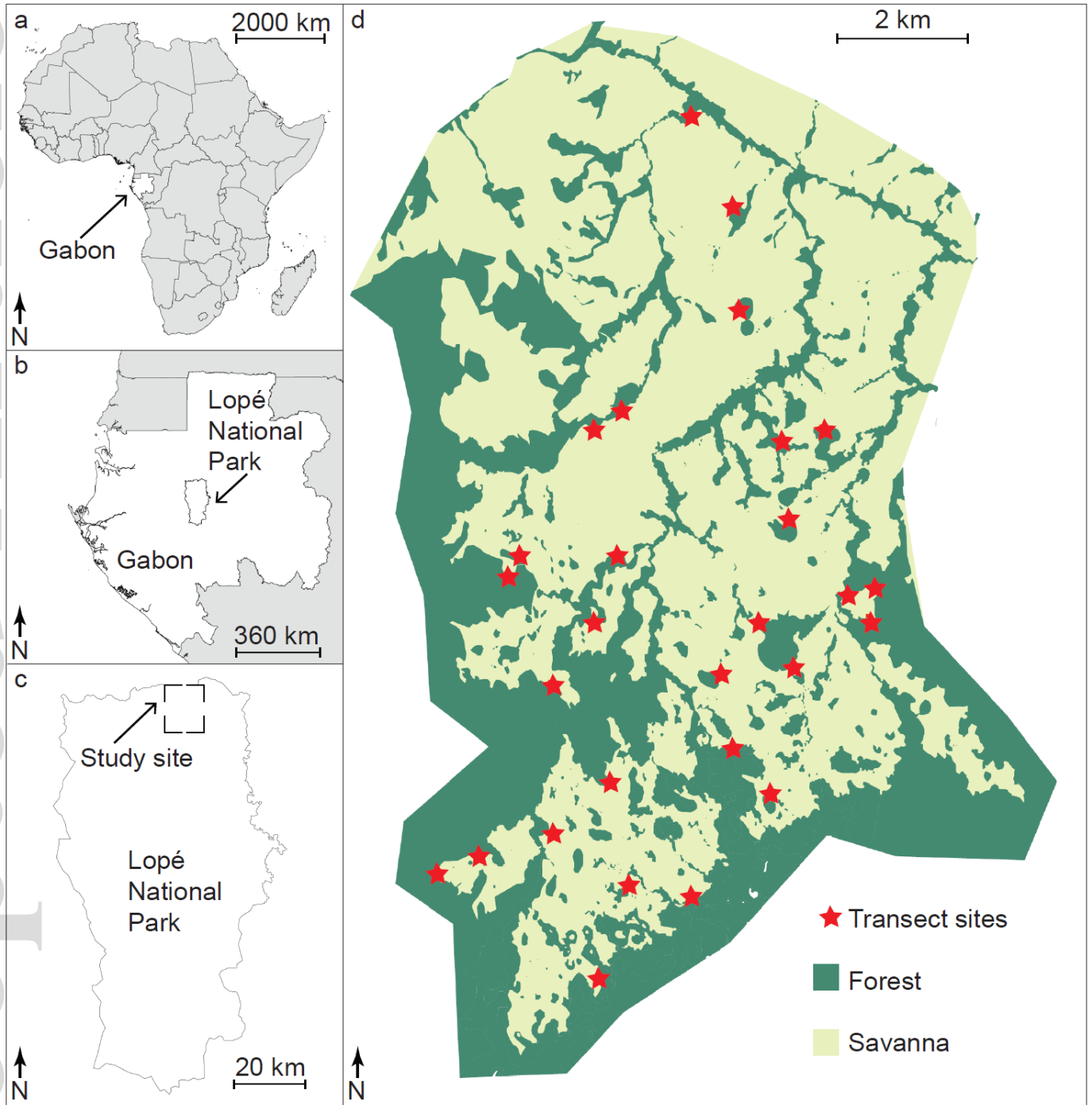
FIGURE 2

FIGURE 3

FIGURE 4
