
The role of fire and elephants in shaping a Central African forest-savanna mosaic

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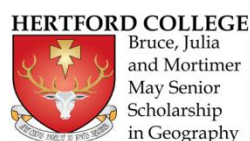
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Abstract

This thesis aimed to investigate the ecology of a forest-savanna transition in Central Africa, with a specific focus on how it was affected by fire and elephants. It had three objectives, each of which was addressed through a research article. The data presented in these articles were collected at forty forest-savanna transition sites in the forest-savanna mosaic of Lopé National Park, Gabon.

The objective of the first article, entitled “**Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions**”, was to empirically describe the fire suppression threshold and the interactive abiotic and biotic controls on it. Results from this work showed fires to become less intense and less hot as they approached the forest-savanna transition. These changes in fire behaviour were induced by a change in grass species composition, not by changes in grass biomass. Approaching the forest-savanna transition, the grass community shifted from one dominated by a fine, dry, highly flammable species, to one dominated by a thick-culmed, slower drying species. This shift was accompanied by a shift to higher levels of tree canopy cover. This article showed how fire was mediated by grass species composition, which was mediated by tree canopy cover, which was in turn mediated by fire. It thus elucidated on the mechanism that allows forest and savanna to co-exist in tropical mosaicked landscapes.

The objective of the second article, entitled “**Distinct transition tree community suggests possible antiquity of forest-savanna mosaics**”, was to assess whether a distinct transition tree community could be identified at the forest-savanna transition, and to investigate its ecology. Results from this work showed that a distinct woody community existed at the forest-savanna transition. This community was intermediately fire resistant, with a suite of functional traits suited to survive at the interface of forest and savanna, rather than in the interior of either. The species in this transition community were not forest gap species forming a community representing one successional stage, but rather showed signs of being a stable community that had experienced multiple recruitment events. The presence of such a unique woody community at the transition suggested that this mosaic, and the fire regime that maintained it, are ancient.

The objective of the third article, entitled “**The role of forest elephants in shaping tropical forest-savanna co-existence**”, was to quantify forest elephant use of the forest-savanna transition, assess the drivers of this use, and determine the consequences for transition dynamics. Results from this work showed that the forest-savanna transition was an important foraging site for forest elephants. Forest elephant foraging here was strongly seasonal and driven by fruit availability. Unlike savanna elephants, forest elephants foraged relatively non-destructively, and had little direct effect on woody vegetation structure. However, their frequent use of the transition created substantial paths, which acted as fire breaks during savanna burning.

Inadvertently, forest elephants thus protected the fire-sensitive forest interior from burning.

This thesis concluded that fire is the main determinant of forest-savanna transition dynamics and vegetation distribution in mosaics, and likely has been for millennia. Although forest elephants did not have the ability to create and maintain an open canopy in the same way as fire, their foraging at the forest edge reinforced the fire-mediated feedbacks that allow forest and savanna to co-exist in this landscape.

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Table of Contents

Abstract	1
Acknowledgements	4
List of figures	10
List of tables	18
Chapter 1: Introduction.....	21
1.1 Thesis rationale	22
1.2 Thesis aim and objectives	28
1.3 Thesis structure	30
1.4 References	31
Chapter 2: Literature review.....	34
2.1 Forest-savanna transitions as components of dynamic mosaicked landscapes ..	35
2.2 How does fire affect the forest-savanna transition?	40
2.3 How does fire affect the tree community at the forest-savanna transition?	47
2.4 How do the effects of fire and forest elephants interact at the forest-savanna transition?.....	47
2.5 References	57
Chapter 3: Field site description.....	67
3.1 An introduction to the field site	68
3.2 Vegetation.....	72
3.3 Climate	77
3.4 Fire	79
3.5 Forest elephants.....	81
3.6 References	82
Chapter 4: Methods.....	85
4.1 Sampling the forest-savanna transition.....	86
4.2 Grasses, flammability, and fire behaviour.....	91
4.3 Tree communities and functional traits.....	93
4.4 Forest elephants, camera traps, and damage to trees.....	95
4.5 References	101

Chapter 5: Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions	102
5.1 Abstract and key words	104
5.2 Introduction.....	106
5.3 Materials and Methods.....	110
5.4 Results.....	122
5.5 Discussion.....	132
5.6 Acknowledgements.....	138
5.7 References.....	139
5.8 Supplementary material	143
 Chapter 6: Distinct fire-adapted transition tree community suggests forest-savanna mosaics are ancient.....	 148
6.1 Abstract and key words	150
6.2 Introduction.....	151
6.3 Materials and Methods.....	156
6.4 Results.....	165
6.5 Discussion.....	175
6.6 Acknowledgements.....	182
6.7 References.....	183
6.8 Supplementary material	187
 Chapter 7: The role of forest elephants in shaping tropical forest-savanna co-existence	 203
7.1 Abstract and key words	205
7.2 Introduction.....	207
7.3 Materials and Methods.....	213
7.4 Results.....	221
7.5 Discussion.....	229
7.6 Acknowledgements.....	236
7.7 References.....	237
7.8 Supplementary material	243
 Chapter 8: Conclusions and Synthesis.....	 251
8.1 Summary of key findings	252
8.2 Synthesis	259
8.3 References.....	264

List of figures

Figure 1.1: Map of the location of Gabon within the African continent (a) and the forest-savanna mosaic field site within Lopé National Park (b) (Agence Nationale des Parcs Nationaux, 2006).

Figure 2.1: Distribution of forest and savanna across sub-Saharan Africa and the rest of the tropics. Areas where rainfall is too low to support a closed canopy are deterministically low tree cover systems (savanna and grasslands), and areas where rainfall is high are deterministically forest. Areas where rainfall is intermediate (1000 – 2500 mm MAP) are where either forest or savanna may exist as alternative stable states (bistable areas). These areas are coloured as to whether they currently support closed canopy forest, or open canopy savanna/grasslands. Figure from Staver *et al.* (2011b).

Figure 2.2: A diagrammatic representation of forest and savanna as alternative stable states, using a ball in basin analogy. The solid red ball sits in either a forest or savanna state (green basin). In (a), both forest and savanna are stable states, and so if disturbed (blue arrows) the ball will move up and down the sides of its current basin (stable state), but rolling into the adjacent basin is difficult as stabilising feedbacks exist to reinforce the initial state of the ball. In (b), the system is perturbed and the ball rolls into the adjacent basin and the stable state shifts, in this case from savanna to forest. This will occur either if an extreme perturbation affects the system (shown by the arrow on the left panel) or if resilience of the system is gradually eroded over time, making even small perturbations likely to cause a shift in state (shown by the arrow on the right panel). Figure based on Beisner *et al.* (2003).

Figure 2.3: Showing fire-resistance functional traits of savanna tree species. The top panel shows cross sections of a savanna tree sapling where (a) shows the thick insulating bark accumulated by these species, (b) and (c) shows how these species bury their buds deep in the bark layer to further protect them and (c) how they have more than one bud per leaf axil to facilitate resprouting after fire. The bottom panel shows a savanna tree that has been dug out of the ground, where (d) shows the enlarged underground organ of this tree, in which large amounts of starch are stored to be mobilized after burning, enabling quick recovery of lost photosynthetic material.

Figure 2.4: How savanna (a) and forest (b) elephants look different to one another. The shape of their heads is distinct from one another, and the forest elephant is smaller with a longer tail.

Figure 2.5: An old forest elephant dung pile in the forest, in which tree seedlings are clearly shown to be germinating, likely as a result of the seeds the elephant ate. Such a site is common, and shows the important role forest elephants play in tree seed dispersal and recruitment.

Figure 3.1: Photographs of different parts of the forest-savanna mosaic in Lopé National Park. Abrupt transitions between the open canopy savanna and closed canopy forest can be seen.

Figure 3.2: Photographs of the savannas that are typical of the field site. In the top panel a gallery forest can be seen in background, immediately bordering the savanna. In the bottom panel, the tree in the foreground is *Crossopteryx febrifuga*, the most common woody species in these savannas.

Figure 3.3: Photographs of the different forest sub-types occurring in the study site. a) Gallery forest and b) forest patches or “bosquets” within the savanna (outlined), c) colonising forest in a savanna that has been fire suppressed, d) the interior of the densely vegetated *Marantaceae* forest, and e) Prof. Kate Parr at the edge of the mature forest, next to a big tree and standing amidst a sparsely vegetated understorey.

Figure 3.4: Mean monthly rainfall (blue bars) and cumulative water deficit (blue line) (calculated following Aragão *et al.*, 2007) in each month of the year in Lopé National Park. Shaded pink blocks show the short and long dry seasons that occur annually.

Figure 3.5: Photographs of emaciated forest elephants foraging at the forest-savanna transition during the late dry season (August/September) during this study.

Figure 3.6: Photographs of two of the fire fronts that resulted from the experimental burns in this study.

Figure 4.1: Map of the forest-savanna mosaic of the field site and the location of the forty high and low fire frequency transects within it (Agence Nationale des Parcs Nationaux, 2006).

Figure 4.2: Showing the layout of each transect at the forest-savanna transition. Field definitions of vegetation types were physiognomic, and used only to ensure sufficient sampling, rather than in quantitative analysis. a) In each transect, 25 m of savanna was sampled, followed by the entire transition, followed by 10 m of forest. b) At each site, an elephant path ran along the edge of the savanna.

Figure 4.3: a) An example of the simple apparatus used to measure flammability traits of the grass species, this image shows the set up to measure maximum combustion rate, whereby a piece of grass is burnt and the speed at which it loses weight is recorded. b) One of the thermocouples used to measure fire intensity and temperature, the data logger was wrapped in a fire blanket and aluminium foil, leaving only the thermocouple wire outside, which was attached to a metal rod at 30 cm above the ground.

Figure 4.4: a) Laying the transect across the forest-savanna transition, and b) measuring the diameters (at 10 cm above the ground) of the trees inside it before c) tagging and recording the tree species and d) measuring each tree's crown dimensions. Pictured here are Guy Antoine Kamba (b and c) and Eddy Milamizokou Nappo (a and d), members of the field team.

Figure 4.5: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the landing screen (top), classification window (bottom) and elephant count window (inset). More details can be found in the appendix of **Chapter 7**.

Figure 4.6a: A selection of the images captured by the camera traps, which included forest elephants as well as gorillas, leopards, chimpanzees, mandrills, and pangolins.

Figure 4.6b: A selection of the images captured by the camera traps, which included forest elephants as well as gorillas, leopards, chimpanzees, mandrills, and pangolins.

Figure 5.1: Map showing the location of a) Lopé National Park in Gabon, b) the study area within the park, and c) the eighteen forest-savanna transition transect sites (Agence Nationale des Parcs Nationaux, 2006).

Figure 5.2: Mean canopy leaf area index (LAI) and mean grass biomass (tons.ha⁻¹) across forest-savanna transitions in 18 regularly burnt transects. The median point (and interquartile range) of fire extinction is shown by “X” (and a solid black line). The zero point on the x-axis represents the edge of the savanna. Positive distances on the x-axis are in the savanna and towards its interior, while negative distances are across the transition and towards the forest interior. Points and error bars show the mean and its standard error. The fitted curves show the results of Border-and-Ecotone Detection Analysis (BEDA) (Hennenberg et al., 2008). The detected border for LAI was 0 m into the savanna (at the savanna edge), where LAI = 3.1 (shown as dark green * on the figure). The ecotonal area for LAI was between -1.4 m and 1.3 m into the savanna (2.7 m wide, shown by dark green shaded rectangle). The border for grass biomass was 1 m into the savanna, where grass biomass = 2.2 (shown as light green * on the figure). The

ecotonal area for grass biomass is between -1.8 m and 3.7 m into the savanna (5.6 m wide, shown by light green shaded rectangle).

Figure 5.3: Fire intensity (kW.m^{-1}) at different distances into the savanna (m) as measured in 18 burnt transects across forest-savanna transitions. Points represent measured intensities, and the line represents the generalised linear model fitted to these points (model fitted with the gamma distribution and a log link, with transect included as a random effect: $\text{df}=68$, intercept = 5.4 ($p<0.0001$), slope = 0.06 ($p<0.0001$), marginal R^2 using the trigamma estimate = 0.11). Positive distances on the x-axis are towards the savanna interior, negative distances (across the transition and towards the forest interior) were not measured in the experimental set-up.

Figure 5.4: Mean recorded temperatures ($^{\circ}\text{C}$) after temperature first crossed a threshold of a) 150°C or b) 60°C for thermocouples placed at 0 m, 10 m, or 20 m into the savanna. Time 0 was the point at which the temperature first exceeded the threshold. Shaded ribbon shows standard error around the mean. The area under each curve represents the total thermal dose (150°C threshold: 0 m = 16456°C , 10 m = 19911°C , 20 m = 20908°C ; 60°C threshold: 0 m = 25030°C , 10 m = 25043°C , 20 m = 22601°C). Time spent above each threshold was the distance between first and last recording of the threshold temperature (150°C threshold: 0 m = 65 s, 10 m = 70 s, 20 m = 79 s; 60°C threshold: 0 m = 223 s, 10 m = 202 s, 20 m = 166 s).

Figure 5.5: a) Total and per species grass biomass (tons.ha^{-1}) and b) tree canopy leaf area index across 18 regularly burnt forest-savanna transition transects. The zero point on the x-axis represents the edge of the savanna, while positive distances are towards the savanna interior. Points and error bars show the mean and its standard error. Different letters indicate significant differences in the variable at different distances into the savanna as determined by Kruskal-Wallis tests (significance noted at $p<0.05$).

Figure 5.6: a) Mean weight loss (% initial weight) over time during combustion and b) mean fuel moisture content over time during ambient air drying of the three dominant grass species: *Anadelphia afzeliana*, *Hyparrhenia diplandra*, and *Imperata cylindrica*. In (a), the solid line shows the fitted Boltzmann curve for each species (*A. afzeliana*: $p<0.01$, $\text{df}=212$; *H. diplandra*: $p<0.01$, $\text{df}=185$; *I. cylindrica*: $p<0.01$, $\text{df}=208$). In (b), points and error bars show the mean and its standard error; constant moisture content was reached after 8 days for *I. cylindrica* (at 17 %), after 10 days for *A. afzeliana* (at 14%), and after 13 days for *H. diplandra* (at 25 %); ignition point was reached at 19 % moisture content for both *A. afzeliana* (after 4 days) and *I. cylindrica* (after 5 days), and never reached for *H. diplandra*.

Figure S5.1: Calibration of disc pasture meter (DPM) in the study site, Lopé National Park, Gabon. Each point represents one calibration plot. Each calibration plot was 1 m x 1 m, in which the mean of five DPM measurements (one in each corner and one in the middle of the plot) was associated with the clipped grass biomass of the plot (dry weight after drying to constant mass in oven). The line represents the calibration equation, where the intercept was set to zero: Grass biomass (tons.ha⁻¹) = DPM height (cm) * 0.2675 (linear model: p<0.0001, adjusted R² = 0.94, F = 56.3, df = 17).

Figure S5.2: The method for calculating rate of spread of the fire front using thermocouples. Rate of spread was determined using the formula: $ROS = \frac{T_x - T_y}{D_{x,y}}$ where ROS is rate of spread (m.s⁻¹), T_x and T_y are the times (seconds) that

thermocouples x and y show their temperature peaks (ie. the time the fire front is assumed to cross the location of each thermocouple), with x being the first and y being the second thermocouple that the fire front passes, and D_{x,y} being the distance (m) between thermocouple x and y. In this example we calculate two rates of spread for one fire front, the ROS between thermocouples 3 and 5, and between thermocouples 5 and 7. Diagrams show: a) the layout of the thermocouples (labelled 1-9) within the savanna at varying distances (0, 10 and 20 m), and the movement of an approaching fire front (arrows) that crosses first thermocouple 3, then 5, then 7; b) calculation of the distance (D) between thermocouples 3 and 5; and c) calculation of the time that temperature peaks (T) for thermocouples 3, 5, and 7. In each transect, multiple rate of spread calculations could be performed. In this example, for instance, rate of spread could also be calculated between thermocouples 6 and 8, and between thermocouples 2 and 4.

Figure S5.3: Experimental set-up to test plant scale maximum combustion rate of each grass species.

Figure 6.1: Map of a) the study area and the forty transect sites and b) their location within the broader region of Lopé National Park in c) Gabon (Agence Nationale des Parcs Nationaux, 2006).

Figure 6.2: Split Moving Window Dissimilarity Analysis (SMWDA) and Moving Window Regression Analysis (MWRA) for high (a) and low (b) fire frequency transects. SMWDA z-scores are shown by solid coloured lines, MWRA slopes by solid black lines. *s indicate detected ecotone locations (turning points), ↑ and adjoining lines indicate width of ecotones (maximum and minimum of regression slopes in MWRA). Horizontal dotted lines at y=1.645 (coloured lines) and y=0 (black lines) mark the significance

thresholds for SMWDA and turning points in MWRA respectively. The detected communities are denoted on the x-axis.

Figure 6.3: Profiles of high (a) and low (b) fire frequency transects based on actual data collected. Diagram shows where, on average, the trees of each species were found along the transect. All trees are drawn to scale for mean height and canopy dimensions per species. Tree density depicted is proportional to a transect 5 m wide, allowing representation of the correct ratios of whole trees. Tree species canopies are colour-coded according to which community they were part of.

Figure 6.4: Principal Components Analysis using community weighted mean fire-resistance traits of transect blocks (n=98). Sample blocks of transects are colour-coded according to detected communities determined by SMWDA and MWRA (savanna, transition, and forest). The Principle Component 1 axis explained 60% of the variation in the data. The Principle Component 2 axis explained 14% of the variation in the data.

Figure 6.5: Frequency histogram showing trunk diameter distribution of each tree species in the transition community.

Figure 6.6: Mean canopy leaf area index (LAI) (a) and mean grass biomass (tons.ha⁻¹) (b) along high (red circles) and low (blue triangles) fire frequency transects. Communities are shown on the x-axis, with the width of the transition in high (red) and low (blue) fire frequency transects shaded. Different letters indicate significant differences in LAI or grass biomass between vegetation types (LAI: $\chi^2=280$, $p<0.0001$, $df=2$, mean LAI: savanna = 1.5, transition = 4.4, forest = 5.0; grass biomass: $\chi^2=1401$, $p<0.0001$, $df=2$, mean grass biomass (tons.ha⁻¹): savanna = 3.9, transition = 0.1, forest = 0.0). Error bars show standard error around the mean.

Figure S6.1: Photographs of the study site, Lopé National Park, Gabon, showing a) the mosaic of forest and savanna, b) a sharp forest-savanna transition as seen from the air and c) the forest-savanna transition as seen from the ground.

Figure S6.2: Diagram of transect, spanning three field-defined vegetation types. Vegetation types were defined in the field using physiognomic characteristics. Savanna was defined to be where grass cover was continuous, woody canopy cover discontinuous, and visibility was >5 m; transition where grass cover became discontinuous, woody canopy cover became vertically and horizontally continuous, and visibility was <5m, and the forest where the woody canopy was vertically discontinuous with the understory vegetation and visibility was >5 m. The entire field-defined transition was sampled, as well as an adjacent 25 m savanna and 10 m forest. Transects

were 2 m wide, of variable length, and were sampled in 1 m increments (1 m x 2 m blocks). Transect sites were randomly selected in GIS by placing points on a line that ran across all forest-savanna transitions and then selecting a subset of these using a random number generator. Sites were then deemed acceptable if they met the following criteria: > 100 m from other transect sites, > 50m road/river/marsh, associated forest or savanna patch was >50m wide, > 50m from another forest edge (ie. forest finger is not too narrow), not on very steep slope, not on obviously rocky substrate, not across an obvious tree-fall gap, easily accessible by car or foot (< 2 hours walk each way).

Figure S6.3a: Bark thickness allometries for each focal species. Adjusted R^2 and p values for each species extracted from linear models.

Figure S6.3b: Tree height:diameter allometries for each focal species. Adjusted R^2 and p values for each species extracted from linear models.

Figure 7.1: Map showing the location of a) Lopé National Park in Gabon, b) the study area within the park, and c) the 40 camera trap locations across high and low fire frequency sites within the forest-savanna mosaic (Agence Nationale des Parcs Nationaux, 2006).

Figure 7.2: a) Mean elephant density at the forest edge (May 2016-July 2017) as calculated from camera traps. Shaded area shows standard error around the mean. Horizontal lines show previously estimated forest elephant densities in other vegetation types in the landscape, as well as the mean annual density in this study. Shaded pink blocks show the long dry season that occurs annually. b) Total fruit availability score (monthly mean from 1986-2018) for the forest edge and interior. c&d) Showing the relationship between forest elephant density at the forest edge and fruit availability at the forest edge (c) (linear model, slope=0.000077, intercept=1.8, adjusted R^2 =0.55, p <0.005, df =12) and the forest interior (d) (linear model, slope=0.000083, intercept=2.7, adjusted R^2 =-0.07, p =0.70, df =12).

Figure 7.3: a) Proportion of trees in each size class incurring different types of forest elephant damage. Note that the y-axis has been compressed for display purposes. b) Table of which size class trees forest elephants prefer to browse in each preference categories of species. c) Size distribution of trees for species avoided, somewhat preferred, and strongly preferred by forest elephants. No significant differences were between observed (coloured bars) and expected (dotted lines) frequencies of stems in each size class, or between frequencies of stems in each preference categories (in χ^2 tests p was always > 0.5)

Figure 7.4: a) Grass biomass and b) tree canopy cover (leaf area index, LAI) around the forest elephant path that runs along the edge of the savanna, parallel with the edge of the forest. Positive distances from the forest edge are in the savanna, negative distances in the forest. Different letters indicate significant differences between sites where the path acted as a fire-break, vs those in which it did not as determined by Kruskal-Wallis tests ($p < 0.05$).

Figure S7.1: Camera trap images of emaciated forest elephants, captured during this study at the end of the dry season (August/September 2017).

Figure S7.2: Photographs of the study site showing a) the sharp transitions between forest and savanna and the location of the forest edge and b) an example of the elephant path that runs along the forest edge and how it acts as a fire break during burning.

Figure S7.3a: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the landing screen (top), classification window (bottom) and elephant count window (inset).

Figure S7.3b: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the pre-classification tutorial.

Figure S7.3c: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the field guide that citizen scientists can consult during classification.

Figure S7.4: Fruit availability score (mean monthly 1986-2018) for each species in the phenology dataset.

Figure S7.5: A heavily used forest elephant path in the savanna interior that shows no ability to act as a fire-break.

Figure 8.1: A diagram summarising the findings of the thesis.

List of tables

Table 5.1: Flammability traits for the three main grass species: *Anadelphia afzeliana*, *Hyparrhenia diplandra*, and *Imperata cylindrica*. The “Method” column indicates whether the trait value was determined at the whole plant scale using field-based measurements (“field”) or from laboratory-based measurements made on mixed plant parts analysed in a calorimeter (“laboratory”). Where applicable, values show the mean ($\pm$ standard error). Different letters indicate significant differences ($p < 0.05$) after pairwise comparison of mean ranks in Kruskal-Wallis tests.

Table S5.1: Fire behaviour and climate-related metrics measured during burning of 18 forest-savanna transition transect sites.

Table S5.2: Linear models where fire behaviour metrics were examined as a function of climate-related metrics. Significant effects ($p < 0.05$) are marked with an *. With the exception of fuel moisture content and mean and maximum wind speed on maximum temperature, no significant effects of climate-related metrics on fire behaviour metrics were found.

Table 6.1: Showing i) the p-value of χ^2 tests on observed versus expected frequencies of focal tree species in each communities, and whether the associated residuals (Pearson standardised) were positive or negative; and ii) the p-value of indicator value tests run on each focal species to test if it was a significant indicator species for one of the communities. Significant results ($p < 0.05$ or residual > 2.13) are marked with an *. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Table S6.1: Mean functional trait values for each focal tree species. Different letters indicate significant differences in mean values between species ($p < 0.05$) according to Kruskal-Wallis tests.

Table S6.2: The ecology, according to the literature, of the seventeen focal species of the study. The table shows a summary of the available literature, both that which originates from within the study site (Lopé National Park, Gabon), and from further afield.

Table S6.3a: Showing, for adult trees, i) the χ^2 and p-value of tests on observed versus expected frequencies of focal tree species in each vegetation type, and the associated

residuals (Pearson standardised); and ii) the indicator value and associated p-value for each focal species to test if it was a significant indicator species for one of the vegetation types. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Table S6.3b: Showing, for juvenile trees, i) the χ^2 and p-value of tests on observed versus expected frequencies of focal tree species in each vegetation type, and the associated residuals (Pearson standardised); and ii) the indicator value and associated p-value for each focal species to test if it was a significant indicator species for one of the vegetation types. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Table S6.4: An extract from the census data (abundance and basal area) collected by White *et al.* (2001)¹ in savanna (regularly burnt), colonising forest (a.k.a. savannas where fire had been suppressed for > 10 years and become forest encroached) and various mature forest (fire-free) vegetation types. In 1 ha plots across different vegetation types all trees > 5cm diameter were identified and measured. Vegetation types covered the hypothesised stages of forest succession: savanna to colonising forest to monodominant *Aucoumea klaineana* forest to young *Marantaceae* forest to older mixed *Marantaceae* forest. Other old/mature forest types are also shown.

Table S6.5: Summarising the ecology of the African congeneric species of the transition tree community. All congeners are listed in the table, except for genus *Psychotria*, which had too many congeners to list and thus only the species in the most closely related clades were used (according to Andersson, 2002)¹.

Table 7.1: Degree to which tree species at the forest edge are preferred (preference ratio >1), somewhat preferred (preference ratio <1), or avoided (preference ratio = 0) by forest elephants.

Table S7.1: All data sets used in calculation of the “fruit availability score”.

Chapter 1:

Introduction

By:

Anabelle W. Cardoso



Photo: Anabelle W. Cardoso

1.1 Thesis rationale

Questions about what determines vegetation distribution have puzzled ecologists for some time. At continental scales, it is mostly determined by climate (Whittaker, 1962; Holdridge, 1967), with mean annual precipitation (MAP) limiting maximum tree cover and differentiating open-canopied savanna from closed-canopied forest (Sankaran *et al.*, 2005). However, this deterministic relationship breaks down at the landscape scale. Forest-savanna mosaics, common across the tropics, are the quintessential example of this breakdown (Parr *et al.*, 2014). In these landscapes, despite MAP predicting forest, both forest and savanna often co-exist (Sankaran *et al.*, 2005; Staver *et al.*, 2011a). Other abiotic factors, like soil, offer incomplete explanations to this vegetation distribution conundrum (Bond, 2010; Favier *et al.*, 2012). The disequilibrium of certain tropical landscapes with MAP has been attributed to disturbance, specifically by large consumers of plant biomass (Bond, 2005). Mammal herbivores, like elephants, and fire are cited as the two most important consumers in the tropics (Bond, 2005). Their relative importance varies between landscapes, as does the disturbance regime they execute on forest and savanna within the same landscape (Hirota *et al.*, 2011; Staver *et al.*, 2011a,b; Archibald & Hempson, 2016; Charles-Dominique *et al.*, 2018).

The most readily observable difference in disturbance between forests and savannas is their fire regime. Savannas have an open canopy of scattered trees and a continuous heliophilic C4 grassy understorey (Ratnam *et al.*, 2011). This grass layer seasonally dries and becomes flammable, resulting in savannas experiencing the highest fire

frequencies on earth (Mouillot & Field, 2005). This regular surface-fire regime consumes tree saplings within the flame zone and prevents them from transitioning into larger size classes, thus maintaining an open canopy (Grady & Hoffmann, 2012; Hoffmann *et al.*, 2012). In contrast, forests are tree-dominated; they have a closed canopy and a shade-tolerant understorey (Ratnam *et al.*, 2011). The abundance of adult size class trees in forests shade out C4 grasses and usually exclude fire, thus maintaining a closed canopy (Hoffmann *et al.*, 2012). Fire therefore mediates stabilising feedbacks that reinforce forest and savanna distribution (Hirota *et al.*, 2011; Staver *et al.*, 2011c,b). This, combined with their ability to co-exist in a single mosaicked landscape, has led to the proposal that, at intermediate levels of MAP, forest and savanna are alternative stable states (Hirota *et al.*, 2011; Staver *et al.*, 2011c,b; Dantas *et al.*, 2016).

In Africa, mammal herbivores, specifically elephants, also enact different disturbance regimes on forest and savanna. For the most part, these differences can be attributed ecological differences between forest-dwelling forest elephants (*Loxodonta cyclotis* (Matschie, 1900)) and savanna-dwelling savanna elephants (*L. africana* (Blumenbach, 1797)). These two species mostly do not overlap in range, and therefore landscapes are usually disturbed by either one or the other. Savanna elephants, like fire, maintain the open canopy of savannas by toppling large trees or repeatedly damaging their canopy and bark which eventually results in the tree dying (Laws, 1970; Midgley *et al.*, 2005; Asner & Levick, 2012; Morrison *et al.*, 2015). The effects of forest elephant disturbance are less well understood. They may reduce canopy closure by breaking saplings in the

understorey (Terborgh *et al.*, 2016) and maintaining open patches within the continuous forest with their feeding behaviour (Klaus *et al.*, 1998; Turkalo *et al.*, 2013). On the other hand, they may reinforce the closed canopy of the forest by dispersing seeds and promoting tree recruitment (Blake *et al.*, 2009).

The different disturbance regimes of forest and savanna interface with one another at the forest-savanna transition. The transition acts as a boundary between forest and savanna, reinforcing their distribution by separating their disturbance regimes. However, forest and savanna distribution is not stable and both biomes can alternatively expand and contract through time (Maley, 2002; Aleman & Staver, 2018). When shifts in distribution occur, the transition is the most dynamic zone of change, acting as the frontier of forest or savanna advancement or retraction (Favier *et al.*, 2004; Oliveras & Malhi, 2016; Aleman & Staver, 2018). The transition's role in vegetation distribution is thus disproportionately important relative to the amount of space it occupies in a landscape (Oliveras & Malhi, 2016). Despite this, we know relatively little about the disturbance regime the transition actually experiences and how this affects its dynamics through time.

Addressing this knowledge gap is crucial as forest and savanna are expected to be amongst the most vulnerable vegetation types to climate and land-use change in the future, with forest-savanna transitions being especially sensitive to these changes (Higgins & Scheiter, 2012; Moncrieff *et al.*, 2014; Aleman *et al.*, 2016; Oliveras & Malhi, 2016). Both fire and elephants are already being significantly impacted by

anthropogenic activity. There is evidence that global burnt area has started to decrease over the past 18 years, especially in savannas, as a result of agricultural expansion and intensification (Andela *et al.*, 2017). Furthermore, forest elephant populations have drastically declined across Africa as a result of ceaseless hunting pressure (Maisels *et al.*, 2013). These changes in disturbance regime will no doubt exert considerable pressure on the forest-savanna transition, but without an understanding of the magnitude or direction of this pressure it is difficult to appropriately manage tropical landscapes to avert catastrophic losses in ecosystem function.

The aim of this thesis was to investigate the ecology of forest-savanna transitions, with a specific focus on how they are affected by fire and elephants. The field site for this research was the forest-savanna mosaic of Lopé National Park (LNP), located in Gabon in Central Africa (**Fig. 1.1**). The mosaic in LNP is ancient, with the savanna parts of the mosaic pre-dating the parts of the forest adjacent to it (Peyrot *et al.*, 2003). This ancient savanna has been regularly burnt as part of the fire management program since 1993, and likely for at least 5000 years prior (White, 2001; Jeffery *et al.*, 2014). LNP experiences relatively low hunting pressure and is home to one of the world's largest forest elephant populations, with the highest ever estimated densities of forest elephants located inside the study site (3 elephants.km⁻²; White *et al.*, 1993; White, 1994; Maisels *et al.*, 2013). Together, these factors make LNP one of the most intact and “natural” tropical forest-savanna mosaic landscapes globally, and thus an excellent model system for this study.

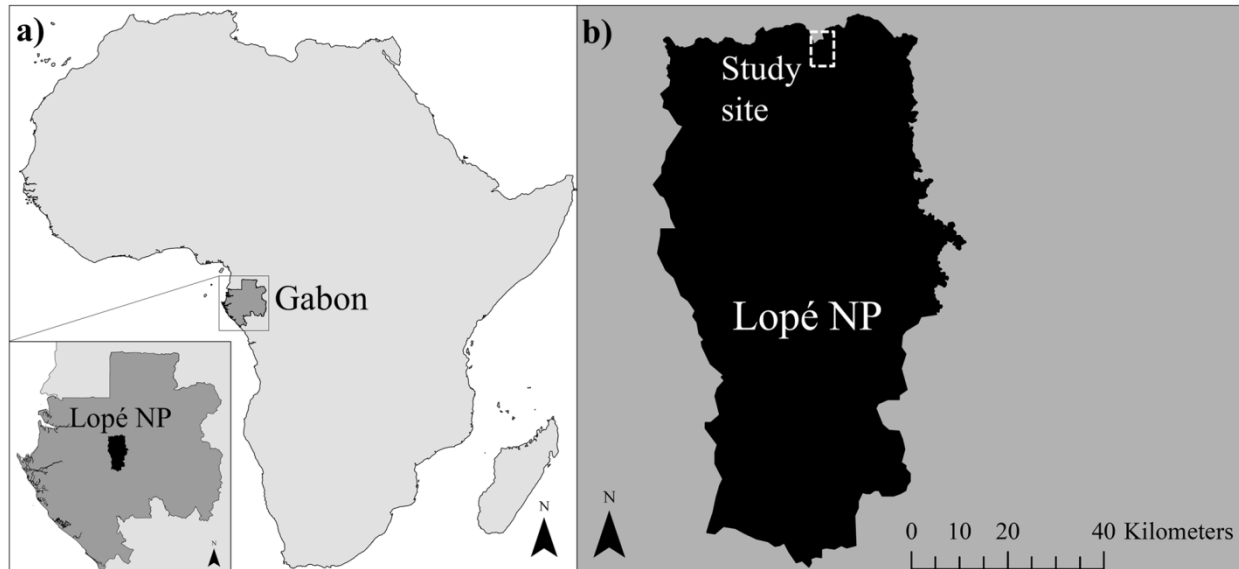


Figure 1.1: Map of the location of Gabon within the African continent (a) and the forest-savanna mosaic field site within Lopé National Park (b) (Agence Nationale des Parcs Nationaux, 2006).

The field site experiences relatively high annual rainfall for a savanna (approximately 1400 mm), and in landscapes with this level of precipitation previous studies have predicted fire to be a more dominant disturbance than herbivory (Archibald & Hempson, 2016). The research presented in this thesis thus begins, in **Chapter 5**, by characterising the fire regime experienced by the forest-savanna transition. This chapter focuses on quantifying fire behaviour changes that occurred around the point of fire suppression between forest and savanna, and explores the role of biotic, namely grassy fuel, and abiotic, namely canopy shading, mediators of this fire regime. As fire regimes can filter trees into distinct communities based on their functional traits (Hoffmann *et al.*, 2003; Charles-Dominique *et al.*, 2015), in **Chapter 6** this thesis investigates whether the fire regime of the transition resulted in development of a distinct woody vegetation type that is different to both forest and savanna. Additionally,

this chapter assesses the importance of regular burning for maintaining the transition and the other vegetation types of the mosaic. In addition to fire being a regular feature in the field site, forest elephant biomass is also exceptionally high (White, 1994). Elephants are known ecosystem engineers, and they anecdotally make frequent use of the transition, where their paths are thought to act as moderate fire breaks (Sukumar, 2003; Oliveras & Malhi, 2016). Thus, in **Chapter 7**, this thesis characterises forest elephant use of the forest-savanna transition, focusing specifically on how this use may be interacting with the effects of fire to determine transition dynamics, and thus forest and savanna distribution, in the mosaic over time.

1.2 Thesis aim and objectives

This thesis aimed to investigate the ecology of forest-savanna transitions, with a specific focus on how they are affected by fire and elephants. This aim was addressed through three research articles, each of which had a guiding objective.

Objective 1: To empirically describe the fire suppression threshold and the interactive abiotic and biotic controls on it.

To fulfil this objective the following research questions were addressed:

Q1) Is there evidence for a fire suppression threshold within the forest-savanna transition?

Q2) Does fire behaviour change within the savanna before reaching the threshold in **(Q1)**?

Q3) To what extent are any fire behaviour changes in **(Q2)** a function of shifts in biotic factors, like grass, and/or abiotic factors, like shading?

Objective 2: To assess whether a distinct transition tree community could be identified at the forest-savanna transition, and to investigate its ecology.

To fulfil this objective the following research questions were addressed:

Q2) Do tree species in the forest-savanna mosaic filter into distinct communities?

Q1) Is there a detectable transition in the forest-savanna mosaic?

Q3) Does fire maintain the diversity of tree communities in the forest-savanna mosaic?

Objective 3: To quantify forest elephant use of the forest-savanna transition, assess the drivers of this, and determine the consequences for transition dynamics.

To fulfil this objective the following research questions were addressed:

Q1) Is the forest-savanna transition an important forage resource for forest elephants?

Q2) Which species do forest elephants prefer to browse at the forest-savanna transition, and is this reflected in these species' size demography?

Q3) Is forest elephant activity at the forest-savanna transition important for preventing savanna fires from burning into the forest?

1.3 Thesis structure

This thesis is article-based and presented according to the requirements for the University of Oxford's DPhil degree in Geography and the Environment. The thesis is organized into eight chapters. **Chapter 1** introduces the thesis and sets out the specific aims and research questions it will be addressing. **Chapter 2** sets the research into a broader context by reviewing the literature and identifying the research gaps the thesis fills. **Chapter 3** describes the field site where the research took place, and **Chapter 4** briefly explains the methodology used. **Chapters 5, 6, and 7** address the three main objectives of the thesis by presenting the three research articles produced. Finally, the conclusions and implications of the research are discussed in **Chapter 8**.

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Chapter 2:

Literature review

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Photo: Anabelle W. Cardoso

2.1 Forest-savanna transitions as components of dynamic mosaicked landscapes

The forest-savanna transition is the most widespread ecotone in the tropics (Torello-Raventos *et al.*, 2013). Ecotones were first defined by Odum in 1959 as “transitions between two or more communities; junction zones or tension belts which may have considerable linear extent but are narrower than the adjoining community areas themselves”. The forest-savanna transition thus occupies a three-dimensional space in the landscape and exists as more than just a conceptual two-dimensional delineation between tree-dominated forest and grass-dominated savanna. Because of this, the transition has a width and occupies a belt of space between forest and savanna.

Forest-savanna transitions are the characteristic feature of forest-savanna mosaics, where forest and savanna fragments interlock with one another across a single landscape (Oliveras & Malhi, 2016). Forest-savanna mosaics are a widespread feature of the tropics, occurring in places of intermediate rainfall, where this rainfall falls seasonally (Lehmann *et al.*, 2011). Natural forest-savanna mosaics covered 3.2 million hectares of the tropics in 1997 (Achard *et al.*, 2002). Forest-savanna mosaics are dynamic, with fire playing a universally important role in determining the distribution of forest and savanna across them (Favier *et al.*, 2004; Hoffmann *et al.*, 2005; Müller *et al.*, 2007; Silva *et al.*, 2008; Trauernicht *et al.*, 2012; Dantas *et al.*, 2013a; Ibanez *et al.*, 2013; Charles-Dominique *et al.*, 2015). Such mosaics cover 9% (or 2.72 million km²) of

Africa, where they are usually ancient and biodiverse landscapes of high conservation value (Walters *et al.*, 2013; Parr *et al.*, 2014).

Forests pre-date savannas as a vegetation type, and covered much of Africa until 6-8 Ma, when they retreated under the pressure of advancing savannas (Cerling *et al.*, 1993, 1997). The success of savannas was driven by the rise to dominance of their C4 grasses (Edwards *et al.*, 2010). This rise was facilitated by lower atmospheric CO₂ concentrations, which gave a competitive advantage to grasses using the C4 photosynthetic pathway over trees using the C3 pathway (Edwards *et al.*, 2010). This competitive advantage was enhanced by the other evolved traits of C4 grasses, specifically their high growth and slow decay rates which promoted fire by increasing flammable fuel loads (Bond, 2008). C4 grasses flourished with fire, as they were able to rapidly recover after burning and outcompete trees for resources, thus further promoting fire and the expansion of the savanna (Bond, 2008). The last 2.6 Ma have seen periods of both savanna advancement, when climate is drier and atmospheric CO₂ is lower, as well as periods of forest expansion, when climate is wetter and atmospheric CO₂ is higher (Prentice *et al.*, 2011). The forest-savanna transition is therefore dynamic through space, oscillating with climate on decadal to millennial timescales (Maley, 2002).

In Central Africa, movement of the forest-savanna transition has been affected by both climate and human use of the landscape (White, 2001a). The “Late Holocene Rainforest Crisis” of approximately 2.5 ka saw large-scale forest retreat with concomitant

savanna expansion across the region (Maley, 2002). Attributing a single cause to this change is complex, as both global climatic and local human land use changes were occurring. There is evidence that climate was drier during this period, making conditions more favourable for savanna expansion (Vincens *et al.*, 1999). However, Neolithic and early Iron Age farmers were also moving into the area, likely both exploiting the more open conditions and exacerbating them by cutting down trees to make charcoal for smelting iron (Schwartz, 1992; Malhi, 2018). Iron age populations reached a maximum around 1.9 ka, during which time slash-and-burn agricultural practices and the use of fire for hunting and iron smelting would have maintained the forest-savanna mosaics of the region (Oslisly *et al.*, 2013).

Following this, a wetter climate from 1.4 ka would have favoured forest expansion, especially in forest-savanna mosaics (Ngomanda *et al.*, 2009). This effect may have been exacerbated by decreases in human population in the area as people moved to climates more suitable for crop cultivation (Oslisly, 1995; Oslisly *et al.*, 2013). Human populations reappeared in the forest-savanna mosaics, specifically those of our field site, around 700 ya, and persisted until the 1870s when French colonisers reached the area (Oslisly, 1995). As a result of this long and complex history, many Central African landscapes presently carry signatures of past climate and human activity (White, 2001a; Malhi, 2018).

The fluctuations in the balance between forest and savanna observed in the past are likely to be insignificant compared to the unprecedentedly fast and extreme

fluctuations that will likely be induced by the current acceleration in anthropogenic climate and land use change (IPCC, 2007; Steffen *et al.*, 2015; Aleman *et al.*, 2016, 2018). Forest-savanna transitions are the most sensitive part of the landscape to these changes, since minor changes in environmental drivers can result in major changes in their structure and function (Oliveras & Malhi, 2016). Presently, anthropogenically induced climate changes, specifically increases in atmospheric CO₂, increases in global temperature, and increased precipitation over Central Africa are all expected to favour forest expansion at the expense of savannas (IPCC, 2007; Bond & Midgley, 2012; James & Washington, 2013). Savanna loss will be further aggravated by land use changes, especially in west and Central Africa, where a lack of protected areas makes these savannas some of the most vulnerable in the tropics (Aleman *et al.*, 2016). Loss of savanna to expanding forest has already been observed at multiple African sites (Schwartz *et al.*, 1996; Favier *et al.*, 2004; Mitchard *et al.*, 2009; Aleman *et al.*, 2018), including in Lopé National Park where this study takes place (Nana, 2005; Palla *et al.*, 2011; Jeffery *et al.*, 2014).

Extreme changes in vegetation distribution will benefit neither forest nor savanna. A degraded forest where grass has invaded may look like a savanna, and a fire-suppressed savanna where trees have encroached may look like a forest, but neither possess the astounding biodiversity or ecological functionality of their intact counterparts (Bond & Parr, 2010; Ratnam *et al.*, 2011; Veldman & Putz, 2011; Parr *et al.*, 2014; Veldman *et al.*, 2015; Veldman, 2016; McCleery *et al.*, 2018). It is worthwhile noting that while the devastating loss of charismatic tropical forests to waves of

deforestation has received widespread attention (e.g. Achard *et al.*, 2002; Malhi *et al.*, 2008; Hansen *et al.*, 2013), the equally concerning loss of ancient and biodiverse tropical savannas has received notably less attention (Parr *et al.*, 2014).

Although the balance between forest and savanna is dynamic, there are stabilising feedbacks that exist within both systems. Up until now, these feedbacks, mediated by fire and mammal herbivores, are what have allowed these ecologically opposite vegetation types to co-exist in mosaicked tropical landscapes for thousands of years (Bond, 2005; Hirota *et al.*, 2011; Staver *et al.*, 2011a,b; Hoffmann *et al.*, 2012a; Archibald & Hempson, 2016).

2.2 How does fire affect the forest-savanna transition?

The C4 grasses that dominate the understorey of tropical savannas are fast-growing, allowing them to accumulate large amounts of biomass quickly (Ehleringer & Monson, 1993; Gignoux *et al.*, 2006). This biomass dries out seasonally but decomposes slowly, allowing large amounts of flammable fuel to collect (Knapp & Seastedt, 1986; Ehleringer & Monson, 1993; Bond, 2008). When this fuel burns, as it regularly does (Mouillot & Field, 2005), trees caught in the flame zone lose their above-ground biomass (top-kill), and must resprout repeatedly to persist in the system (Bond & Midgley, 2001). Long-term persistence within the grass layer is common in savanna trees, and many individuals live for decades stuck in the fire-trap created by recurrent burning (Higgins *et al.*, 2000; Grady & Hoffmann, 2012). To escape the fire-trap, trees must grow sufficiently large in the time between consecutive fires to elevate their canopy out of the flame zone and must have accumulated sufficiently thick bark so as to protect their cambium during burning (Bond & Midgley, 2000; Lawes *et al.*, 2011; Hoffmann *et al.*, 2012a). This happens rarely (Wakeling *et al.*, 2011), and so the open canopy of the savanna that facilitates a flammable understorey continues to exist.

In contrast, forests have a closed canopy that shades out heliophilic C4 grasses from the understorey, eliminating the continuous layer of fine, dry fuels needed for fire to percolate (Hennenberg *et al.*, 2006; Archibald *et al.*, 2009; Hoffmann *et al.*, 2012b; Abades *et al.*, 2014). The closed canopy also creates a more still and humid micro-climate, making the system even less flammable (Uhl & Kauffman, 1990; Hennenberg *et*

al., 2008). Trees can thus establish in the understorey and grow into the canopy layer unimpeded by regular burning, reinforcing the closed canopy that facilitated this in the first place (Hoffmann *et al.*, 2012a).

In forest-savanna mosaics, these fire-mediated stabilising feedbacks are what allow forest and savanna to co-exist in one landscape (Hoffmann *et al.*, 2012a; Dantas *et al.*, 2016). Their co-existence, and the sharp boundaries between them, have led to the proposal that, when maximum tree cover is not limited by water availability (1000 – 2500 mm MAP), forest and savanna are alternative stable states (Hirota *et al.*, 2011; Staver *et al.*, 2011a,b) (**Fig. 2.1**). To be an alternative stable states means that either state, forest or savanna in this case, can exist at a point in space in time (Beisner *et al.*, 2003). Each state reinforces its presence via stabilising feedbacks, and thus changes between states are rare, and neither smooth nor easily reversible (Hirota *et al.*, 2011; Staver *et al.*, 2011b).