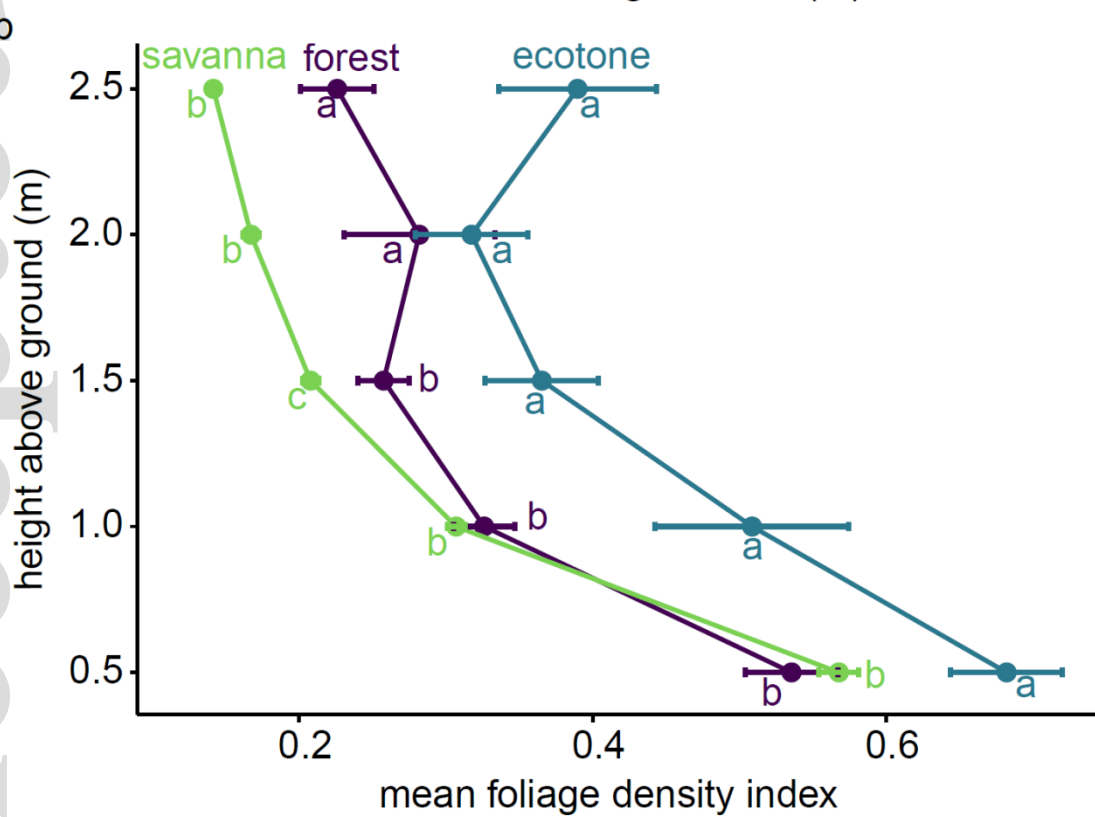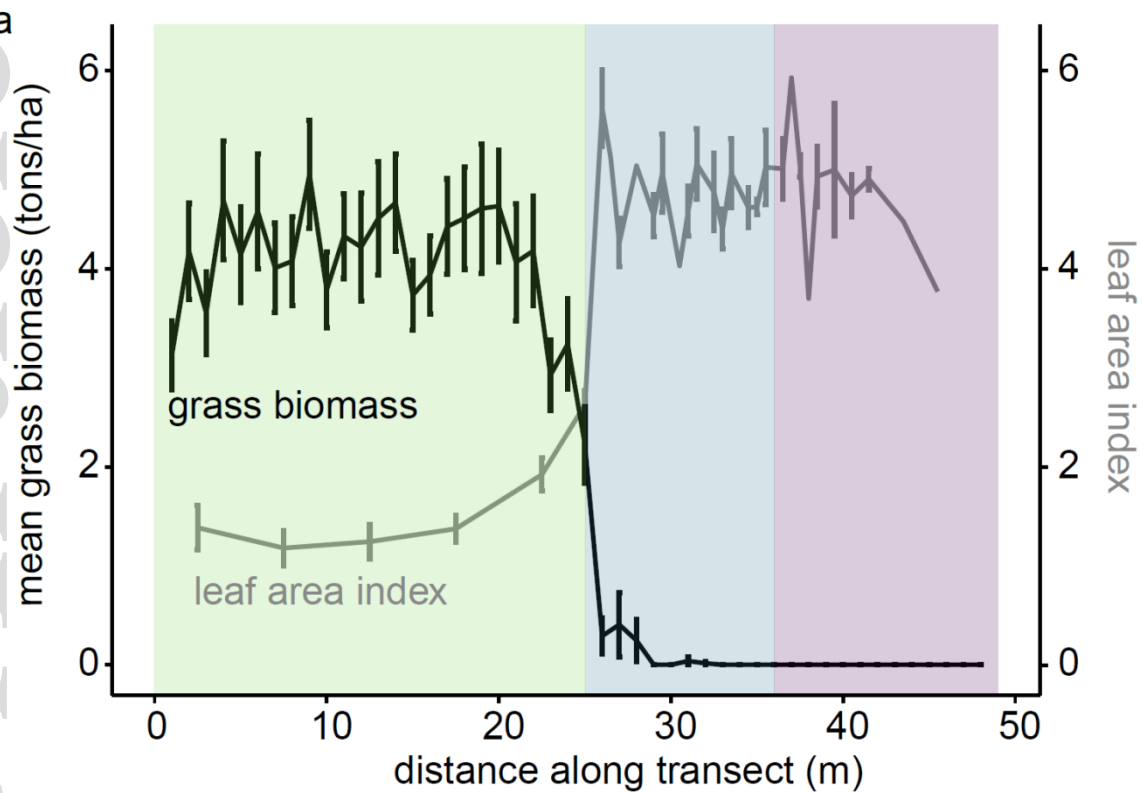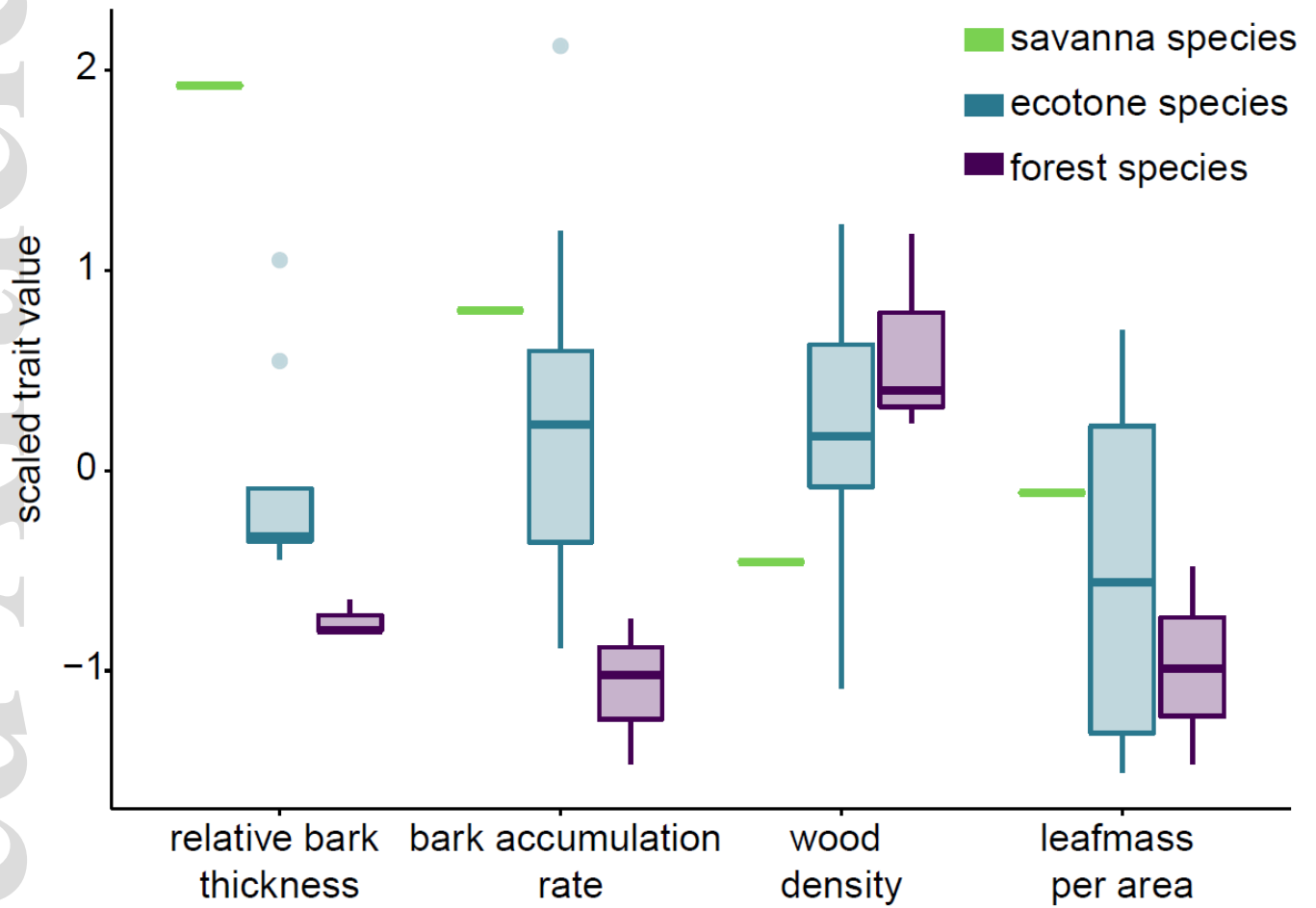
FIGURE 5

a

b

FIGURE 6

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