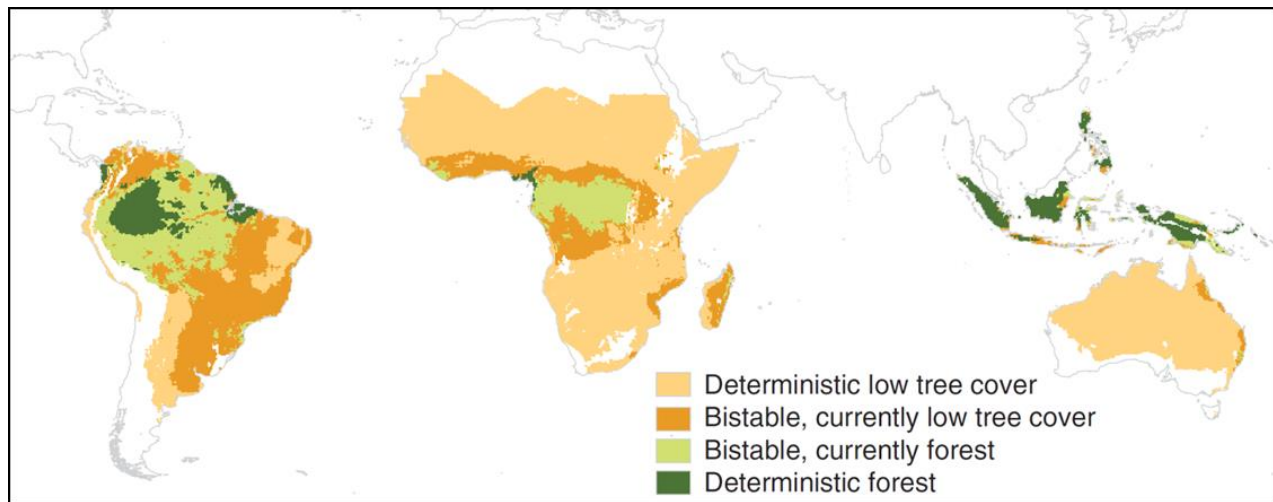


Figure 2.1: Distribution of forest and savanna across sub-Saharan Africa and the rest of the tropics. Areas where rainfall is too low to support a closed canopy are deterministically low tree cover systems (savanna and grasslands), and areas where rainfall is high are deterministically forest. Areas where rainfall is intermediate (1000 – 2500 mm MAP) are where either forest or savanna may exist as alternative stable states (bistable areas). These areas are coloured as to whether they currently support closed canopy forest, or open canopy savanna/grasslands. Figure from Staver *et al.* (2011b).

Shifts between alternative stable states occur suddenly and are difficult to predict (Scheffer & Carpenter, 2003). They are triggered by individual extreme perturbations to the system, or by repeated small perturbations that accumulate and erode the resilience of the system over time, or by a combination of both (Beisner *et al.*, 2003; Scheffer & Carpenter, 2003) (**Fig. 2.2**). A shift from savanna to forest can occur if fire becomes suppressed, giving the trees persisting within the grass the opportunity to grow to canopy height. It can also occur if nutrients, including air enriched with CO₂, are added to the system, allowing the trees to grow faster in the interval between fires, thus effectively lengthening the fire-free interval and gradually increasing the proportion of trees that escape the fire trap until a closed canopy forms (Bond & Midgley, 2000; Hoffmann *et al.*, 2012a). Conversely, a shift from forest to savanna can occur if an

extremely intense fire storm, caused by very dry, very hot, and very windy weather, burns into a forest edge, opening up the canopy and allowing grasses to establish (Barlow & Peres, 2008; Archibald *et al.*, 2017). It can also occur if persistent drought conditions allow even low intensity fire to repeatedly penetrate the forest, eventually killing forest trees that are replaced by grasses (Nepstad *et al.*, 2001; Cochrane & Laurance, 2002; Barlow & Peres, 2008; Hennenberg *et al.*, 2008; Brando *et al.*, 2012; Balch *et al.*, 2013, 2015; Silvério *et al.*, 2013). Under normal circumstances however, both of these circumstances are suitably rare, and the feedbacks maintaining co-existence suitably strong, that neither forest nor savanna has completely eliminated the other.

Forest and savanna are not universally considered to be alternative stable states at intermediate levels of MAP. Critics of this theory have published research showing that the statistical methods used on remote sensing data to detect multiple stable states at continental scales may produce results showing that a discontinuity in tree cover exists, when no such pattern is present in reality (Hanan *et al.*, 2014). This criticism was addressed by using validation data to show that the originally detected discontinuities were mostly reflected in reality (Staver & Hansen, 2015). In the case where forest and savanna are able to co-exist in a single landscape with sharp boundaries between them, physical and chemical soil properties have been cited as the key underlying cause (Lloyd *et al.*, 2009, 2015). Given these underlying soil differences, regular savanna burning is thus mathematically shown to be able to make these boundaries appear sharper than they actually are (Lloyd & Veenendaal, 2016). Supporting that no true

sharp boundaries between forest and savanna exist, field studies taking into account all layers of vegetation have found there to be no detectable boundary between the two vegetation types at all (Veenendaal *et al.*, 2014). It should be noted however that differences in underlying soil of vegetation types can be induced, rather than causal, of the overlying vegetation (Jobbágy & Jackson, 2004).

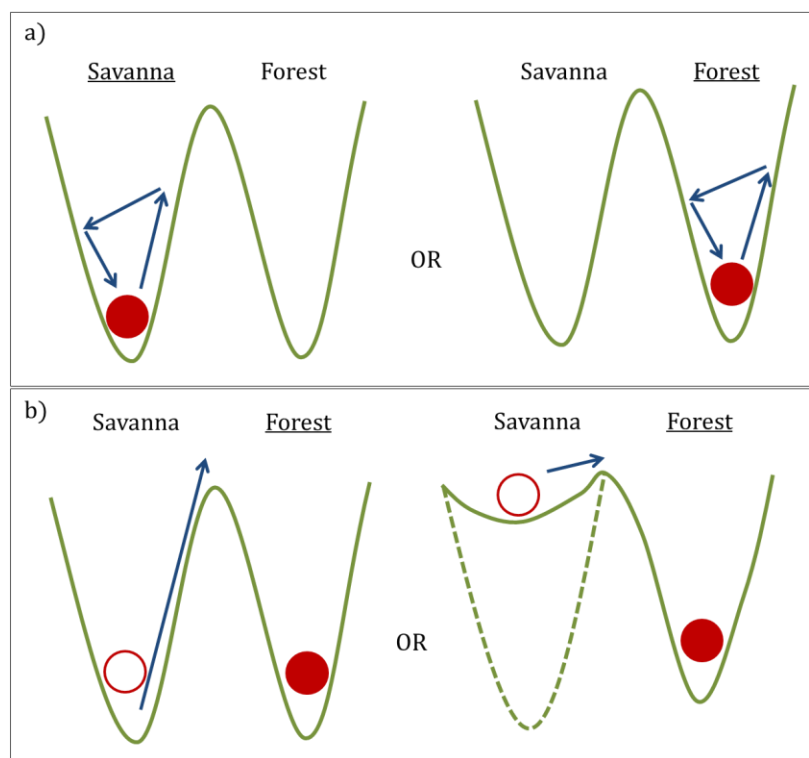


Figure 2.2: A diagrammatic representation of forest and savanna as alternative stable states, using a ball in basin analogy. The solid red ball sits in either a forest or savanna state (green basin). In (a), both forest and savanna are stable states, and so if disturbed (blue arrows) the ball will move up and down the sides of its current basin (stable state), but rolling into the adjacent basin is difficult as stabilising feedbacks exist to reinforce the initial state of the ball. In (b), the system is perturbed and the ball rolls into the adjacent basin and the stable state shifts, in this case from savanna to forest. This will occur either if an extreme perturbation affects the system (shown by the arrow on the left panel) or if resilience of the system is gradually eroded over time, making even small perturbations likely to cause a shift in state (shown by the arrow on the right panel). Figure based on Beisner *et al.* (2003).

The mechanism that prevents savanna fires from burning into forests is largely driven by differences in fuel flammability, mediated by differences in tree canopy cover. Although forests have sufficient amounts of fuel biomass to support a fire, these fuels are of high bulk density and moist, unlike the fine dry grassy fuels of the savanna (Biddulph & Kellman, 1998; Hennenberg *et al.*, 2006; Hoffmann *et al.*, 2012b). This is driven by the forest's higher tree canopy cover, which both directly shades out flammable grasses, and indirectly prevents fuel from drying to the point of ignition, as it otherwise would if the same fuel were in an open canopy savanna (Uhl & Kauffman, 1990; Biddulph & Kellman, 1998). The importance of canopy cover in determining where fires extinguish has been demonstrated repeatedly, both in south American (Hoffmann *et al.*, 2012a) and in Southern African (Archibald *et al.*, 2009) systems. Empirical evidence shows that once tree cover reaches a threshold level (leaf area index of 3, or a canopy cover of 40 %), fires fail to percolate and become eliminated from the understorey (Archibald *et al.*, 2009; Hoffmann *et al.*, 2012a; Abades *et al.*, 2014). The point at which canopy cover is high enough to induce a loss of fire from the system is known as the fire-suppression threshold (Hoffmann *et al.*, 2012a).

However, fire is not purely a binary disturbance, either present or absent in a system. Rather, its effects on vegetation dynamics are variable, determined largely by how intense it is (Higgins *et al.*, 2000). Fire intensity is a measure of how much energy a fire front releases as it moves across a landscape (Byram, 1959). It is the product of heat yield, or how much energy a unit of fuel releases as it burns, the biomass of the fuel consumed during burning, and the rate of spread, or speed of movement, of the fire

front (Byram, 1959). Fire intensity is thus determined by the prevailing weather conditions, especially wind, and by the flammability of the fuels being burned (Gill & Zylstra, 2005; Bradstock, 2010). Flammability is the ability of plant biomass to burn. Specifically, it describes how easily fuel catches alight (ignitability), how well it burns (combustibility), and how long it continues to burn for (sustainability) (Anderson, 1970; Gill & Zylstra, 2005). Flammability varies between fuel types (e.g. between woody trees and herbaceous grasses), and between plant species of the same fuel type (Simpson *et al.*, 2016a). It can also be influenced by weather conditions, for example recent rain events can increase fuel moisture levels and decrease fuel flammability (Biddulph & Kellman, 1998).

Recent studies have shown that flammability can vary significantly between grass species (Simpson *et al.*, 2016b). A separate study showed that variation in flammability between grasses and forbs can affect fire behaviour (Wragg *et al.*, 2018). A third study showed that grass species composition can change near the forest-savanna transition (Charles-Dominique *et al.*, 2018). Together, these imply that grass species composition and fire behaviour may change at the forest-savanna transition, suggesting that the mechanism preventing fire from spreading in to the forest interior from the burning savanna may be more complex than originally thought. Describing and explaining this complexity is what **Chapter 5** of this thesis addresses.

2.3 How does fire affect the tree community at the forest-savanna transition?

Functional traits are features of a plant that directly or indirectly affect its fitness by influencing growth, reproduction, and survival (Calow, 1987; Keddy, 1992; Violle *et al.*, 2007). Where in a landscape a plant species can persist, or its niche, is determined by its functional traits (Hutchinson, 1957). Different species that survive in similar niches may thus have similar suites of functional traits that allow them to persist under similar environmental constraints. Fire is a strong selective force in forest-savanna mosaicked landscapes, and filters trees into communities according to their functional traits (Hoffmann *et al.*, 2003; Müller *et al.*, 2007; Dantas *et al.*, 2013b; Charles-Dominique *et al.*, 2015, 2017). This leads to differences between forest and the savanna tree communities, namely that savanna tree species are fire-resistant but usually require light, while forest tree species are fire sensitive but can establish and persist in the shady forest understorey (Scholes & Archer, 1997; Hoffmann *et al.*, 2003; Geiger *et al.*, 2011; Gignoux *et al.*, 2016).

Being fire resistant requires savanna trees to invest in a resource-expensive suite of traits. Fire kills trees either by damaging the xylem or the phloem (hydraulic or stem-girdling death), or the cambium and the buds (meristematic death) (Midgley *et al.*, 2011). To prevent this, savanna trees accumulate thick bark quickly, which helps to insulate their xylem, phloem, cambium, and buds from lethal temperatures (Bond & Van Wilgen, 1996; Michaletz & Johnson, 2007; Dantas *et al.*, 2013b; Charles-Dominique *et*

al., 2017). Savanna trees also position their buds deep into their bark, which helps to insulate them from high temperatures, and often have more than bud per leaf axil (accessory buds), which facilitates resprouting after burning (Burrows *et al.*, 2008; Charles-Dominique *et al.*, 2015). They also store significant amounts of starch underground in large swollen root structures, which can be quickly mobilised to support canopy re-growth after burning (Bowen & Pate, 1993; Maurin *et al.*, 2014) (**Fig. 2.3**). In contrast, forest trees do not have to survive regular burning, and so investment in fire-resistance traits is a poor evolutionary strategy for them because it diverts resources away from other, more relevant, plant functions. Forest tree species are more likely to invest either in traits that allow them to grow fast and take advantage of ephemeral light gaps, or in traits that allow them to live longer and tolerate shade and other potential stressors through time (Wright *et al.*, 2010).

Trees at the forest-savanna transition are exposed to fire less frequently than those in the savanna interior, but a more frequently than those in the forest interior (Kellman & Meave, 1997). More recently, a study in a South African forest-savanna mosaic has shown that, although the gradient in canopy cover and fire regime between forest and savanna is abrupt, intermediate levels of canopy closure within the forest-savanna transition do exist (Charles-Dominique *et al.*, 2018). This study hypothesised that this intermediate level of canopy cover is associated with fires that are intermediately intense, and a tree community that is intermediately fire-resistant (Charles-Dominique *et al.*, 2018). The distinctness of this supposed tree community at the forest-savanna

transition, specifically its species composition, physical characteristics, and functional traits, was assessed in **Chapter 7** of this thesis.

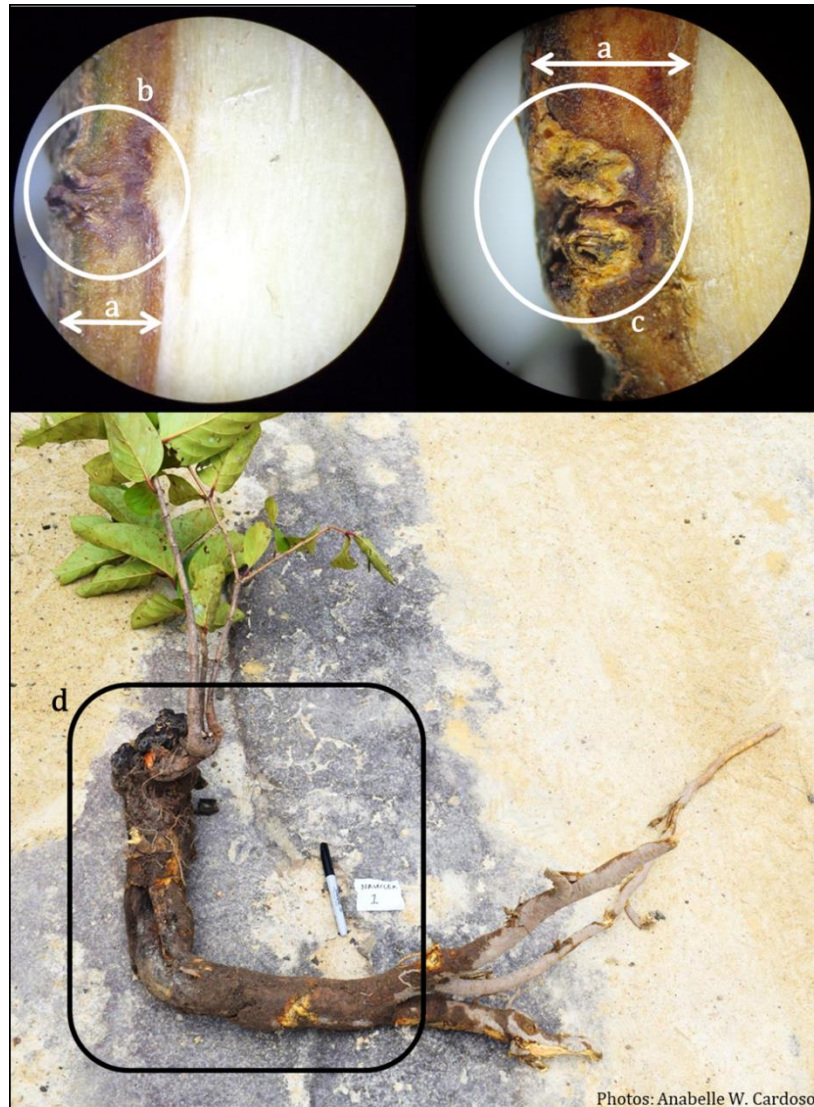


Figure 2.3: Showing fire-resistance functional traits of savanna tree species. The top panel shows cross sections of a savanna tree sapling where (a) shows the thick insulating bark accumulated by these species, (b) and (c) shows how these species bury their buds deep in the bark layer to further protect them and (c) how they have more than one bud per leaf axil to facilitate resprouting after fire. The bottom panel shows a savanna tree that has been dug out of the ground, where (d) shows the enlarged underground organ of this tree, in which large amounts of starch are stored to be mobilized after burning, enabling quick recovery of lost photosynthetic material.

2.4 How do the effects of fire and forest elephants interact at the forest-savanna transition?

Most of what we know about how elephants affect vegetation comes from research on savanna elephants living in savanna landscapes (Terborgh *et al.*, 2018). In these circumstances, elephants tend to promote the persistence of savanna via preventing canopy closure (Wing & Buss, 1970; Pellegrini *et al.*, 2017). This occurs both directly, as a result of their feeding preferences and social behaviour, and indirectly, as a result of their interactions with fire (Wing & Buss, 1970).

Savanna elephants usually have a net negative effect on tree cover. Although they are mixed feeders, browsing on trees as well as grazing on grasses, their browsing habits are notable destructive (Laws, 1970; Wing & Buss, 1970). In addition to aggressively browsing on the canopy, they also strip the bark off the trunk of the tree, which can lead to ring-barking and subsequent tree death (Laws, 1970). Savanna elephants also frequently uproot entire canopy size trees, significantly decreasing the number of canopy-size individuals, although whether this is for nutritional or social reasons is unknown (Laws, 1970; Ben-Shahar, 1993, 1996; Jacobs & Biggs, 2002; Midgley *et al.*, 2005; Shannon *et al.*, 2008; Asner & Levick, 2012). Even low-intensity elephant damage to trees, if repetitive, can significantly alter savanna dynamics, and is the primary cause of large tree mortality in certain sites, exceeding the effects of both fire and rainfall (Morrison *et al.*, 2015). The effect that elephants have on tree cover is so profound that they are able to shift a system from a dense woodland savanna to more open savanna

without fire being present (Pellegrini *et al.*, 2014). So destructive is the nature of the savanna elephant that they have historically been culled in certain national parks in Southern Africa (Dickson & Adams, 2009).

As a result of the direct reduction in canopy cover by savanna elephants, more light can reach the understorey. This can lead to increases in grass biomass, facilitating the penetration of fire into the system, which in turn maintains and enhances a more open canopy (Wing & Buss, 1970). So profound is the effect of elephants on tree cover, that in places where productivity is high, if the fire-interval is long enough then elephants become an integral component of maintaining canopy openness, as fire alone is unable to do so (Pellegrini *et al.*, 2014). The effects of elephants and fire on tree cover can also be additive, as elephants prefer to browse on previously burnt trees and fire causes more damage to trees already damaged by elephant browsing (Shannon *et al.*, 2011; Vanak *et al.*, 2012).

In contrast to our understanding of savanna elephants' effects on vegetation in savanna environments, we know much less about the effects of elephants on vegetation in forest environments. Both forest elephants and Asian elephants (*Elephas maximus*) forage in forests, but because it is difficult to directly observe elephants in such environments we know little about how this foraging effects forest dynamics (Terborgh *et al.*, 2018). Asian elephants seem to be important for seed dispersal in forests (Sekar *et al.*, 2017), seem to favour monocotyledonous browse and this are able to reduce the abundance of

such species when they are present, and may also affect tree seedling recruitment patterns through their browsing preferences (Terborgh *et al.*, 2018).

This study however focusses on forest elephants, which are the only species of elephant found in the study site. Forest elephants are a genetically distinct species from the congeneric savanna elephant (Rohland *et al.*, 2010; Ishida *et al.*, 2018). The International Union for Conservation of Nature (IUCN) considers forest and savanna elephants as one group, and classifies them as “vulnerable”, or facing a high risk of extinction in the wild (IUCN, 2018). Their reason for not separating African elephants into two species is that, despite good genetic evidence existing for this, all species and sub-species are not yet properly delineated, and it does not want hybrids between groups to be inappropriately conserved (IUCN, 2018). They do however note that African elephant vulnerability varies significantly across its range, and we know from previous work that the forest elephant populations of Central Africa are some of the most vulnerable due to high hunting pressure for both meat and ivory (Blake *et al.*, 2007; Maisels *et al.*, 2013; Poulsen *et al.*, 2017).

Forest elephants are ecologically different to savanna elephants (**Fig. 2.4**). The forest elephant is smaller than the savanna elephant and lives in smaller family groups (White *et al.*, 1993). The distribution of savanna elephants is largely determined by surface water availability (Chamaillé-Jammes *et al.*, 2007; Landman *et al.*, 2012; Davies *et al.*, 2018). In contrast, because water is usually abundant and well-distributed in tropical forests, forest elephant distribution is determined by forage availability (Blake, 2002).



Figure 2.4: How savanna (a) and forest (b) elephants look different to one another. The shape of their heads is distinct from one another, and the forest elephant is smaller with a longer tail.

Unlike the mixed-feeding savanna elephant, forest elephants are largely frugivorous, likely due to a combination of the forest understorey lacking elephant-accessible and preferred browse, and an abundance of fruiting tree species being available (White *et al.*, 1993; Blake, 2002). Forest elephant movement is thus likely to be influenced by fruiting seasons and the distribution of fruit-bearing trees across the landscape (White, 1992; Blake, 2002). Subsequently, forest elephants play a vital role in seed dispersal

and consequently are important components of maintaining forest community structure (Blake *et al.*, 2009). They have thus been referred to as “mega-gardeners of the forest”, or as the “tree planters of the Congo basin” (Blake *et al.*, 2009; Campos-Arceiz & Blake, 2011) (**Fig. 2.5**). The loss of forest elephants would likely lead to large-scale tree recruitment failure, and their presence is thus essential for forest ecosystem function (Blake *et al.*, 2009).



Figure 2.5: An old forest elephant dung pile in the forest, in which tree seedlings are clearly shown to be germinating, likely as a result of the seeds the elephant ate. Such a site is common, and shows the important role forest elephants play in tree seed dispersal and recruitment.

However, like their savanna elephant relatives, forest elephants can also be destructive. Their feeding behaviour can maintain and possibly create open patches within the continuous forest. For example, they are attracted to tree-fall gaps by the abundance of accessible vegetation in the understorey, and their heavy browsing may slow forest succession in these areas (White, 2001b). They also trample vegetation and eat the mud around salt-licks, preventing the colonization of these areas by denser vegetation (Klaus *et al.*, 1998; Turkalo *et al.*, 2013). Although forest elephants can't reach the canopy, they browse extensively on the saplings in the forest understorey, affecting tree recruitment patterns (Terborgh *et al.*, 2016). This may be the reason that forests containing elephants have an understorey that is less diverse and comprised of different species than the overstorey (Terborgh *et al.*, 2016). It may also be the underlying cause of the frequently observed patches of monodominant trees in the understorey, despite the overstorey being diverse (Terborgh *et al.*, 2016). Such phenomena are virtually undocumented in tropical forests that lack elephants and other mega-fauna, for example in the Amazon (Terborgh *et al.*, 2016).

Contrary to what their name might suggest, forest elephants are not restricted to the forest interior. They frequently make use of the more open habitats within their range, including the forest-savanna transition (White & Abernethy, 1997; Oliveras & Malhi, 2016). Here, forest elephants and fire interact, and may be having a significant effect on transition dynamics. Despite this, almost everything we know about these potential interactions is based on studies of savanna elephants. Establishing how forest and savanna elephants differ in their interactions with fire, and how this may affect

vegetation dynamics, is therefore crucial for appropriate management of dynamics tropical landscapes. This need is made even more pressing by the continued population decline of forest elephants, shortening the time and locations where assessment of their ecological function can still viably be made (Blake *et al.*, 2007; Maisels *et al.*, 2013; Poulsen *et al.*, 2017). Addressing this need is the focus of **Chapter 7** of this thesis.

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Chapter 3:

Field site description

By:

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Photo: Anabelle W. Cardoso

3.1 An introduction to the field site

Our study takes place in the forest-savanna mosaic of Lopé National Park (LNP), Gabon. Gabon is a medium-sized African country, spanning 267 667 km² (Lee *et al.*, 2006). It lies on the equator and is bordered to the east and the south by the Republic of Congo, to the north by Equatorial Guinea and Cameroon, and to the west by the Atlantic Ocean. 80% of Gabon is covered by tropical forest, with savannas found in the south, the center, and in the east (Lee *et al.*, 2006). Gabon is mega-diverse, home to 198 species of mammal, including more apes and forest elephants than any other African country, and 6,000 – 10,000 species of plants (Letouzey, 1968; Emmons *et al.*, 1983; Tutin & Fernandez, 1983; Maisels *et al.*, 2013).

Gabon's 13 national parks cover more than 10% of the country, and were gazetted in 2002. This was largely spurred by the work of conservationist Mike Fay, who, together with a team that included photographer Michael Nichols, traversed a 2000 km “mega-transect” across Gabon and into the Congo basin over 456 days. The resulting photographs and astounding biodiversity documented were used to make a compelling, and ultimately successful, case for the implementation of a network of national parks across Gabon (Quammen & Nichols, 2000, 2001, 2002, 2003; Lee *et al.*, 2006).

LNP is the second largest of Gabon's national parks, covering nearly 5000 km². It sits just below the equator and is bordered in the north by the Ogooué river, one of Africa's largest rivers that drains near all the water in Gabon, and to the east and west by the

Offoué and Mingoué rivers respectively (White & Abernethy, 1997). LNP is 120 km long, with the southern part of the park covered by continuous, closed canopy, tropical rainforest, and the northern and eastern edges by 800 km² of forest-savanna mosaic (**Fig. 3.1**). The mosaicked landscape of the Lopé-Okanda region, which includes our field site, was designated a UNESCO world heritage site in 2007 (UNESCO, 2007).

The field site was first scientifically written about by Aubréville in 1967, who described it as “a strange forest-savanna mosaic” and hypothesised it to have originated from a process of savanna recolonisation after prehistoric forest retreat in drier climates. Nicolas (1977) agreed with him, but both Descoings (1974) and Fontes (1978) proposed that the savannas are more likely to be the result of past human occupation. De Foresta (1990) and Schwartz *et al.* (1990) took an intermediate viewpoint, and proposed the currently accepted explanation, which is that the mosaic is natural in origin but has been maintained since by anthropogenic fires.

The broader middle Ogooué valley around the field site has historically been occupied by multiple groups of people. Stone Age people occupied the area at least 5 ka, and likely much before than this, followed by the arrival of early Iron Age people around 2.4 ka and again around 1.9 ka (Oslisly, 1995; White & Abernethy, 1997; White, 2001). Following this, there was a hiatus in human occupation from 1.4 ka to 700 a, followed by resettlement of late Iron Age people from 700 a onwards (Oslisly, 1995; White & Abernethy, 1997). No matter the origin, the mosaic is ancient, and has been dated using carbon isotopes to be at least 9 ka (Oslisly *et al.*, 1996). It should be noted that this date

has been questioned, and the concerns raised also addressed (Oslisly *et al.*, 1997; Schwartz, 1997).

More recently, the park was lightly selectively logged for Okoumé (*Aucoumea klaineana*) trees between 1965 and 1980 (White, 1992, 1995). Currently, the park experiences negligible levels of fire wood harvesting and very low levels of hunting, as population density around the park is low.



Photo: Anabelle W. Cardoso



Photo: Kathryn Jeffery

Figure 3.1: Photographs of different parts of the forest-savanna mosaic in Lopé National Park. Abrupt transitions between the open canopy savanna and closed canopy forest can be seen.

3.2 Vegetation

The savannas in the mosaic are classified as Middle Ogooué savannas (van de Weghe, 2011) (**Fig. 3.2**). In the field site, they are historically dominated by the grasses *Anadelphia afzeliana* (Rendle, 1919), *Hyparrhenia diplandra* ((Hack.) Stapf 1919), *Andropogon pseudapricus* (Stapf 1919) and *Schizachyrium platyphyllum* ((Franch.) Stapf 1919) (Descoings, 1974; Fontes, 1978; White, 1992). During fieldwork for this study we observed them to be dominated by the above species, with the exception of *A. pseudapricus*, and the addition of *Imperata cylindrica* ((L.) P.Beauv. 1812), *Ctenium newtonii* (Hack 1887) and *Panicum nervatum* (Stapf 1920). Woody species diversity in the savannas is low, and historically comprises only *Crossopteryx febrifuga* ((Afzel. Ex G.Don) Benth. 1849), *Sarcocephalus latifolius* ((Sm.) E.A.Bruce 1947), *Psidium guineense* (Sw. 1788) (an alien shrub), *Bridelia ferruginae* (Benth. 1849), and *Psorospermum febrifugum* (Spach 1961) (Descoings, 1974; Fontes, 1978; White, 1992). During fieldwork for this study we observed only the first three of these species within the savanna.



Figure 3.2: Photographs of the savannas that are typical of the field site. In the top panel a gallery forest can be seen in background, immediately bordering the savanna. In the bottom panel, the tree in the foreground is *Crossopteryx febrifuga*, the most common woody species in these savannas.

The forest of the mosaic is classified as continuous Lower Guineo-Congolian rainforest (White, 1983). Some forest sub-types occur outside of the continuous forest block, surrounded by savanna (**Fig. 3.3**). For example, gallery forest is found along rivers in both the forest and the savanna, and is generally low in stature and a mix of forest specialist and pioneer species (White & Abernethy, 1997). In addition to gallery forests, isolated forest patches, or “bosquets”, also occur within the savanna. These are hypothesised to have originated during human occupation, where ancient villages protected them as plantations or sacred forests (White & Abernethy, 1997). Colonising forest can also be found within the savanna, especially in smaller savanna patches that have been protected from burning. These forests are characterised by high abundances of forest pioneer species, specifically *Aucoumea klaineana* (Pierre 1896), *Lophira alata* (Banks ex P.Gaertn. 1805) and *Sacoglottis gabonensis* ((Baill.) Urb. 1877) trees, which often form dense, monodominant stands (White & Abernethy, 1997; White, 2001). These dense stands are the precursor to the more mature *Marantaceae* forest, which is characterised by a relatively light understorey covered by an impenetrable layer of herbaceous plants from the *Zingiberaceae* and *Marantaceae* families (White & Abernethy, 1997; White, 2001). The successional stage succeeding this is the mature forest, which has a dark, cool, sparsely vegetated understorey and a very diverse tree community, with more than 100 species able to be found in a hectare, and some trees that are estimated to be over 1000 years old (White & Abernethy, 1997).

Please visit <https://youtu.be/cUSripeylw8> to view an accompanying video of the mosaic of LNP.



Figure 3.3: Photographs of the different forest subtypes occurring in the study site. a) Gallery forest and b) forest patches or “bosquets” within the savanna (outlined), c) colonising forest in a savanna that has been fire suppressed, d) the interior of the densely vegetated *Marantaceae* forest, and e) Prof. Kate Parr at the edge of the mature forest, next to a big tree and standing amidst a sparsely vegetated understorey.

Limited differences in soil exist across the forest-savanna transition (Cuni-Sanchez *et al.*, 2016). Specifically, no significant differences in C %, total C, total P, cation exchange capacity and bulk density exist between savanna and most forest types (Cuni-Sanchez *et al.*, 2016). The C:N ratio of savanna soils is not significantly different to that of colonising forest or young *Marantaceae* forest, but is significantly higher than the C:N ratio of soils from monodominant *Aucoumea* forest and older *Marantaceae* forest (Cuni-Sanchez *et al.*, 2016). These differences are to be expected, as the regular burning of savannas can decrease their soil N (Pellegrini *et al.*, 2018).

3.3 Climate

The climate of LNP is relatively dry compared to the rest of Gabon, receiving only 1450 mm MAP (mean 1984-2016, Tutin *et al.*, 2016). This is caused by the rain shadow created by the Massif du Chaillu to the west (White & Abernethy, 1997). Rainfall is very seasonal, separated by a long dry season from mid-June to mid-September, and a shorter dry season between mid-December and mid-February, with the latter being less well defined and lasting anywhere from a few days to a month (**Fig. 3.4**, White & Abernethy, 1997). Mean annual humidity does not drop below 70% throughout the year, and maximum daily temperature is 20 - 23 °C (min - max) in the dry season and 26 - 33 °C (min - max) in the wet season, with an annual mean of 24 degrees (2003-2016, White & Abernethy, 1997; Tutin *et al.*, 2016). LNP is unusual in the context of the wider tropics in that the long dry season is also the coldest and cloudiest season, limiting evaporative loss from the forests during this time and allowing them to persist despite long gaps between precipitation events (White & Abernethy, 1997). The long dry season is when fruit in the forest is most scarce, leaving elephants often “visibly emaciated with only skin on their bones” (White & Abernethy, 1997) (**Fig. 3.5**).

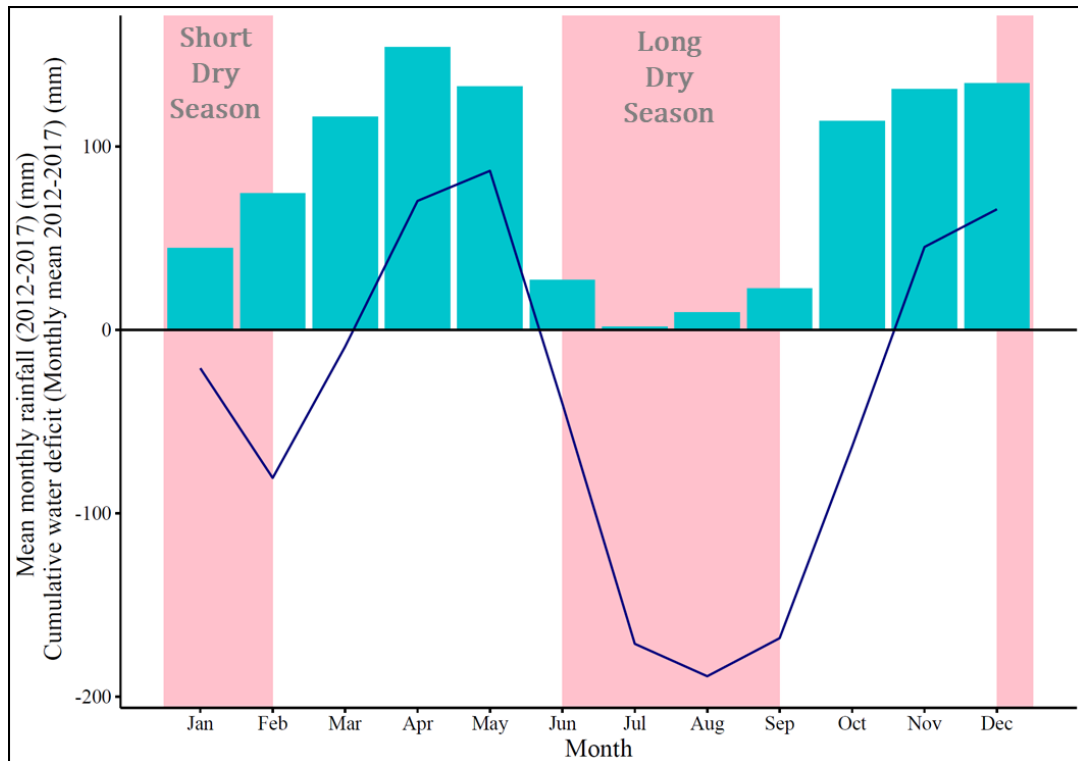


Figure 3.4: Mean monthly rainfall (blue bars) and cumulative water deficit (blue line) (calculated following Aragão *et al.*, 2007) in each month of the year in Lopé National Park. Shaded pink blocks show the short and long dry seasons that occur annually.



Figure 3.5: Photographs of emaciated forest elephants foraging at the forest-savanna transition during the late dry season (August/September) during this study.

3.4 Fire

The loss of savannas to expanding forest edges, known as forest encroachment, is occurring across Central Africa, including in the forest-savanna mosaic of LNP (Schwartz *et al.*, 1996; Favier *et al.*, 2004; Nana, 2005; Mitchard *et al.*, 2009; Palla *et al.*, 2011; Jeffery *et al.*, 2014; Aleman *et al.*, 2018). To combat this and maintain habitat diversity, most savanna patches in LNP have been regularly burnt as part of the park's fire management program since 1993 (Jeffery *et al.*, 2014).

Most savanna patches have been burnt annually, with some burnt every 2-3 years, and a few being protected from fire (Jeffery *et al.*, 2014). Burning occurs over six weeks in the long dry season, between July and September (Jeffery *et al.*, 2014). Savanna patches are burnt in sections, with the limits of these defined by naturally occurring fire-breaks, such as rivers, forest patches, or roads (Jeffery *et al.*, 2014). Historically, fires have been lit in the late afternoon and early evening to make them easier to control (Jeffery *et al.*, 2014). As a product of this practice, the fires have not been very intense, which has likely contributed to their inability to halt forest encroachment in many parts of the landscape (Jeffery *et al.*, 2014).

In contrast to normal burning procedures, during the experimental burns of this study we attempted maximize fire intensity by lighting fires in the hottest part of the day (**Fig. 3.6**). Fires were started at multiple points in a line across the savanna, i.e. everyone in the field team formed a line and we walked through the savanna throwing down

matches. Where we started fires depended on the direction of the wind and local topography, again always trying to maximize fire intensity by starting head fires at the bottom of hills where possible. In light of this increased intensity, the historical natural fire-breaks that delimit savanna sections from one another were redefined.



Figure 3.6: Photographs of two of the fire fronts that resulted from the experimental burns in this study.

3.5 Forest elephants

The forest elephant's range covers 38% of Central Africa, but only 9% of this falls within protected areas (Blanc *et al.*, 2007). Gabon covers just under a quarter of their range and is home to over half of the remaining population (Blanc *et al.*, 2007; Maisels *et al.*, 2013). Many of the Gabonese forest elephants live in LNP, and this density is concentrated around the northern part of the park, around the forest-savanna mosaic where this study takes place (Maisels *et al.*, 2006, 2013). This makes LNP one of the only places in Africa where one can answer questions about forest elephant ecology using relatively intact forest elephant populations.

The forest-savanna mosaic of LNP is so attractive to elephants that they are anecdotally drawn to it from across the region. The causes of this attraction haven't been investigated, but are likely a combination of the abundant forage in the area and the low hunting pressure creating a safe oasis for them to flee to after facing encounters with hunters elsewhere. The latter explanation is supported by frequent field encounters with elephants, during which it was hard to tell which party was more scared.

3.6 References

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Chapter 4:

Methods

By:

Anabelle W. Cardoso



Photo: Anabelle W. Cardoso

4.1 Sampling the forest-savanna transition

40 transects were sampled across two fire treatments: 18 “low fire frequency” (savanna burnt 0-3 times in the last 10 years and not burnt in the last 3 years) and 22 “high fire frequency” (savanna burnt 1-3 times in the last 3 years) (**Fig. 4.1**). Transects were erected and sampled between 9 May and 25 August 2016. Each site’s vegetation was sampled before it was burned. Fires took place between 15 July and 2 September 2016. One camera trap was erected at each site and monitored forest elephant activity for one year.

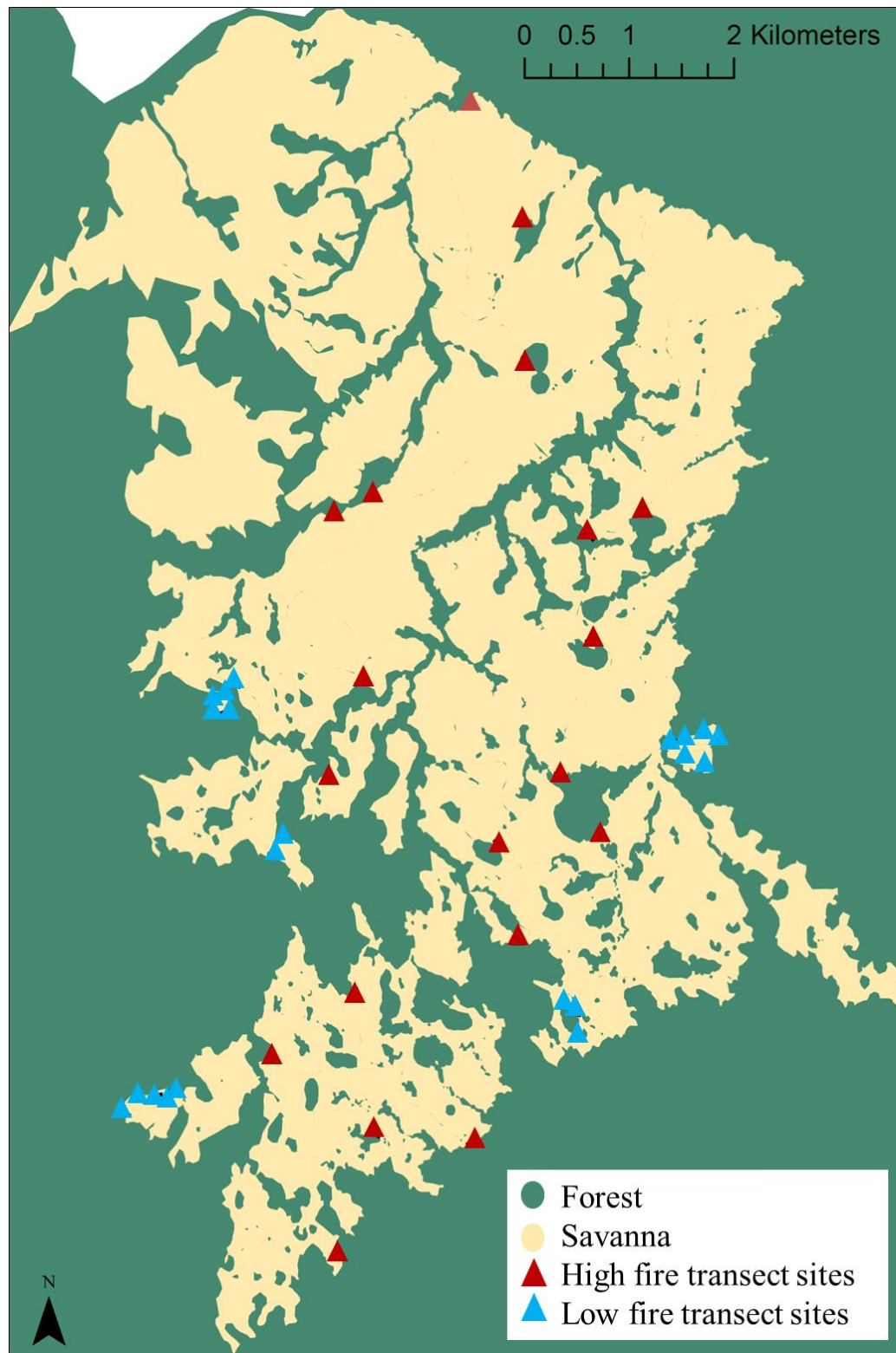


Figure 4.1: Map of the forest-savanna mosaic of the field site and the location of the forty high and low fire frequency transects within it (Agence Nationale des Parcs Nationaux, 2006).

Sites were chosen randomly, by first dropping numbered points 20 m apart along all forest-savanna transitions in the mosaic using Geographic Information Systems (ArcGIS v10.3,(ESRI, 2014)), and then using a random number generator to select points. The first 18 suitable low fire frequency and 22 suitable high fire frequency sites were chosen. To be considered suitable, sites had to be transitions between grass-dominated savannas (*cf. Pteridophyte* savannas found in parts of the park) and closed canopy forest, at least 50 m from any large tree fall gaps that could be influencing vegetation patterns. Both forest and savanna patches had to be at least 50 m wide, and at least 100 m away from other sites. Sites were deemed unsuitable if within 50 m of a river, marsh, or salt-lick, or on a steep slope or rocky substrate, as these factors can affect fire and elephant behaviour. Sites had to be accessible by car and within 30 min walking distance from the car, as the hours safe to work in the field prohibited very long work days, making sites further away impractical to sample. Sites were excluded if they were unsafe to work in with respect to elephants, as was the case with many of the low fire frequency savanna areas. Many of these areas were heavily overgrown, making them simultaneously very attractive to elephants and very difficult for us to see elephants at a safe distance.

Each transect spanned savanna, transition, and forest vegetation types, as defined in the field. Field definitions of vegetation types were to ensure sufficient sampling, and were not used in quantitative analysis. Definitions were physiognomic, and were the result of consensus between at least three members of the field team. Savanna was defined to be where grass cover in the understorey was continuous, tree cover in overstorey was a

discontinuous, and visibility across the landscape was at least 5 m. The transition was defined to be where understorey grass cover became discontinuous, there was vertical continuity between the understorey and overstorey layers, tree cover in the overstorey was continuous, and visibility across the landscape was limited to less than 5 m. The forest was defined to be where grass was completely eliminated from the understorey, the understorey became relatively open and was once again vertically discontinuous with the overstorey, and visibility across the landscape again increased to more than 5 m.

In order to ensure sufficient sampling of all vegetation types, each transect covered 25 m of field-defined savanna, the entire field-defined transition, and 10 m of field defined forest (**Fig. 4.2**). Each transect was 2 m wide and, depending on the length of the field-defined transition, of variable length (37 – 48 m). At each site, an elephant path divided the savanna from the transition (i.e. had continuous grass on one side and none, or very discontinuous, grass on the other).

Fieldwork for this research had three main components. First, at each transect site, the grass community and its flammability traits were assessed, and how these affected fire behaviour at the forest-savanna transition was determined. Following this, the tree community and its functional traits at the forest-savanna transition were assessed, and the role of fire in determining these was investigated. Finally, forest elephant use of the sites was evaluated using camera traps and an assessment of their damage to trees at the forest-savanna transition was performed.

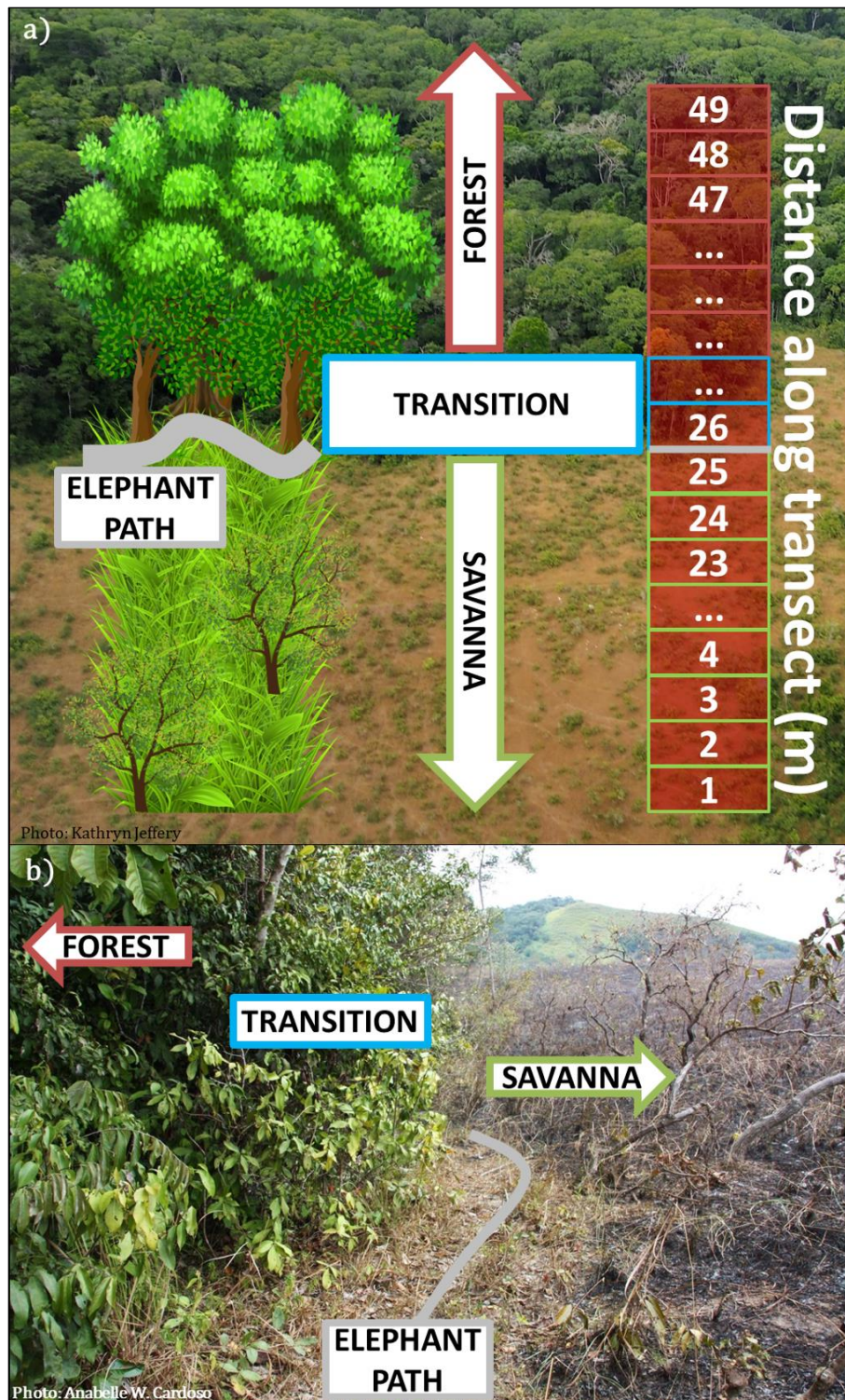


Figure 4.2: Showing the layout of each transect at the forest-savanna transition. Field definitions of vegetation types were physiognomic, and used only to ensure sufficient sampling, rather than in quantitative analysis. a) In each transect, 25 m of savanna was sampled, followed by the entire transition, followed by 10 m of forest. b) At each site, an elephant path ran along the edge of the savanna.

4.2 Grasses, flammability, and fire behaviour

Grass species composition and percentage ground cover of each species along each transect was assessed. Grass biomass along the transect was measured using a disc pasture metre calibrated for the site. These measures were combined to assess changes in the grass species community along the transect. The dominant species in the grass community then had their flammability traits assessed using a modified version of the methods proposed by Simpson *et al.* (2016) (**Fig. 4.3a**). The degree of canopy closure along the transect, i.e. how much light is reaching the understorey, was measured using photographs taken with a fish-eye lens, which were converted into leaf area index values via post-hoc image analysis. Once sampling had been completed, all the high fire frequency sites were burnt and fire intensity and temperature metrics were assessed using Type K thermocouples (**Fig. 4.3b**). This information allowed links between grass community composition, canopy closure, grass' flammability traits, and fire behaviour, to be drawn. Details on this methodology can be found in **Chapter 5**.

The methods applied here, specifically those for assessing grass species flammability in the field, were low cost, required very little equipment and technical skill, and produced remarkably consistent results. Advances like this are crucial for African tropical ecology, as money and capacity are often the limiting factor for local research.



Figure 4.3: a) An example of the simple apparatus used to measure flammability traits of the grass species, this image shows the set up to measure maximum combustion rate, whereby a piece of grass is burnt and the speed at which it loses weight is recorded. b) One of the thermocouples used to measure fire intensity and temperature, the data logger was wrapped in a fire blanket and aluminium foil, leaving only the thermocouple wire outside, which was attached to a metal rod at 30 cm above the ground.

4.3 Tree communities and functional traits

All trees with a diameter at 10 cm above the ground larger than 3 cm were tagged and their species and canopy dimensions recorded (**Fig. 4.4**). Smaller trees were sampled in smaller nested transect that ran along the left hand side of the main transect. The location of each tree along the transect was recorded, and used in statistical analyses to look for delineations between savanna, transition, and forest tree communities.

The tree species that contributed the most to biomass and occurred most commonly in the transects had a range of functional traits measured. These traits included: absolute bark thickness, bark thickness as a proportion of stem diameter, the rate of bark production (bark's allometric coefficient), wood density, tree height to trunk diameter ratio, ground area covered by the canopy, canopy volume, leaf mass per unit of leaf area, and leaf size. In addition, the degree of tree canopy cover was estimated using leaf area indices. Together with the data collected on fire behaviour, data on functional traits were used to link species patterns at the forest-savanna transition and the underlying processes causing them. Details on this methodology can be found in **Chapter 6**.

After collecting an abundance of data on community composition and functional traits, results showed that the original physiognomic field-definitions of vegetation type were well supported by quantitative analysis. This is important for tropical ecology where resources may be limited and conditions challenging, as it enables the quick-and-dirty

identification of vegetation types in the field, with the knowledge that such an approach is supported by data.



Figure 4.4: a) Laying the transect across the forest-savanna transition, and b) measuring the diameters (at 10 cm above the ground) of the trees inside it before c) tagging and recording the tree species and d) measuring each tree's crown dimensions. Pictured here are Guy Antoine Kamba (b and c) and Eddy Milamizokou Nappo (a and d), members of the field team.

4.4 Forest elephants, camera traps, and damage to trees

Most, if not all, previous research on elephant-fire interactions has focused on savanna elephants. There is very little known about the forest elephants, and with good reason. Forest elephants are difficult to observe directly as large swathes of their habitat are relatively impenetrable tropical forest (Terborgh *et al.*, 2016). They are also under immense pressure from hunting, and so tend to be scared of, or aggressive towards, human researchers in the field. This research circumvented this issue by using unobtrusive movement and heat triggered camera traps (Agressor No Glow, Bushnell, Kansas, USA). This enabled, for the first time, an investigation into the ecology of the elusive forest elephant at the forest-savanna transition.

At each transect site the elephant path at the edge of the savanna was graded based on how intensely it appeared to be used. Elephant damage to the surrounding trees was also recorded at the end of the camera trapping period, so that their preferences and intensity of browsing could be assessed. A motion and heat sensitive camera trap, which was set to trigger up to once per second, was then erected. Each camera trap monitored forest elephant activity at the site for between 11 and 13 months. Using this data, links between forest elephant activity and fire behaviour, and how this was helping to facilitate forest-savanna mosaic stability through time, were able to be described. Details on this methodology can be found in **Chapter 7**.

The camera traps captured over a million images, making manual analysis by one person infeasible. Consequently, through collaboration with the citizen science platform Zooniverse.org, an interactive website called “Elephant Expedition” was created (**Fig. 4.5**). Interested members of the public, or citizen scientists, visited the website and clicked through images from the camera traps, identifying the animals and counting how many forest elephants they could see. Through an extensive social media campaign and with the help of the Zooniverse.org network, by the end of the project “Elephant Expedition” had more than 10 000 registered volunteers. Volunteers appeared to really enjoy working on the project. One volunteer, who was in hospital receiving chemotherapy, said that the project was a great way to pass the time and feel like part of something, that it allowed her to no longer feel excluded by her illness. Another volunteer said that he had learnt so much from the project, and especially valued all the connections he had had with people on the online talk boards. He went to say that the project had ignited in him a love of elephants, made his evenings so much more fun, and that he was grateful to the project for opening his eyes to how much he was capable of doing. Many of the volunteers expressed their sadness that the project was ending, saying that they would miss the elephants.

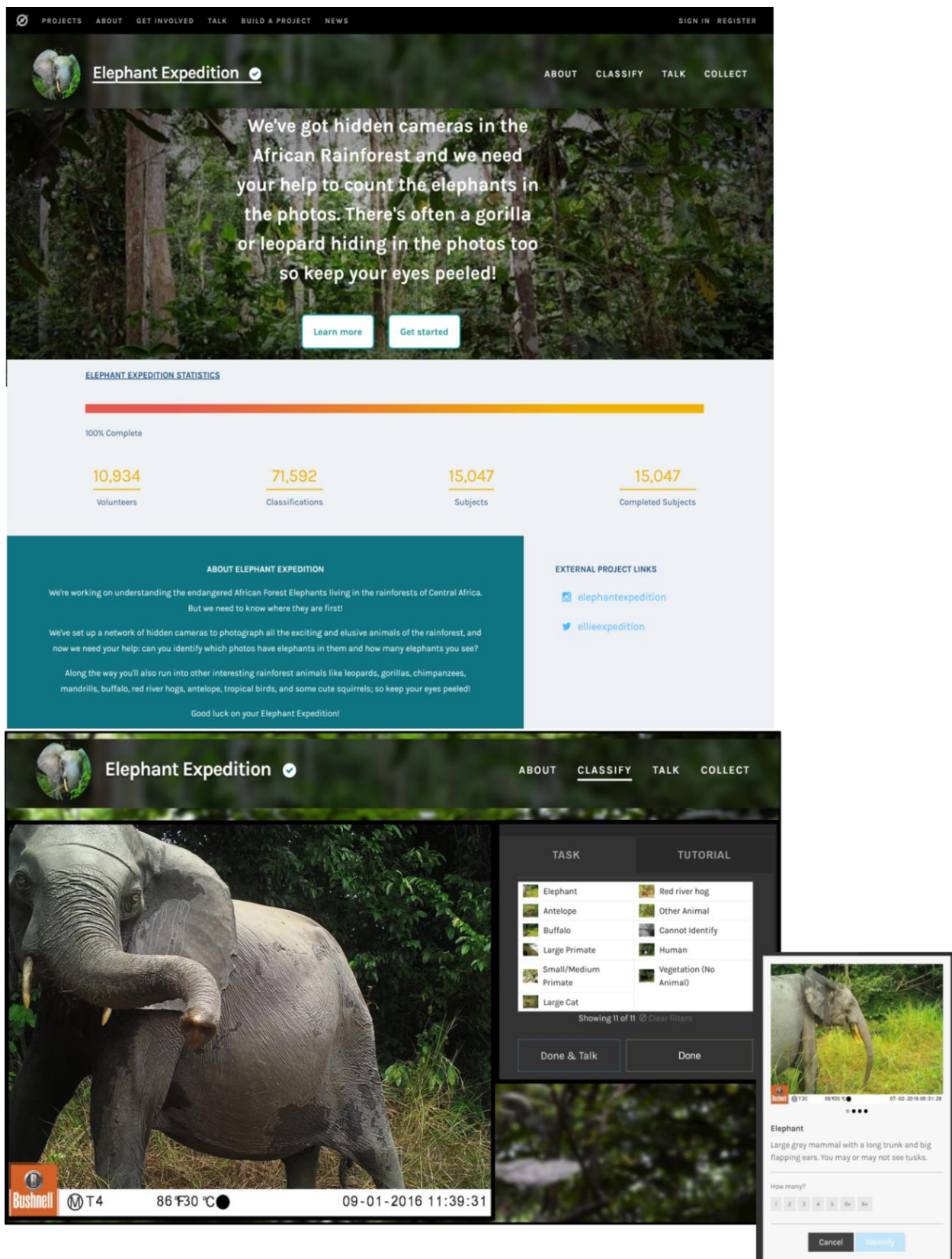


Figure 4.5: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the landing screen (top), classification window (bottom) and elephant count window (inset). More details can be found in the appendix of **Chapter 7**.

The project also received some attention from the press, and was featured on Mongabay.com's blog as well as on the University of Oxford's science blog. Most recently, it was featured in the print version of BBC wildlife magazine as part of a feature on citizen scientists. Overall, the citizen science experience was hugely valuable. A lot was learnt through this process, and the level of time investment made by members of the public, and their genuine interest in conservation, was constantly humbling. The scale of the response could not have been anticipated, and serves as a lesson about the importance of communicating one's science to a broader audience. Many wonderful images of the local wildlife were also captured (**Fig. 4.6**).



Figure 4.6a: A selection of the images captured by the camera traps, which included forest elephants as well as gorillas, leopards, chimpanzees, mandrills, and pangolins.



Figure 4.6b: A selection of the images captured by the camera traps, which included forest elephants as well as gorillas, leopards, chimpanzees, mandrills, and pangolins.

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Chapter 5:

Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions

By:

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Photo: Anabelle W. Cardoso

This chapter starts by characterising fire behaviour at the forest-savanna transition. It then goes on to explore drivers of fire behaviour at the transition, namely those relating to grass community composition and flammability. By doing so, it is able to describe the mechanisms which mediate fire behaviour at the forest-savanna transition, an essential first step in understanding how fire affects transition vegetation dynamics.

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Kathryn J. Jeffery, David Lehmann, and Josue Edzang Ndong, assisted with finessing the methodology and provided support in the field. Ian McGregor and Claire M. Belcher assisted with data collection. All these authors also provided constructive comments during writing of the manuscript.

5.1 Abstract and key words

Forest-savanna mosaics are maintained by fire-mediated positive feedbacks; whereby forest is fire suppressive and savanna is fire promoting. Forest-savanna transitions therefore represent the interface of opposing fire regimes. Within the transition there is a threshold point at which tree canopy cover becomes sufficiently dense to shade out grasses and thus suppress fire. Prior to reaching this threshold, changes in fire behaviour may already be occurring within the savanna. Such changes are neither empirically described nor their drivers understood. Fire behaviour is largely driven by fuel flammability. Flammability can vary significantly between grass species and grass species composition can change near forest-savanna transitions. This study measured fire behaviour changes at eighteen forest-savanna transition sites in a vegetation mosaic in Lopé National Park in Gabon, central Africa. The extent to which these changes could be attributed to changes in grass flammability was determined using species-specific flammability traits. Results showed simultaneous suppression of fire and grass biomass when tree canopy leaf area index (LAI) reached a value of 3, indicating that a fire suppression threshold existed within the forest-savanna transition. Fires became less intense and less hot prior to reaching this fire suppression threshold. These changes were associated with higher LAI values, which induced a change in the grass community, from one dominated by the highly flammable *Anadelphia afzeliana* to one dominated by the less flammable *Hyparrhenia diplandra*. Changes in fire behaviour were not associated with changes in total grass biomass.

This study demonstrated not only the presence of a fire suppression threshold but the mechanism of its action. Grass composition mediated fire-behaviour within the savanna prior to reaching the suppression threshold, and grass species composition was mediated by tree canopy cover which was in turn mediated by fire-behaviour. These findings highlight how biotic and abiotic controls interact and amplify each other in this mosaicked landscape to facilitate forest and savanna co-existence.

Key words: Forest-savanna mosaic, Transition, Ecotones, Fire behaviour, Edge effects, Flammability, Alternative stable states, Grass functional traits.

5.2 Introduction

Forest and savanna distribution can largely be predicted by mean annual precipitation (MAP), which is a key determinant of total tree cover (Sankaran *et al.*, 2005). Landscapes where MAP is higher are deterministically closed canopy forests, and landscapes where MAP is lower are deterministically open canopy savannas (Staver *et al.*, 2011a). However, this predictability falls away in locations where MAP is intermediate (1000-2000 mm p.a.). In these places, whether the system is forest or savanna is not deterministic, and either of these states may be observed (Staver *et al.*, 2011a). Landscapes that are not deterministically forest or savanna are common (Staver *et al.*, 2011a), and as a result forest and savanna co-occur so frequently that the forest-savanna transition is the most widespread ecotone in the tropics (Torello-Raventos *et al.*, 2013). Forest-savanna transitions are especially common in forest-savanna mosaics, where patches of pyrophilic savanna interlock with patches of pyrophobic forest. The opposing fire regimes of forest and savanna meet at the forest-savanna transition, with fire behaviour able to determine the transition's location and dynamics (Oliveras & Malhi, 2016). This makes fire a key determinant of vegetation distribution in mesic tropical landscapes (Hirota *et al.*, 2011; Staver *et al.*, 2011a; Hoffmann *et al.*, 2012a; Dantas *et al.*, 2016), and yet changes in fire behaviour at the forest-savanna transition and the biotic and abiotic drivers of this are not well understood.

Within the forest-savanna transition exists the fire suppression threshold (Hoffmann *et al.*, 2012a). This is the point at which tree canopy cover becomes sufficient to exclude heliophilic C4 grasses and create a moist and less windy micro-climate, thus eliminating fire from the understorey (Hoffmann *et al.*, 2012a). Above this threshold of canopy cover, fire-sensitive forest tree species succeed while savanna tree species are competitively excluded by the lack of light, and so a forest state persists (Hoffmann *et al.*, 2003; Gignoux *et al.*, 2016). Below this threshold, C4 grasses flourish and seasonally become dry and burn (Bond & Van Wilgen, 1996), killing trees caught in the flame zone, or removing their aerial biomass and forcing them to resprout repeatedly, thus maintaining the open canopy of the savanna (Grady & Hoffmann, 2012). While the fire suppression threshold has been demonstrated at certain sites (Hoffmann *et al.*, 2012a; Dantas *et al.*, 2013; Ibanez *et al.*, 2013a; Charles-Dominique *et al.*, 2018), its existence more broadly, as well as the role that fire plays in maintaining forest-savanna mosaics, has been questioned (Lloyd & Veenendaal, 2016).

The fire suppression threshold does, to some extent, consider fire to be a binary variable within the ecosystem: either present below the threshold, as in savanna, or absent above the threshold, as in forest. However, the probability that fire top-kills trees is not binary, and varies with changes in fire behaviour (Higgins *et al.*, 2000). Fire behaviour is determined by the properties of the fuels (i.e. their flammability), and is further altered by the prevailing weather conditions (e.g. high wind speeds and temperatures can cause extreme fire-storms, Bradstock *et al.*, 2010). Flammability is the ability of fuel to burn, or “to start and sustain a flame” and is driven not by a single

plant trait, but by group of traits that determine the probability and behaviour of fire (Pausas *et al.*, 2017). These traits dictate the fuel's ignitability, or ability to start a fire, its combustibility, or how well it burns, and its sustainability, or how long it burns for (Gill & Zylstra, 2005). Broadly, flammability traits are those relating to the fuel's load (biomass quantity), its intrinsic properties (biomass quality), how wet it is (fuel moisture), and how it arranges spatially (biomass connectivity and aeration) (Gill & Zylstra, 2005; Simpson *et al.*, 2016).

The flammability of the grasses that fuel savanna fires can vary significantly between species (Simpson *et al.*, 2016). Some previous studies have investigated species-level grass flammability traits in a laboratory (Simpson *et al.*, 2016) using models (*cf.* field experiments) to make inferences about landscape-scale fire behaviour. Conversely, other studies investigated savanna landscape-scale fire behaviour in detail (Wragg *et al.*, 2018), but did not address species-level flammability traits to explain the observed patterns. Studies that investigate fire behaviour and flammability at forest-savanna transitions tend to consider all savanna grassy fuel as equally flammable at a given biomass and moisture content (Hennenberg *et al.*, 2006; Balch *et al.*, 2008; Hoffmann *et al.*, 2012b), and don't examine variation in flammability between grass species. Studies that show that grass species composition does change at the transition acknowledge that such changes will likely affect fire behaviour (Charles-Dominique *et al.*, 2018), but do not empirically measure grass species flammability traits.

Grass species composition can vary across the savanna, specifically approaching the forest-savanna transition and the fire suppression threshold (Charles-Dominique *et al.*, 2018). These changes are likely to be affecting fire behaviour and may be playing a crucial role in maintaining the forest-savanna mosaic via their interaction with the fire suppression threshold. To the best of our knowledge however, no study has yet empirically linked grass species-specific flammability traits with grass community composition changes and fire behaviour changes at the forest-savanna transition.

The objective of this study was to empirically describe the fire suppression threshold and the interactive abiotic and biotic controls on it. We did this at 18 forest-savanna transition sites in a mosaic landscape in Lopé National Park in Gabon, central Africa. Specifically, we posed the following research questions:

Q1) Is there evidence for a fire suppression threshold within the forest-savanna transition?

Q2) Does fire behaviour change within the savanna before reaching the threshold in (Q1)?

Q3) To what extent are any fire behaviour changes in (Q2) a function of shifts in biotic factors, like grass, and/or abiotic factors, like shading?

5.3 Materials and Methods

Study site

Lopé National Park (LNP), Gabon, is a mosaic of Middle Ogooué savannas (van de Weghe, 2011) and continuous Lower Guineo-Congolian rainforest (White, 1983). The landscape is characterised by sharp transitions between vegetation types and there is almost always a forest elephant path running along the edge of the savanna, parallel to the edge of the forest. Mean annual rainfall is 1442 mm (1984-2016), mean annual temperature is 24 °C (2003-2016), and mean annual humidity is 81 % (2003-2016) (Tutin *et al.*, 2016). LNP has a short (mid-December to mid-February) and a long (mid-June to mid-September) dry season, with prescribed burning occurring in the latter. Prescribed fires have been used since 1993 as a way to maintain the savanna component of the mosaic, which is at risk of being lost to encroaching forest (Jeffery *et al.*, 2014). Both the savanna and fire are ancient features of the landscape (White, 2001; Peyrot *et al.*, 2003).

The study was performed at eighteen forest-savanna transition transects across the mosaic (**Fig. 5.1**). Transects covered forest and savanna patches that were at least 50 m wide. Transects were selected randomly and were at least 100 m from one another and 50 m from a road or river. Transects covered 25 m of savanna and 10 m of forest as well as the width of the transition vegetation belt between the two. Transects were 2 m wide but of variable length (37 – 48 m), as the width of the transition varied between sites. Delineation of these vegetation types was done on a physiognomic basis. Savanna was

defined as where grass cover was continuous, woody canopy cover discontinuous, and visibility at eye level (1.6m) >5 m. The transition was then defined to start where grass cover became discontinuous, woody canopy cover became continuous, the tree canopy layer was vertically continuous with the understorey layers, and visibility was <5m. The transition was defined to end and the forest begin where tree canopy layer became vertically discontinuous with the understorey again, and visibility increased to >5 m. Transects were sampled in adjacent 1 m increments (1 m x 2 m block) with positive distances indicating blocks into the savanna, negative distances indicating blocks towards the forest, and zero distances denoting blocks at the edge of the savanna. At each site, an elephant path divided the savanna from the transition (i.e. the path had continuous grass on one side and none, or very discontinuous, grass on the other).

The fire suppression threshold

This study considered a fire suppression threshold to exist at the forest-savanna transition if: i) fire could be empirically demonstrated to be suppressed and ii) the point of fire suppression coincided with a threshold level of canopy leaf area index (LAI) (previously estimated to occur at 3 (Hoffmann *et al.*, 2012a) or 1.5 (Charles-Dominique *et al.*, 2018)) at which grass biomass becomes eliminated from the understorey.

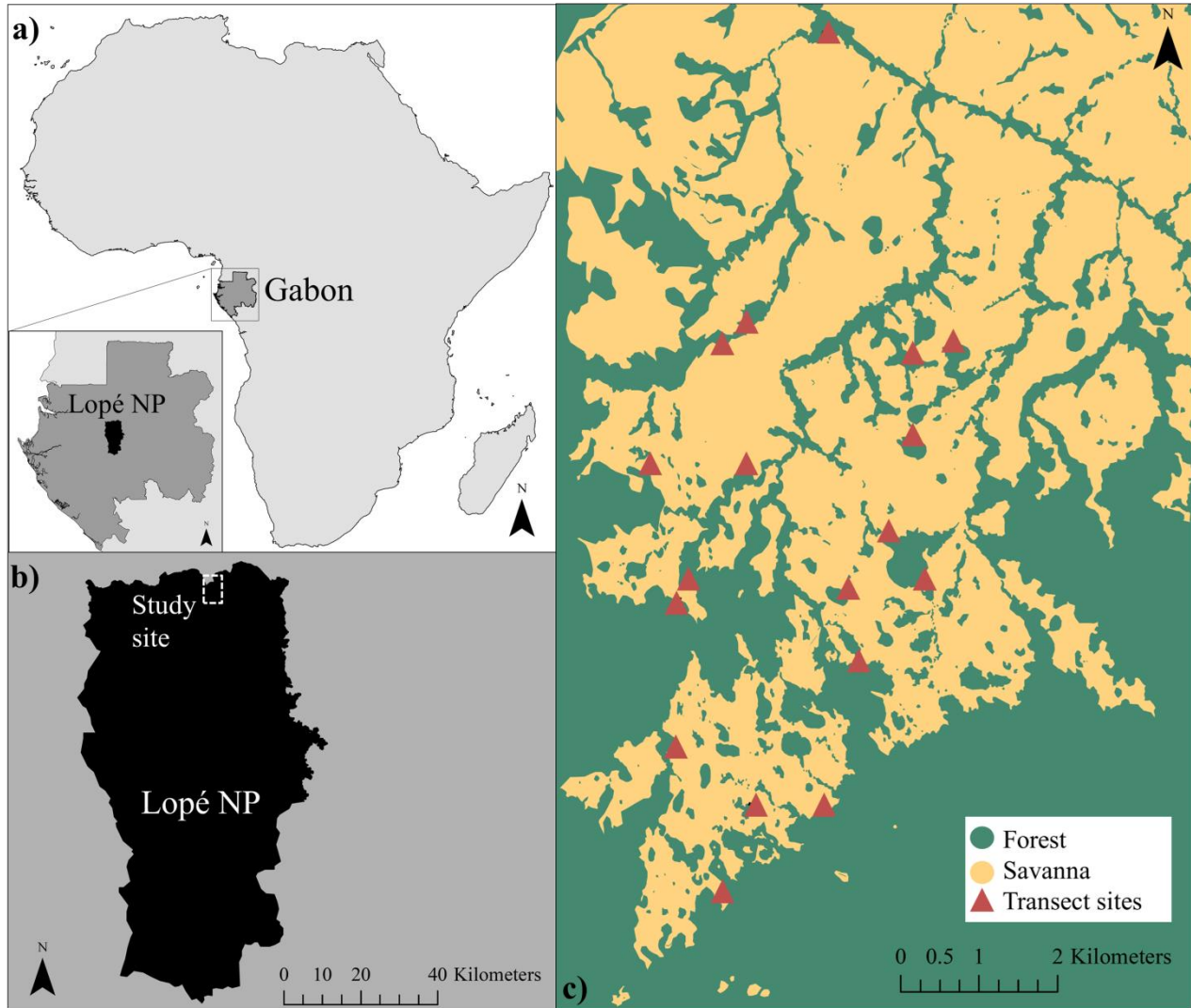


Figure 5.1: Map showing the location of a) Lopé National Park in Gabon, b) the study area within the park, and c) the eighteen forest-savanna transition transect sites (Agence Nationale des Parcs Nationaux, 2006).

The location of fire suppression relative to the edge of the savanna was assessed visually via burn scars on the day of burning. All transects were burned in the middle of the day during the dry season between 16 July and 2 September 2016. All fires were lit with matches between the late morning and afternoon from multiple point sources arranged in a line at least 100 m from the transect, and each fire progressed as a

continuous fire front. The direction of wind during burning was consistent (North-West origin), therefore whether the transect faced windward or leeward dictated whether the fire arrived as a head or flank fire.

Canopy leaf area index (LAI) ($\text{leaf area} \cdot \text{ground area}^{-1}$) is the ratio of ground area covered by canopy and is a proxy for understorey shading. It was calculated from hemispherical photographs taken at 1 m above ground level every 5 m in the savanna and forest and every 1 m in transition (Nikkor fish-eye lens 10.5mm F2.8G AF DX IF ED) (Marthews *et al.*, 2014). Photographs were converted into LAI estimates using post-hoc image analysis in Hemisfer (v2.16, Schleppi *et al.*, 2007; Thimonier *et al.*, 2010).

Grass biomass was measured every 1 m along the transect using a disc pasture meter (DPM) calibrated for the site (**Fig. S5.1**).

Border-and-Ecotone Detection Analysis (BEDA) (Hennenberg *et al.*, 2008) was applied to the resulting LAI and grass biomass data locate and characterise their borders and ecotones. A border is a boundary between two environments, in this case forest and savanna, at which the magnitude of change in a measured variable, in this case LAI and grass biomass, is the greatest. The width of the detected border, or its ecotone, represents the intermediate environments where the conditions on either side of border exert an influence on one another (also known as “depth of edge influence”; Hennenberg *et al.*, 2008). If a measured variable has a threshold response then its ecotone will be narrow as the self-reinforcing feedbacks either side of the ecotone make

the adjacent environments comparatively more stable spaces to occupy than the intermediate ecotone (Beisner *et al.*, 2003). BEDA fits a sigmoidal non-linear function with four-parameters using the formula:

$$f(x) = \frac{a + (c - a)}{1 + e^{(x-b)/d}}$$

where a and c are the upper and lower asymptotes (mean environmental conditions either side of the border), b is the inflection point where the change in the variable is strongest (location of the border), d is the steepness of change in the variable between the asymptotes, with $b+2d$ and $b-2d$ representing the width of the ecotonal area (Hennenberg *et al.*, 2008). BEDA was performed in R using the command *drm* in package *drc* (Ritz *et al.*, 2015). If a fire suppression threshold exists, we expect the detected border in LAI and grass biomass to be co-located with the point of fire suppression. We also expect the associated ecotones to be narrow (a few metres wide), indicating a threshold response.

Fire behaviour

Fire behaviour changes from the interior towards the edge of the savanna were assessed as i) fire intensity changes and ii) changes in fire temperature metrics. The weather during burning was also measured so that its effects could be accounted for.

Fire intensity

We estimated fire intensity using Byram's (1959) equation:

$$I = H \cdot w \cdot r$$

where I is the fire-line intensity in kW.m^{-1} , H is the heat yield of the fuel (kJ.g^{-1}), w is the mass of fuel combusted (g.m^{-2}) and r is the rate of spread of the fire front (m.sec^{-1}). Heat yield of fuel was assumed to be constant at 16.89 kJ.g^{-1} (Trollope, 1998). The mass of fuel combusted was the difference between pre-fire grass biomass (as determined by DPM) and post-fire grass biomass, which was the dry biomass of a 1 m^2 clipped area after fire. Rate of spread, the biggest determinant of fire intensity, was measured using thermocouples. Type-K thermocouples and Hobo Onset data loggers (model UX100-014M) logged temperature at 30 cm above the ground (estimated minimum flame height based on the minimum grass height) at 1 second intervals. At each site either five (at 9 transects) or nine (at 9 transects) thermocouples were set up in the savanna in a $20 \text{ m} \times 20 \text{ m}$ square, with one edge of the square running along the edge of the savanna. A thermocouple was always placed at each corner and in the centre of the square, and, when using 9 thermocouples, also at the midpoints of the four sides. Each thermocouple was therefore at a known distance into the savanna (0, 10, or 20 m) and from other thermocouples. Rate of spread was then the time taken for the fire front to pass between thermocouples, where the point at which a fire front passed a thermocouple was the peak temperature recorded by that thermocouple (**Fig. S5.2**).

Fire intensity was then assessed as a function of distance into the savanna using a generalised linear model (*glmer* in package *lme4*), using a gamma distribution and a log link, where transect was included as a random effect.

Fire temperature metrics

Fire temperature metrics calculated were i) maximum temperature (°C), ii) time spent above a temperature threshold (s), and iii) total thermal dose above this threshold (°C).

Maximum temperature was the highest value recorded by the thermocouple during burning. Time spent above a temperature threshold was the cumulative time (seconds) a thermocouple recorded temperatures hotter than a threshold temperature. Total thermal dose above a temperature threshold was the area under the curve that resulted from plotting temperature as a function of time (T), where T_0 was the point at which the temperature first exceeded the threshold. Area under the curve was calculated by summing all temperatures recorded above the threshold (since temperatures were recorded at 1 second intervals) (Kennard *et al.*, 2005).

Fire temperature metrics were assessed at two temperature thresholds: 60 and 150 °C. 60 °C is the lethal temperature for plant cells (Alexandrov, 1964), and 150 °C is useful for inter-study comparison as time spent above 150 °C is associated with fire severity and corresponds with calorimeter measurements (Pérez & Moreno, 1998), while total thermal dose above 150 °C corresponds with pyrometer measurements (Kennard *et al.*, 2005).

Temperature metrics were calculated for each thermocouple, therefore at 0, 10, and 20 m in to the savanna, away from the savanna edge. Thermocouples were positioned on

the savanna side of the elephant path, so as to measure fire behaviour before the fire front reached the discontinuity in grass created by the path.

Fire weather

In order to account for the effect of weather on fire behaviour air temperature (°C), relative humidity (%), wind speed (km.hr⁻¹) , and wind direction (°) were recorded using a portable weather station (Kestrel 5500L). From this, vapour pressure deficit (VPD) was calculated using the formula (Monteith, 2013):

$$VPD (KPa) = 1 - \frac{Relative\ Humidity\ (\%)}{100} * (610.7 * 10^{\frac{7.5 * Temperature\ (^{\circ}C)}{237.3 + Temperature\ (^{\circ}C)}}).$$

We also calculated the fire danger index (FDI) (Meikel et al., 2012) which incorporates both meteorological (air temperature, relative humidity, wind speed) and fuel moisture variables (amount of and days since last rainfall event). FDIs vary between 0 and 100 and were categorised into danger classes following Meikel et al. (2012). Immediately before each burn, a grass sample was collected in the savanna section of the transect and its fuel moisture level subsequently assessed on a dry mass basis using the formula:

$$Fuel\ moisture\ content\ (\%) = \frac{wet\ weight - dry\ weight}{dry\ weight}.$$

Relationships between each of these weather variables and each measured fire behaviour variable were assessed using linear models.

Grass flammability

Grass species composition was assessed along the transect by visually estimating the % cover of each grass species representing > 1 % total cover in 5 m x 2 m blocks. % ground cover estimates were then proportionally transformed into biomass estimates for each species using the total biomass estimates from the DPM. Biomass changes for each species were then plotted as a function of distance into the savanna (from savanna edge) and significance of observed changes assessed at $p < 0.05$ using Kruskal-Wallis tests. Although woody species were present in the transect, these were not considered in this study as savannas have a surface fire regime mostly fueled by grasses.

Species-specific flammability traits were measured on the three most abundant grass species, *Hyparrhenia diplandra*, *Anadelphia afzeliana*, and *Imperata cylindrica*, which together accounted for more than 80 % of the total grass biomass in the transects. Flammability traits were categorised as i) combustion-, ii) moisture-, or iii) biomass-related traits, but these are inextricably linked and should be interpreted as such. Fully mature and sunlit individuals for flammability trait sampling were collected outside the transects, within a 300 m radius of one another, on the same day at the beginning of the dry season (beginning of their natural curing season). Flammability traits were measured at two scales: whole plant (representing a field-based measure) and plant parts in a calorimeter (representing a laboratory-based measure). Differences between flammability traits of each species were assessed using Kruskal-Wallis tests, where significance was noted at $p < 0.05$.

Combustion-related traits

Maximum combustion rate (g.s^{-1}) is the maximum mass loss rate a plant or plant material exhibits during burning (aka peak mass loss rate). The field-based measure of this trait was based on the protocol of (Simpson *et al.*, 2016) and measured on ten plants per species. A plant was supported on a scale before igniting at the base by two matches (**Fig. S5.3**). During combustion, sample weight was recorded every 0.2 seconds via post-hoc analysis of a video of the scale's display screen during combustion. Weight was then plotted as a function of time and the resulting sigmoidal curve fitted using command *drm* in package *drc* (Ritz *et al.*, 2015). The inflection point of the curve represents the point where mass was being lost most quickly. Three seconds of data either side of this point were fitted with a linear model, the slope of which represents the whole plant maximum combustion rate (Simpson *et al.*, 2016). Prior to ignition, plants were clipped to 10 g (9.95 – 10.05 g) to enable inter-specific comparison since maximum combustion rate is strongly biomass dependant (Simpson *et al.*, 2016). Two of the three species were not ignitable under field conditions so we dried all samples in a field oven at approximately 50 °C for three days before testing. All but one sample ignited successfully. Three samples were excluded due to large pieces of biomass having fallen off the scale during burning.

To calculate the laboratory-based measure of maximum combustion rate we burnt three dried samples for each species using a cone calorimeter (following ASTM standard E1354). 10 – 40 g of cut up grass material was placed in a mesh basket 15cm wide and 368 cm^3 such that an equal volume of fuel was compared between each burn.

Samples were subjected to a constant heat radiation of 35 kW.m^{-2} and their maximum combustion rate measured. Heat of combustion (kJ.g^{-1}) (how much heat energy is released during burning); peak heat release rate (kW.m^{-2}) (analogous to maximum fire intensity); and time to ignition (s) (how long it takes for a sample to ignite) were also measured.

Moisture-related traits

These were all field-based measurements and were assessed using a novel experimental process to give insight into the curing process of whole plants during the dry season. Twenty-six plants of each species were clipped to constant biomass for each species and air dried in a ventilated room. Ambient air temperature and relative humidity during drying showed little variation (mean temperature ($\pm$ standard error): $25.3 \text{ }^{\circ}\text{C}$ (± 0.1), mean humidity ($\pm$ standard error): 89% (± 0.3). The samples were weighed every day until constant weight, and then were oven dried and moisture content determined on a dry mass basis. Moisture content at harvest (% dry biomass), number of days air drying before reaching constant weight, and the moisture content when at constant weight (% dry biomass) were recorded. Moisture content at the point when half of samples becomes ignitable (% dry biomass) was determined by holding a lit match to the base of a subset of the samples (between three and ten samples per day), and noting on which day, and therefore which moisture content, half of this subset ignited and combusted.

Biomass-related traits

These were field based measurements. Dry biomass per plant (g) was the mean biomass of five large, mature, sunlit plants per species after they had been oven dried to constant weight. Biomass density (g.cm^{-1}) was measured on the same five plants and gives a measure of the vertical distribution of biomass (Simpson *et al.*, 2016). Each plant was cut into five or more equal length sections (15 to 40 cm depending on plant height), each of which were weighed both fresh and after oven drying to constant weight. Biomass density was then the slope of the linear model fitted to log transformed cumulative dry biomass as a function of log transformed cumulative vertical height. Slopes equalling 1 indicate that biomass is equally distributed along the length of the plant, while slopes <1 and >1 indicate biomass is concentrated towards the top or the bottom of the plant respectively. Leaf surface area to volume (SA/V) ratio was calculated using five leaves from each of three plants per species. Leaf surface area was determined via post-hoc analysis of flatbed scanner images (Pérez-Harguindeguy *et al.*, 2013), leaf volume was determined using callipers to measure leaf thickness at three locations per leaf and multiplying this by the surface area (Simpson *et al.*, 2016).

5.4 Results

Evidence for a fire suppression threshold (Q1)

Fire was empirically demonstrated to be suppressed. The majority of fires self-extinguished within 1 m of leaving the savanna (median point of fire extinction ($\pm$ inter-quartile range) = -1 ($\pm$ 1.8) m from savanna edge) (**Fig. 5.2**).

The point of fire suppression coincided with a threshold in canopy leaf area index (LAI) at which grass biomass became eliminated from the understorey. The detected border in tree canopy LAI (1 m from the field-defined savanna edge, at LAI= 3.1) was co-located with the border in grass biomass (0 m from the savanna edge at grass biomass = 2.2 tons.ha⁻¹), both of which occurred near simultaneously with the median point of fire suppression (-1 m from the savanna edge) (**Fig. 5.2**). The ecotonal areas of both tree canopy LAI and grass biomass were narrow, spanning 2.7 m and 5.6m respectively (**Fig. 5.2**).

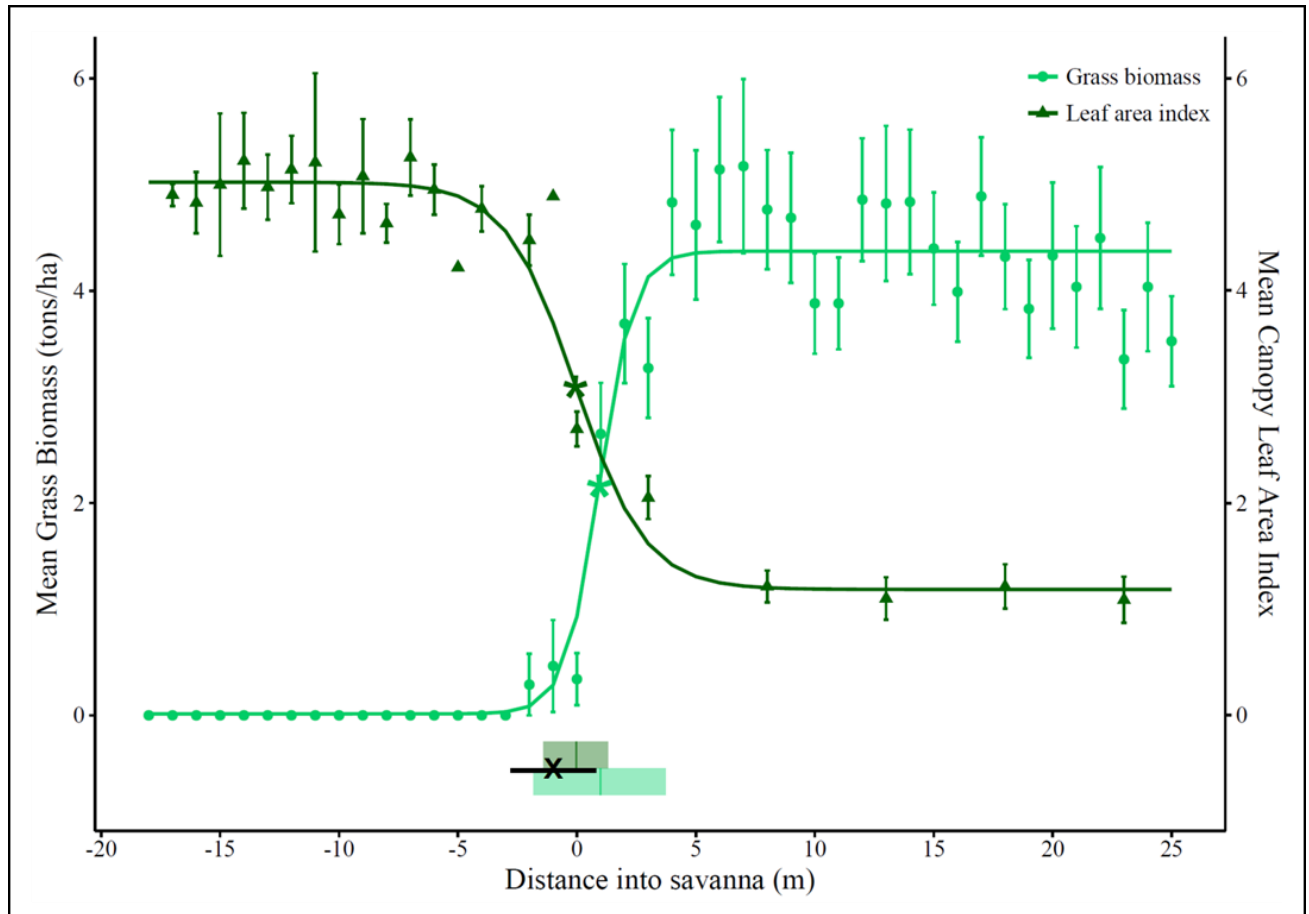


Figure 5.2: Mean canopy leaf area index (LAI) and mean grass biomass ($\text{tons}\cdot\text{ha}^{-1}$) across forest-savanna transitions in 18 regularly burnt transects. The median point (and interquartile range) of fire extinction is shown by “X” (and a solid black line). The zero point on the x-axis represents the edge of the savanna. Positive distances on the x-axis are in the savanna and towards its interior, while negative distances are across the transition and towards the forest interior. Points and error bars show the mean and its standard error. The fitted curves show the results of Border-and-Ecotone Detection Analysis (BEDA) (Hennenberg et al., 2008). The detected border for LAI was 0 m into the savanna (at the savanna edge), where LAI = 3.1 (shown as dark green * on the figure). The ecotonal area for LAI was between -1.4 m and 1.3 m into the savanna (2.7 m wide, shown by dark green shaded rectangle). The border for grass biomass was 1 m into the savanna, where grass biomass = 2.2 (shown as light green * on the figure). The ecotonal area for grass biomass is between -1.8 m and 3.7 m into the savanna (5.6 m wide, shown by light green shaded rectangle).

Changes in fire behaviour (Q2)

Fire intensity decreased as it reached the edge of the savanna (**Fig. 5.3**). This decrease, although significant, was not of great magnitude, due to the high variability in fire intensity.

Of greater magnitude were the decreases in fire temperature metrics closer to the edge of the savanna. Maximum recorded flame temperatures at the edge of the savanna were significantly lower at the savanna edge than those recorded in the savanna interior (Kruskal-Wallis, $\chi^2=15.7$, $df=2$, $p<0.001$; mean ($\pm$ standard error) maximum temperature at different distances into the savanna: 0 m = 358 ($\pm$ 26) °C, 10 m = 444 ($\pm$ 32) °C, and 20 m = 511 ($\pm$ 20) °C). Additionally, thermal dose at a threshold of 150 °C was lower at the edge of the savanna than in the savanna interior as was time spent above this threshold (area under the curve at different distances into the savanna: 0 m = 16456 °C, 10 m = 19911 °C, 20 m = 20908 °C; time above 150 °C at different distances into the savanna: 0 m = 65 s, 10 m = 70 s, 20 m = 79 s; **Fig. 5.4a**). We observed the reverse for a 60 °C threshold, where thermal dose and time spent above this threshold temperature were greater at the edge of the savanna than towards the savanna interior (area under the curve at different distances into the savanna: 0 m = 25030 °C, 10 m = 25043 °C, 20 m = 22601 °C; time above 60 °C at different distances into the savanna: 0 m = 223 s, 10 m = 202 s, 20 m = 166 s; **Fig. 5.4b**).

Climate-related metrics measured during the burns showed relatively little variability and were not generally found to be significantly affecting fire behaviour (**Table S5.1, S5.2**).

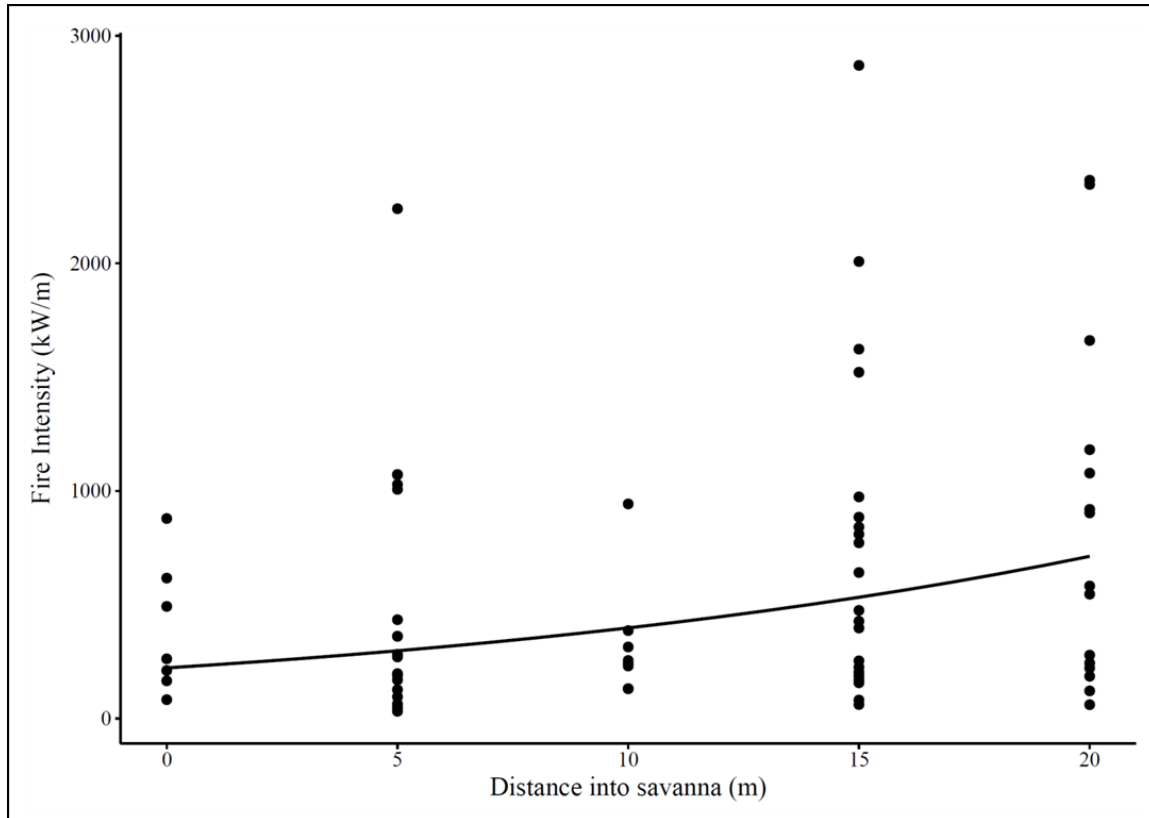


Figure 5.3: Fire intensity ($\text{kW}\cdot\text{m}^{-1}$) at different distances into the savanna (m) as measured in 18 burnt transects across forest-savanna transitions. Points represent measured intensities, and the line represents the generalised linear model fitted to these points (model fitted with the gamma distribution and a log link, with transect included as a random effect: $\text{df}=68$, intercept = 5.4 ($p<0.0001$), slope = 0.06 ($p<0.0001$), marginal R^2 using the trigamma estimate = 0.11). Positive distances on the x-axis are towards the savanna interior, negative distances (across the transition and towards the forest interior) were not measured in the experimental set-up.

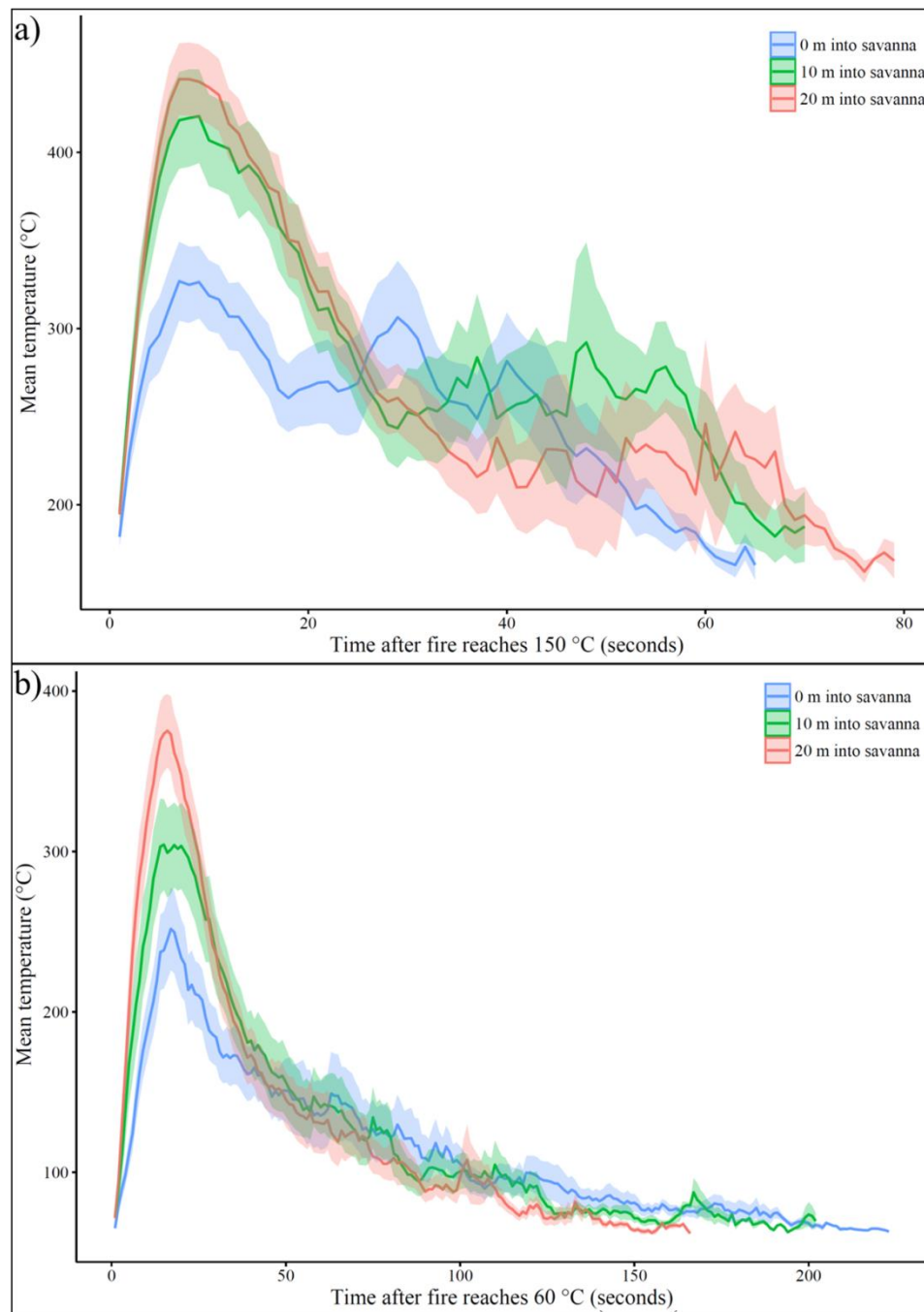


Figure 5.4: Mean recorded temperatures (°C) after temperature first crossed a threshold of a) 150 °C or b) 60 °C for thermocouples placed at 0 m, 10 m, or 20 m into the savanna. Time 0 was the point at which the temperature first exceeded the threshold. Shaded ribbon shows standard error around the mean. The area under each curve represents the total thermal dose (150 °C threshold: 0 m = 16456 °C, 10 m = 19911 °C, 20 m = 20908 °C; 60 °C threshold: 0 m = 25030 °C, 10 m = 25043 °C, 20 m = 22601 °C). Time spent above each threshold was the distance between first and last recording of the threshold temperature (150 °C threshold: 0 m = 65 s, 10 m = 70 s, 20 m = 79 s; 60 °C threshold: 0 m = 223 s, 10 m = 202 s, 20 m = 166 s).

Grass community composition and flammability (Q3)

Changes in fire behaviour were accompanied by significant changes in grass community composition, but not by changes in total grass biomass (**Fig. 5.5a**). *Hyparrhenia diplandra* had the highest biomass at almost all distances into the savanna, and showed significant increases in biomass approaching the edge. The second most dominant species, *Anadelphia afzeliana*, significantly decreased in biomass closer to the savanna edge. The least dominant species, *Imperata cylindrica*, showed no significant changes in biomass. Changes in grass species composition were accompanied by significant changes in tree canopy LAI (**Fig. 5.5b**). The increase in tree canopy LAI corresponded with an increase in *H. diplandra* and a decrease in *A. afzeliana*.

Field- and laboratory-based measurements of combustion-related traits showed *H. diplandra* to be the least flammable species, with *A. afzeliana* and *I. cylindrica* showing similar flammability traits to one another (**Table 5.1**). In field-based measurements *H. diplandra* maximally combusted less than a third as much weight per second of burning than the other two species (**Table 5.1, Fig. 5.6a**). Laboratory-based measurements revealed *H. diplandra* to also have a significantly lower heat of combustion than the other two species. Conversely, for laboratory-based measurements, *A. afzeliana* was found to have the lowest and *I. cylindrica* the highest maximum combustion rates respectively. Laboratory-based measurements also showed that *I. cylindrica* had the highest peak heat release rate, while *A. afzeliana* had the lowest. These same measurements showed *A. afzeliana* and *H. diplandra* to have significantly faster ignition times, nearly half those of *I. cylindrica*.

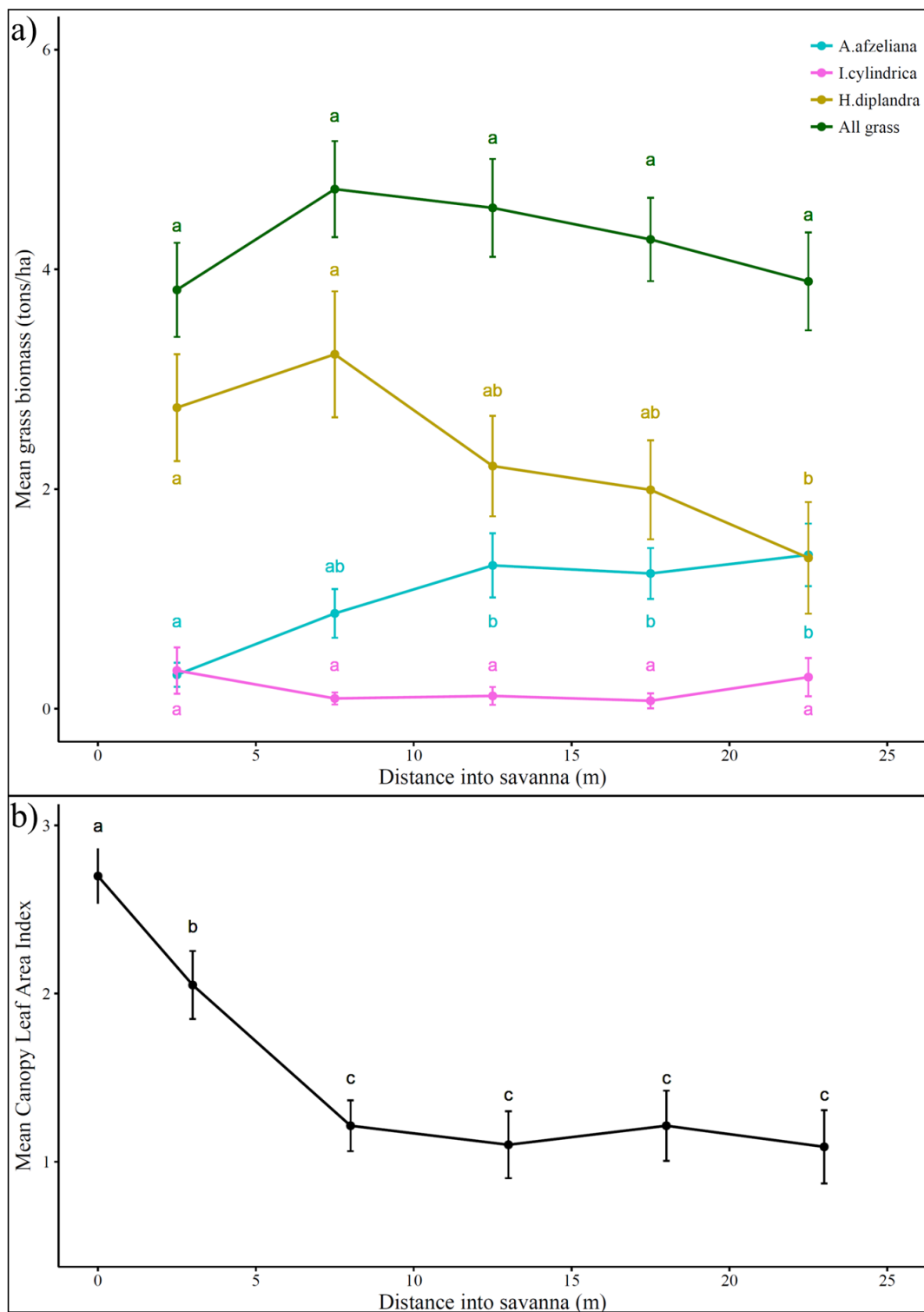


Figure 5.5: a) Total and per species grass biomass (tons.ha⁻¹) and b) tree canopy leaf area index across 18 regularly burnt forest-savanna transition transects. The zero point on the x-axis represents the edge of the savanna, while positive distances are towards the savanna interior. Points and error bars show the mean and its standard error. Different letters indicate significant differences in the variable at different distances into the savanna as determined by Kruskal-Wallis tests (significance noted at p<0.05).

Based on combustion-related flammability traits, *A. afzeliana* and *I. cylindrica* have a similar flammability to one another and are significantly more flammable than *H. diplandra*. However, when also considering moisture-related flammability traits, *A. afzeliana* is the most and *H. diplandra* the least flammable of the three dominant grass species.

Field-based measurement of moisture-related flammability traits revealed *A. afzeliana* to be the most flammable of the three species. *A. afzeliana* had a significantly lower *in situ* moisture content (89%) than *H. diplandra* (133%) or *I. cylindrica* (149%) (**Table 5.1**), with a six- to fourteen- fold higher biomass per plant compared to the other two species. *A. afzeliana* also reached an equilibrium moisture content after fewer days of air drying (10 days) than *H. diplandra* (13 days), and this equilibrium moisture content was significantly lower in *A. afzeliana* (14 %) than *H. diplandra* (25%) or *I. cylindrica* (17%). Both *A. afzeliana* and *I. cylindrica* reached ignition point at 19 % moisture content (after 4 and 5 days respectively), while *H. diplandra* reached neither ignition point nor 19 % moisture content during air drying.

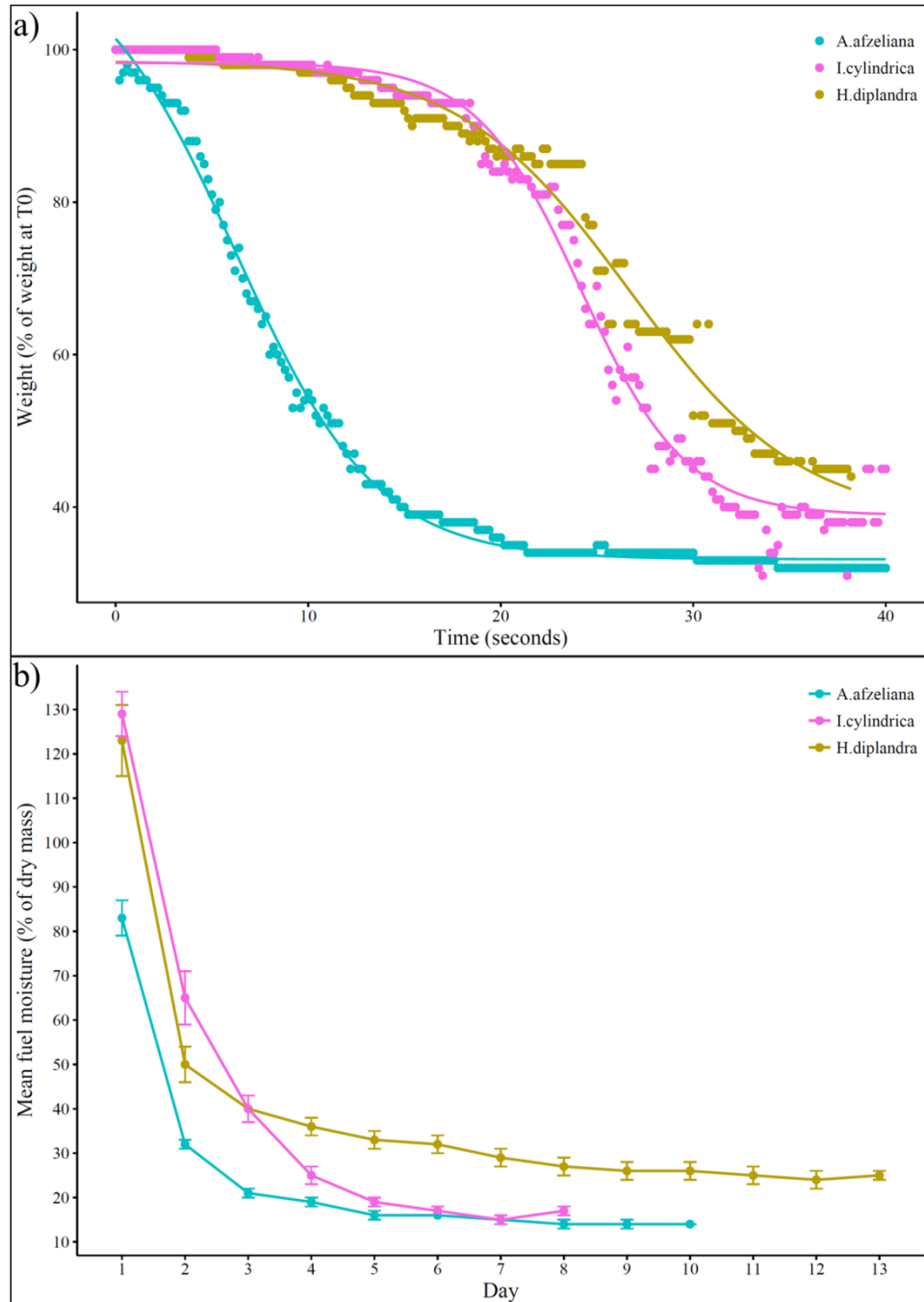


Figure 5.6: a) Mean weight loss (% initial weight) over time during combustion and b) mean fuel moisture content over time during ambient air drying of the three dominant grass species: *Anadelphia afzeliana*, *Hyparrhenia diplandra*, and *Imperata cylindrica*. In (a), the solid line shows the fitted Boltzmann curve for each species (*A. afzeliana*: $p < 0.01$, $df = 212$; *H. diplandra*: $p < 0.01$, $df = 185$; *I. cylindrica*: $p < 0.01$, $df = 208$). In (b), points and error bars show the mean and its standard error; constant moisture content was reached after 8 days for *I. cylindrica* (at 17 %), after 10 days for *A. afzeliana* (at 14%), and after 13 days for *H. diplandra* (at 25 %); ignition point was reached at 19 % moisture content for both *A. afzeliana* (after 4 days) and *I. cylindrica* (after 5 days), and never reached for *H. diplandra*.

Table 5.1: Flammability traits for the three main grass species: *Anadelphia afzeliana*, *Hyparrhenia diplandra*, and *Imperata cylindrica*. The “Method” column indicates whether the trait value was determined at the whole plant scale using field-based measurements (“field”) or from laboratory-based measurements made on mixed plant parts analysed in a calorimeter (“laboratory”). Where applicable, values show the mean ($\pm$ standard error). Different letters indicate significant differences ($p < 0.05$) after pairwise comparison of mean ranks in Kruskal-Wallis tests.

Flammability traits	Method		Flammability traits of grass species	<i>Anadelphia afzeliana</i>	<i>Hyparrhenia diplandra</i>	<i>Imperata cylindrica</i>
	Combustion-related	Field	Maximum combustion rate (g.s ⁻¹)	0.56 ($\pm$ 0.06) a	0.20 ($\pm$ 0.06) b	0.57 ($\pm$ 0.13) a
		Laboratory	Maximum combustion rate (g.s ⁻¹)	0.38 ($\pm$ 0.01) a	0.40 ($\pm$ 0.01) ab	0.48 ($\pm$ 0.03) b
			Heat of combustion (kJ.g ⁻¹)	16.5 ($\pm$ 0.5) a	14.5 ($\pm$ 0.3) b	15.9 ($\pm$ 0.3) a
			Peak heat release rate (kW.m ⁻²)	562 ($\pm$ 24) a	527 ($\pm$ 22) ab	661 ($\pm$ 31) b
			Time to ignition (s)	16 ($\pm$ 0.5) a	17 ($\pm$ 0.5) a	27 ($\pm$ 0.5) b
	Moisture-related	Field	Moisture content at harvest (% dry biomass)	89 ($\pm$ 6) a	133 ($\pm$ 9) b	149 ($\pm$ 21) b
			Number of days air-drying before reaching constant weight	10 ($\pm$ 0) a	13 ($\pm$ 0) b	8 ($\pm$ 0) c
			Moisture content at constant weight (% dry biomass)	14 ($\pm$ 0) a	25 ($\pm$ 8) b	17 ($\pm$ 1) c
			Moisture content half of samples became ignitable (“ignition point”) (% dry biomass)	19	19	never reached
	Biomass-related	Field	Dry biomass per plant (g)	28 ($\pm$ 2) a	154 ($\pm$ 9) b	11 ($\pm$ 0.5) c
			Biomass density (g.cm ⁻¹)	4.4 ($\pm$ 1.5) a	6.6 ($\pm$ 1.1) a	13.0 ($\pm$ 0.7) b
			Leaf surface area:volume ratio	229 ($\pm$ 38) a	97 ($\pm$ 12) b	74 ($\pm$ 7) b

5.5 Discussion

This study demonstrated not only the existence of a fire suppression threshold in this system, but also that its mode of action was mediated by grass community composition which was in turn mediated by the degree of tree canopy cover. This provides support for the hypothesis that forest and savanna are alternative stable states (Sankaran *et al.*, 2005; Hirota *et al.*, 2011; Staver *et al.*, 2011b,a), and highlights the important role of grasses play in the positive feedback loops allowing both states to co-exist in forest-savanna mosaicked landscapes.

A fire suppression threshold existed within the forest-savanna transition (Q1)

We determined the fire suppression threshold to be where tree LAI reached a value of 3. At this point, fires self-extinguished and grass biomass was eliminated from the understorey. Our results support previous findings from South American savannas, where the fire suppression threshold was also proposed to occur when tree LAI reached a value of 3 (Hoffmann *et al.*, 2012). In Southern African savannas, estimates of the fire suppression threshold were where tree canopy cover reached 40 % (Archibald *et al.*, 2009) or where tree LAI reached a value of 1.5 (Charles-Dominique *et al.*, 2018), with discrepancies between the latter estimate and the South American estimate attributed to methodological differences or differences in leaf angle and tree architecture.

The presence of narrow ecotones in both tree cover and grass biomass support the hypothesis that fire-mediated positive feedback loops are maintaining both forest and savanna as alternative stable states of a single mosaicked landscape (Hoffmann et al., 2012; Staver et al., 2011; Staver & Levin, 2012). Any intermediate ecotonal conditions at the forest-savanna transition quickly equilibrated with the more stable conditions of one or the other adjacent environments.

Fires became less intense and less hot prior to reaching the fire suppression threshold (Q2)

Fire behaviour showed significant changes near the edge of the savanna prior to reaching the fire suppression threshold, becoming less intense, reaching lower maximum temperatures, and delivering a lower thermal dose. Although such changes are not entirely unexpected, this is the first empirical exploration of the physical width over which the fire suppression threshold acts. These findings also emphasise the need for fire studies to consider fire as a continuous rather than a binary variable, especially at the forest-savanna transition.

Decreases in fire intensity and heat at the forest-savanna transition have important implications for forest encroachment. Forest encroachment is the process whereby savanna is lost due to expanding forest. It can be mitigated to some extent by intense fires that kill encroaching saplings (van Wilgen *et al.*, 1990; Smit *et al.*, 2010). As this study demonstrated, fires of the critical intensity needed to kill the majority of tree saplings ($> 3000 \text{ kW.m}^{-1}$, van Wilgen *et al.*, 1990) are distinctly lacking from the forest-

savanna transition. This poses management challenges as the forest-savanna transition is exceptionally vulnerable to forest encroachment (Favier *et al.*, 2004), and there is thus potential for savanna habitat to be lost here. Such losses have already been observed in the less frequently burnt parts of the landscape (Jeffery *et al.*, 2014).

Although some heat metrics (those at the 60 °C threshold) did increase closer to the transition, this is unlikely to be sufficient to kill anything but the very smallest tree seedlings. Plant cell death does occur above 60 °C, however thermocouples did not measure temperatures inside the relevant plant tissue. Plant tissue is protected from lethal temperatures by bark and other surrounding tissue (Midgley *et al.*, 2011) while the canopy leaf cells are unlikely to have experienced lethal heat plumes as there was an absence of flame-associated temperatures (>300 °C) closer to the edge (Wotton *et al.*, 2012).

Changes in fire behaviour were mediated by changes in grass species composition and flammability, which was mediated by tree canopy cover (Q3)

We showed fire to decrease in intensity and temperature while total grass biomass remained high. These changes in fire behaviour showed strong links with grass species dominance patterns and the associated species-level flammability traits. This study provides the first empirical demonstration of such patterns, and confirms the combined inferences made by previous studies (Simpson *et al.*, 2016; Charles-Dominique *et al.*, 2018; Wragg *et al.*, 2018).

Whole-plant moisture-related flammability traits were especially important in determining landscape-scale fire behaviour changes, confirming the importance of including fuel moisture metrics in fire-behaviour models (Rothermel, 1972; Scott & Burgan, 2005). For example, although *Anadelphia afzeliana* and *Imperata cylindrica* are approximately equally combustible, curing simulations showed that *A. afzeliana* would be drier and therefore faster combusting than *I. cylindrica* at any given point in the burning season. Similarly, curing simulations showed that *Hyparrhenia diplandra* is unlikely to ever cure sufficiently *in situ* to become flammable, likely due to the high ambient relative humidity levels, and will therefore act to reduce fire intensity and temperature. Both of these inferences were confirmed by field measurements of fire behaviour. The low *in situ* flammability of *H. diplandra* was further confirmed by post-burn field observations of its leaves resprouting vigorously from the nodes all the way up the scorched-black culms. This indicates that this species' low flammability traits decreased fire intensity sufficiently to protect dormant buds in the canopy.

The importance of moisture-related flammability traits is confirmed by there being key differences between laboratory-based and field-based flammability traits of the three dominant grass species. When equal volumes of dry samples were assessed using a calorimeter, no clear pattern of which species was the most flammable emerged, with each more flammable in one metric while less flammable in another. However, when whole plants were burnt, *A. afzeliana*, and to a lesser extent *I. cylindrica*, were shown to be the most flammable, and *H. diplandra* the least, a finding that correlated with observed landscape-level fire behaviour patterns. The discrepancy between the two

approaches is due to the combustion of oven-dried samples in the calorimeter, and thus an inability to account for differences in moisture-related flammability traits. Since field-based flammability measurements were key for determining landscape-scale fire behaviour, we recommend that future research mimics field moisture conditions within calorimeter-based measurements otherwise incorrect conclusions may be drawn.

Changes in grass species composition occurred simultaneously with an increase in tree canopy cover (LAI). Tree LAI alters understorey habitat both directly, by decreasing the amount of light reaching the understorey, and indirectly, by creation of a cooler, more humid, more fertile environment (Scholes & Archer, 1997). Although the micro-climate of the understorey was not measured in this study, the point at which tree LAI started to significant increase corresponded closely with previous estimates of how far into the savanna the forest's micro-climatic envelope extends (Ibanez et al. 2013). This indicates that, in addition to the direct effect of light reduction, increasing tree LAI alters grass species composition approaching the edge of the savanna indirectly via changes to the micro-climate. In addition to this indirect effect tree LAI is having on fire behaviour, the inextricable direct effect that a cooler and more moist micro-climate might have on fire behaviour should not be overlooked, although a thorough investigation of this was beyond the scope of this study.

Conclusion

This study showed that the fire suppression threshold at forest-savanna transitions was not a simple on-off switch, but a mechanism mediated by interacting biotic and abiotic

factors that cause fire behaviour to change before the threshold is reached. We demonstrated here how the more shade-tolerant grasses are also less flammable, largely as a result of their moister culms. Although not previously described, we suspect that such a phenomenon is widespread, and it would be fascinating to explore whether similar patterns occur at other tropical forest-savanna transitions.

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5.8 Supplementary material

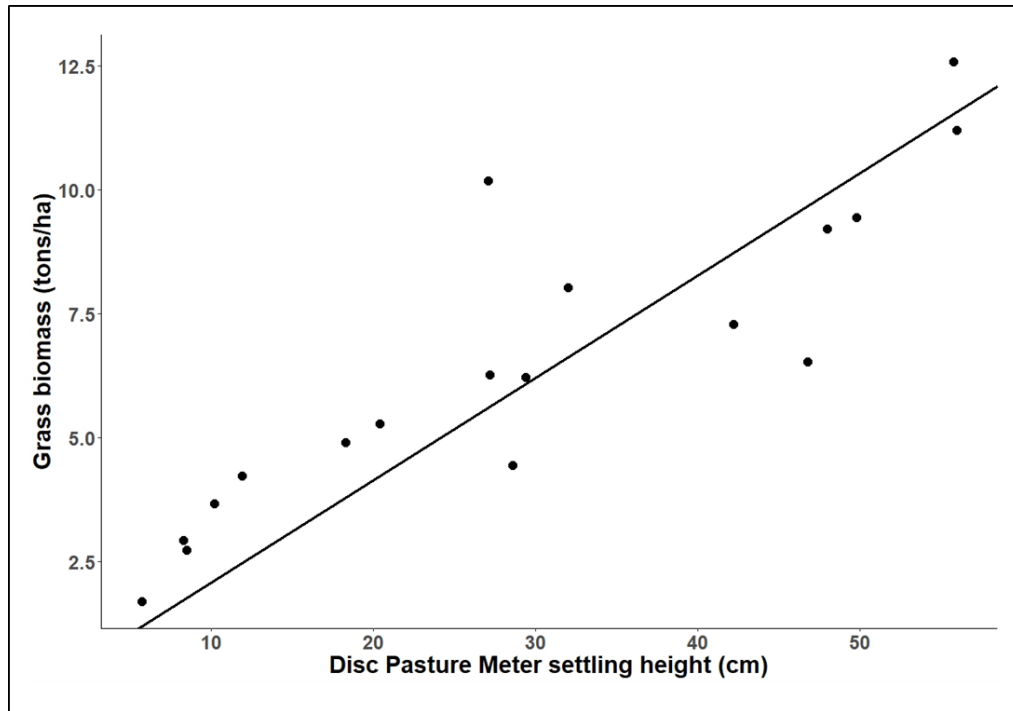


Figure S5.1: Calibration of disc pasture meter (DPM) in the study site, Lopé National Park, Gabon. Each point represents one calibration plot. Each calibration plot was 1 m x 1 m, in which the mean of five DPM measurements (one in each corner and one in the middle of the plot) was associated with the clipped grass biomass of the plot (dry weight after drying to constant mass in oven). The line represents the calibration equation, where the intercept was set to zero: Grass biomass ($\text{tons} \cdot \text{ha}^{-1}$) = DPM height (cm) * 0.2675 (linear model: $p < 0.0001$, adjusted $R^2 = 0.94$, $F = 56.3$, $df = 17$).

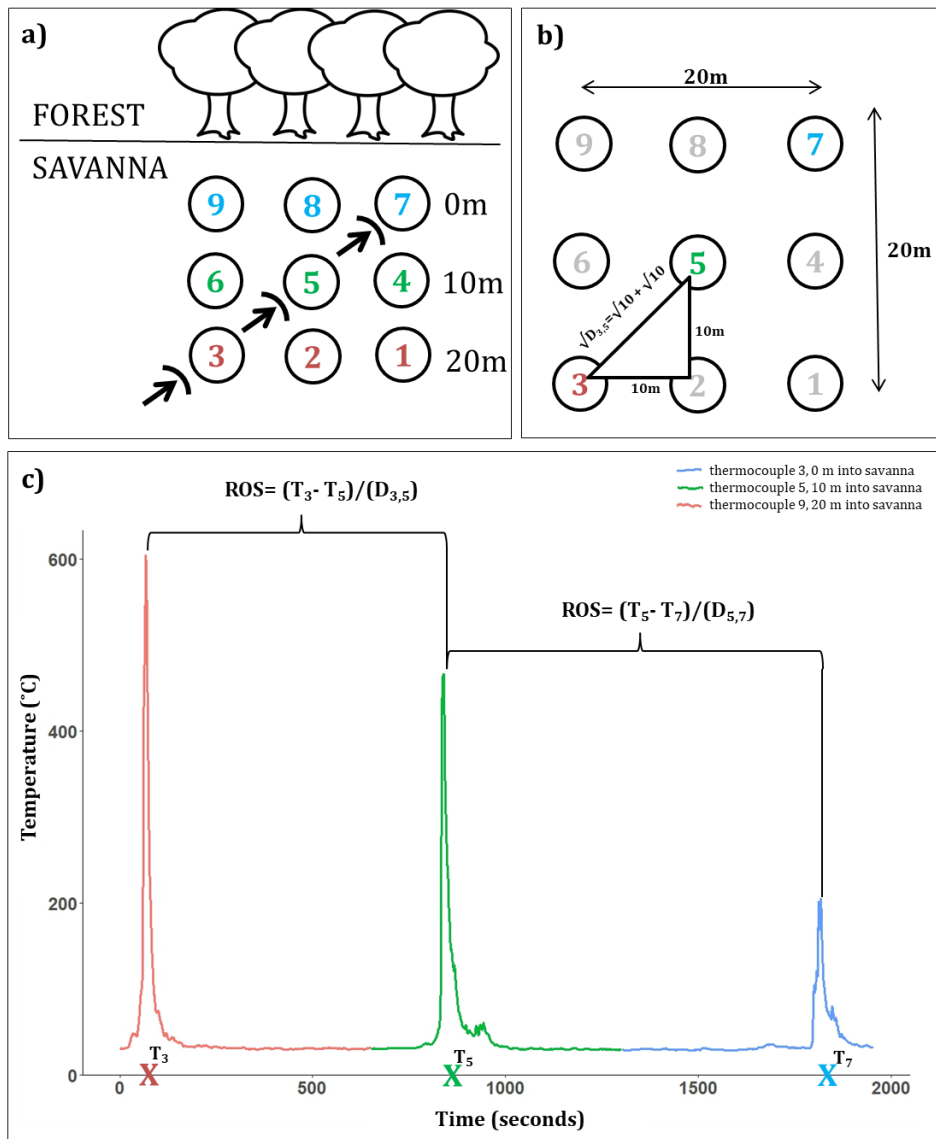


Figure S5.2: The method for calculating rate of spread of the fire front using thermocouples. Rate of spread was determined using the formula: $ROS = \frac{T_x - T_y}{D_{x,y}}$ where ROS is rate of spread ($m \cdot s^{-1}$), T_x and T_y are the times (seconds) that

thermocouples x and y show their temperature peaks (ie. the time the fire front is assumed to cross the location of each thermocouple), with x being the first and y being the second thermocouple that the fire front passes, and $D_{x,y}$ being the distance (m) between thermocouple x and y. In this example we calculate two rates of spread for one fire front, the ROS between thermocouples 3 and 5, and between thermocouples 5 and 7. Diagrams show: a) the layout of the thermocouples (labelled 1-9) within the savanna at varying distances (0, 10 and 20 m), and the movement of an approaching fire front (arrows) that crosses first thermocouple 3, then 5, then 7; b) calculation of the distance (D) between thermocouples 3 and 5; and c) calculation of the time that temperature peaks (T) for thermocouples 3, 5, and 7. In each transect, multiple rate of spread calculations could be performed. In this example, for instance, rate of spread could also be calculated between thermocouples 6 and 8, and between thermocouples 2 and 4.

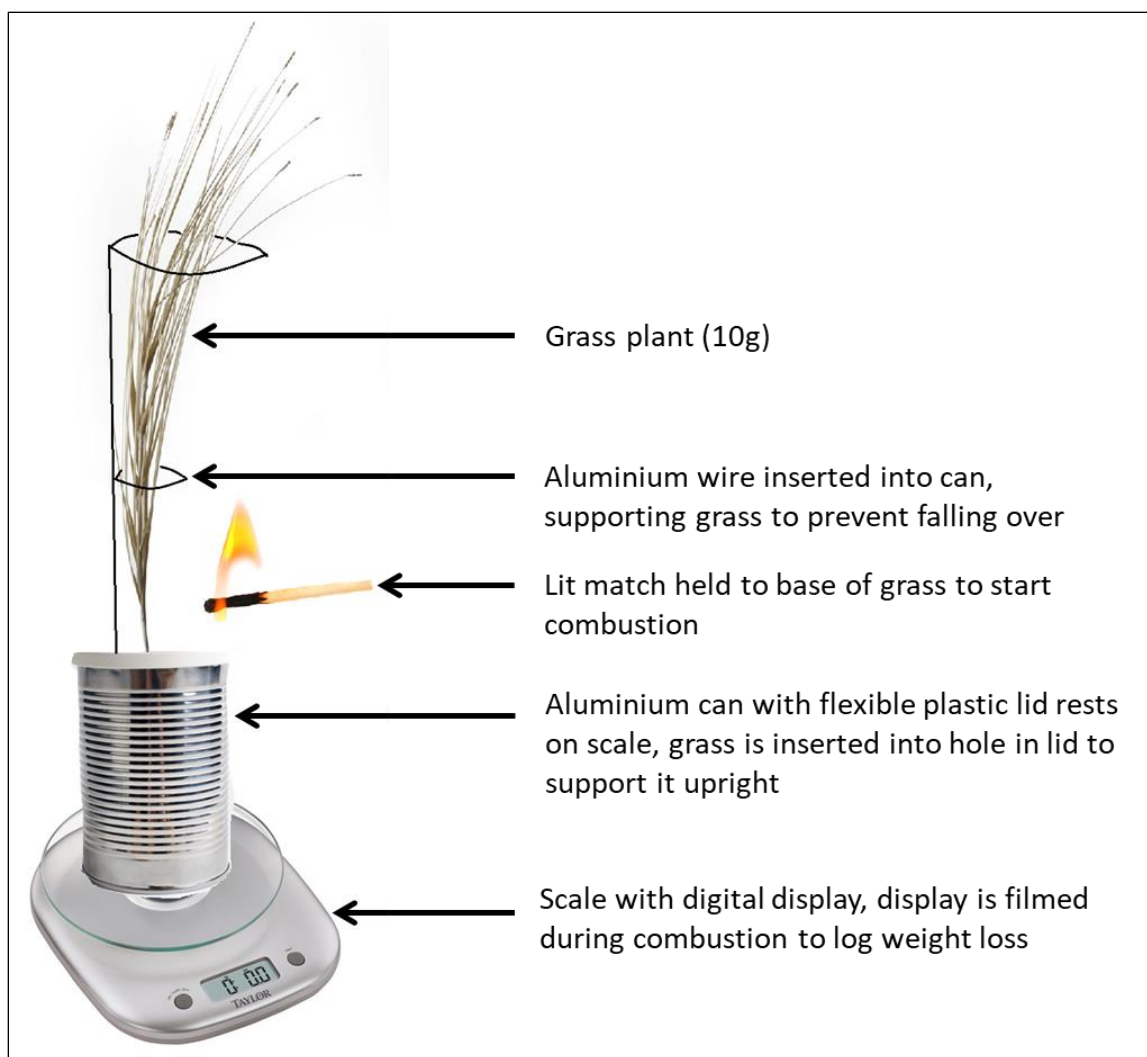


Figure S5.3: Experimental set-up to test plant scale maximum combustion rate of each grass species.

Table S5.1: Fire behaviour and climate-related metrics measured during burning of 18 forest-savanna transition transect sites.

	Metric measured during burning	Median ($\pm$ inter-quartile range)
Fire behaviour	Point of fire self-extinction (m into savanna)	-1 ($\pm$ 1.8)
	Maximum fire line intensity (kW.m ⁻¹)	902 ($\pm$ 499)
	Maximum temperature (°C)	595 ($\pm$ 53)
Climate-related	Fire danger index (using mean wind speed) (0-100)	40 ($\pm$ 6)
	Fire danger index (using maximum wind speed) (0-100)	46 ($\pm$ 6)
	Fuel moisture content (% dry mass)	35 ($\pm$ 12)
	Mean wind speed (km.hr ⁻¹)	5.4 ($\pm$ 1.9)
	Maximum wind speed (km.hr ⁻¹)	16.2 ($\pm$ 3.1)
	Relative humidity (%)	65 ($\pm$ 2)
	Ambient air temperature (°C)	28.6 ($\pm$ 0.5)
	Vapour pressure deficit (kPa)	1.36 ($\pm$ 0.48)

Table S5.2: Linear models where fire behaviour metrics were examined as a function of climate-related metrics. Significant effects ($p < 0.05$) are marked with an *. With the exception of fuel moisture content and mean and maximum wind speed on maximum temperature, no significant effects of climate-related metrics on fire behaviour metrics were found.

<u>Climate-related metrics</u>	<u>Fire behaviour metrics</u>								
	Point of fire self-extinction (m into savanna)			Maximum fire line intensity (kW.m ⁻¹)			Maximum temperature (°C)		
	p	Slope (+/-)	Adjusted R ²	p	Slope (+/-)	Adjusted R ²	p	Slope (+/-)	Adjusted R ²
Fire danger index (using mean wind speed) (0-100)	0.53	-	-0.04	0.38	-	-0.01	0.57	+	-0.04
Fire danger index (using maximum wind speed) (0-100)	0.41	-	-0.02	0.52	-	-0.04	0.34	+	-0.01
Fuel moisture content (% dry mass)	0.23	-	0.03	0.34	+	-0.01	0.01*	+	0.33
Mean wind speed (km.hr ⁻¹)	0.51	-	-0.03	0.46	+	-0.03	0.04*	+	0.21
Maximum wind speed (km.hr ⁻¹)	0.42	-	-0.02	0.48	+	-0.03	0.05*	+	0.18
Relative humidity (%)	0.59	+	-0.05	0.20	+	0.05	0.46	+	-0.02
Ambient air temperature (°C)	0.61	-	-0.05	0.45	-	-0.03	0.34	-	-0.01
Vapour pressure deficit (kPa)	0.54	-	-0.04	0.29	-	0.01	0.39	-	-0.01

Chapter 6:

Distinct transition tree community suggests possible antiquity of forest-savanna mosaics

By:

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Photo: Anabelle W. Cardoso

The previous chapter characterised fire behaviour at the forest-savanna transition, and found fires to become less intense and less hot as they approached the edge of the savanna. This prompts exploration of whether these fire conditions, distinct from the adjacent forest and savanna, have led to the development of a woody community that is uniquely suited to this niche. This chapter explores this, and describes the ecology of the tree community at the forest-savanna transition.

This paper is under review at *New Phytologist*.

The ideas and research questions, study design, methods, data collection, data analysis, and writing presented in this chapter are the work of the first author, Anabelle W. Cardoso. These activities greatly benefitted from the contributions of Yadvinder Malhi, Imma Oliveras, Katharine A. Abernethy, and William J. Bond, who also made substantial contributions during the writing of the manuscript.

Kathryn J. Jeffery, David Lehmann, and Josue Edzang Ndong, assisted with finessing the methodology and provided support in the field. Lee J. T. White provided data used in this study. All these authors also provided constructive comments during writing of the manuscript.

6.1 Abstract and Key words

Transitions in forest-savanna mosaics represent the interface of opposing fire regimes. Whether a compositionally and functionally distinct woody community has evolved to exploit this space is unknown. The ecology of such a community would provide insight of the stability of the mosaic through time, and the role that fire plays in facilitating the co-existence of multiple vegetation types in one landscape. Within a Central African forest-savanna mosaic we investigated the ecology of the woody transition community using data from forty vegetation transects. We used functional traits to link species assemblage patterns with environmental processes causing them. Results showed a distinct, intermediately fire resistant transition tree community existed. Seven tree species were identified as forming this community, which had the stem size distribution of a stable community and not a forest gap community. Burning is essential to maintain this landscape, as under decreased fire frequency the early signs of forest encroachment were observed. The presence of a distinct transition community at the forest-savanna transition suggests that savanna and forest have been interfacing with one another here for a long time. Although not previously recognised, the distinct transition community identified here is likely to be a feature of all ancient forest-savanna mosaics.

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

6.2 Introduction

Tropical forest and savanna are two ecologically opposite vegetation types that mosaic with one another across 9 % of Africa (Parr *et al.*, 2014). Forest-savanna mosaics are characterised by an abundance of sharp transitions between vegetation types. Such mosaics are of high conservation value as their diversity of habitats allows them to support forest and savanna specialist fauna in a single landscape (Walters *et al.*, 2013). However, they are also particularly vulnerable to change as the forest edge can expand or retreat through time (Maley, 2002; Mitchard *et al.*, 2009; Aleman *et al.*, 2018). Despite their importance and dynamic nature, the ecology of transitions in forest-savanna mosaics remains poorly understood (Oliveras & Malhi, 2016).

Forest-savanna transitions, defined here as where the forest edge meets the savanna, occupy a unique niche in mosaicked landscapes: the interface of two opposing fire regimes. Closed-canopy forests very rarely burn as they lack high-flammability fuels (grasses) (Hoffmann *et al.*, 2012b) and have a fire-suppressing cool, humid, and still micro-climate (Uhl & Kauffman, 1990). In contrast, open-canopy wooded grassland savannas are fire-promoting, and their highly productive and seasonally dry grass layer supports some of the highest fire frequencies on earth (Mouillot & Field, 2005). Differences in the fire regime causes the tree communities of these vegetation types to be compositionally and functionally distinct: forest tree species are fire-sensitive and savanna tree species are fire-resistant (Hoffmann *et al.*, 2003; Charles-Dominique *et al.*, 2015b). Between the forest and savanna lies the transition, which experiences an

intermediate fire regime (Cardoso *et al.*, **Chapter 5**). As such, an intermediately fire-resistant tree community may exist here. Such a community would likely play an important role in determining the vulnerability of savanna to encroachment from forest and vice versa.

In order to better understand the ecology of forest-savanna transitions it is important to explore both their species composition patterns and the processes that may affect these (Cadenasso *et al.*, 2003). Patterns in species assemblages can be used to identify the location of the transition and identify the species community that lives there. Discontinuities in species assemblage patterns, such as borders and their associated ecotones, are especially useful for this. We define a border (following Hennenberg *et al.*, 2005) as the boundary between two vegetation communities at which point the magnitude of change between them is the greatest, and ecotones as the width of the zone of substantial change either side of the border. An ecotone is often referred to as a “transition zone”, and can be sharp and narrow or gradual and wide, but refers *only* to the width around one border that separates two communities. More than one border and multiple non-overlapping ecotones however suggest that more than one community is present (Walker *et al.*, 2003). For example, in forest-savanna mosaics, two borders and non-overlapping ecotones between forest and savanna suggests three communities are present: forest, savanna, and transition; while a single border suggests only two: forest and savanna with an intermediate ecotone or “transition zone”.

Patterns in species composition are inextricably linked to underlying processes (Fagan *et al.*, 2003). In forest-savanna mosaics, fire is one of the key processes affecting vegetation patterns, filtering plant communities based on their fire-resistance traits (Charles-Dominique *et al.*, 2017). Investment in fire-resistance traits is associated with allocation trade-offs (Rosell *et al.*, 2014), so species will only do so if fire is a strong selective pressure in the system. For example, savanna tree species tend to have thick bark as this helps to insulate their trunks from heat during the frequent surface fires they have to contend with (Hoffmann *et al.*, 2003). In contrast, forest tree species live in a virtually fire-free environment and therefore do not need to invest in fire-resistance traits. Instead, because light availability is so variable in closed-canopy forests, forest tree species invest either in traits that allow for fast growth, allowing them to take advantage of ephemeral light gaps, or in traits that increase their longevity, allowing them to tolerate shade and other stresses over longer lifespans (Wright *et al.*, 2010). While the suite of functional traits associated with forest and savanna tree species is relatively well described (Hoffmann *et al.*, 2003), similar information on the species at the transition, who experience intermediate fire pressure (Cardoso *et al.*, **Chapter 5**) and light availability (Charles-Dominique *et al.*, 2018), has not yet been described.

To date, studies on transitions between forest and more open environments have largely focused on anthropogenically created forest edges and the negative “edge influence” effects on forest vegetation associated with these (Harper *et al.*, 2005). The few studies on natural transitions in forest-savanna mosaics focus only 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.*, 2004; Ibanez *et al.*, 2013c), 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.*, 2013b). While these are all valuable contributions, an exploration of transition vegetation as an entity distinct from forest and savanna is still needed.

The ecology of the forest-savanna transition has implications for the long-term dynamics and stability of mosaicked landscapes. Mosaics with a long evolutionary history of fire-mediated co-existence of forest and savanna are more likely have a distinct transition tree community capable of thriving in the intermediate fire regime of the interface. This tree community might be expected to contain stems of all size classes, suggesting that it has existed long enough for there to be multiple recruitment events. Conversely, mosaics that are ephemeral and of more recent origin are more likely to have a transition community where all of the stems are of similar size classes, suggesting that they recruited simultaneously and potentially represent only a single successional stage.

We explore the woody community across transitions in a fire-managed forest-savanna mosaic using data from 40 transects in Lopé National Park in Gabon, Central Africa. The objective of this study was to assess whether a distinct transition tree community could be identified at the forest-savanna transition, and to investigate its ecology. Specifically, we investigated the following research questions:

Q1) Is there a detectable transition in the forest-savanna mosaic?

1.1) Can at least two borders and non-overlapping ecotones be detected between savanna and forest?

1.2) Can any detected transition (in 1.1) be distinguished from the forest and savanna in a multi-variate functional trait space?

Q2) Do tree species in the forest-savanna mosaic filter into distinct communities?

2.1) Which tree species form the transition community?

2.2) Does the size class distribution of the transition community suggest it is in equilibrium or a single successional stage?

Q3) Does fire maintain the diversity of tree communities in the forest-savanna mosaic?

3.1) Is the distinction between forest, transition, and savanna less clear when fire frequency is low (*cf.* high)?

3.2) How do the communities of the forest-savanna mosaic change when fire frequency is low (*cf.* high)?

6.3 Materials and Methods

Study site

Lopé National Park (LNP), Gabon, is a forest-savanna mosaic with sharp transitions between Middle Ogooué savannas (van de Weghe, 2011) and Lower Guineo-Congolian rainforest (White, 1983) (**Fig. S6.1**). The average rainfall is 1442 mm p.a. (1984-2016), average temperature is 24 °C (2003-2016), and average humidity is 81 % (2003-2016) (Tutin *et al.*, 2016). There is a short (mid-December to mid-February) and a long (mid-June to mid-September) dry season. Prescribed burning occurs in the long dry season, with fire being used in this landscape for more than 5000 years (White, 2001; Jeffery *et al.*, 2014).

Vegetation transects

We set up 40 transects across two fire frequency treatments: 18 “low fire” (savanna burnt 0-3 times in the last 10 years and not burnt in the last 3 years) and 22 “high fire” (savanna burnt 1-3 times in the last 3 years) (**Fig. 6.1**). The distinction between high and low fire frequency sites was made as a) “high fire” sites were visually very distinct (less overgrown) from sites that were burnt any less frequently and b) high rainfall African savannas, like the one in this study, have the highest grass species richness, evenness, and diversity when burnt every 1-3 years (Smith *et al.*, 2013) (i.e. “high fire” sites), thus we interpreted all fire frequencies lower than this (i.e. “low fire” sites) to represent a departure from the “natural” fire regime of the area.

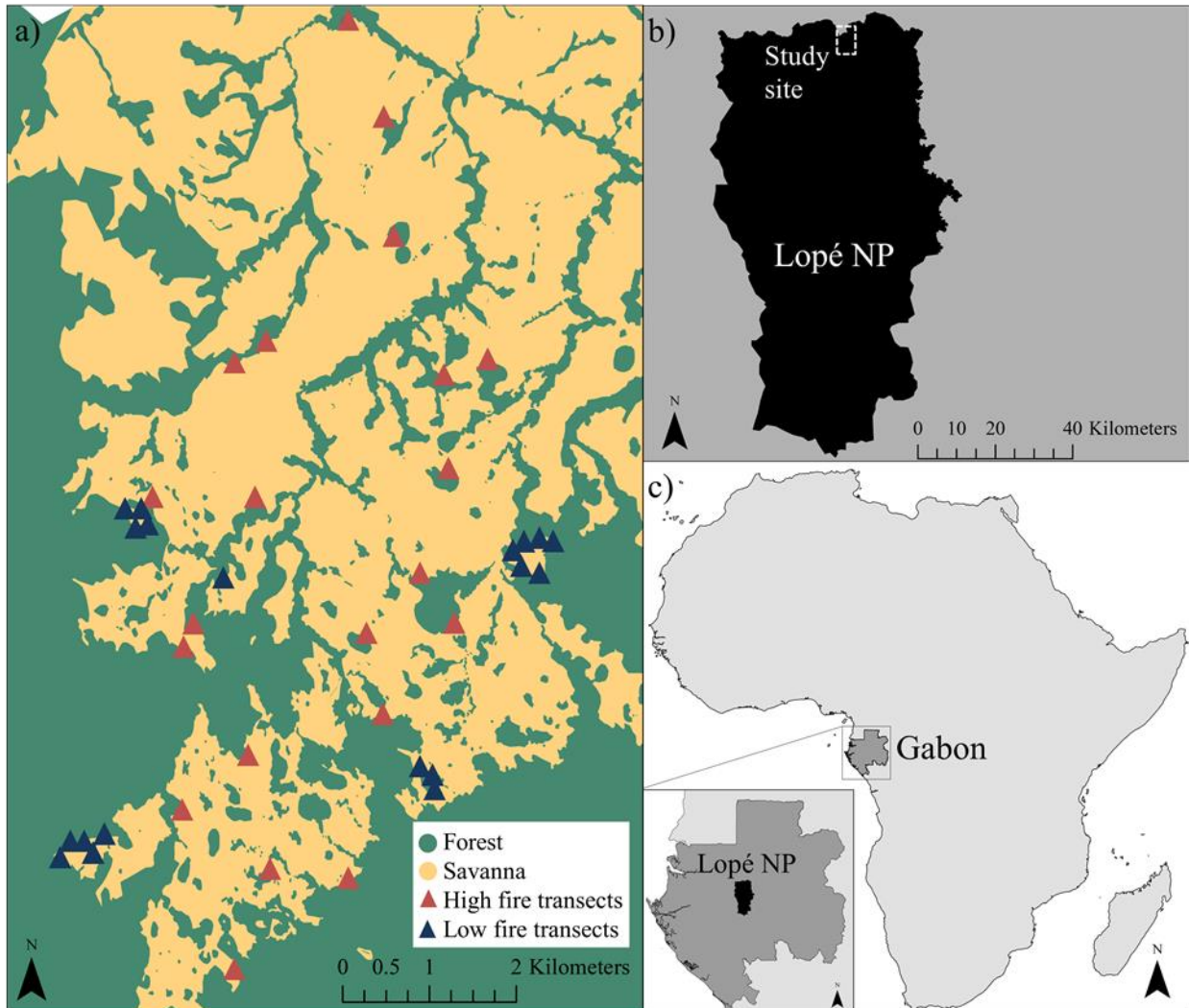


Figure 6.1: Map of a) the study area and the forty transect sites and b) their location within the broader region of Lopé National Park in c) Gabon (Agence Nationale des Parcs Nationaux, 2006).

Transects were 2 m wide and started in the savanna, 25 m from the forest edge, before crossing the hypothesised transition, which was of variable length, and then covering 10 m of forest (**Fig. S6.2**). These delineations of savanna, transition, and forest were applied in the field and were only to ensure adequate sampling and were not used as classifications in the data analysis. Field definitions were physiognomic for ease of

application: savanna was where grass cover was continuous, woody canopy cover discontinuous, and visibility >5 m; transition was where grass cover became discontinuous, woody canopy cover became continuous, the canopy was vertically continuous with the understorey layers, and visibility was <5 m; and forest was where the woody canopy remained continuous, but became vertically discontinuous with the understorey, and visibility was >5 m. Transects were sampled in adjacent 1 m increments (1 m x 2 m block), starting in the savanna and progressing towards the forest interior. Distances up to 25 m along the transect were therefore in the savanna, with distances greater than 25 m along the transect falling either in the transition or the forest. Transects were sampled along their length in 1 m blocks (each 2 m wide).

All trees with a basal diameter (measured at 10 cm above ground) > 3 cm were classed “established” trees and their location, species, basal diameter, height, and canopy dimensions (length, breadth, depth) noted. Within a nested sampling strip 20 cm wide on the left hand side of the transect all stems with a basal diameter <3 cm and a height >30 cm were classed “juvenile” saplings and their location, species, height, and basal diameter noted. Grass biomass was measured every 1 m using a disc pasture meter calibrated for the site (Dorgeloh, 2002; Cardoso *et al.*, **Chapter 5**).

Functional traits

Functional traits were sampled on the woody species representing 85 % of total woody basal area sampled in the transects (**Table S6.1**).

Bark investment (mm of bark per mm of trunk diameter) represents the importance of bark production (Ibanez *et al.*, 2013a). Bark thickness was taken to be the median of three thickness measurements (using digital callipers) on one 4 cm² sample of bark removed from the trunk at 30 cm above the ground; while trunk diameter was taken at the point of bark sampling (using a diameter tape), measured on a minimum of nine individuals per species. From these data, the allometric coefficient of bark was determined (allometric coefficient_{bark}). This is a species-level measure of the speed of bark production, where coefficients <1 indicate a disproportionally higher investment in bark at smaller diameters, >1 disproportionally higher at larger diameters, and ≈1 proportional investment in bark with diameter (Jackson *et al.*, 1999). It was calculated by determining 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. S6.3a**). Previous work has found savanna trees to have coefficients <1 and forest trees to have coefficients >1 (Hoffmann *et al.*, 2003).

The relative size of species' underground storage organs (cross-sectional area of root at the widest point per basal area of trunk) was determined, with larger values implying more carbohydrates available to fuel canopy regrowth after burning (Bond & Midgley, 2003). Species values were taken to be the mean ratios of three dug-up saplings (measured using digital callipers).

Woody density (g of dry wood mass per cm³ of wood volume) is linked to many tree functions, for example growth and mortality rates (Chave *et al.*, 2009). This was

calculated for each species as the mean oven dry mass of three twigs ($\pm 1\text{-}2\text{ cm}$ diameter) divided by their respective volumes (after bark was removed; Marthews *et al.*, 2014).

The relative tree height to trunk diameter (cm of tree height per mm of trunk diameter) gives a measure of how tall the trees of a species are. Tree height (measured using laser hypsometer Nikon TruPulse 360R) was divided by trunk diameter (measured using diameter tape) for every tree in the transects, and the species value was the mean of all trees of each species. From these data the allometric coefficient of tree height (allometric coefficient_{height}) was determined (similarly to allometric coefficient_{bark}), giving a measure of how quickly trees are accumulating height (Feldpausch *et al.*, 2011) (**Fig. S6.3b**). All trees had their canopy dimensions (canopy depth, width, and length) measured (using a measuring tape). From this, the ratios between canopy area (cm²) and tree basal area (cm²) and canopy volume (cm³) and tree height (m) could be determined. These ratios show, relative to its size, how much shade a tree may create and the volume of space it is filling with photosynthetic leaf material relative. Canopy area was calculated as the area of an ellipse, canopy volume as the volume of an ellipsoid sphere, and tree basal area as the area of a circle. For each species these were the mean ratios of all trees in the transects.

Leaf mass per area (LMA, g of leaf mass per cm² of leaf area) gives a measure of how thick leaves are and was calculated by converting leaf images (excluding petioles) (using desktop scanner Canon LiDE 120) to leaf pixel area via post-hoc image analysis

in MatLab (v8.0, Marthews et al. 2014) and 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. Using these leaf scans, the mean leaf area (cm² of leaf area) of each species was also determined as a measure of leaf size.

Canopy leaf area index (LAI, canopy leaf area per unit of ground area) was measured as a proxy for understorey shading. We calculated canopy LAI from hemispherical photographs (every 5 m in savanna and forest and every 1 m in transition) taken 1 m above ground level (Nikkor fish-eye lens 10.5mm F2.8G AF DX IF ED) and converted into LAI values using post-hoc image analysis in Hemisfer (v2.16, Schleppi *et al.*, 2007; Thimonier *et al.*, 2010) according to Marthews *et al.* (2014).

Data analysis

In order to increase the number of trees in the analyses and facilitate the detection of statistically significant patterns, data on established trees from individual transects were combined to produce two “merged” transects: one for transects experiencing high and one for low fire frequencies. Each transect block therefore represented the mean composition of all blocks that were sampled at that location along the transect.

Split moving window dissimilarity analysis (SMWDA) and moving window regression analysis (MWRA) were combined to detect the location of borders and the width of their associated ecotones along the transects (Ludwig & Cornelius, 1987). SMWDA

calculates the dissimilarity of adjacent half-windows by comparing their squared Euclidean distances based on presence-absence matrices. Dissimilarities are 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). The mean dissimilarity of five half-window sizes (1-5 m) was used to reduce the scale dependency of the results (Erdős *et al.*, 2014). MWRA then calculates the degree of change in z-scores along the transect by calculating the slope of each z-score using the two scores either side via a moving window (Hennenberg *et al.*, 2005; R script for all SMWDA performed available in Erdős *et al.*, 2014). Borders were determined to be the peaks in z-scores >1.645 (95% confidence interval) from SMWRA that were also detected as turning points (slope=0) by the MWRA (Hennenberg *et al.*, 2005). The width of each border's ecotone was determined to be the distance between the maximum and minimum of the slope from the MWRA (Hennenberg *et al.*, 2005). Detected borders thus denoted locations of significant discontinuities in species composition along the transects, and when they were associated with no-overlapping ecotones indicated the potential presence of multiple tree communities (Walker *et al.*, 2003). Each transect could then be divided into forest, transition, or savanna.

A principal components (PCA) analysis (function *prcomp* in package *stats*) was used to assess whether these forest, transition, and savanna could be distinguished from one another in a multi-variate functional trait space (Legendre & Legendre, 1998). The community weighted mean (based on tree basal area) for each trait was calculated for each community in each transect (according to the detected communities in SMWA and

MWRA) and these were then input as samples into the PCA (scaled and centered). Kruskal-Wallis tests (function *kruskal* in package *agricolae*) were used to test for significant differences in principle component scores between the communities.

We then assessed whether tree species in the transects could be classified into distinct savanna, transition, and forest communities. χ^2 tests (function *pchisq* in package *stats*) were used to compare observed frequencies of adult stems in each species with expected frequencies, which assumed the density of stems was equal between forest, transition, and savanna. To assess post-hoc the source of the significant χ^2 values, we calculated the Pearson standardised residual for forest, transition, and savanna using the formula: $\frac{\text{observed} - \text{expected}}{\sqrt{\text{expected}}}$. Positive residuals that were greater than 2.128 (p was adjusted for multiple comparisons within each species) were noted to be a significant (Sharp, 2015). A significant residual indicated that there were significantly higher than expected stems of that species in that community. Indicator species for each community were also sought using indicator value analysis (Dufrêne & Legendre, 1997; De Caceres & Legendre, 2009). This enabled identification of which species were both abundant in a specific community (i.e. high specificity) and are also predominantly found in that community (i.e. fidelity). Indicator values were calculated using the function *indval* in the package *labdsv*. Tree species that had significant χ^2 values, had a significant residual for the transition community only, and were significant indicator species for the transition were classified as being part of the transition community. Similar criteria were applied to species in the savanna and forest communities.

To assess whether detected communities were also associated with distinct LAI environments or grass biomasses we used Kruskal-Wallis tests. The relationship between grass biomass and distance from the forest edge was assessed using linear models.

Statistical significance was noted at $p < 0.05$. All statistical analyses were performed in R (v3.5.0; R Development Core Team, 2018).

6.4 Results

A transition was detected between savanna and forest (Q1)

Borders, or significant peaks in dissimilarity (i.e. where SMWDA mean Z-score > 1.96) that coincided with turning points (i.e. where MWRA slope=0), were detected at two points in high and three points in low fire frequency transects (marked by * in **Fig. 6.2**). The ecotones associated with these borders (i.e. the distance between the maximum and minimum MWRA slope value either side of each border) were non-overlapping in high fire frequency transects, indicating that three distinct tree communities were present. In low fire frequency transects, two of the three ecotones were overlapping, therefore only two true ecotones were present despite there being three borders, and thus here too three distinct tree communities were indicated.

Using the outer limits of the ecotones, when fire frequency was high the savanna was found in the first 27 m along the transect, the transition between 27 m and 36 m, and the forest along the remainder of the transect (**Fig. 6.2a**). When fire frequency was low, the savanna was found in the first 25 m along the transect, the transition between 25 m and 42 m, and the forest along the remainder of the transect (**Fig. 6.2b**). A diagrammatic representation the distribution of the trees in these three vegetation communities along the transects of both fire regimes can be found in **Fig. 6.3**. There is an absence of larger trees in this diagram, especially in the forest, as a result of the transects being too small to effectively sample trees in larger size classes (*cf.* no larger trees being present in the area).

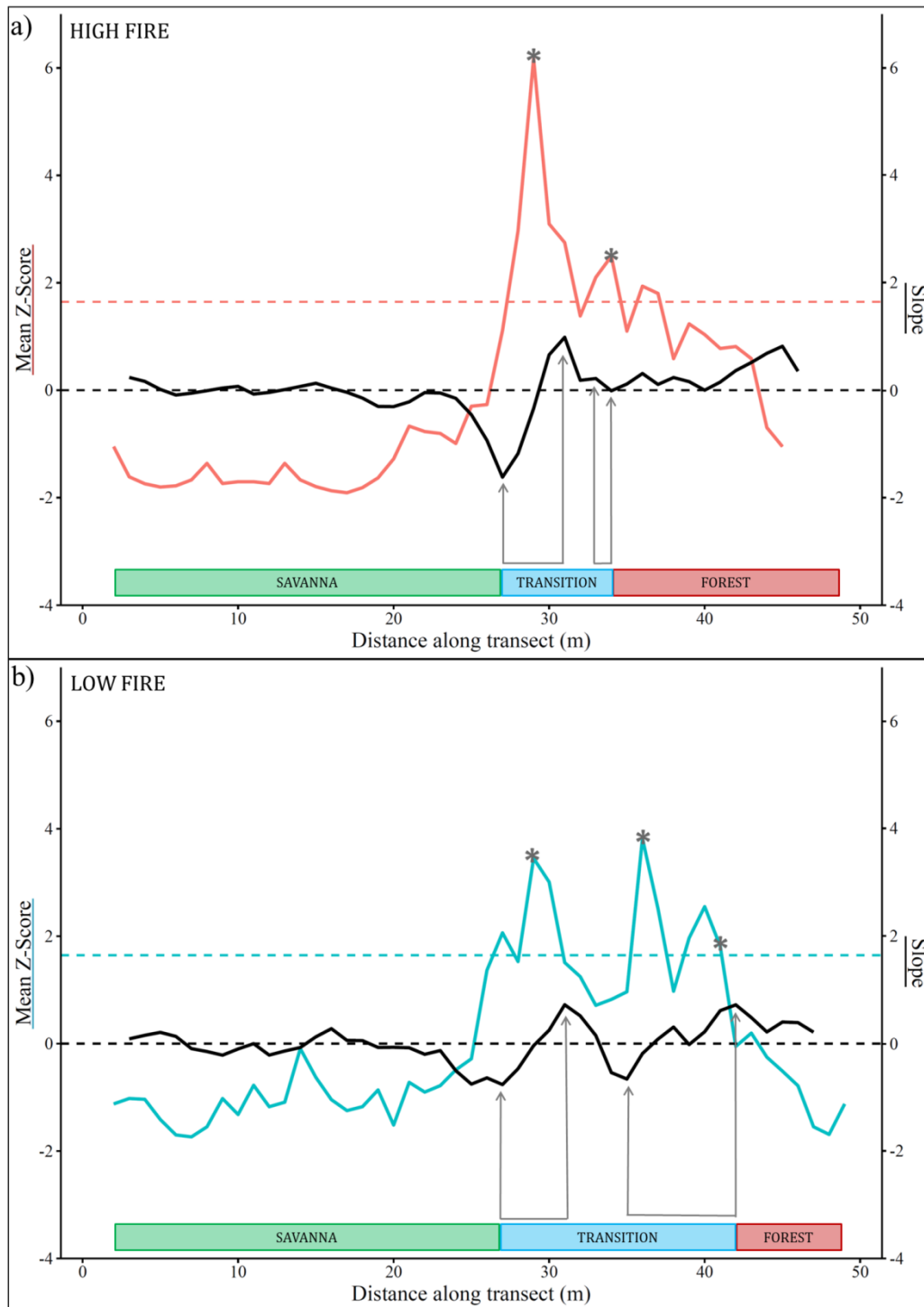


Figure 6.2: Split Moving Window Dissimilarity Analysis (SMWDA) and Moving Window Regression Analysis (MWRA) for high (a) and low (b) fire frequency transects. SMWDA z-scores are shown by solid coloured lines, MWRA slopes by solid black lines. *s indicate detected ecotone locations (turning points), $\uparrow$ and adjoining lines indicate width of ecotones (maximum and minimum of regression slopes in MWRA). Horizontal dotted lines at $y=1.645$ (coloured lines) and $y=0$ (black lines) mark the significance thresholds for SMWDA and turning points in MWRA respectively. The detected communities are denoted on the x-axis.

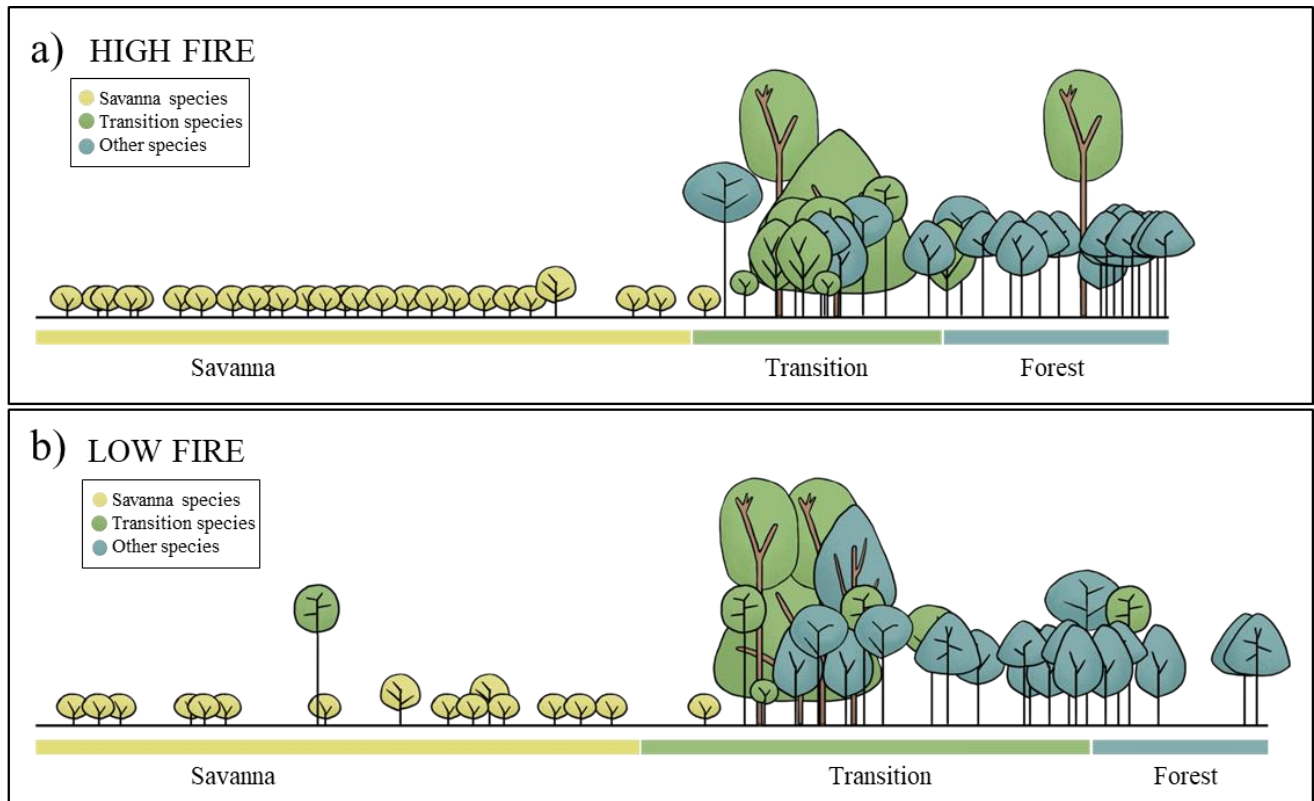


Figure 6.3: Profiles of high (a) and low (b) fire frequency transects based on actual data collected. Diagram shows where, on average, the trees of each species were found along the transect. All trees are drawn to scale for mean height and canopy dimensions per species. Tree density depicted is proportional to a transect 5 m wide, allowing representation of the correct ratios of whole trees. Tree species canopies are colour-coded according to which community they were part of.

The transition was able to be distinguished from forest and savanna in a multi-variate functional trait space. The PCA analysis (n=98) indicated that 74 % of the variation between communities could be explained by the first (PC1) and second (PC2) principal components (60 % by PC1 and 14 % by PC2) (**Fig. 6.4**). Visually, there is some overlap between the transition and forest, while the savanna is more distinct. However, PC1 scores were significantly different between all three communities ($\chi^2=61.5$, $p<0.0001$, $df=2$, mean PC1 scores: savanna = -2.4, transition = 1.4, forest = 2.2). Higher PC1 scores

were associated with increased bark investment, larger allometric coefficients_{bark}, and greater relative size of the underground storage organ. Lower PC1 scores were associated with increased wood density, and larger tree height:diameter, canopy area:basal area, allometric coefficients_{height}, and, to a lesser extent, canopy volume: tree height. PC2 scores were not significantly different between the three communities ($\chi^2=2.7$, $p=0.26$, $df=2$, mean PC2 scores: savanna = 0.17, transition = -0.1, forest = -0.2). Higher PC2 scores were associated with larger leaf areas and higher LMA values. When examined individually, functional traits generally showed significant differences between savanna and the other two communities (**Table S6.3**). The transition usually had mean trait values intermediate to those of the savanna and the forest, however was not usually significantly different to the forest. The exception to this was bark investment, which was significantly different between the three communities.

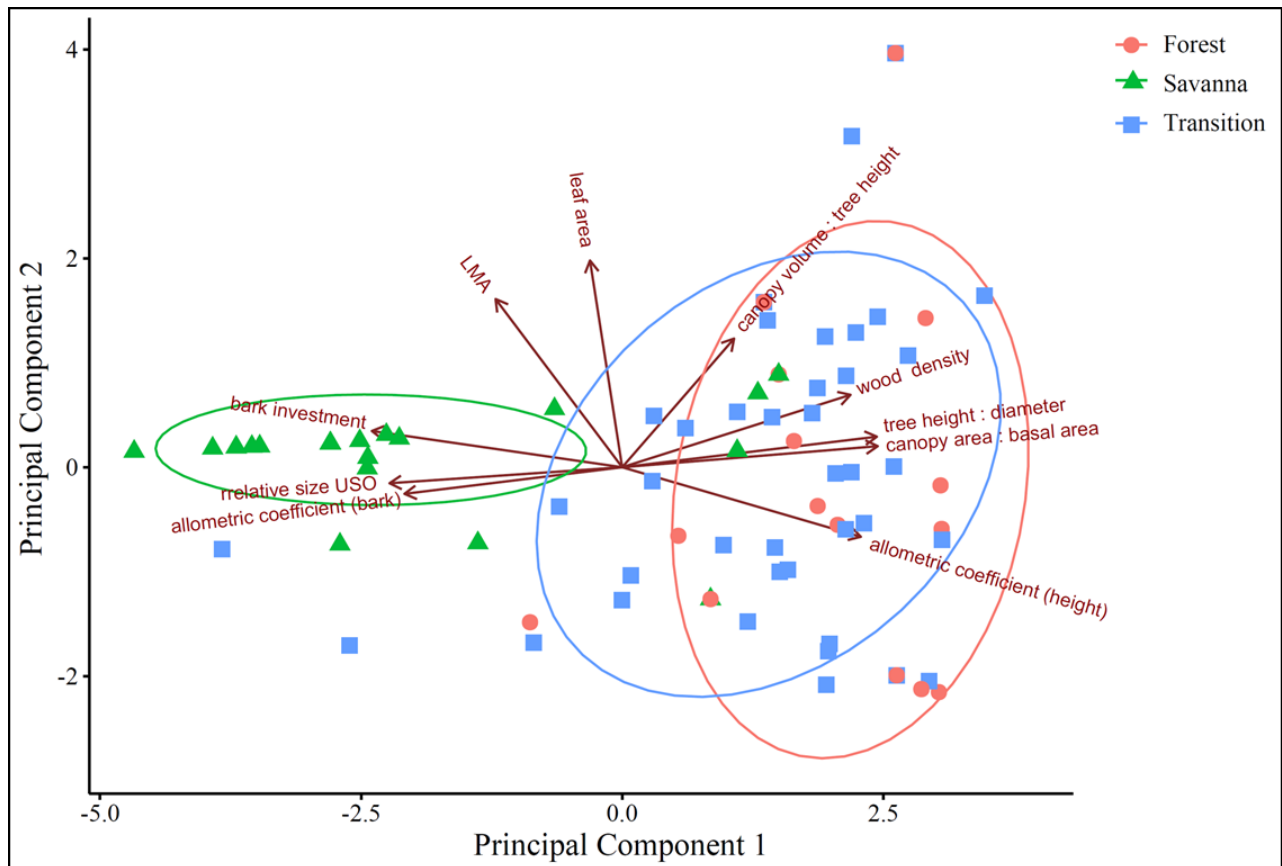


Figure 6.4: Principal Components Analysis using community weighted mean fire-resistance traits of transect blocks (n=98). Sample blocks of transects are colour-coded according to detected communities determined by SMWDA and MWRA (savanna, transition, and forest). The Principle Component 1 axis explained 60% of the variation in the data. The Principle Component 2 axis explained 14% of the variation in the data.

A distinct suite of tree species made up the transition community (Q2)

Seventeen species were found to make up 85% of the total basal area of the woody species measured in the transects. These species are listed in **Table S6.2**, and the literature on their ecology summarised. Of these seventeen species, seven were classified as being part of the transition tree community: *Antidesma vogelianum*, *Barteria fistulosa*, *Cnestis ferruginea*, *Millettia versicolor*, *Lophira alata*, *Psychotria vogeliana*, and *Sacoglottis gabonensis*. These transition tree species each had

significantly higher than expected abundances in the transition, and were significant indicator species for the transition (**Table 6.1, Table S6.3a**). Additionally, two species were classified as forming the savanna tree community: *Crossopteryx febirfuga* and *Sarcocephalus latfolius*. These species had significantly, in the case of the former, and near significantly, in the case of the latter, higher than expected abundances in the savanna, and also were significant indicator species for the savanna. No species were able to be confidently classified into the forest tree community. Similar analysis of juvenile tree stems supported the patterns detected in analysis of adult stems (**Table S6.3b**).

Histograms of stem size distribution for each of the species in the transition tree community all showed approximate reverse J-curve demography distribution, with each species having stems in multiple size classes (**Fig. 6.5**).

Table 6.1: Showing i) the p-value of χ^2 tests on observed versus expected frequencies of focal tree species in each communities, and whether the associated residuals (Pearson standardised) were positive or negative; and ii) the p-value of indicator value tests run on each focal species to test if it was a significant indicator species for one of the communities. Significant results ($p < 0.05$ or residual > 2.13) are marked with an *. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Species	χ^2 Tests (Observed vs Expected Frequencies)				Indicator Value Tests	
	χ^2 p-value	Residuals			Vegetation type	Indicator Value p-value
		Savanna	Transition	Forest		
<i>Antidesma vogelianum</i>	0.001*	-	+*		Transition	0.012*
<i>Aucoumea klaineana</i>	0.008*	-	+*	-	Transition	0.817
<i>Barteria fistulosa</i>	< 0.0001*	-	+*	-	Transition	0.003*
<i>Cnestis ferruginae</i>	< 0.0001*	-	+*	-	Transition	0.003*
<i>Crossopteryx febrifuga</i>	< 0.0001*	+*	-	-	Savanna	0.001*
<i>Cryptosepalum staudtii</i>	< 0.0001*	-	+*	+	Transition	0.363
<i>Diospyros dendo</i>	< 0.0001*	-	+*	+*	Transition	0.025*
<i>Diospyros zenkeri</i>	< 0.0001*	-	+*	+*	Transition	0.131
<i>Gomphia flava</i>	< 0.0001*	-	+*	+	Transition	0.339
<i>Lophira alata</i>	< 0.0001*	-	+*	+	Transition	0.001*
<i>Millettia versicolor</i>	< 0.0001*	-	+*	+	Transition	0.049*
<i>Ouratea myrioneura</i>	< 0.0001*	-	+*	+*	Transition	0.002*
<i>Psychotria vogeliana</i>	< 0.0001*	-	+*	-	Transition	0.003*
<i>Sacoglottis gabonensis</i>	< 0.0001*	-	+*	+	Transition	0.001*
<i>Sarcocephalus latifolius</i>	0.091	+	-	-	Savanna	0.040*
<i>Vitex doniana</i>	0.139	-	+	-	Transition	0.123
<i>Xylopia aethiopica</i>	< 0.001*	-	+*	+	Transition	0.679

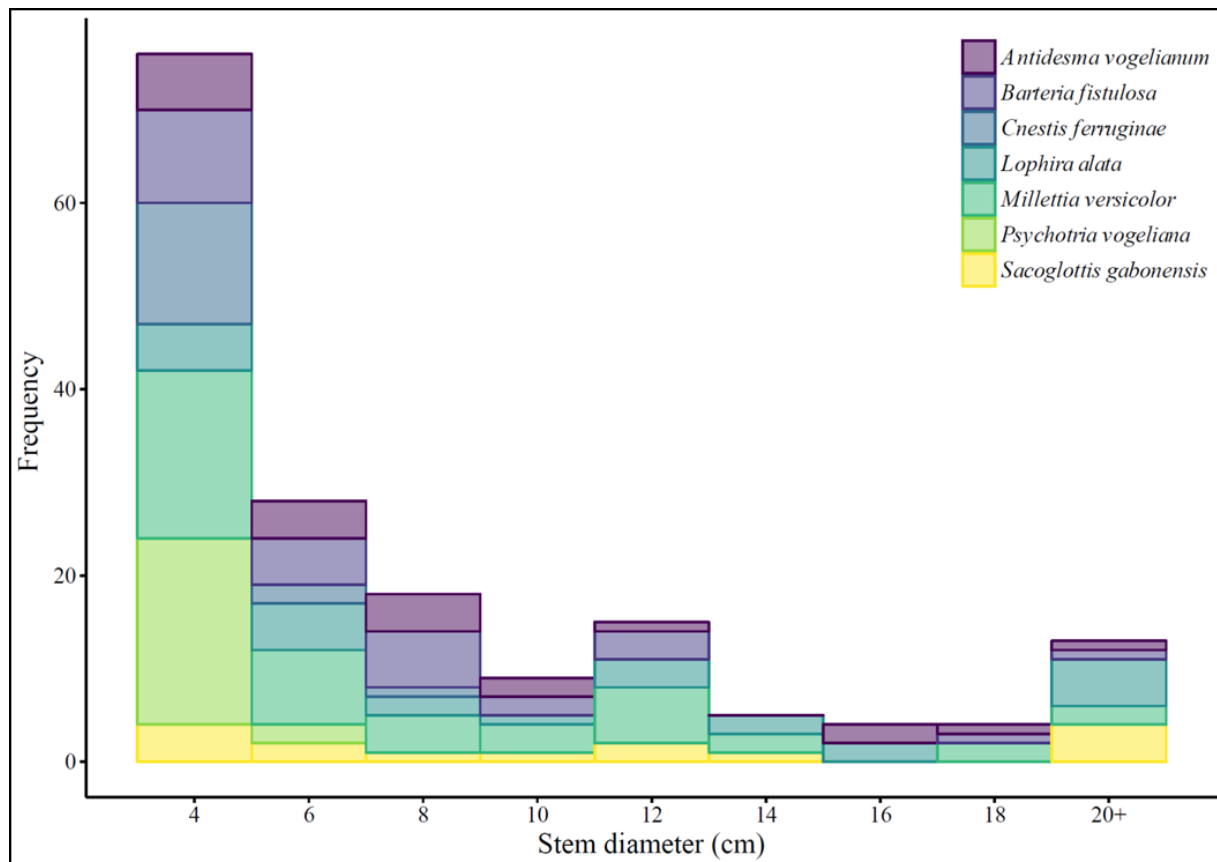


Figure 6.5: Frequency histogram showing trunk diameter distribution of each tree species in the transition community.

Fire maintains the diversity of communities in the forest-savanna mosaic (Q3)

The distinction between tree communities became less clear at low fire frequencies. The transition was wider in low fire frequency sites (17 m vs 9 m), however the distinction between the transition and adjacent forest and savanna was less clear with peaks in dissimilarity being lower (i.e. borders less clear), and ecotones being more gradual (i.e. wider and less clearly defined) (**Fig. 6.2**).

LAI was significantly different between savanna, transition, and forest ($\chi^2=280$, $p<0.0001$, $df=2$, mean LAI: savanna = 1.5, transition = 4.4, forest = 5.0). No significant differences in LAI were found between savannas of different burn treatments (**Fig. 6.6a**; $\chi^2=101$, $p=0.75$, $df=1$, mean savanna LAI: high fire = 1.5, low fire = 1.5). However, the relationship between grass biomass and distance into the savanna was significant in low but not high fire transects (low fire: intercept = 395, slope = 5.3, adjusted $R^2=0.32$, $p<0.005$, $df=24$; high fire: intercept = 520, slope = 0.1, adjusted $R^2=-0.3$, $p>0.95$, $df=24$), indicating a significant decrease in savanna grass biomass approaching the transition in low but not high fire frequency transects (**Fig. 6.6b**).

When fire frequency was low, juveniles of the transition tree community did now exhibit strong savanna colonising behaviour (**Table S6.3b**). Notably, under these low fire frequency conditions, *A. klaineana* was the species with the highest proportion of its juvenile stems in the savanna (80 %), with other species (excluding the savanna species *C. febrifuga*) having less than half of this (maximum 29 % by *B. fistulosa*).

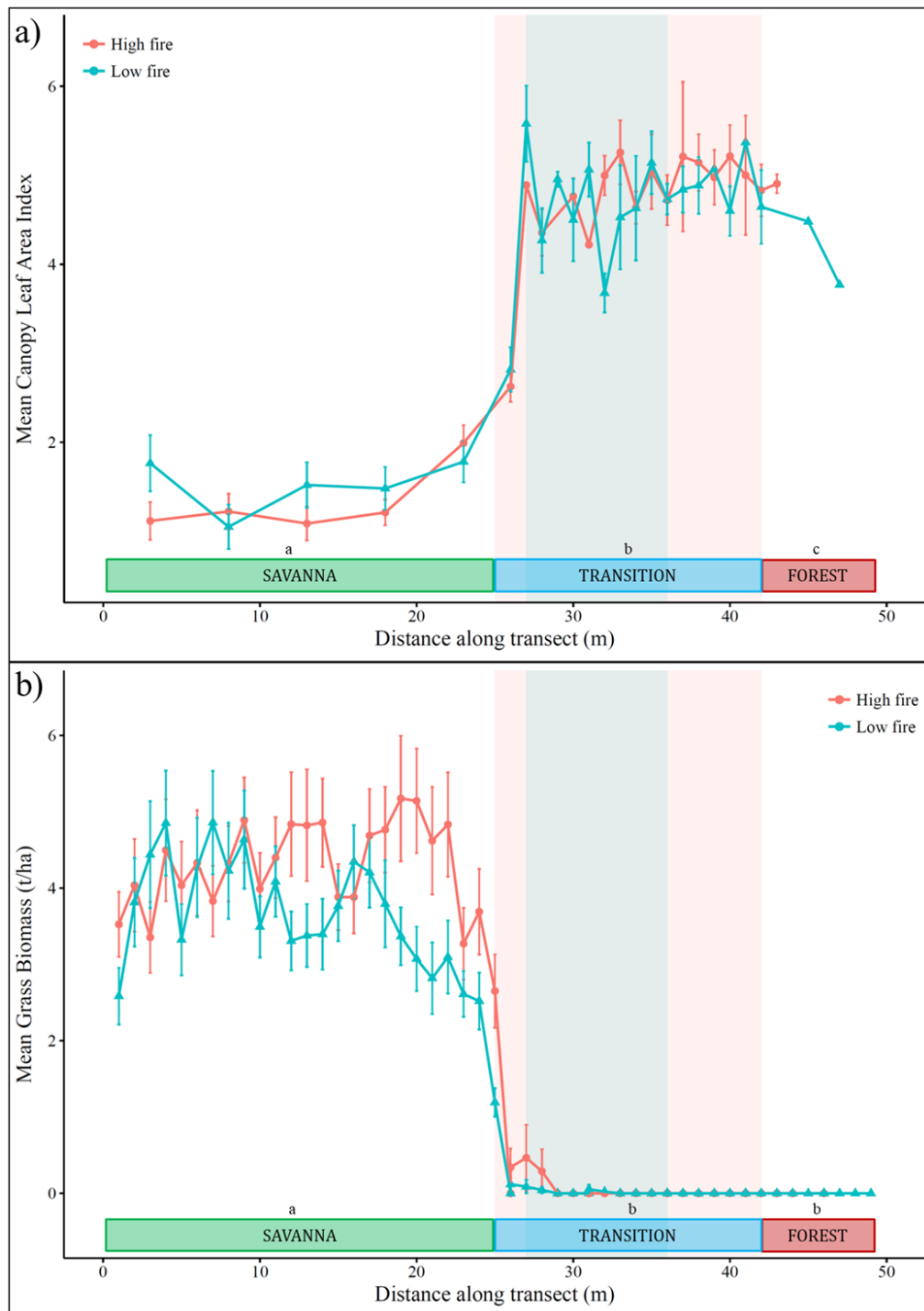


Figure 6.6: Mean canopy leaf area index (LAI) (a) and mean grass biomass (tons.ha⁻¹) (b) along high (red circles) and low (blue triangles) fire frequency transects. Communities are shown on the x-axis, with the width of the transition in high (red) and low (blue) fire frequency transects shaded. Different letters indicate significant differences in LAI or grass biomass between vegetation types (LAI: $\chi^2=280$, $p<0.0001$, $df=2$, mean LAI: savanna = 1.5, transition = 4.4, forest = 5.0; grass biomass: $\chi^2=1401$, $p<0.0001$, $df=2$, mean grass biomass (tons.ha⁻¹): savanna = 3.9, transition = 0.1, forest = 0.0). Error bars show standard error around the mean.

6.5 Discussion

This study demonstrates the existence of a distinct transition tree community within this tropical forest-savanna mosaic. This community was able to be differentiated functionally, specifically on the basis of its intermediate investment in fire resistance. Seven tree species made up the transition community. Under decreased fire frequencies, none of these transition species displayed savanna colonisation behaviour, although the transition became less distinct from adjacent forest and savanna and grass biomass showed some decreases.

A distinct transition was detected between savanna and forest (Q1)

That multiple non-overlapping ecotones could be detected between savanna and forest is strong evidence that a community of edge, or ecotone, specialist species has assembled at the forest-savanna transition in this mosaic. This community is well adapted to the intermediate fire regime it experiences, investing intermediately in fire resistance functional traits, specifically bark. Bark increases tree stem insulation during burning by decreasing xylem cavitation and necrosis of the cambium (Bova & Dickinson, 2005; Midgley *et al.*, 2011). Even though the difference in bark investment between transition and forest communities is moderate, insulation increases with the square of bark thickness (Hoffmann *et al.*, 2003; Pausas, 2015), therefore even this small increase will grant the transition community significant gains in fire-resistance relative to the forest.

The transition community's ability to thrive under intermediate fire intensity and light availability conditions confers fitness advantages at the forest-savanna transition, but makes the community ill-suited to thrive in the interior of either adjacent vegetation type. Intermediate investment in bark is likely to be insufficient to survive the high intensity fires of the savanna interior. However, it is also likely to make this community uncompetitive in the forest interior, as even intermediate bark investment will divert resources away from competitive traits necessary to survive in the resource-limited forest understorey. That the transition community continues to exist despite there being apparently few other places in which it can persist suggests that the forest-savanna mosaic that creates these intermediate conditions has been in existence for some time.

Given that forest tree species can be extremely fire sensitive and that burning can have catastrophic effects on tropical forests (Pinard *et al.*, 1999; Brando *et al.*, 2012), the importance of a intermediately fire resistant transition tree community that can buffer the forest interior from savanna fires should not be underestimated.

A distinct suite of tree species made up the transition community (Q2)

The transition community comprised seven tree species, which exhibited an inability to establish and thrive in the interior of either adjacent forest or savanna environments. The first question that arises from this finding is whether this is a transition tree community, or simply a subset of forest gap species that are exploiting the high light conditions at the forest edge. A forest gap community would, by nature, be ephemeral;

with many of the pioneering species recruiting at the time of gap formation and growing quickly, before experiencing high mortality rates a few years later once shade levels rose, leading to a fairly flat stem size distribution (Brokaw, 1985). However, the stem size distribution of the transition community (**Fig. 6.5**), reflects what we expect from a more stable community that has had continuous or multiple recruitment events. This indicates that the transition tree community is unlikely to be a forest gap community. This conclusion is supported by none of the transition species having been recorded in census plots done in the interior of the mature forest in the study site (White, 2001;**Table S6.4**).

Although the transition community is not one of forest gap species, some of the species within the community display pioneering behaviour – not into forest gaps but into savanna when fire is suppressed (*L. alata* and *S. gabonensis*, **Table S6.2**). This suggests that there are two components to the transition community; one that is somewhat fire sensitive and unable to survive in the frequently burnt savanna interior, but can expand its range if released from regular burning, and a second that is also somewhat fire sensitive but is unable to expand even under decreased burning. The grassy component of savannas can exert significant competitive pressure on trees for above and below ground resources, making it especially difficult for trees to establish in savannas (Scholes & Archer, 1997). The tree species able to compete with grasses when fire is removed from the system are thus especially interesting components of the transition community as they may provide clues as to why certain tree species were able to survive in the regularly burnt grasslands of Africa to create the savannas we observe today.

It is thus interesting to consider how the transition community came to be arise. One hypothesis is that it speciated *in situ* at the forest-savanna transition, evolving to thrive in the unique fire and light conditions here. This would necessarily imply that the both the transition community and the forest-savanna mosaic are ancient. While an attractive hypothesis, this kind of sympatric speciation would have required runaway reproductive isolation to occur very quickly (Caisse & Antonovics, 1978). While this is theoretically possible, it is often the case that species are more likely to move into an area where they already have some of the adaptations necessary for success, than to evolve those adaptation *in situ* (Donoghue, 2008).

Another hypothesis for the origin of the transition community is then that these species evolved elsewhere and subsequently successfully colonised the forest-savanna transition in the study site. Supporting this hypothesis is the fact that all but one (*L. alata*) of the species in the transition community are also found in the coastal forests and savannas of Mayombe (*cf.* the inland savannas and forests of Bateke), and most of these are able to disperse long distances via either bats or birds (*A. vogelianum*, *B. fistulosa*, *C. ferruginea* and *P. vogeliana*; Sosef *et al.*, 2006; **Table S6.2**). If this were the case, it leads us to wonder in which specific kinds of habitats the species of the transition community then originally evolved in prior to this dispersal. While finding a definitive answer to this is outside of the scope of this study, examining the available literature on each transition species' closest congenics provides some insight.

Most of the African congeners of the transition community were forest (*cf.* savanna) species (**Table S6.5**). This is as expected since the tropical forest is an older and more extensive biome than the tropical savanna, and thus will tend to be a donor rather than a recipient of species (Donoghue & Edwards, 2014). Within the forest, the majority of congeners of the transition community occupied ecological niches associated with higher light availability: riparian environments, secondary forest or anthropogenically degraded landscapes, and swampy or seasonally flooded areas. Although less common, a fair number of congeners also favoured savanna environments, dry forests, woodlands, and thickets, as well as coastal habitats. A full phylogenetic analysis of the transition community would add immensely to the interpretation of the results of this study.

Fire maintains the diversity of vegetation types in the forest-savanna mosaic (Q3)

Significant differences in canopy leaf area index (LAI) between savanna, forest, and transition suggest the presence of multiple fire-related thresholds. LAI and grass biomass both changed significantly between the savanna and the transition, suggesting the existence of a fire suppression threshold, at which point canopy cover suppresses grasses and thus fire (Hoffmann et al., 2012). Further evidence for this threshold exists in the observed self-extinguishing of fires within 1 m of grass becoming eliminated from the understorey (2 m into the transition) (Cardoso *et. al.*, **Chapter 5**). There were also significant differences in LAI between the transition and the forest, implying that a “deep-shade” threshold also likely exists, whereby forest trees cast deeper shade than is necessary to exclude savanna grasses, and thus exclude transition species which are

only semi-shade tolerant, and further decrease the flammability of the system (Charles-Dominique, 2018).

Savannas of the low fire frequency transects had not yet been sufficiently encroached to reach the fire suppression threshold, but vegetation types were becoming more homogenous as the early stages of forest encroachment began. The transition's borders are further apart and its ecotones wider and more gradual in low fire frequency savanna. Furthermore, although LAI is not significantly higher in low fire than regularly burnt savannas, grass biomass did decrease significantly closer to the savanna-transition interface, a phenomenon not observed in regularly burnt savannas.

Although juvenile tree stems in the savanna were rare, the vast majority of the stems that were present here were from the species *A. klaineana*. This is a heliophilic forest species that forms monodominant early-successional forest stands in old unburnt savannas (White, 2001). Interestingly, this species has an ability to root sucker (Leroy-Duval, 1974), a trait usually associated with increased survival in regularly burnt environments as it enables the spatial spread of risk and resources (Charles-Dominique *et al.*, 2015a). However, *A. klaineana* is fire sensitive (White, 2001) and completely absent, even at larger diameters, from high fire transects. In low fire transects however it grows rapidly (Engone Obiang *et al.*, 2013), needing just under 22 years for its bark to grow 6mm thick (**Fig. S6.3a**), the threshold thickness required for a sapling to have a 50 % chance of avoiding top-kill in a low intensity fire (Hoffmann *et al.*, 2012). This makes *A. klaineana* an excellent indicator species of forest encroachment as it is

unlikely to be found in stable frequently burnt savannas that are at relatively low risk of becoming forests, but when it is found it indicates that under the prevailing conditions the savanna will become forest encroached within the next 22 years.

Conclusion

This study has demonstrated the unique ecology of the forest-savanna transition in the context of forest-savanna mosaics in Central Africa. In doing so, we provide evidence of the value of both forest and savanna components co-existing in mosaicked landscapes, and suggest that such co-existence is likely natural and ancient. Our approach can be applied across the tropics, and may be especially useful when attempting to establish the antiquity of a mosaicked landscape in the absence of long-term data. This study also demonstrates that regularly burning the savanna component is essential to maintain the habitat diversity in these ancient and natural landscapes. Such a finding is important as savannas have historically been frequently misclassified as degraded forests, leading to the active promotion of their destruction for the cause of “forest restoration” (Veldman *et al.*, 2015), often via enforcing fire suppression policies (Durigan & Ratter, 2016). Our work helps to remedy such misconceptions and provides further support for forest-savanna mosaics having previously unrecognised unique features and a high conservation value (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.

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6.8 Supplementary material



Figure S6.1: Photographs of the study site, Lopé National Park, Gabon, showing a) the mosaic of forest and savanna, b) a sharp forest-savanna transition as seen from the air and c) the forest-savanna transition as seen from the ground.

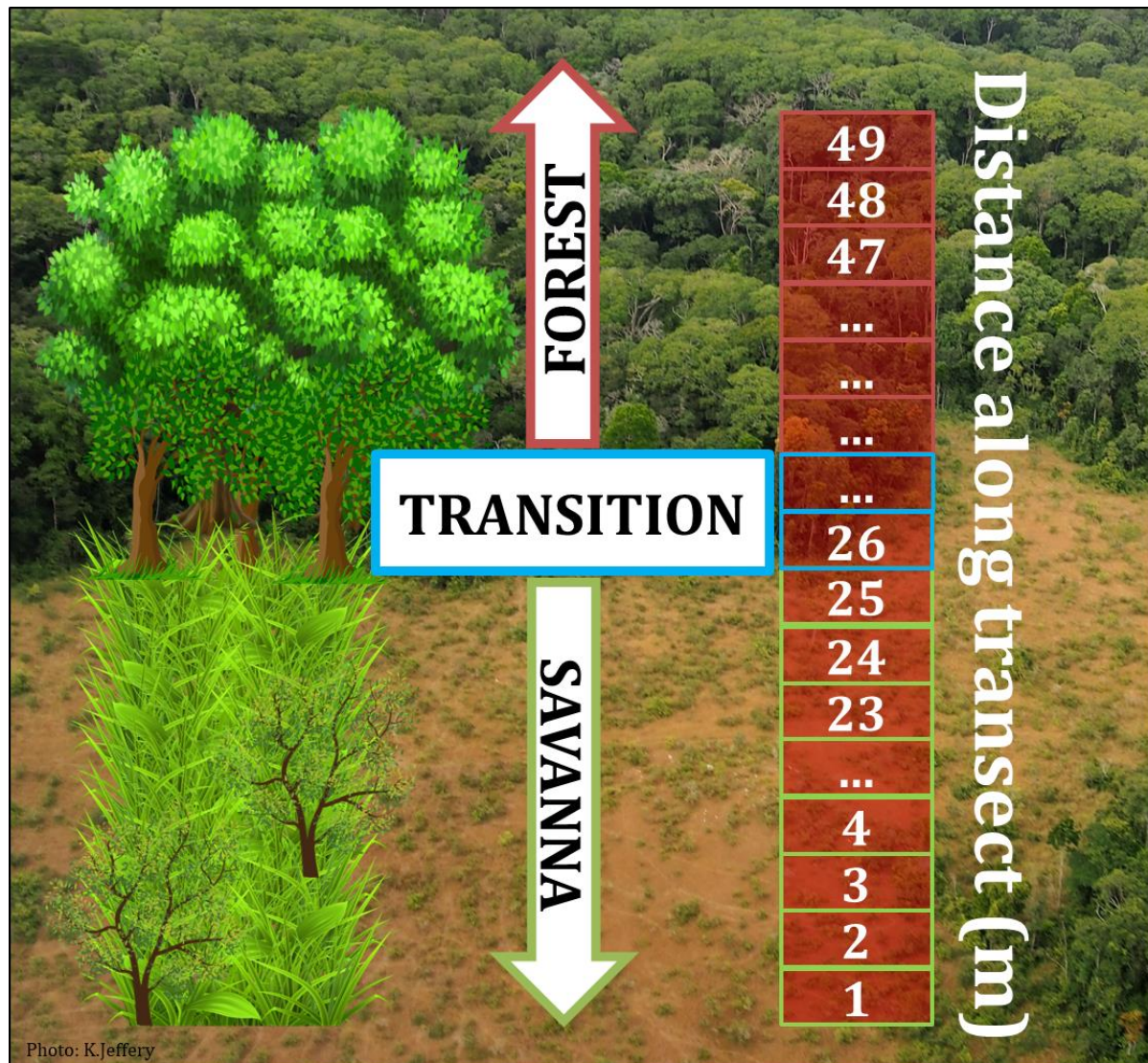


Figure S6.2: Diagram of transect, spanning three field-defined vegetation types. Vegetation types were defined in the field using physiognomic characteristics. Savanna was defined to be where grass cover was continuous, woody canopy cover discontinuous, and visibility was >5 m; transition where grass cover became discontinuous, woody canopy cover became vertically and horizontally continuous, and visibility was <5 m, and the forest where the woody canopy was vertically discontinuous with the understory vegetation and visibility was >5 m. The entire field-defined transition was sampled, as well as an adjacent 25 m savanna and 10 m forest. Transects were 2 m wide, of variable length, and were sampled in 1 m increments (1 m x 2 m blocks). Transect sites were randomly selected in GIS by placing points on a line that ran across all forest-savanna transitions and then selecting a subset of these using a random number generator. Sites were then deemed acceptable if they met the following criteria: > 100 m from other transect sites, > 50 m road/river/marsh, associated forest or savanna patch was >50 m wide, > 50 m from another forest edge (ie. forest finger is not too narrow), not on very steep slope, not on obviously rocky substrate, not across an obvious tree-fall gap, easily accessible by car or foot (< 2 hours walk each way).

Table S6.1: Mean functional trait values for each focal tree species. Different letters indicate significant differences in mean values between species ($p < 0.05$) according to Kruskal-Wallis tests.

Species	Bark investment (mm.mm ⁻¹)	Allometric coefficient bark (ln mm bark thickness.ln mm trunk diameter ⁻¹)	Relative size of underground storage organ (area of root:basal area of stem)	Wood density (no bark) (g.cm ⁻³)	Tree height : diameter (cm.mm ⁻¹)	Allometric coefficient height (ln cm tree height.ln mm trunk diameter ⁻¹)	Canopy volume : tree height (cm ³ .m ⁻¹)	Canopy area : basal area (cm.cm ⁻¹)	Leaf mass per area (g.cm ⁻²)	Leaf area (cm ²)
<i>Antidesma vogelianum</i>	0.03ef	0.54	1.7abc	0.7bc	5.1d	0.96	1273bcde	1273de	68.4ef	7h
<i>Aucoumea klaineana</i>	0.03e	0.56	1.9abcd	0.5g	9.0ab	0.89	1353a	1130cde	145.2a	106e
<i>Barteria fistulosa</i>	0.03ef	0.49	1.3cd	0.6cde	7.7bc	0.86	589cde	1189cd	128.8bc	191b
<i>Cnestis ferruginea</i>	0.04cd	0.92	2.4ab	0.5fg	10.3ab	0.80	N/A (lianescent shrub)		62.2ef	181b
<i>Crossopteryx febrifuga</i>	0.12a	0.73	2.1ab	0.6ef	2.6e	0.58	183f	345g	112.8bcd	148bcde
<i>Cryptosephalum staudtii</i>	0.04de	0.65	1.3cd	0.6cd	7.9bc	1.03	831abcd	1965a	56.8f	114de
<i>Diospyros dendo</i>	0.02h	0.40	1.4bcd	0.6cd	7.3c	0.88	925bcde	1357abc	77.6ef	59fg
<i>Diospyros zenkeri</i>	0.02fg	0.51	1.5abcd	0.6cd	7.4bc	0.99	1572abcde	1633ab	58.4f	104ef
<i>Gomphia flava</i>	0.02gh	0.47	1.2d	0.7ab	9.1ab	0.76	578abc	1773a	97.8cde	154bcd
<i>Lophira alata</i>	0.04de	0.70	1.5abcd	0.6de	7.6bc	0.90	1217abc	624ef	94.7de	109e
<i>Millettia versicolor</i>	0.08b	0.59	1.7abcd	0.7ab	7.5c	0.76	815bcde	1441bcd	64.6ef	218a
<i>Ouratea myrioneura</i>	0.03fg	0.39	1.3cd	0.8ab	10.2ab	0.81	743ab	1728a	96.5cde	169bc
<i>Psychotria vogeliana</i>	0.07b	0.79	1.4bcd	0.6c	8.6b	0.70	272e	1749a	96.0cde	201ab
<i>Sacoglottis gabonensis</i>	0.04de	0.65	1.2d	0.7b	7.4c	0.84	9434ab	1583abc	126.1b	35gh
<i>Sarcocephalus latifolius</i>	0.14a	0.77	3.1a	0.4h	2.7e	0.61	730de	423fg	113.1bc	187b
<i>Vitex doniana</i>	0.06cd	0.48	1.3cd	0.5h	4.5d	0.93	1231f	243g	117.9bc	116cde
<i>Xylopia aethiopica</i>	0.06bc	0.68	1.3cd	0.5gh	8.5bc	0.77	3413abc	1234abcd	118.5bc	15gh

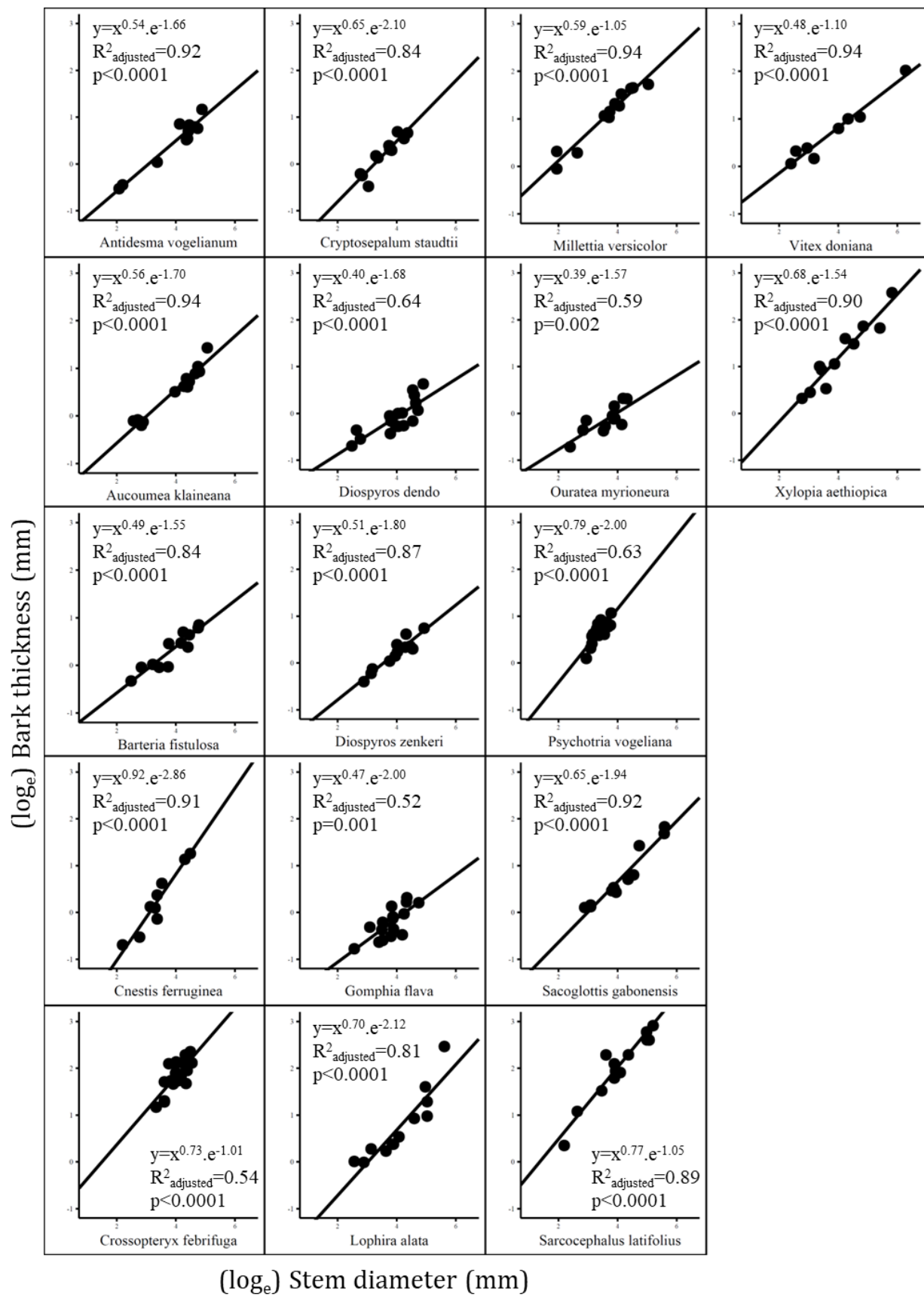


Figure S6.3a: Bark thickness allometries for each focal species. Adjusted R^2 and p values for each species extracted from linear models.

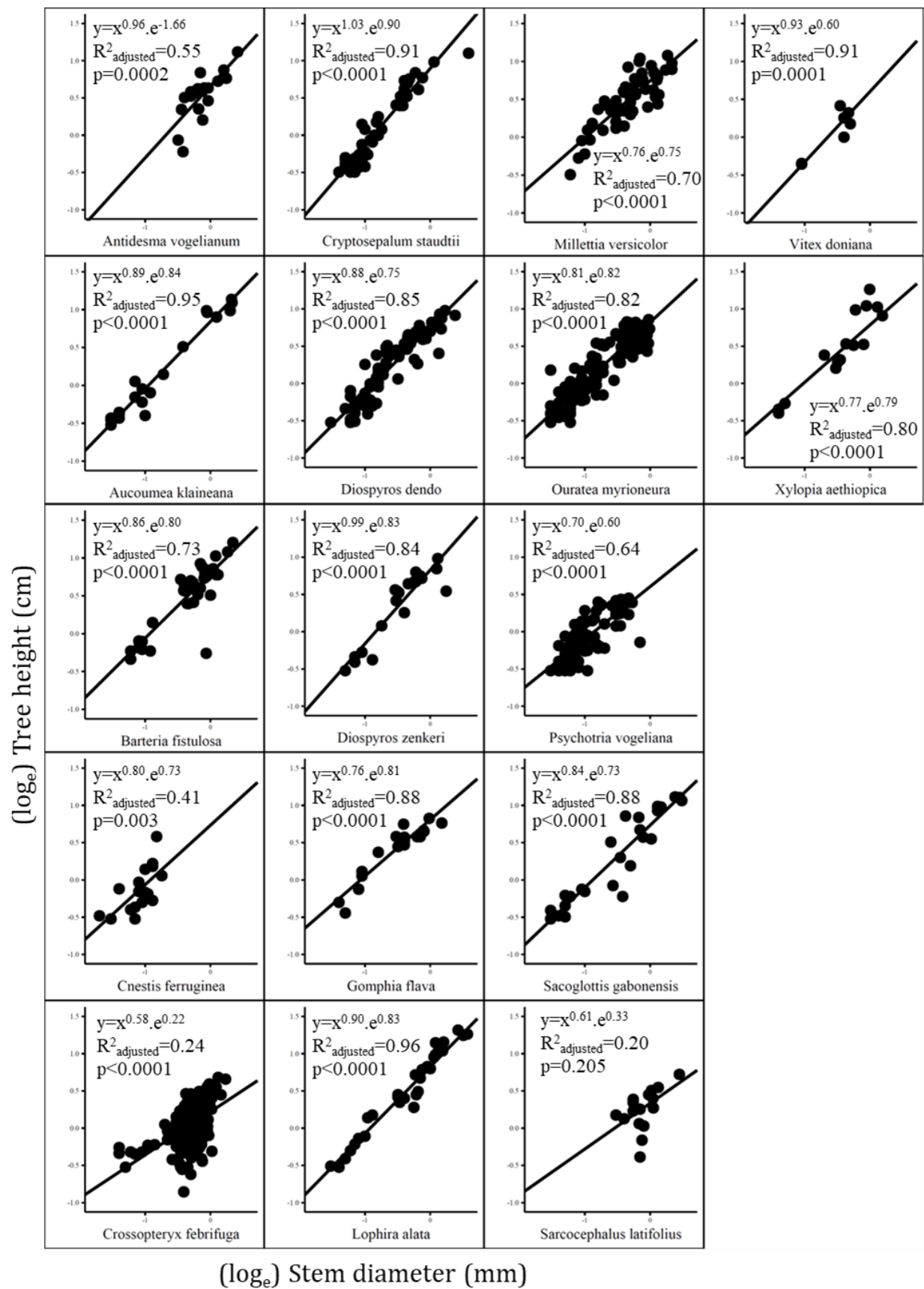


Figure S6.3b: Tree height:diameter allometries for each focal species. Adjusted R^2 and p values for each species extracted from linear models.

Table S6.2: The ecology, according to the literature, of the seventeen focal species of the study. The table shows a summary of the available literature, both that which originates from within the study site (Lopé National Park, Gabon), and from further afield.

Species	Classified vegetation type in this study		Species ecology according to literature	References
<i>Antidesma vogelianum</i>	Transition	Study site	A savanna edge species. Bird and animal dispersed, including by elephant.	1
		Across Africa	Found in transitional and montane rainforest in Tanzania, the rainforest (annual rainfall >3000mm) in Nigeria, and in the mountain foothill forest in Cameroon.	2, 3, 4, 5
<i>Aucoumea klaineana</i>	Forest	Study site	A forest pioneer species. Fire sensitive. Can form mono-dominant stands in younger forest types. Regenerates well in open conditions. Root sucker. Little regeneration in the forest understory, only occurs when colonising savanna.	1
		Across Africa	Tropical rainforest tree. Long-lived. Does not regenerate within the forest. Virtually endemic to Gabon, but also found in small areas in Equatorial Guinea, Cameroon, and Republic of Congo.	6, 7
<i>Barteria fistulosa</i>	Transition	Study site	A young and disturbed forest species. Can form dense stands. Bat dispersed.	1
		Across Africa	Found in the forest understory of Nigeria, Cameroon, and the Congo river basin. Patchy distribution in the forest understory, low density (about 0.1-10 trees per hectare), can form denser stands on river edges, most abundant on gully margin forests and secondary forest in clearings within mature forest, often also found along trails and heavily logged sites. In other west African forests, it grows well in elephant-created disturbed patches within the forest.	8
<i>Cnestis ferruginea</i>	Transition	Study site	A savanna edge species. Also found in young forest, and occasionally within the forest interior. Bird dispersed.	1
		Across Africa	No literature available.	
<i>Crossopteryx febrifuga</i>	Savanna	Study site	A common savanna species.	1
		Across Africa	Found in guinean savanna of Côte d'Ivoire and miombo woodlands of Zimbabwe.	9, 10
<i>Cryptosepalum staudtii</i>	Transition	Study site	A gallery forest species.	1
		Across Africa	No literature available.	
<i>Diospyros dendo</i>	Forest	Study site	A forest understory species. Found in most forest types, favours rocky areas with thin soil.	1
		Across Africa	Found in the Congo's natural tropical forest.	11
<i>Diospyros zenkeri</i>	Forest	Study site	A forest understory species. Found in most forest types, favours rocky areas with thin soil.	1
		Across Africa	Found in the understory of the interior of old secondary rainforests, and the understory of the edge of young secondary rainforests in Gamba and Gabon.	12
<i>Gomphia flava</i>	Forest	Study site	A forest understory species. Found in most forest types, favours rocky areas with thin soil.	1
		Across Africa	Part of the swamp guild of trees in Ghana, also found in submontane wet forest at mid-altitude, often associated with forest margins and among secondary scrub in South Sudan.	13, 21

Table S6.2 (continued):

Species	Classified vegetation type in this study		Species ecology according to literature	References
<i>Lophira alata</i>	Forest	Study site	A forest pioneer species. Fire sensitive. Can be a dominant component of younger and gallery forests. Wind dispersed but large seeds.	1
		Across Africa	In Gabon, it is a forest pioneer species, can form mono-dominant forest, often associated with <i>A. klaineana</i> and <i>S. gabonensis</i> . Also found in littoral forest of Congo and mixed forest, lowland wet and evergreen littoral and semi-deciduous forest of Cameroon. Long lived and light demanding.	14, 15, 16
<i>Millettia versicolor</i>	Transition	Study site	A savanna edge species. Can also fringe rocky outcrops within the forest, or be found within forest patches in the savanna. Coppices vigorously after breaking. Dehiscent dispersal.	1
		Across Africa	No literature available.	
<i>Ouratea myrionura</i>	Forest	Study site	A forest understory species. Found in most forest types, favours rocky areas with thin soil.	1
		Across Africa	No literature available.	
<i>Psychotria vogeliana</i>	Transition	Study site	A savanna edge species. Bird and mammal dispersed.	1
		Across Africa	Found in the undergrowth of teak plantations in Benin where it is used as an indicator species of sandy plateau soils associated with the least productive plantations.	17
<i>Sacoglottis gabonensis</i>	Transition	Study site	A forest pioneer species. Common in younger forest types. Fire sensitive. Can form mono-dominant stands at savanna-forest transitions, especially in savanna patches enclosed by forest. Good savanna coloniser. Common in younger forest types. Casts deep shade at forest edge and shades out grasses thus suppressing fire. Coppices after breaking. Elephant dispersed.	1
		Across Africa	Part of the swamp guild of trees in Ghana. Also found in the forests Côte d'Ivoire, the littoral humid forest and clusters of forest pioneer species in the savanna of the Congo. A dominant tree in coastal rainforest of west and central Africa.	1, 18, 19, 20, 21
<i>Sarcocephalus latifolius</i>	Savanna	Study site	A savanna species.	1
		Across Africa	Found in palm savannas and dry Combretum savannas in Uganda where it prefers thickets, well drained soils, or brushland and has slow regeneration. Also found in forest-savanna mosaic in Côte d'Ivoire and in savanna plains or grasslands between equatorial forests and tropical deserts in Mali. Also found in Ghana in savanna woodland where hillsides and the central valley are thickets and dry forest and the surrounding plains are grassland.	22, 23, 24, 25
<i>Vitex doniana</i>	Ubiquitous	Study site	A savanna edge species. Also occasionally found in moist areas of the savanna, as well as gallery forest and in low lying areas.	1
		Across Africa	Found in the guinean savannas of Benin and in Malawi.	26, 27
<i>Xylopia aethiopica</i>	Transition	Study site	A gallery forest species. Fast growing, thrives in open conditions.	1
		Across Africa	Found widely in wet swampy soil across west and central Africa, can be found in clusters of forest pioneer species in the savanna, where it co-occurs with <i>A. klaineana</i> . Light-demanding, short-lived forest species. Is also part of the pioneer guild of trees in Ghana and is also found in Mali.	20, 21, 28

Table S6.2 (continued):

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Table S6.3a: Showing, for adult trees, i) the χ^2 and p-value of tests on observed versus expected frequencies of focal tree species in each vegetation type, and the associated residuals (Pearson standardised); and ii) the indicator value and associated p-value for each focal species to test if it was a significant indicator species for one of the vegetation types. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Species	χ^2 Tests (Observed vs Expected Frequencies)					Indicator Value Tests		
	χ^2	p	Residuals			Vegetation type	Indicator value	p
			Savanna	Transition	Forest			
<i>Antidesma vogelianum</i>	30.13	0.001	- 3.16	5.02	-1.11	Transition	0.15	0.012
<i>Aucoumea klaineana</i>	9.69	0.008	-1.62	2.62	-0.67	Transition	0.02	0.817
<i>Barteria fistulosa</i>	18.17	< 0.0001	-2.28	3.53	-0.60	Transition	0.22	0.003
<i>Cnestis ferruginae</i>	25.00	< 0.0001	-2.85	4.08	-0.03	Transition	0.19	0.003
<i>Crossopteryx febrifuga</i>	142.52	< 0.0001	7.29	-8.48	-4.18	Savanna	0.84	0.001
<i>Cryptosepalum staudtii</i>	26.61	< 0.0001	-3.07	4.36	0.03	Transition	0.05	0.363
<i>Diospyros dendo</i>	64.94	< 0.0001	-4.41	3.70	5.66	Transition	0.18	0.025
<i>Diospyros zenkeri</i>	27.25	< 0.0001	-2.86	2.49	3.46	Transition	0.09	0.131
<i>Gomphia flava</i>	23.93	< 0.0001	-2.96	3.70	1.16	Transition	0.07	0.339
<i>Lophira alata</i>	23.72	< 0.0001	-2.95	3.71	1.09	Transition	0.34	0.001
<i>Millettia versicolor</i>	42.10	< 0.0001	-3.94	4.90	1.57	Transition	0.18	0.049
<i>Ouratea myrioneura</i>	81.26	< 0.0001	-5.31	5.25	5.07	Transition	0.27	0.002
<i>Psychotria vogeliana</i>	32.58	< 0.0001	-2.98	4.77	-1.14	Transition	0.24	0.003
<i>Sacoglottis gabonensis</i>	28.61	< 0.0001	-3.07	4.36	0.03	Transition	0.20	0.001
<i>Sarcocephalus latifolius</i>	4.78	0.091*	1.33	-1.42	-1.05	Savanna	0.14	0.04
<i>Vitex doniana</i>	3.94	0.139	-0.91	1.58	-0.62	Transition	0.08	0.123
<i>Xylopia aethiopica</i>	15.03	< 0.001	-2.38	2.76	1.4	Transition	0.06	0.679

Table S6.3b: Showing, for juvenile trees, i) the χ^2 and p-value of tests on observed versus expected frequencies of focal tree species in each vegetation type, and the associated residuals (Pearson standardised); and ii) the indicator value and associated p-value for each focal species to test if it was a significant indicator species for one of the vegetation types. Species forming the transition community (significant positive residual only in the transition and significant indicator value for the transition) are in bold.

Species	χ^2 Tests (Observed vs Expected Frequencies)					Indicator Value Tests		
	χ^2	p	Residuals			Vegetation type	Indicator value	p
			Savanna	Transition	Forest			
<i>Antidesma vogelianum</i>	na	na	na	na	na	na	na	na
<i>Aucoumea klaineana</i>	1.45	0.486	0.6	-1.0	0.2	Savanna	0.05	0.465
<i>Barteria fistulosa</i>	7.20	0.027	-1.3	2.3	-0.7	Transition	0.11	0.046
<i>Cnestis ferruginae</i>	9.55	0.009	-1.9	2.3	0.8	Transition	0.13	0.096
<i>Crossopteryx febrifuga</i>	1.87	0.392	0.7	-0.5	-1.0	Savanna	0.15	0.042
<i>Cryptosepalum staudtii</i>	47.7	<0.0001	-3.8	5.7	-0.6	Transition	0.07	0.306
<i>Diospyros dendo</i>	92.18	<0.0001	-5.3	4.5	6.6	Transition	0.15	0.102
<i>Diospyros zenkeri</i>	11.46	0.003	-2.1	2.6	0.8	Transition	0.06	0.262
<i>Gomphia flava</i>	8.90	0.012	-1.8	2.0	1.2	Transition	0.07	0.223
<i>Lophira alata</i>	16.29	0.0003	-2.1	3.4	-0.8	Transition	0.16	0.010
<i>Millettia versicolor</i>	17.25	0.0002	-2.3	3.4	-0.1	Transition	0.09	0.209
<i>Ouratea myrioneura</i>	99.36	<0.0001	-6.1	7.4	2.8	Transition	0.38	0.002
<i>Psychotria vogeliana</i>	189.04	<0.0001	-7.8	11.3	-0.5	Transition	0.57	0.001
<i>Sacoglottis gabonensis</i>	9.13	0.010	-1.5	2.5	-0.8	Transition	0.13	0.055
<i>Sarcocephalus latifolius</i>	na	na	na	na	na	na	na	na
<i>Vitex doniana</i>	1.08	0.584	0.7	-0.8	-0.4	Savanna	0.03	1.000
<i>Xylopia aethiopica</i>	3.90	0.14	-1.0	1.6	-0.5	Transition	0.06	0.244

Table S6.4: An extract from the census data (abundance and basal area) collected by White *et al.* (2001)¹ in savanna (regularly burnt), colonising forest (a.k.a. savannas where fire had been suppressed for > 10 years and become forest encroached) and various mature forest (fire-free) vegetation types. In 1 ha plots across different vegetation types all trees > 5cm diameter were identified and measured. Vegetation types covered the hypothesised stages of forest succession: savanna to colonising forest to monodominant *Aucoumea klaineana* forest to young *Marantaceae* forest to older mixed *Marantaceae* forest. Other old/mature forest types are also shown.

	Savanna		Colonising forest		Monodominant <i>A.klaineana</i> forest		Young <i>Marantaceae</i> Forest		Mature <i>Marantaceae</i> Forest		Old Montane Forest		Old Riverine Forest	
Species	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹	stems.ha ⁻¹	m ² .ha ⁻¹
<i>Antidesma vogelianum</i>	0.00	0	0.40	43	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Aucoumea klaineana</i>	0.00	0	1.84	51	22.29	175	39.76	117	2.40	8	5.20	8	0.00	0
<i>Barteria fistulosa</i>	0.00	0	1.00	155	0.80	92	0.11	8	0.00	0	0.00	0	0.00	0
<i>Cnestis ferruginea</i>	0.00	0	0.02	5	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Crossopteryx febrifuga</i>	1.29	340	0.87	148	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Cryptosepalum staudtii</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Diospyros dendo</i>	0.00	0	0.00	0	0.23	40	0.74	106	0.57	110	0.00	0	0.00	0
<i>Diospyros zenkeri</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Gomphia flava</i>	0.00	0	0.02	5	0.11	38	0.00	0	0.00	0	0.00	0	0.00	0
<i>Lophira alata</i>	0.00	0	1.14	52	3.57	129	1.83	102	2.67	21	0.00	0	0.20	3
<i>Millettia versicolor</i>	0.00	0	0.13	5	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Ouratea myrioneura</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Psychotria vogeliana</i>	0.00	0	0.01	2	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Sacoglottis gabonensis</i>	0.00	0	0.83	89	2.91	88	2.32	10	0.00	0	0.00	0	0.00	0
<i>Sarcocephalus latifolius</i>	0.01	3	0.15	5	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Vitex doniana</i>	0.00	0	0.05	2	0.00	0	0.00	0	0.00	0	0.00	0	1.63	8
<i>Xylopia aethiopica</i>	0.00	0	0.81	48	0.29	15	0.12	15	0.00	0	0.00	0	0.00	0

¹White, L. T. J. (2001). Forest-savanna dynamics and the origins of "Marantaceae Forest" in the Lope' Reserve, Gabon. In B. Weber, L. White, A. Vedder, & L. Naughton-Treves (Eds.), *African rain forest ecology and conservation* (pp. 165–182). New Haven, Connecticut: Yale University Press.

Table S6.5: Summarising the ecology of the African congeneric species of the transition tree community. All congeners are listed in the table, except for genus *Psychotria*, which had too many congeners to list and thus only the species in the most closely related clades were used (according to Andersson, 2002)¹.

[illegible]

Table S6.5 cont.:

Family	Genus	Species	Region	Evergreen or semi-deciduous broadleaf forest	Gallery forest or riparian vegetation	Swampy, marshy, or seasonally flooded forest	Dry forest, thicket, scrub, or woodland	Forest edge or mugh	Secondary or disturbed forest, anthropogenically degraded vegetation	Savanna	Beach or coastal vegetation	Other notes
Leguminosae	Milletia	orientalis	Madagascar									
Leguminosae	Milletia	pilosa	W.Africa									
Leguminosae	Milletia	psilopetala	C.Africa									
Leguminosae	Milletia	pugensis	E.Africa									
Leguminosae	Milletia	rhodantha	W.Africa									
Leguminosae	Milletia	sacculii	E.Africa									
Leguminosae	Milletia	spini	C.Africa									
Leguminosae	Milletia	thoussii	C.Africa									
Leguminosae	Milletia	thomingii	W.S.Africa									
Leguminosae	Milletia	eteldiana	G-S.Africa									
Leguminosae	Milletia	sanagana	W.Africa									
Leguminosae	Milletia	sensei	E.Africa									
Leguminosae	Milletia	aukaimata	S.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	angustidentata	C.Africa									
Leguminosae	Milletia	aromatica	S.Africa									
Leguminosae	Milletia	aura	Madagascar									
Leguminosae	Milletia	bartei	W.C.Africa									
Leguminosae	Milletia	bequaerti	C.Africa									
Leguminosae	Milletia	bussi	E.Africa, Madagascar									
Leguminosae	Milletia	cadane	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	drysophylla	W.C.Africa									
Leguminosae	Milletia	comosa	C.Africa									
Leguminosae	Milletia	conraui	W.Africa									
Leguminosae	Milletia	coruscans	W.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	drilagi	W.Africa									
Leguminosae	Milletia	disodor	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	dubia	C.Africa									
Leguminosae	Milletia	dua	C.Africa									
Leguminosae	Milletia	elongatistyla	E.Africa									
Leguminosae	Milletia	ericarpa	E.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	evaulolata	C.Africa									
Leguminosae	Milletia	fulgens	S.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	gargapiniara	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	goossensii	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	goosvlei	G-S.Africa									
Leguminosae	Milletia	gracilis	S.Africa									
Leguminosae	Milletia	grandis	S.Africa									
Leguminosae	Milletia	griffoniana	W.C-S.Africa									
Leguminosae	Milletia	hodii	C.Africa									
Leguminosae	Milletia	hykbia	C.Africa									
Leguminosae	Milletia	hypodanra	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	impressa	E-S.Africa									
Leguminosae	Milletia	irivani	W.Africa									
Leguminosae	Milletia	lami	C.Africa									
Leguminosae	Milletia	lance-alberti	C.Africa									
Leguminosae	Milletia	lance-podii	W.Africa									
Leguminosae	Milletia	lascoursvillensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	laurentii	C.Africa									
Leguminosae	Milletia	lebrunii	C.Africa									
Leguminosae	Milletia	lecontei	C.Africa									
Leguminosae	Milletia	lameoides	Madagascar									

Table S6.5 cont.:

Family	Genus	Species	Region	Evergreen or semi-deciduous broadleaf forest	Galler forest or riparian vegetation	Swampy, marshy, or seasonally flooded forest	Dry forest, thicket, scrub, or woodland	Forest edge or margin	Secondary or disturbed forest, anthropogenically degraded vegetation	Savanna	Beach or coastal vegetation	Other notes
Leguminosae	Milletia	leoneis	W.Africa									
Leguminosae	Milletia	le-testui	C.Africa									
Leguminosae	Milletia	leucantha	E.Africa									
Leguminosae	Milletia	limbata	C.Africa									
Leguminosae	Milletia	lucens	W.Africa									
Leguminosae	Milletia	lundersis	W.C.Africa									
Leguminosae	Milletia	macroura	C.Africa									
Leguminosae	Milletia	makandensis	S.Africa									Geoxyle suffutes (underground tree)
Leguminosae	Milletia	manni	W.C.Africa									
Leguminosae	Milletia	marangensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	marundensis	C.Africa									
Leguminosae	Milletia	micans	E.Africa									
Leguminosae	Milletia	midraedi	W.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	mosambicensis	S.Africa									
Leguminosae	Milletia	raffae	Madagascar									
Leguminosae	Milletia	rutens	S.Africa									
Leguminosae	Milletia	ryangensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	oyemensis	W.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	pallens	W.Africa									
Leguminosae	Milletia	paucijuga	E.Africa									
Leguminosae	Milletia	richardsoni	Madagascar									
Leguminosae	Milletia	schliebenii	E.Africa									
Leguminosae	Milletia	seicandra	E.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	soyauvi	C.Africa									
Leguminosae	Milletia	speciosa	S.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	stenopetala	C.Africa									
Leguminosae	Milletia	stipellatissima	C.Africa									
Leguminosae	Milletia	stuhmannii	S.Africa									
Leguminosae	Milletia	tsiku	W.Africa									
Leguminosae	Milletia	tanensis	E.Africa									
Leguminosae	Milletia	tadaraoensis	Madagascar									
Leguminosae	Milletia	tridoni	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	thomii	C.Africa									
Leguminosae	Milletia	urphyllodes	C.Africa									
Leguminosae	Milletia	usamensis	E-S.Africa									
Leguminosae	Milletia	varieddroveni	C.Africa									
Leguminosae	Milletia	vaneclei	W.Africa									
Leguminosae	Milletia	vellensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	zediani	W.Africa									
Leguminosae	Milletia	tipindensis	W.Africa									
Leguminosae	Milletia	tipoda	S.Africa									
Proportion of species				0.19	0.44	0.18	0.22	0.21	0.19	0.20	0.07	
Rubiaceae	Psychotria	vogelliana	W.C.Africa									
Rubiaceae	Psychotria	cryptogramma	E.Africa									
Rubiaceae	Psychotria	fauzola	E.Africa									
Rubiaceae	Psychotria	ingensis	E.Africa									
Rubiaceae	Psychotria	leucopoda	E.Africa									
Rubiaceae	Psychotria	humilis	W.Africa									
Rubiaceae	Psychotria	bauria	W.C.Africa									
Rubiaceae	Psychotria	schweinfurthii	W.C.Africa									

Table S6.5 cont.:

Family	Genus	Species	Region	Evergreen or semi-deciduous broadleaf forest	Gallery forest or riparian vegetation	Swampy, marshy, or seasonally flooded forest	Dry forest, thicket, scrub, or woodland	Forest edge or margin	Secondary or disturbed forest, anthropogenically degraded vegetation	Savanna	Barb or coastal vegetation	Other notes
Leguminosae	Milletia	leoneis	W.Africa									
Leguminosae	Milletia	le-testui	C.Africa									
Leguminosae	Milletia	leucantha	E.Africa									
Leguminosae	Milletia	limbataensis	C.Africa									
Leguminosae	Milletia	luensis	W.Africa									
Leguminosae	Milletia	luridensis	W.C.Africa									
Leguminosae	Milletia	macraea	C.Africa									
Leguminosae	Milletia	makondensis	S.Africa									Geoxyle suffrutes (underground tree)
Leguminosae	Milletia	manni	W.C.Africa									
Leguminosae	Milletia	marangensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	marundensis	C.Africa									
Leguminosae	Milletia	micans	E.Africa									
Leguminosae	Milletia	mildredae	W.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	mossambicensis	S.Africa									
Leguminosae	Milletia	nathaliae	Madagascar									
Leguminosae	Milletia	nubans	S.Africa									
Leguminosae	Milletia	nyangensis	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	oymensis	W.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	pallens	W.Africa									
Leguminosae	Milletia	paucijuga	E.Africa									
Leguminosae	Milletia	richardsoni	Madagascar									
Leguminosae	Milletia	schieberii	E.Africa									
Leguminosae	Milletia	seicantha	E.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	soyauui	C.Africa									
Leguminosae	Milletia	speciosa	S.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	stenopectala	C.Africa									
Leguminosae	Milletia	stipitatisima	C.Africa									
Leguminosae	Milletia	stuhnamii	S.Africa									
Leguminosae	Milletia	takou	W.Africa									
Leguminosae	Milletia	tanensis	E.Africa									
Leguminosae	Milletia	tadaracensis	Madagascar									
Leguminosae	Milletia	thidlori	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	thomaei	C.Africa									
Leguminosae	Milletia	urphyllodes	C.Africa									
Leguminosae	Milletia	usaramensis	E-S.Africa									
Leguminosae	Milletia	varieddrovoni	C.Africa									
Leguminosae	Milletia	vamedei	W.Africa									
Leguminosae	Milletia	vellerii	C.Africa	na	na	na	na	na	na	na	na	
Leguminosae	Milletia	zechian	W.Africa									
Leguminosae	Milletia	zipindensis	W.Africa									
Leguminosae	Milletia	zipoda	S.Africa									
Proportion of species				0.19	0.44	0.18	0.22	0.21	0.19	0.20	0.07	
Rubiaceae	Psychotria	vogelliana	W.C.Africa									
Rubiaceae	Psychotria	cryptogramma	E.Africa									
Rubiaceae	Psychotria	faucida	E.Africa									
Rubiaceae	Psychotria	tingensis	E.Africa									
Rubiaceae	Psychotria	leucopoda	E.Africa									
Rubiaceae	Psychotria	humilis	W.Africa									
Rubiaceae	Psychotria	bauria	W.C.Africa									
Rubiaceae	Psychotria	schwanfuthii	W.C.Africa									

Table S6.5 cont.:

Family	Genus	Species	Region	Evergreen or semi-deciduous broadleaf forest	Gallery forest or riparian vegetation	Swampy, marshy, or seasonally flooded forest	Dry forest, thicket, scrub, or woodland	Forest edge or margin	Secondary or disturbed forest, anthropogenically degraded vegetation	Savanna	Beach or coastal vegetation	Other notes
Rubiaceae	Psychotria	cinerea	W.E. Africa									
Rubiaceae	Psychotria	limbatae	C. Africa									
Rubiaceae	Psychotria	plantaginifolia	C. Africa									
Rubiaceae	Psychotria	tenuissima	C. Africa									
Rubiaceae	Psychotria	verschuerenii	C. Africa									
Rubiaceae	Psychotria	heterosicta	G.E. Africa									
Rubiaceae	Psychotria	lala	G.E.-S. Africa									
Rubiaceae	Psychotria	mucronata	G.E.-S. Africa									
Rubiaceae	Psychotria	nairbianis	G.E.-S. Africa									
Rubiaceae	Psychotria	peduncularis	G.E.-S. Africa									
Rubiaceae	Psychotria	punctata	G.E.-S. Africa									
Rubiaceae	Psychotria	spthamea	G.E.-S. Africa									
Rubiaceae	Psychotria	tambassica	G.E.-S. Africa									
Rubiaceae	Psychotria	volensii	G.E.-S. Africa									
Rubiaceae	Psychotria	butzei	G.-S. Africa									
Rubiaceae	Psychotria	holsti	E. Africa									
Rubiaceae	Psychotria	mionboda	E. Africa									
Rubiaceae	Psychotria	linearispala	E.-S. Africa									
Rubiaceae	Psychotria	pumila	E.-S. Africa									
Rubiaceae	Psychotria	brachyantha	W.C. Africa									
Rubiaceae	Psychotria	brachyanthodes	W.C. Africa									
Rubiaceae	Psychotria	calva	W.C. Africa									
Rubiaceae	Psychotria	luens	W.C. Africa									
		Proportion of species		0.73	0.09	0.09	0.09	0.09	0.09	0.18	0.09	
Humiriaceae	Sacoglottis	gabonensis	W.C. Africa									Fire sensitive, forest pioneer
		Proportion of species		1.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	

¹Andersson, L. (2002). Relationships and generic circumscriptions in the Relationships Psychotria complex (Rubiaceae , Psychotrieae). Syst. Geogr. Plants 72, 167–202.

Chapter 7:

The role of forest elephants in shaping tropical forest-savanna co-existence

By:

Anabelle W. Cardoso, Yadvinder Malhi, Imma Oliveras, Kathryn J. Jeffery, Emma Bush, David Lehmann, Josue Edzang Ndong, Simon L. Lewis, Nicolas Labriere, Edmond Dimoto, Lee T. J. White, William J. Bond, and Katharine A. Abernethy



Having explored the role of fire in shaping forest-savanna transitions in the previous two chapters, this chapter investigates how this role interacts with the effects of forest elephants. Like for when exploring fire in the previous chapters, this chapter begins by characterising the disturbance regime forest elephants enact on the vegetation of the forest-savanna transition, and how this directly affects vegetation structure. It then assesses the indirect effects of forest elephants on vegetation structure by examining interactions with fire. This chapter brings together the findings of the first two chapters on how fire affects vegetation at the transition, integrates them with findings on the effects of forest elephants, and draws conclusions on the interactive role that both play in determining forest-savanna transition dynamics.

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The ideas and research questions, study design, methods, data collection, data analysis, and writing presented in this chapter are the work of the first author, Anabelle W. Cardoso. These activities greatly benefitted from the contributions of Katharine A. Abernethy, Yadvinder Malhi, Imma Oliveras, and William J. Bond, who also made substantial contributions during the writing of the manuscript.

Kathryn J. Jeffery, David Lehmann, and Josue Edzang Ndong assisted with finessing the methodology, provided field support, and helped collect data. Emma Bush, Simon L. Lewis, Nicolas Labriere, Edmond Dimoto, and Lee T. J. White provided data used in this study. All authors provided constructive comments during writing of the manuscript.

7.1 Abstract and Key words

Forest edges, where a closed canopy gives way to open savanna, are dynamic features of tropical landscapes. While the role of fire in determining edge dynamics has been relatively well explored, the role of mega-herbivores is much less understood. Here, we focus on the forest elephant, and the effects this mega-herbivore's foraging has on forest edge dynamics. Using forty camera traps we investigated sites at the forest edges of the forest-savanna mosaic in Lopé National Park, Gabon. We collected 1.2 million images between May 2016 and June 2017 which were classified by over 10 000 volunteers through an online citizen science platform. These data were combined with a 33-year phenology dataset on elephant-favoured fruiting tree species in this landscape, and field measurements of elephant browsing preferences and damage. Our results showed a strong relationship between forest elephant density at the forest edge and fruit availability here. When fruit availability at the forest edge was high, forest elephant density here was nearly double the highest densities ever reported in any other part of the landscape (7.5 elephants.km⁻² in this study vs the previous highest estimate of 4 elephants.km⁻²). Even outside of this high density period, forest elephant density at the forest edge (2.2 elephants.km⁻²) was more than double what other studies estimate density to be in closed canopy forests with low human hunting pressure (1 elephant.km⁻²). Forest elephants were selective browsers at the forest edge, preferring certain species, and trees 3-4 m tall. Their browsing was relatively non-destructive, in comparison to savanna elephants, and had little effect on tree size demography. Forest elephants' heavily used paths acted as fire breaks during savanna

burning, making them inadvertent protectors of the fire sensitive forest. Forest elephant's heavy use of the forest edge helps to reinforce the stabilising feedbacks that allow forest and savanna to co-exist in tropical landscapes.

Key words: Ecosystem engineer, Alternative stable states, Forest elephants, *Loxodonta cyclotis*, Fire, Forest-savanna mosaic, Gabon.

7.2 Introduction

Elephants are the largest living mega-herbivore and have significant impacts on the ecosystems they inhabit. They are part of many obligate seed dispersal mutualisms and so affect tree recruitment patterns, they are important distributors of key nutrients across landscapes, and their herbivory and trampling can determine species composition and vegetation structure, which dictates global ecosystem services such as carbon accumulation and storage (Campos-Arceiz & Blake, 2011; Beaune *et al.*, 2013; Wolf *et al.*, 2013; Terborgh *et al.*, 2016; Bunney *et al.*, 2017; Pellegrini *et al.*, 2017; Rosin *et al.*, 2017; Poulsen *et al.*, 2018). African elephants form two genetically and ecologically distinct groups (Rohland *et al.*, 2010; Ishida *et al.*, 2011; Maisels *et al.*, 2013): the savanna elephant, *Loxodonta africana* (Blumenbach, 1797), and the physically smaller forest elephant, *L. cyclotis* (Matschie, 1900). Although both species have faced drastic population declines (Ripple *et al.*, 2015), recently the most severe of these has been experienced by the forest elephants of Central Africa (Blake *et al.*, 2007; Maisels *et al.*, 2013; Poulsen *et al.*, 2017). A thorough understanding of the ecological role of elephants is therefore necessary, before this functionality is lost forever. While this need has been relatively well-addressed for savanna elephants, a similar understanding of forest elephants is severely lacking (Breuer *et al.*, 2016; Poulsen *et al.*, 2018).

As their name suggests, forest elephants are a forest-dwelling species, with their current range mostly enclosed within the rainforests of Central Africa (Maisels *et al.*,

2013). Their abundance across this range, however, varies significantly between forest types (White *et al.*, 1993). Perhaps counterintuitively, density is often higher in the more open-canopied parts of the forest: forest clearings, the relatively open-canopied *Marantaceae*, *Lophira alata*, or riverine forests (White *et al.*, 1993; Blake, 2002), and colonising forest patches linked with past human occupation (Barnes *et al.*, 1991; Barnes, 1999). One explanation for this is that the increased light of an open canopy and the secondary forest vegetation that grows on abandoned human settlements increases elephant-favoured browse, which is otherwise scarce in the understory of closed canopy forest interior (Barnes *et al.*, 1991; Barnes, 1999; Blake, 2002). By this logic, forest edges, considered in this study as locations where forest transitions into savanna, may also be a favoured foraging site for forest elephants, as their relatively high light conditions allow them to support an abundance of elephant accessible browse (Cardoso *et al.*, **Chapter 7**). Although forest elephants are anecdotally observed at the forest edge (Momont, 2007; Oliveras & Malhi, 2016), their use of this habitat type is yet to be quantified.

Elephant density in different habitat types is neither uniform nor constant, for example savanna elephant density is largely dictated by surface water availability (Chamaillé-Jammes *et al.*, 2007). In contrast, because surface water is abundant and well distributed in the forest, in the absence of human pressure forest elephant density is determined by forage availability (Barnes *et al.*, 1991; White, 1992; Blake, 2002; Yackulic *et al.*, 2011). A large component of forest elephant forage is fruit, but, as fruit availability can be strongly seasonal (White, 1994a), there are times when forest

elephants may rely more heavily on browse to fulfil their nutritional needs. At such times, forest elephants may need to leave the forest interior and seek alternative foraging sites (Blake, 2002). The forest edge may be such an alternative foraging site, as, in addition to abundant and accessible browse, it is also home to multiple elephant-favoured fruiting species that may have complementary phenology to the fruit trees in the forest interior (White *et al.*, 1993; White, 1994a; Momont, 2007). In the study site, the time when forest elephants struggle most to find sufficient fruit in the forest interior is the end of the dry season, when the proportion of fruit in their dung is at a minimum, and they are often “visibly emaciated with only skin on their bones” (White, 1992; White & Abernethy, 1997; Momont, 2007) (**Fig. S7.1**).

Forest edges are dynamic and expand and contract on decadal to millennial timescales with changes in climate and ancient human influence on the landscape (Maley, 2002; Favier *et al.*, 2004; Aleman & Staver, 2018; Aleman *et al.*, 2018). Forest edges are a natural feature of the forest elephant’s range, and so understanding the effect that these mega-herbivores have on this dynamic part of the landscape is important. If forest elephants are exploiting the forest edges as foraging sites, this is likely to have direct effects on edge dynamics. For example, if they trample seedlings and snap saplings at the forest edge, as is observed in the forest interior, they may decrease seedling survival and influence tree recruitment patterns (Terborgh *et al.*, 2016; Rosin *et al.*, 2017), which could lead to contraction of the forest edge. Similarly, contraction of the forest edge may occur if forest elephants, like savanna elephants, target medium-sized trees and cause their widespread mortality (Morrison *et al.*, 2015). Conversely, if forest

elephants disperse seeds and promote tree recruitment at the forest edge (Blake *et al.*, 2009), as is observed in the forest interior, their use of the edge may promote forest expansion. If forest elephants are selective foragers and browse on certain species over others, as is observed in savanna elephants (Owen-Smith & Chafota, 2012), their effects may be observed more strongly in certain tree species.

In addition to these direct effects, forest elephants may also be having indirect effects on forest edge dynamics via interactions with fire. Tropical savannas are some of the most frequently burnt systems on earth, and although the trees in savannas have evolved to cope with this regular burning, forest trees are fire sensitive (Hoffmann *et al.*, 2003; Mouillot & Field, 2005). During savanna burning, mechanisms at the forest edge prevent the penetration of fire into the forest interior (Cardoso *et al.*, **Chapter 5**). These mechanisms include increased tree canopy cover at the forest edge shading out grasses and thus reducing fuel biomass and continuity, which prevents fire from percolating (Archibald *et al.*, 2009; Hoffmann *et al.*, 2012; Abades *et al.*, 2014). Forest elephants can also decrease fuel biomass by eating grass, and reduce fuel continuity by repeated trampling along paths, creating fire-breaks which will increase forest protection from burning and thus reinforce landscape resilience.

Understanding forest elephant effects on forest edge dynamics is especially crucial currently, as although the forest edge has fluctuated in the past, the current acceleration in human-induced climate and land use change is likely to cause unprecedented changes to it across the tropics (IPCC, 2007; Bond & Midgley, 2012; James &

Washington, 2013; Malhi *et al.*, 2014; Steffen *et al.*, 2015; Aleman *et al.*, 2016). One of the most widespread changes currently observable is the loss of savannas across sub-Saharan Africa as a result of expanding forest (Favier *et al.*, 2004; Mitchard *et al.*, 2009; Jeffery *et al.*, 2014). This process, known as forest encroachment, leads to a loss of biodiversity and ecosystem functionality (Parr *et al.*, 2014; Veldman *et al.*, 2015; Veldman, 2016). Elephants have the potential to mitigate such losses, as they can maintain or even create more open landscapes (Wing & Buss, 1970; Owen-Smith, 1987, 2011; Asner & Levick, 2012). To date, however, all the studies investigating how elephants decrease tree cover have focussed exclusively on savanna elephants. While it is often assumed that forest elephants exert similar structuring effects, such assumptions have not yet been tested.

Gabon, in Central Africa, is a stronghold for forest elephant conservation and is home to most of the remaining global population (Maisels *et al.*, 2013). Our study site, Lopé National Park (LNP), has some of the highest recorded forest elephant densities in Africa (4 elephants.km⁻² in *Sacoglottis gabonensis* forest during fruiting season; White, 1994b). The objective of this study was to quantify forest elephant use of the forest edge, assess the drivers of this, and determine the consequences for forest edge dynamics. Historically, such a study would have been near impossible as direct observation of forest elephants is rare due to their tendency to avoid humans and their largely impenetrable habitat (Terborgh *et al.*, 2016; Turkalo *et al.*, 2018). We solved this issue by using 40 motion- and heat-triggered camera traps set up at forest edges in the forest-savanna mosaic of LNP. This allowed us to unobtrusively monitor forest

elephants at high space and time resolution. We combined these data with field measurements of fruit phenology, vegetation structure, and elephant browsing preferences and damage around each camera trap location to address the following research questions and hypotheses:

Q1) Is the forest edge an important forage resource for forest elephants?

H_{1.1}: Forest elephant density at the forest edge will be higher, or seasonally higher, than previous density estimates made in the forest interior (White, 1994b).

H_{1.2}: There are distinct seasonal patterns in elephant use of the forest edge that correlate with seasonal patterns in fruit and browse availability at the forest edge vs in the forest interior.

Q2) Which species do forest elephants prefer to browse at the forest edge, and is this reflected in these species' size demography?

H_{2.1}: Forest elephants are selective browsers at the forest edge, showing preferences for certain species and avoiding others.

H_{2.2}: Forest elephants will prefer to browse on smaller size class stems at the forest edge, as noted by (Terborgh *et al.*, 2016), and thus a demographic bottleneck will be observed in the larger size classes of their preferred species, with no such bottleneck observable in the species they avoid.

Q3) Is forest elephant activity at the forest edge important for preventing savanna fires from burning into the forest?

H_{3.1}: Forest elephant's paths that are more heavily used and have less grass around them act as fire-breaks at the forest edge during savanna burning.

7.3 Materials and Methods

Study site

The study site was the forest-savanna mosaic in the northern part of Lopé National Park (LNP), Gabon, in central Africa. Here, Middle Ogooué savannas (van de Weghe, 2011) interlock with continuous Lower Guineo-Congolian rainforest (White, 1983), with sharp transitions, or ecotones, between them (**Fig. S7.2a**). An elephant path is nearly always observed running along the edge of the savanna, parallel to the forest edge (**Fig. S7.2b**).

Mean annual rainfall in LNP is 1442 mm (1984-2016), mean annual temperature is 24 °C (2003-2016), and mean annual humidity is 81 % (2003-2016) (Tutin *et al.*, 2016). LNP has a short (mid-December to mid-February) and a long (mid-June to mid-September) dry season, with prescribed burning occurring in the latter. Savanna burning has been used as a management tool since 1993 (Jeffery *et al.* 2014), and has been present in the landscape for at least the last 5000 years (White, 2001).

Forest elephant density

Forest elephant density at the forest edge was estimated at 40 points using motion- and heat-triggered camera traps (Agressor No Glow, Bushnell, Kansas, USA). Cameras were attached to trees at 1-1.5 m above ground, focusing perpendicularly towards the elephant path, so as to be the most likely to capture a passing elephant, whilst also not being directly in the elephant's way and inciting them to destroy the camera. Camera

trap sites covered two fire treatments: 19 sites were “low fire frequency” (savanna burnt 0-3 times in the last 10 years and not burnt in the last 3 years) and 21 were “high fire frequency” (savanna burnt 1-3 times in the last 3 years) (**Fig. 7.1**).

The camera traps could be triggered up to once per second and ran from May 2016 to June 2017. This resulted in 1.2 million images, making manual analysis by a small research team unfeasible. Images were thus classified by >10 000 interested members of the public (citizen scientists) via an interactive web interface (“Elephant Expedition”, created in collaboration with Zooniverse.org, available at <https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>, **Fig. S7.3**). Images containing animals were retired after ten independent classifications, and the count of forest elephants recorded. Each image was associated with up to ten potentially conflicting classifications, so we applied a plurality algorithm that assigned each image a single aggregated classification (Swanson et al. 2015, script available at https://github.com/zooniverse/Data-digging/tree/master/example_scripts/R_code/survey-tasks/generalized). The assigned animal was the one with the highest number of “votes”, and the assigned number of elephants in the image was the median count. Considering that elephants are readily distinguishable from other animals in the study site, that images with animals were classified by ten volunteers, and that the high trigger frequency resulted in multiple images usually being captured during the same elephant visit, we have a high level of confidence in the data obtained from citizen science classifications (Kosmala *et al.*, 2016).

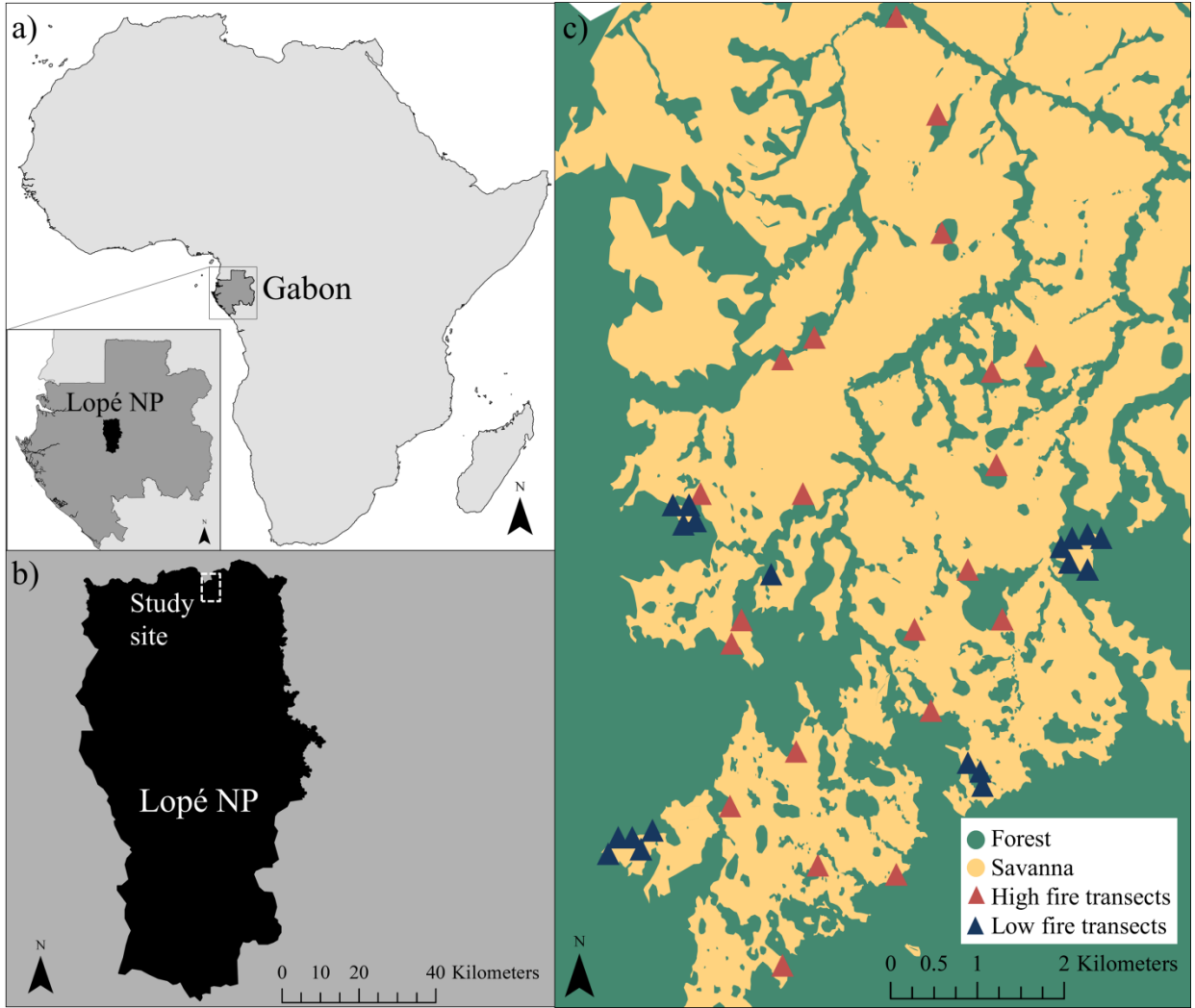


Figure 7.1: Map showing the location of a) Lopé National Park in Gabon, b) the study area within the park, and c) the 40 camera trap locations across high and low fire frequency sites within the forest-savanna mosaic (Agence Nationale des Parcs Nationaux, 2006).

To obtain forest elephant density estimates for each site we applied a random encounter model (REM) (Rowcliffe *et al.*, 2008; Cusack *et al.*, 2015) using the formula:

$$D = \left[\left(\frac{y}{t} \cdot \frac{\pi}{v \cdot r(2 + \theta)} \right) \right] * \text{mean group size}.$$

Here, D is the density of elephants (elephants.km⁻²). $\frac{y}{t}$ is the trapping rate, or total number of independent capture events (y) divided by the total camera effort (t , hrs). Forest elephants move in cohesive groups and the camera trap can be triggered up to once per second, therefore independent capture events were peaks in elephant counts separated from other peaks by at least 1800 seconds on either side (find_peaks function, available at https://github.com/stas-g/findPeaks/blob/master/find_peaks.R). To convert the density of independent capture events into elephant density we multiplied by *mean group size* (Rowcliffe *et al.*, 2008), which is the sum of peaks in count of all independent capture events divided by the number of capture events. This is a conservative estimate, as the maximum count of elephants in any one image is the minimum group size. Total camera effort is the number of hours for which the camera was functional. v is the average speed of a forest elephant (a constant 0.334 km.hr⁻¹, Mills 2017). r and θ are the radius (km) and angle (°) of the camera's detection zone (Rowcliffe *et al.*, 2008). These were calculated by walking in front of the camera detection beam from varying distances and directions and measuring where the trap was triggered, and the value applied was the mean of a subset of the cameras ($n=17$, mean $r = 0.00664$ m (max = 0.00360 km, min = 0.01050 km); mean $\theta = 28.8^\circ$ (max = 40° , min = 20°).

Browsing preferences and damage to trees

At each site the first 15 trees to the right and the left of the camera that were >1 m tall and <1m from the elephant path were assessed for elephant damage ($n=1201$). This assessment was done during the last weeks of camera deployment. Tree species and

height class (1–2 m tall, 2–3 m tall, 3–4 m tall, more than 4 m tall) were noted, as was degree of browsing damage (based on Wing & Buss 1970 and Ishwaran 1983):

- 0. No sign of damage.*
- 1. Side branches of canopy broken.*
- 2. Main stem/trunk broken.*
- 3. Entire tree uprooted.*
- 4. Bark stripped.*
- 5. Elephant tusk marks on trunk.*

To assess which species and size classes forest elephants preferred to browse on, we calculated preference ratios (Petrides, 1975) using the formula:

$$\text{Preference ratio} = \frac{\% \text{ damage}}{\% \text{ availability}}$$

where:

$$\% \text{ damage} = 100 * \frac{\text{number of damaged stems in a species or size class}}{\text{number of damaged stems in all species or size classes}}$$

and:

$$\% \text{ availability} = 100 * \frac{\text{number of stems in species or size class}}{\text{number of stems in all species or size classes}}$$

Preference ratios > 1 indicated that a species or size class is preferred by elephants, preference ratios of between 0 and 1 indicated that a species or size class is somewhat preferred by elephants, and preference ratios of 0 indicated that a species or size class is avoided by elephants.

To assess whether elephants were significantly affecting size distribution, differences between observed and expected frequencies were assessed using χ^2 tests. Expected frequencies were calculated under the assumption that browsing preferences had no effect on size class distribution.

Fruit phenology

Fruiting species important to elephants were determined based on detailed studies on forest elephant diet in the study site (White *et al.*, 1994). Fruiting phenology data for the most important of these (38 species) were then collected in the study site over 33 years (1986 to 2018) (Tutin *et al.*, 2018). Individual tree crowns were visually monitored at the beginning of each month. The presence of ripe fruit in the canopy was recorded, as well as the proportion (0, 0.25, 0.5, 0.75, or 1) of the canopy covered by fruit (see (Bush *et al.*, 2018) for details of the method). Species were classified as either forest edge species (those that occurred in the assessment of elephant damage described above) or as forest interior species (those that did not occur in the survey and are described in the literature as forest interior species; White & Abernethy, 1997).

Using these data, a fruit availability score (FAS) for the forest edge (FAS_{edge}) and the forest interior (FAS_{interior}) was calculated for each month. The FAS indicates long-term patterns of fruit availability across the landscape. The FAS assumes that the amount of fruit a tree produces scales isometrically with its crown volume, which scales with the square of trunk radius (Shenkin et al. in review). The FAS also assumes that fruit in the

canopy is not just present or absent, but that the proportion of the canopy covered in fruit can vary. By adjusting the formula for the “ripe fruit score” (Mitani et al. 2002) to account for these assumptions, we calculated the FAS for each habitat type using the formula:

$$FAS = \sum_{i=1}^n p_i * c_i * d_i * r_i^2$$

Here, i is the tree species, p_i is the mean proportion of individual trees in species i that have ripe fruit in their canopy in any given month, c_i is the mean proportion of each fruiting tree’s canopy that is covered in fruit, d_i is the mean density of trees of in species i in that habitat type (forest edge or forest interior) (stems.ha⁻¹), and r_i is the mean radius at breast height (cm) of trees in species i . The mean density and mean radius of each species was determined from existing census data for plots in different habitat types across the study area (**Table S7.1**).

Elephant paths as fire-breaks

High fire frequency sites were burnt between July and September 2016. Fires were set in the hottest part of the day to maximise intensity. Details on the burning conducted can be found in Cardoso *et al.* (**Chapter 5**).

At each site, an elephant path ran along the edge of the savanna, parallel to the forest edge. Each path was graded 1 (lightly used, no clear break in the grass layer but clearly trampled), 2 (intermediately used, some bare ground visible but grass still growing on

the path), or 3 (heavily used, bare ground clearly visible and clear break in grass layer). After burning, whether or not the elephant path had acted as a fire break was noted.

Grass biomass was assessed around the elephant path; specifically at the forest edge and at 1, 2, and 3 m into the savanna and at 1, 2, and 3 m the forest using a disc pasture meter calibrated for the site (Cardoso *et al*, **Chapter 5**). Canopy leaf area index (LAI, canopy leaf area per unit ground area) can determine grass biomass (Hoffmann *et al*, 2012), and so was also assessed using hemispherical photographs (Nikkor fish-eye lens 10.5mm F2.8G AF DX IF ED). Photographs were taken i) in the savanna, 3 m from the forest edge, ii) at the forest edge, and iii) in the forest, 2 m from the forest edge. The images were converted into LAI values using post-hoc image analysis in Hemisfer (v2.16, Schleppi et al., 2007; Thimonier et al., 2010).

Significant differences in grass biomass and LAI between paths that had acted as a fire-break and those that had not were assessed using Kruskal-Wallis tests.

All analyses were performed in R (v3.5.0, R Development Core Team 2018). Significance was noted at $p < 0.05$.

7.4 Results

Forest elephant density at the forest edge was relatively high (H_{1.1}), and was highest when fruit was most abundant here (H_{1.2})

Mean forest elephant density at the forest edge was 3.1 ± 0.2 elephants.km⁻² (mean $\pm$ standard error) between May 2016 to June 2017. However, this density showed strong seasonal patterns. Forest elephant density at the forest edge was highest between August and November (5.1 ± 1.0 elephants.km⁻²), reaching a maximum in September (7.5 ± 1.4 elephants.km⁻²). This seasonal peak exceeds the previous highest ever estimated seasonal density peak of 4 elephants.km⁻² (White, 1994a) (H_{1.1}) (**Fig. 7.2a**). As expected, even outside of this high density period, mean density at the edge remained relatively high (2.2 ± 0.1 elephants.km⁻²), exceeding the mean annual density (1 elephants.km⁻²) previously estimated for closed canopy forests that are relatively unaffected by human hunting (White *et al.*, 1993; Maisels *et al.*, 2013) (H_{1.1}).

As hypothesised, peaks in density coincided with peaks in mean fruit availability at the forest edge, which occurred at the end of the dry season (H_{1.2}) (**Fig. 7.2b**). Mean forest elephant density at the forest edge had a significant positive relationship with fruit availability at the forest edge (H_{1.2}) (**Fig. 7.2c**). However, contrary to our predictions, no significant links were observed between forest elephant density at the forest edge and fruit availability in the forest interior (**Fig. 7.2d**), although one of the lowest mean monthly density estimates of forest elephants at the forest edge (2.2 ± 0.4 elephants.km⁻²) co-occurred (in February 2017) with the forest interior's highest fruit availability

score (**H_{1.2}**). Similarly, one of the lowest times for fruit availability in the forest interior co-occurred (in April 2017) with a minor peak in forest elephant density at the forest edge (2.6 ± 0.6 elephants.km⁻²) (**H_{1.2}**).

Forest elephants are selective (H_{2.1}) but relatively non-destructive browsers, having no appreciable effects on tree size demography (H_{2.2})

Over 1200 individual trees from 54 species were sampled for elephant damage at the forest edge. Twenty-five of these species had less than five trees sampled and so were excluded from analysis (211 trees). Of the remaining 29 species (1143 trees), 9 species showed no elephant damage. Of the remaining 20 species, 11 were somewhat preferred (preference ratio between 0 and 1) and 9 were strongly preferred (preference ratio > 1) by forest elephants (**Table 7.1**).

Of the 22 species that showed some degree of elephant browsing damage, only 6 also produced fruit eaten by elephants, and the rest were presumably targeted only for their browse. Of these 6, peaks in forest elephant density at the forest edge were associated with peaks in fruit availability for the species *Antidesma vogelianum* and *Sacoglottis gabonensis* both of which were species strongly preferred by forest elephants (**Table 7.1, Fig. S7.4**). Peaks in density were associated to a lesser extent with peaks in fruit availability for the species *Psidium guineense*, *Sarcocephalus latifolius*, and *Psychotria vogeliana*, of which the former two were strongly preferred and the latter somewhat preferred by forest elephants.

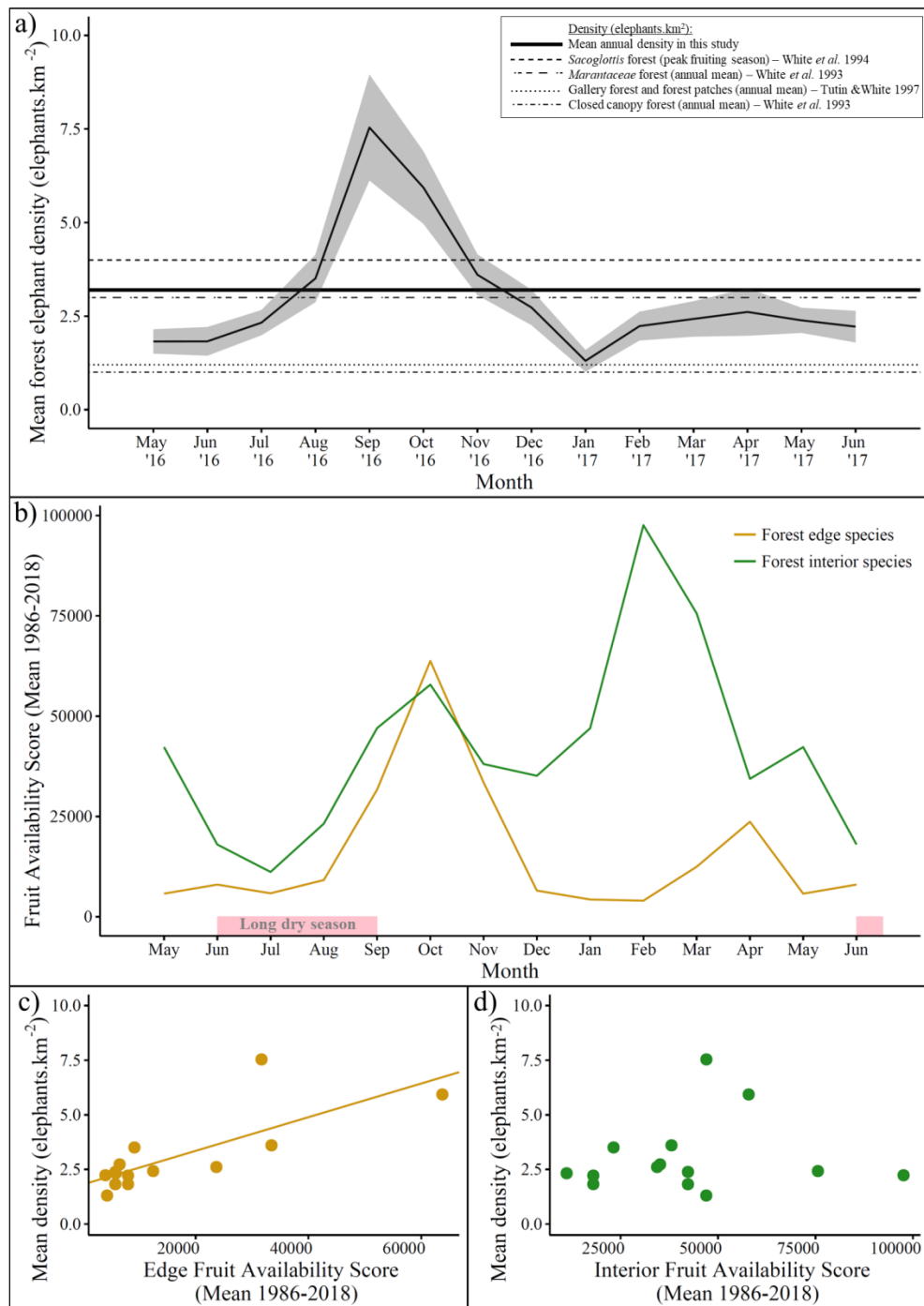


Figure 7.2: a) Mean elephant density at the forest edge (May 2016-July 2017) as calculated from camera traps. Shaded area shows standard error around the mean. Horizontal lines show previously estimated forest elephant densities in other vegetation types in the landscape, as well as the mean annual density in this study. Shaded pink blocks show the long dry season that occurs annually. b) Total fruit availability score (monthly mean from 1986-2018) for the forest edge and interior. c&d) Showing the relationship between forest elephant density at the forest edge and fruit availability at the forest edge (c) (linear model, slope=0.000077, intercept=1.8, adjusted $R^2=0.55$, $p<0.005$, $df=12$) and the forest interior (d) (linear model, slope=0.000083, intercept=2.7, adjusted $R^2=-0.07$, $p=0.70$, $df=12$).

Table 7.1: Degree to which tree species at the forest edge are preferred (preference ratio >1), somewhat preferred (preference ratio <1), or avoided (preference ratio = 0) by forest elephants.

	Species	No. trees sampled	No. trees showing elephant damage	Preference ratio
Strongly preferred	<i>Holarrhena floribunda</i>	9	4	2.78
	<i>Sarcocephalus latifolius</i>	49	18	2.30
	<i>Psidium guineense</i>	24	8	2.09
	<i>Millettia versicolor</i>	129	38	1.84
	<i>Antidesma vogelianum</i>	42	10	1.49
	<i>Vitex doniana</i>	13	3	1.44
	<i>Crossopteryx febrifuga</i>	106	24	1.42
	<i>Sacoglottis gabonensis</i>	84	17	1.27
	<i>Paropsia grewioides</i>	18	3	1.04
Somewhat preferred	<i>Aidia ochroleuca</i>	13	2	0.96
	<i>Psychotria vogeliana</i>	208	29	0.87
	<i>Xylopia aethiopica</i>	44	6	0.85
	<i>Monanthotaxis congolensis</i>	19	2	0.66
	<i>Ouratea myrioneura</i>	82	8	0.61
	<i>Lophira alata</i>	43	4	0.58
	<i>Cryptosepalum staudtii</i>	13	1	0.48
	<i>Tetracera podotricha</i>	13	1	0.48
	<i>Pauridiantha efferata</i>	14	1	0.45
	<i>Cnestis ferruginea</i>	54	3	0.35
	<i>Barteria fistulosa</i>	53	1	0.12
Avoided	<i>Anthocleista vogelii</i>	7	0	0
	<i>Aucoumea klaineana</i>	11	0	0
	<i>Cola lizae</i>	5	0	0
	<i>Diospyros dendo</i>	27	0	0
	<i>Gomphia flava</i>	11	0	0
	<i>Manotes sp.</i>	12	0	0
	<i>Maprounea membranacae</i>	21	0	0
	<i>Pavetta puberula</i>	5	0	0
	<i>Psorospermum tenuifolium</i>	16	0	0

Less than a fifth (16%) of all stems sampled showed some degree of elephant damage. The majority of damage to trees involved branch breaking, followed by main stem snapping (trunk breaking), with uprooting only observed in 0.003% of trees (3 trees, of which only one was taller than 2 m) (**Fig. 7.3a**). Contrary to our predictions that small size trees would experience more damage, forest elephants in this study were found to preferentially damage medium-sized 3–4 m tall trees (**H_{2.2}**) (**Fig. 7.3b**). Despite this preference, and against our expectations, there were no clear effects of forest elephant browsing preferences in tree size demography, with no significant differences between observed and expected frequencies of trees in each size class or between observed and expected frequencies of trees in each preference category (**H_{2.2}**) (**Fig. 7.3c**).

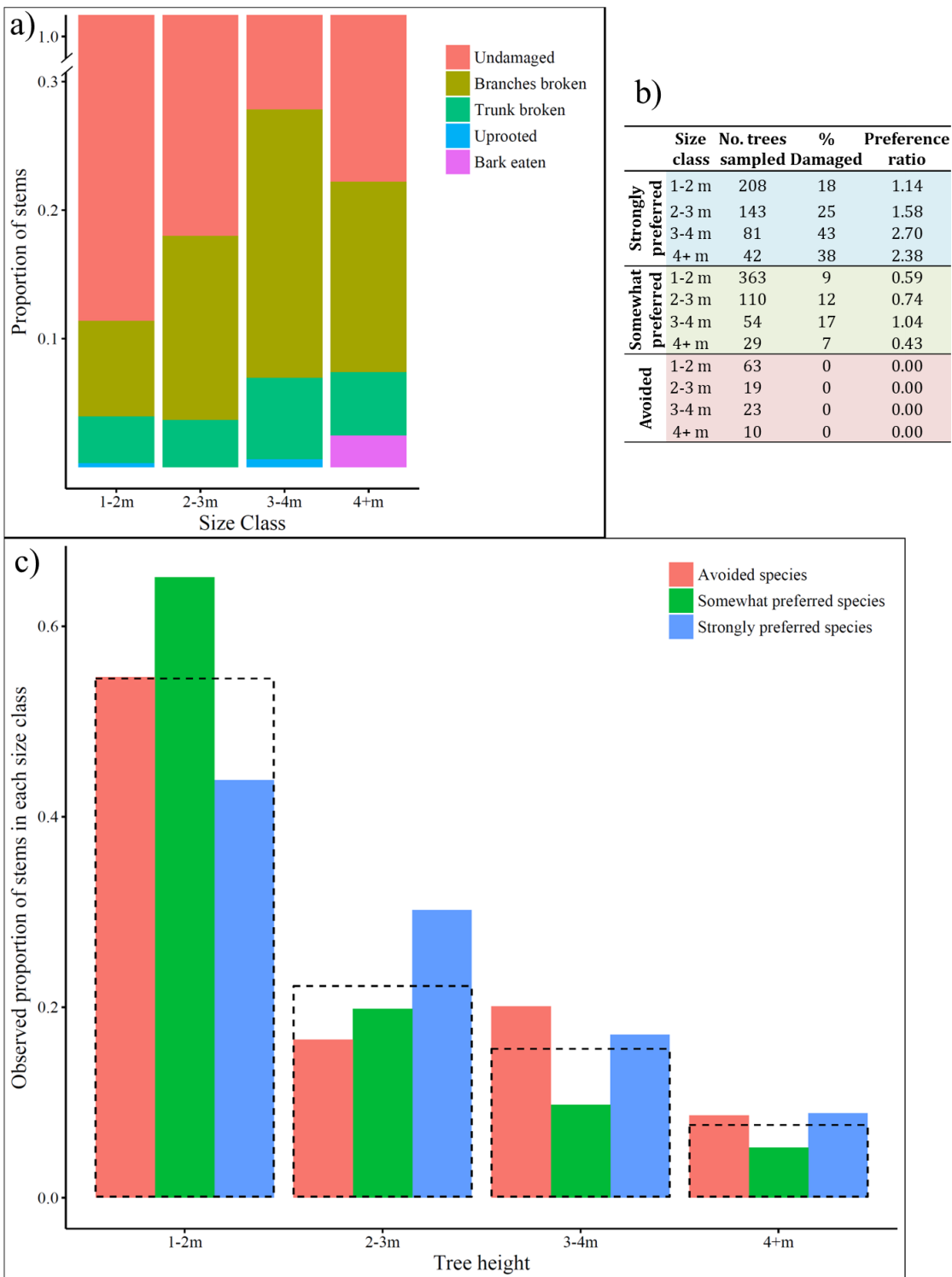


Figure 7.3: a) Proportion of trees in each size class incurring different types of forest elephant damage. Note that the y-axis has been compressed for display purposes. b) Table of which size class trees forest elephants prefer to browse in each preference categories of species. c) Size distribution of trees for species avoided, somewhat preferred, and strongly preferred by forest elephants. No significant differences were between observed (coloured bars) and expected (dotted lines) frequencies of stems in each size class, or between frequencies of stems in each preference categories (in χ^2 tests p was always > 0.5)

The forest elephant paths at the forest edge that acted as fire-breaks were those more heavily used (H_{3.1})

Of the 21 sites that were experimentally burnt, 16 had intermediately (grade 2) and 5 had heavily (grade 3) used elephant paths. No lightly used paths (grade 1) were present. 10 of these 21 elephant paths acted as fire-breaks at the edge of the savanna during burning. Heavily used paths were more likely to act as fire-breaks than intermediately used ones (80% of the grade 3 paths vs 38% of the grade 2 paths acted as fire-breaks) (H_{3.1}). Although not statistically significant, mean annual elephant density was marginally higher in sites with heavily used paths (grade 3) than those with intermediately used paths (grade 2) (Kruskal-Wallis, $\chi^2=1.75$, $df=1$, $p=0.19$; mean ($\pm$ standard error) annual elephant: sites with grade 3 path = $4.0 (\pm 0.8)$ elephants.km², sites with grade 2 path = $2.8 (\pm 0.4)$ elephants.km²). Paths that acted as fire-breaks had marginally less grass biomass around them than paths that didn't act as fire-breaks, however this difference was not statistically significant (**Fig. 7.4a**) (H_{3.1}). This marginal difference was not induced by a higher level of shading, as no significant differences in canopy LAI were found between sites where paths had acted as fire-breaks and sites where they hadn't (**Fig. 7.4b**).

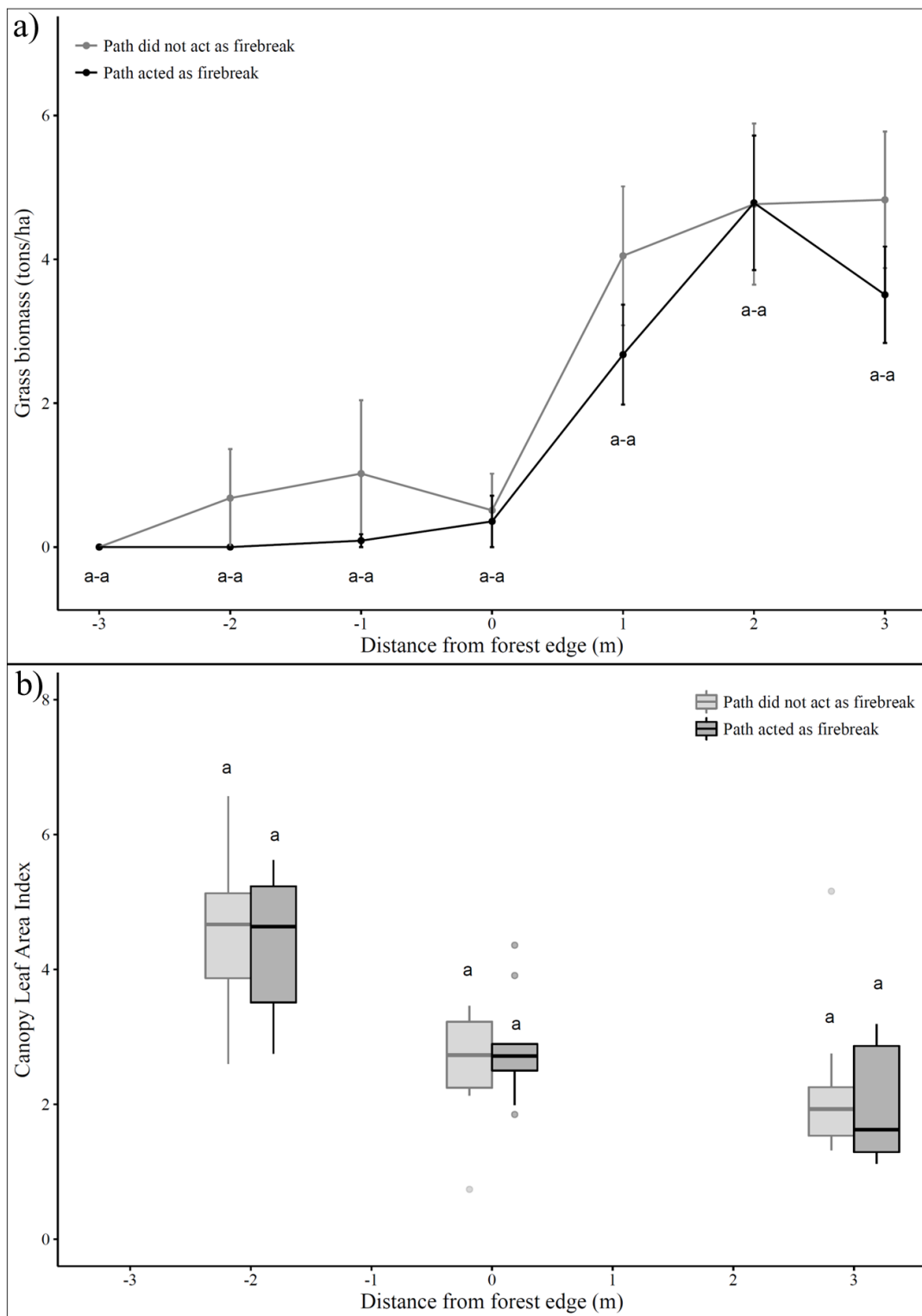


Figure 7.4: a) Grass biomass and b) tree canopy cover (leaf area index, LAI) around the forest elephant path that runs along the edge of the savanna, parallel with the edge of the forest. Positive distances from the forest edge are in the savanna, negative distances in the forest. Different letters indicate significant differences between sites where the path acted as a fire-break, vs those in which it did not as determined by Kruskal-Wallis tests ($p < 0.05$).

7.5 Discussion

The forest edge is an important forage resource for forest elephants (Q1)

Mean forest elephant density was exceptionally high (7.5 elephants.km⁻²) at the end of the dry season (September 2016), approximately double the highest forest elephant density estimate ever made in this landscape (4 elephants.km⁻² in *Sacoglottis gabonensis* forest during fruiting season, White, 1994b). During the rest of the year, forest elephant density at the forest edge remained relatively high (2.2 elephants.km⁻²). This density is lower than previously estimated mean annual density in *Marantaceae* and colonising forests (3 elephants.km⁻², White et al. 1993), but is more than double the estimated mean annual density in closed canopy forests relatively unaffected by human hunting pressure (1 elephants.km⁻² (White *et al.*, 1993; Maisels *et al.*, 2013)). This provides compelling evidence that the forest edge is a key resource for forest elephants, and that forest-savanna mosaics are particularly important landscapes for them for the abundance of forest edges they provide. This conclusion is supported by the findings of Momont (2007), who showed that four collared female forest elephants from the study site preferred the forest-savanna mosaic to the closed canopy forest. It may also explain the patterns in (Maisels *et al.*, 2013), who found that forest elephant density was higher near the forest-savanna mosaic of the study site (northern LNP) than anywhere else in Africa.

Forest elephant density at the forest edge showed a strong seasonal pattern, and was determined by fruit availability here. Forest edge species tended to fruit at the end of

the long dry season, which is when forest elephants in the area are anecdotally struggling the most to meet their nutritional needs (White, 1994a; White & Abernethy, 1997). Elephant density at the edge did not show as clear a relationship with fruit availability in the forest interior, suggesting that the edge is an attractive resource regardless of how abundant fruit may be in the forest interior. The exceptionally high density that occurred at times when edge fruit was most available suggests that forest elephants are being attracted to the forest edge from a wide area, which is in agreement with previous work showing how forest elephant movement can be highly seasonal and correlated with peaks in availability of certain preferred fruiting species (White, 1994a).

In addition to fruit, the forest edge also represents an important browse resource for forest elephants, with many species not producing elephant-preferred fruits but still exhibiting signs of elephant browsing damage. This is supported by previous work that showed the woody community at the forest edge (*cf.* towards the forest interior) to have a significant proportion of its canopy within reach of elephants (Cardoso *et al.*, **Chapter 6**), unlike the understorey of the forest interior (Blake, 2002). Together, this suggests that the forest edge is an important browse resource, in addition to being a fruit resource, for forest elephants.

Forest elephants are selective browsers, however this browsing is relatively non-destructive and not reflected in tree size demography (Q2)

Forest elephants did not browse all species of the forest edge equally and showed a strong preference for some species while avoiding others, as is observed for savanna elephants (Owen-Smith & Chafota, 2012). In addition to showing preferences for different species, forest elephants also showed distinct browsing preferences for trees of certain size classes. Although they most abundantly browsed on trees in the smallest size class (1–2 m tall), when accounting for differences in availability of the size classes, they showed the strongest preference for trees 3–4 m tall. These findings are contrary to our expectations, as prior work has shown forest elephants to browse extensively on trees of smaller size classes (Terborgh *et al.*, 2016). This suggests that the observed preference for trees in larger size classes may simply be an artefact of the fact that these trees are usually older than smaller trees and therefore have had more time to accumulate damage. The trees that the forest elephants most preferred to browse on are resistant to this pressure, able to rapidly resprout and recover. For example, one of their most preferred species, *Millettia versicolor*, is documented to have a strong coppicing ability (White & Abernethy, 1997). A coppicing response to herbivory has been documented in more arid savanna tree species (Staver *et al.*, 2012), however has not yet been thoroughly explored for more mesic forest-savanna transition species.

Forest elephant preferences for trees 3–4 m tall is similar to savanna elephants, who browse extensively on canopy-level trees (>2 m tall), leading to large-scale tree mortality (Morrison *et al.*, 2015). In contrast to savanna elephants, whose browsing

leads to a dearth of trees in larger size classes (Asner *et al.*, 2009), forest elephant browsing had no detectable effects on tree size demography. This is because the overall level of forest elephant damage to trees was relatively low. For example, savanna elephants have been observed to have inflicted damage on up to 90% of trees taller than 2 m (Morrison *et al.*, 2015), while in our study trees of the same size class were only damaged by elephants 28% of the time. Overall, the estimates of elephant damage in this study (16% of all stems) are in line with previous estimates of forest elephant damage from the study site, where they were estimated to be responsible for the snapping of approximately 20% of understorey stems (Terborgh *et al.*, 2016). This finding highlights the stark differences between forest and savanna elephants in terms of their effects on vegetation structure.

African elephants have long been thought of as important for preventing open canopied savanna from being encroached upon by expanding forests, with their widespread extirpation across the continent between the Pleistocene and Holocene even cited as a key contributor to forest expansion in Africa (Owen-Smith, 1987). Later work supported this hypothesis, showing that savanna elephants frequently fell canopy-size trees and are the leading cause of large tree mortality in some savanna landscapes (Asner & Levick, 2012; Morrison *et al.*, 2015). Findings such as these have subsequently been used in models that reconstruct the historical structure of tropical landscapes and show the profound effect the loss of mega-fauna has had on this (Doughty *et al.*, 2015). However, all of these studies focus on savanna elephants, and assume forest elephants likely to fulfill a similar ecological role, since there has been notably little literature to

suggest otherwise. The findings of this study show that the assumption that forest elephants fulfill the same ecological role as savanna elephants is largely incorrect. Most notably, they don't push over large trees like savanna elephants, and in fact they hardly damage trees at all. This isn't due to a lack of accessible size-class trees being available to forest elephants, as many such trees are present at the forest edge. This suggests then, that the tree-felling behaviour of savanna elephants is unique to this species, and may be a socio-sexual behaviour (as suggested by Midgley *et al.* 2005).

The implication of this is that forest elephants aren't able to reduce forest encroachment or maintain open savannas in the way that savanna elephants do. This means that a more nuanced approach is required when modelling the vegetation structure of historical landscapes and when drawing conclusions about the ecological functionality of elephants in Africa. The findings of this work also strongly support that forest and savanna elephants are ecologically distinct species, that their ecological functionality is non-interchangeable, and thus should be considered as separate species in conservation policies (e.g. by the (IUCN, 2018).

Forest elephant activity at the forest edge is important for preventing savanna fires from burning into the forest (Q3)

Approximately half of the forest elephant paths that were part of experimental savanna burning during this study acted as fire breaks, protecting the fire-sensitive forest from burning. To accomplish this ecosystem function, paths needed to be heavily used, with intermediately used paths being only half as effective. From a conservation perspective,

this highlights the importance of maintaining large forest elephant populations within forest-savanna mosaics, as although smaller populations may preserve biodiversity they are likely incapable of fulfilling this ecosystem function. The loss of forest elephants from these landscapes could thus lead to more frequent incursion of fire into forests. Testing this was not possible in this study site as forest edges that aren't associated with elephant paths are near impossible to find, therefore it would be advisable to test this conclusion in landscapes where elephants are locally extinct.

This study did not explicitly investigate the mechanism through which forest elephant paths stopped fire, but our results suggest that the discontinuity in fuel introduced by a wider, more heavily used, elephant path is key. This is supported by our finding that neither grass biomass nor tree canopy cover differed between sites where the elephant path did or did not act as a fire-break. Fires are significantly less intense nearer the forest edge than in the savanna interior (Cardoso *et al.*, **Chapter 5**), and both this reduced intensity, combined with the discontinuity in fuel presented by the elephant path, are essential for forming a fire break. The necessity of both components is demonstrated by field observations of even heavily used elephant paths in the savanna interior never observed to be acting as fire-breaks (**Fig. S7.5**).

Although out of the scope of this study, it would be interesting to investigate how important forest elephants are for the dispersal and recruitment of their most favoured species at the forest edge, and what role these species play in determining forest edge dynamics.

Conclusion

Forest elephants are exceptionally abundant at the forest edge, which is an important fruit and browse resource for them. Forest elephants forage relatively non-destructively compared to their savanna relatives. However, they still play a role in determining forest edge dynamics as their heavily used paths along the forest edge can act as fire-breaks. By inadvertently assisting in the prevention of fires spreading into forests, forest elephants provide a valuable ecosystem service. By reinforcing the fire-related feedbacks that allow forest and savanna to co-exist, forest elephants have probably played a key role in stabilising mosaicked landscapes through time. However, since they are relatively non-destructive, their direct effects on vegetation structure at the forest edge are limited, and they do not exhibit any ability to create a more open canopy. This implies that the maintenance and creation of open-canopied landscapes in Central Africa is primarily the role of fire.

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7.8 Supplementary material



Figure S7.1: Camera trap images of emaciated forest elephants, captured during this study at the end of the dry season (August/September 2017).

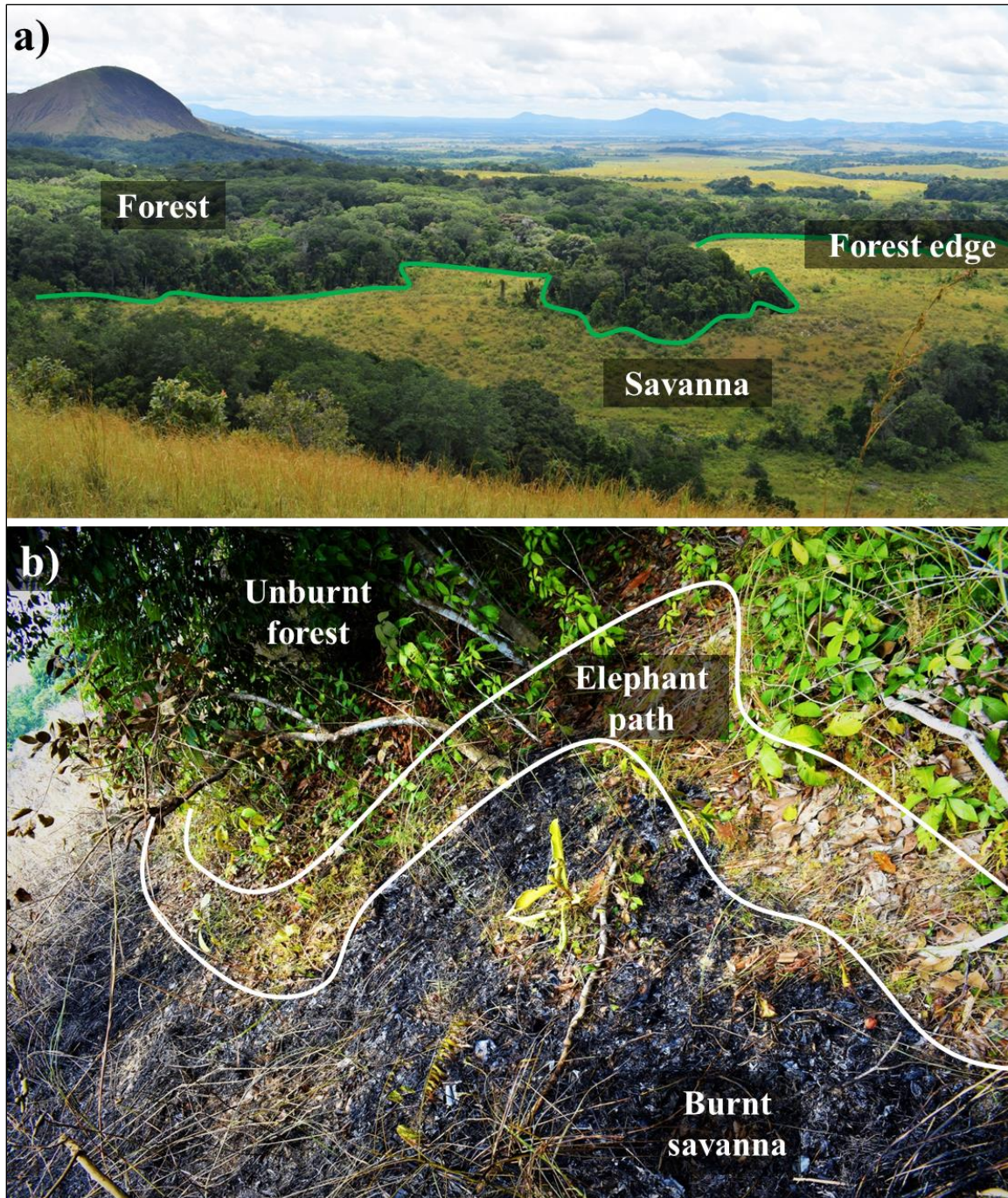


Figure S7.2: Photographs of the study site showing a) the sharp transitions between forest and savanna and the location of the forest edge and b) an example of the elephant path that runs along the forest edge and how it acts as a fire break during burning.

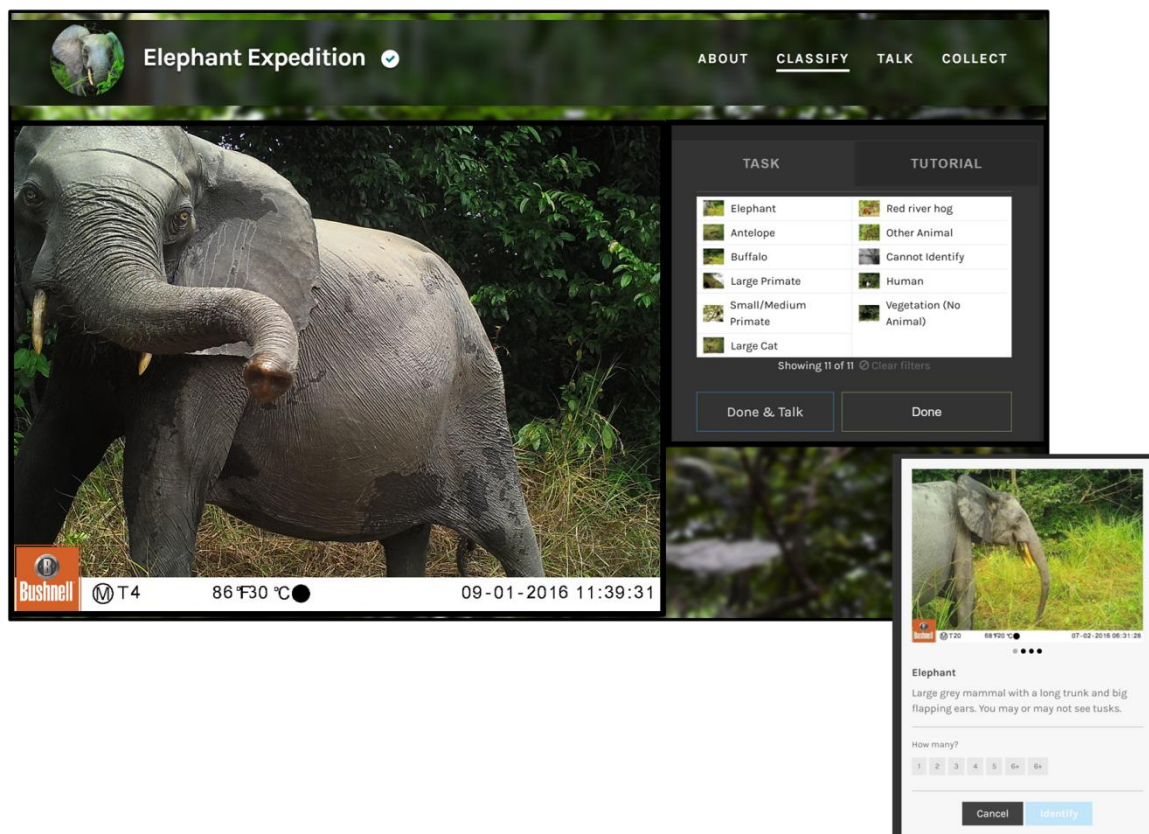
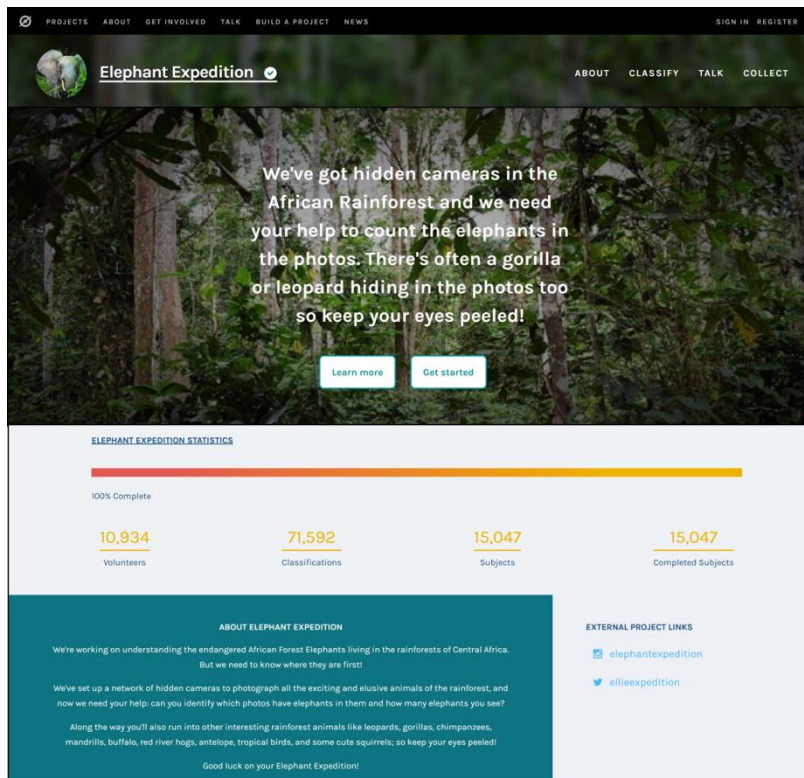


Figure S7.3a: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the landing screen (top), classification window (bottom) and elephant count window (inset).

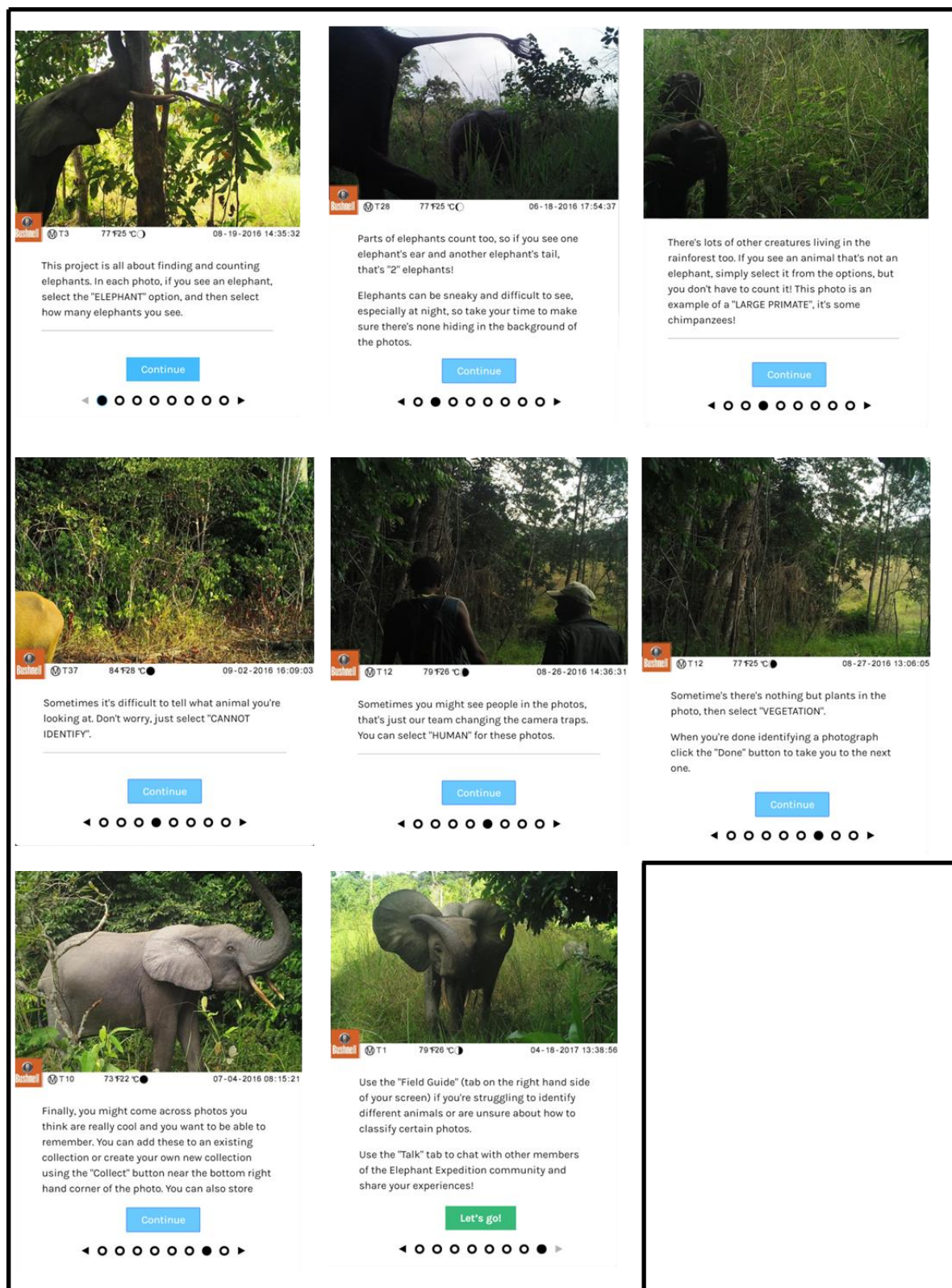


Figure S7.3b: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the pre-classification tutorial.

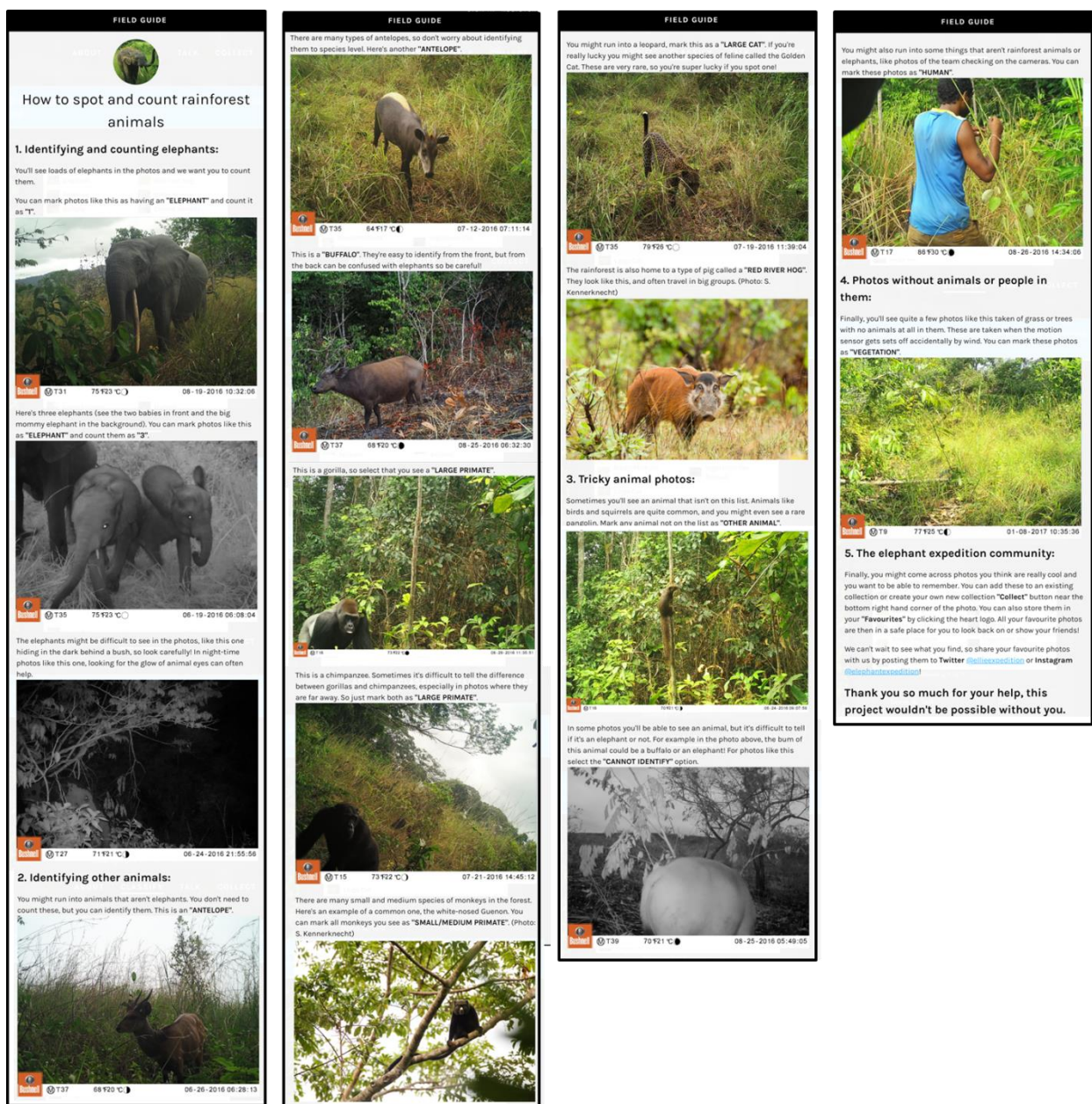


Figure S7.3c: Example of the citizen science web interface, “Elephant Expedition” (<https://www.zooniverse.org/projects/anabellecardoso/elephant-expedition>) showing the field guide that citizen scientists can consult during classification.

Figure S7.4: Fruit availability score (mean monthly 1986-2018) for each species in the phenology dataset.

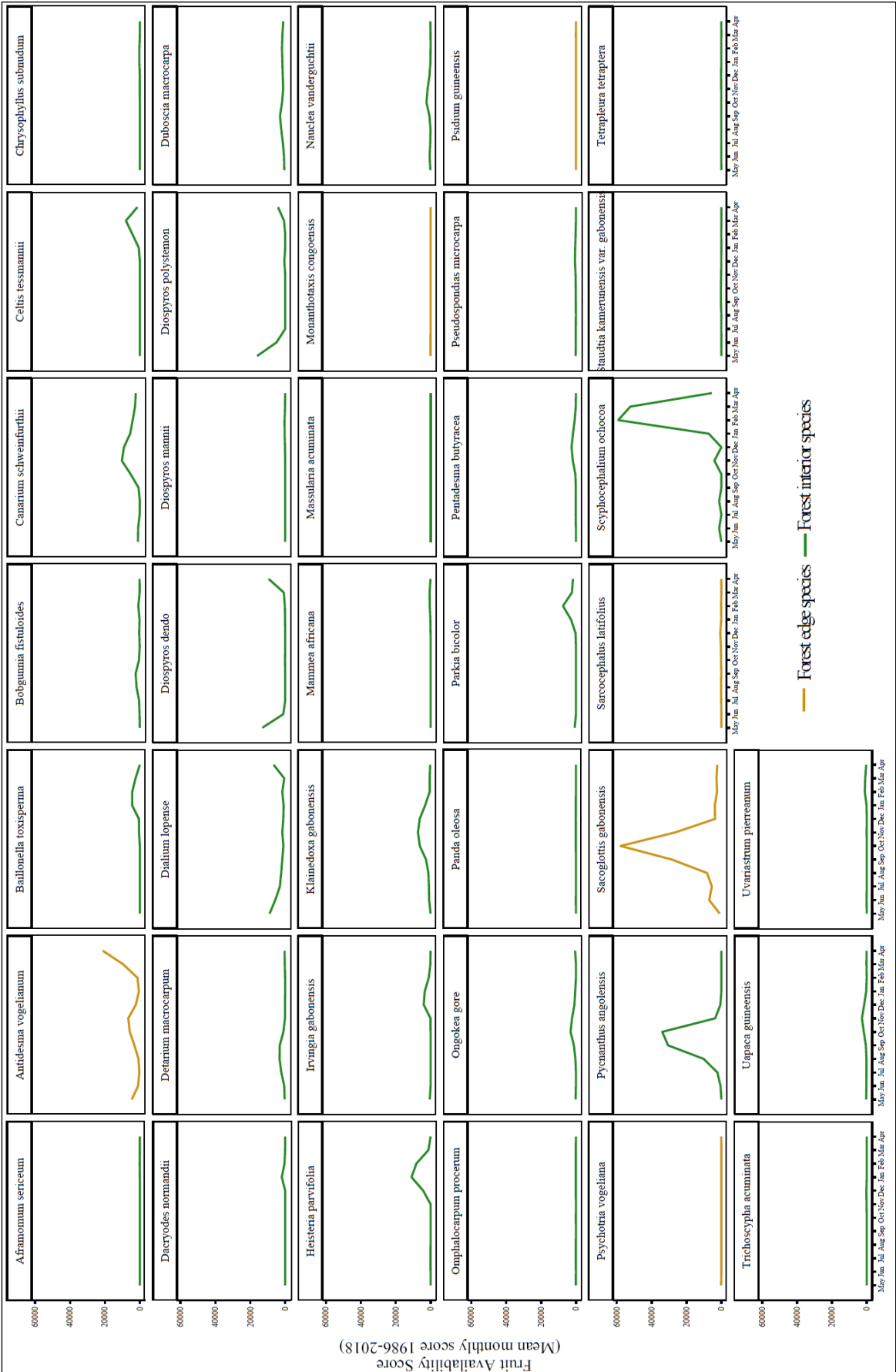




Figure S7.5: A heavily used forest elephant path in the savanna interior that shows no ability to act as a fire-break.

Table S7.1: All data sets used in calculation of the “fruit availability score”.

Data set name	Specific vegetation type	Total plot size (ha)	Data owner
CAYETTE1	Bosquet/Forest patch	0.08	Lee J. T. White
CAYETTE2	Bosquet/Forest patch	0.08	Lee J. T. White
CENTROPLACUS	Bosquet/Forest patch	0.08	Lee J. T. White
CHATEAUDEAU	Bosquet/Forest patch	0.08	Lee J. T. White
COUPONS	Bosquet/Forest patch	0.08	Lee J. T. White
DGG1	Bosquet/Forest patch	0.08	Lee J. T. White
DGG2	Bosquet/Forest patch	0.08	Lee J. T. White
FdAEROPORT1	Bosquet/Forest patch	0.08	Lee J. T. White
FdAEROPORT2	Bosquet/Forest patch	0.08	Lee J. T. White
KLAINEDOXA1	Bosquet/Forest patch	0.08	Lee J. T. White
KLAINEDOXA2	Bosquet/Forest patch	0.08	Lee J. T. White
KLAINEDOXA3	Bosquet/Forest patch	0.08	Lee J. T. White
KOUROU1	Bosquet/Forest patch	0.08	Lee J. T. White
KOUROU2	Bosquet/Forest patch	0.08	Lee J. T. White
LACINFERIEUR	Bosquet/Forest patch	0.08	Lee J. T. White
LACSUPERIEUR1	Bosquet/Forest patch	0.08	Lee J. T. White
LACSUPERIEUR2	Bosquet/Forest patch	0.08	Lee J. T. White
MANDRILL1	Bosquet/Forest patch	0.08	Lee J. T. White
MANDRILL2	Bosquet/Forest patch	0.08	Lee J. T. White
MANDRILL3	Bosquet/Forest patch	0.08	Lee J. T. White
LNL04	Colonising forest	0.5	Nicolas Labriere and Simon Lewis
LNL05	Colonising forest	0.5	Nicolas Labriere and Simon Lewis
LNL06	Colonising forest	0.5	Nicolas Labriere and Simon Lewis
VEGCAT2.1	Colonising forest	0.08	Lee J. T. White
VEGCAT2.2	Colonising forest	0.08	Lee J. T. White
VEGCAT2.3	Colonising forest	0.08	Lee J. T. White
VEGCAT2.4	Colonising forest	0.08	Lee J. T. White
VEGCAT2.5	Colonising forest	0.08	Lee J. T. White
CARDOSO	Forest-savanna transition	12.95	Anabelle W. Cardoso
LOPEL9	Gallery forest	0.08	Lee J. T. White
MBAYEGALLERY	Gallery forest	0.08	Lee J. T. White
MBAYEN5	Gallery forest	0.08	Lee J. T. White
LNL10	Marantaceae forest	1	Nicolas Labriere and Simon Lewis
LNL11	Marantaceae forest	1	Nicolas Labriere and Simon Lewis
LPG02	Marantaceae forest	1	Lee J. T. White
MPAM	Marantaceae forest	2.5	Lee J. T. White
VEGCAT4.1	Marantaceae forest	0.08	Lee J. T. White
VEGCAT4.2	Marantaceae forest	0.08	Lee J. T. White
VEGCAT4.4	Marantaceae forest	0.08	Lee J. T. White
WW94	Marantaceae forest	2.5	Lee J. T. White
LNL12	Mature forest	1	Nicolas Labriere and Simon Lewis
LPG01	Mature forest	1	Lee J. T. White
VEGCAT5.1	Mature forest	0.08	Lee J. T. White
VEGCAT5.2	Mature forest	0.08	Lee J. T. White
VEGCAT5.3	Mature forest	0.08	Lee J. T. White
VEGCAT5.4	Mature forest	0.08	Lee J. T. White
VEGCAT5.5	Mature forest	0.08	Lee J. T. White
LNL08	Mix: Monodominant Okoume, Saccoglottis forest	1	Nicolas Labriere and Simon Lewis
LTJWsite1	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	0.5	Lee J. T. White
LTJWsite2	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	0.5	Lee J. T. White
LTJWsite3	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	0.5	Lee J. T. White
LTJWsite4	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	0.5	Lee J. T. White
LTJWsite5	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	0.5	Lee J. T. White
SEGC94	Mix: Rocky forest, Marantaceae forest and Monodominant Okoume/Azobe	2.5	Lee J. T. White
LNL07	Monodominant Okoume	1	Nicolas Labriere and Simon Lewis
LNL09	Monodominant Okoume	1	Nicolas Labriere and Simon Lewis
VEGCAT3.1	Monodominant Okoume	0.08	Lee J. T. White
VEGCAT3.2	Monodominant Okoume	0.08	Lee J. T. White
VEGCAT3.5	Monodominant Okoume/Azobe	0.08	Lee J. T. White
VEGCAT1.1	Savanna	0.08	Lee J. T. White

Chapter 8:

Conclusions and synthesis

By:

Anabelle W. Cardoso



Photo: Anabelle W. Cardoso

8.1 Summary of key findings

Forests and savannas, the two most widespread biomes in sub-Saharan Africa, both provide a multitude of ecosystem services and are depended upon by millions of people for their livelihoods and wellbeing (Costanza *et al.*, 1998; Olsson & Ouattara, 2013; Ryan *et al.*, 2016). Forest-savanna transitions are sensitive to anthropogenically induced climate and land-use change (Oliveras & Malhi, 2016). However, in order to understand how these changes may affect them, we need to have a good understanding of their ecology. The overall aim of this thesis was thus to investigate the ecology of forest-savanna transitions, with a specific focus on how they were affected by fire and elephants.

This study collected data at of forty transition sites in the forest-savanna mosaic of Lopé National Park in Gabon in Central Africa. Tree and grass communities were assessed and their associated functional traits measured; experimental burns were conducted and fire behaviour was described; and the impacts of forest elephants on the vegetation of the transition were quantified. This work showed that both fire and forest elephants were important drivers of forest-savanna mosaic stability, and highlighted their integral role in facilitating forest and savanna co-existence in mosaicked landscapes.

The three objectives of this thesis were explored through three research articles, the main findings of which are discussed below and summarised in **Figure 8.1**. Following

this, a synthesis of the findings is presented, which includes discussion on the broader implications of the work and potential avenues for future research.

Objective 1: To empirically describe the fire suppression threshold and the interactive abiotic and biotic controls on it.

This objective was addressed in **Chapter 5**, through the research article entitled “**Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions**”.

This study found strong evidence for a fire suppression threshold within the forest-savanna transition, when leaf area index reached a value of 3, as was reported by previous studies in the Brazilian savanna (Hoffmann *et al.*, 2012). In addition, results showed that fire became significantly less intense and less hot prior to reaching this threshold. This implied that the fire suppression threshold did not separate two binary fire regimes, with fire being either present below the threshold or absent above it. Rather, it showed that fire behaviour changes occurred along a gradient and that these changes were being mediated by more than one driver. Specifically, it found that that the changes in fire behaviour were being mediated by grass species composition and flammability traits, which were being mediated by tree canopy cover that was, in turn, being mediated by fire behaviour.

These findings highlighted the importance of accounting for variability in the flammability of grassy fuels, as it affects landscape-scale fire behaviour. Current fire models often fail to do this (e.g. BehavePlus (Heinsch & Andrews, 2010), FARSITE (Finney, 2004), and FlamMap (Finney, 2006)), and apply one fuel model per vegetation type (e.g. “High Load, Very Coarse, Humid Climate Grass” to all grassy areas in a landscape; Scott & Burgan 2005). Even the most advanced models that specifically predict forest and savanna dynamics (eg. FORSAT, Favier *et al.* 2004) make the assumption that a grassy landscape is uniformly flammable under given climatic conditions. As this study showed, assuming all parts of a grassy landscape to be equally flammable will likely result in inaccurate predictions of fire behaviour, which could lead to the application of inefficient or incorrect management strategies.

This study also links species-specific functional traits to community-scale species composition and landscape-scale fire-driven vegetation patterns. While such links have been hypothesised (see Simpson *et al.*, 2016c; Charles-Dominique *et al.*, 2018; Wragg *et al.*, 2018 for examples), this work was the first to empirically demonstrate their existence in the context of forest and savanna co-existence. In addition to the scientific importance of these findings, the methods used for measuring grass species flammability in the field are cheap and easy to replicate, making a contribution to the limited pool of methods available to resource-limited tropical ecologists.

Objective 2: To assess whether a distinct transition tree community could be identified at the forest-savanna transition, and to investigate its ecology.

This objective was addressed in **Chapter 6**, through the research article entitled **“Distinct transition tree community suggests possible antiquity of forest-savanna mosaics”**.

This study found that a distinct woody transition tree community existed between forest and savanna. The community was intermediately fire resistant, and although functionally more similar to the forest than the savanna, was distinct from both. Tree species of the transition community were not a subset of forest gap species, with the community showing signs of being stable through time with multiple recruitment events having occurred, rather than an ephemeral pioneer community. These tree species were also not a subset of savanna species, as their intermediate level of investment in fire-resistance made them unable to survive the regular and intense burning regime of the savanna interior. This transition community is likely acting as a buffer between the contrasting fire regimes of forest and savanna, facilitating their continued co-existence.

The development of a distinct transition tree community points to the antiquity of the forest-savanna mosaic, as both vegetation types must have co-existed for long periods of time for such a specialised tree community to have developed. It also implies that regular burning is essential for the maintenance of the transition as well as the forest

and savanna it delineates. This highlights the importance of considering the transition an ecological entity in its own right, and as an essential stabilising component of fire-maintained forest-savanna mosaics. These results also strongly advocate for the continued burning of this landscape, in order to maintain its diversity of vegetation types, and suggest that similar fire regimes may be appropriate for mosaics across the tropics, in order to mitigate biodiversity losses.

Objective 3: To quantify forest elephant use of the forest-savanna transition, assess the drivers of this, and determine the consequences for transition dynamics.

This objective was addressed in **Chapter 7**, through the research article entitled “**The role of forest elephants in shaping tropical forest-savanna co-existence**”.

This study found mean annual forest elephant density to be higher at the forest-savanna transition than any previous estimates made. This study estimated mean annual elephant density at the transition to be 3.1 elephants.km⁻², in comparison to the previous highest mean annual estimate of 3 elephants.km⁻² for “*Marantaceae* forest” (White *et al.*, 1993) or of 1 elephants.km⁻² for Central African areas not heavily pressured by hunting (Maisels *et al.*, 2013). Forest elephant density at the transition was highest in months where fruit availability at the transition was highest. In addition to fruit, many tree species at the transition were also targeted for their browse. These

findings demonstrated the importance of the forest-savanna transition as a nutritional resource for forest elephants, especially at the end of the dry season when they anecdotally struggle to meet their nutritional requirements (White & Abernethy, 1997).

Despite forest elephant's high density and frequent browsing at the transition, trees here did not show demographic signatures of elephant pressure, and no trees were observed to be fully uprooted. This is in stark contrast with savanna elephants, who are well documented to be significantly more destructive (Laws, 1970; Wing & Buss, 1970; Asner & Levick, 2012; Morrison *et al.*, 2015; Pellegrini *et al.*, 2017). Forest elephant use of the transition did result in well-worn paths here, which acted as fire-breaks and prevented fire from spreading into the forest. This demonstrated how forest elephant activity reinforces the fire suppressing ability of the forest-savanna transition, and showed how fire and forest elephants are inextricably linked components of mosaic stability through time.

This work supported that forest elephants are critical components of tropical ecosystem function (Blake *et al.*, 2009; Campos-Arceiz & Blake, 2011). Our study highlighted the importance of considering the forest-savanna transition as a distinct and important habitat type for forest elephants, and by implication supports the use of fire for maintaining this resource (**Chapter 6**). This study also clearly demonstrated the difference in ecological function between forest and savanna elephants, specifically their different effect on woody vegetation structure, and so supported conclusions

drawn from genetic work on the African elephant that propose these two groups to be distinct species (Rohland *et al.*, 2010; Ishida *et al.*, 2011).

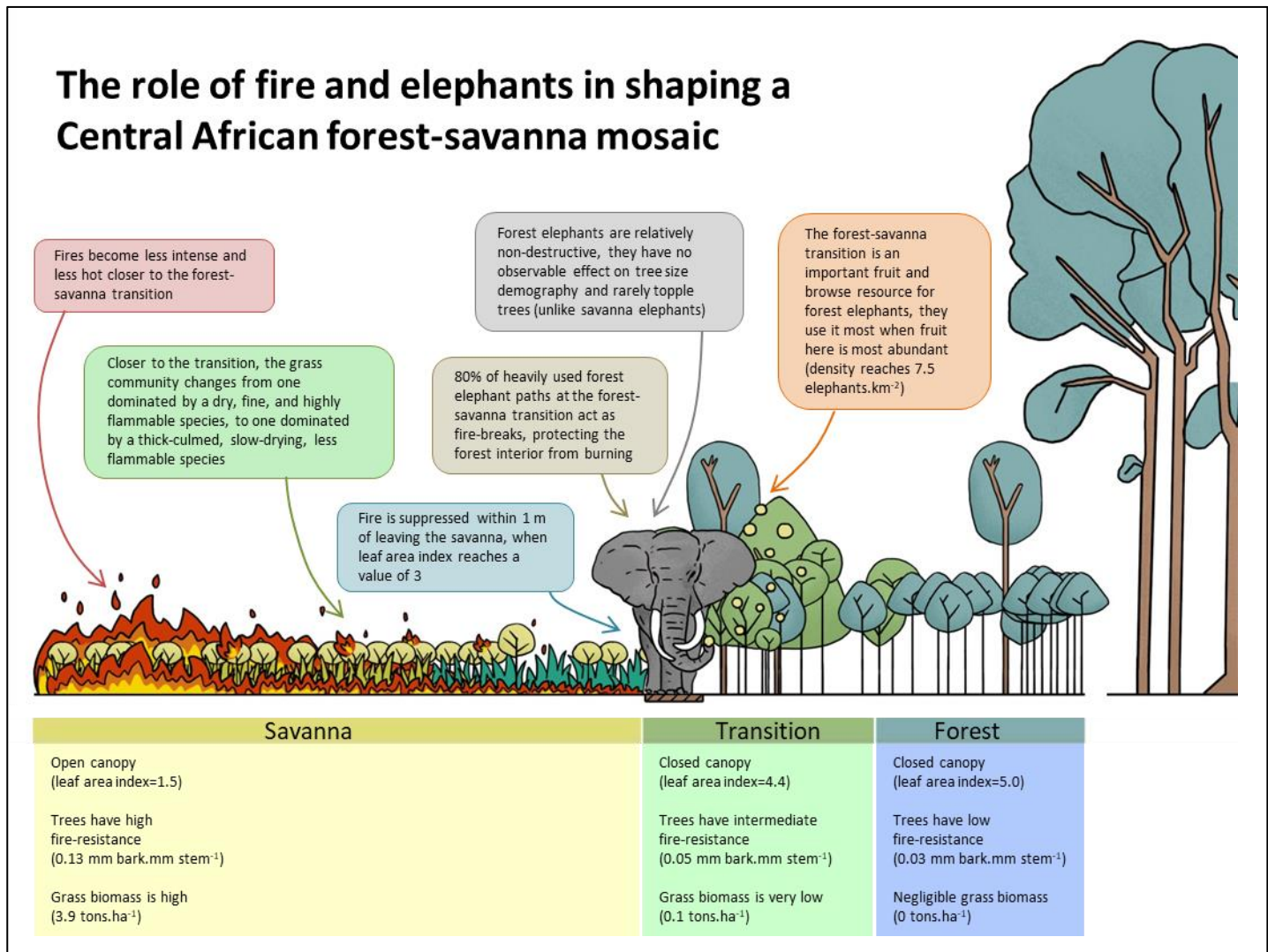


Figure 8.1: A diagram summarising the findings of the thesis.

8.2 Synthesis

This thesis has shown how the forest-savanna transition is being shaped by two major consumers: fire and forest elephants.

This work began by demonstrating how fire is a key determinant of transition vegetation dynamics. It first showed, in **Chapter 5**, how the contrasting fire regimes of forest and savanna interact with one another at the transition, and described the interacting mechanisms that reinforced the fire-suppressing nature of the forest and allowed it to co-exist with fire-promoting savanna. This thesis went on to show, in **Chapter 6**, that the unique tree community had developed at the forest-savanna transition. This tree community was the direct result of the fire suppressing mechanisms this study demonstrated, which create a narrow but widespread niche within mosaicked landscapes. These findings implied that the transition vegetation community, and by association the mosaicked landscape and its fire regime, are ancient. The role of fire in structuring the forest-savanna transition therefore relatively clear: fire-mediated mechanisms facilitate forest and savanna co-existence, and have done so for a very long time.

In addition to giving insight into the past, these findings have important conservation implications for the future. Fire can be a difficult management intervention to promote politically, for example negative attitudes towards fire have led to fire suppression

policies that have wreaked havoc on Brazilian savannas by allowing widespread forest encroachment (Durigan & Ratter, 2016). In the current times of changing climate and fire regimes (Andela *et al.*, 2017), and increasing forest encroachment and savanna loss (Bond & Midgley, 2000; Kgope *et al.*, 2009; Moncrieff *et al.*, 2014; Stevens *et al.*, 2017), changing such negative attitudes towards fire is key. This work highlighted the importance of fire in tropical savannas and helped to frame it as a positive enhancer of ecosystem services rather than a negative destructive force. It did this by showing that the forest edge was resistant to burning and that its interior was protected through multiple interactive mechanisms; thus fire suppression in the adjacent savanna was unnecessary.

This work then went on to explore how forest elephants may have interacted with the effects of fire. The results presented in **Chapter 7** allowed direct investigation of how well some of the commonly accepted truths about savanna elephants apply to forest elephants. Most interestingly, it demonstrated how forest elephants were notably distinct from savanna elephants in their ability to structure vegetation. Forest elephants were shown to be significantly less destructive than savanna elephants. Previous work has implied this (Terborgh *et al.*, 2016), but did not resolve whether this was an innate difference in forest elephant ecology, or simply the result of the canopy layer of their habitat being comprised of trees too big to be pushed over. This study started to solve this mystery, and showed that forest elephants were non-destructive compared to savanna elephants, even when an abundance of elephant-size trees are available to be

pushed over. This work therefore implies that tree uprooting is a learned sexual-social behaviour unique to savanna elephants (Midgley *et al.*, 2005), a hypothesis that warrants further comparative study.

The way forest elephant paths acted as fire-breaks was only possible because the conditions created by the forest-savanna transition meant that the fire was already less intense and less hot by the time it reached the path, and thus could be stopped by this introduced discontinuity in the fuel layer. This demonstrated the complementary role that fire and forest elephants play in stabilising forest and savanna distribution. However, it also begged the question of what would happen if there were no elephant paths. This study was not able to investigate transitions without substantial elephant paths, as these are very rare in the study site. However forest elephants are rare or absent in most other parts of Africa, and so there are multiple locations where comparative studies could, and should, be made.

Such comparative studies are vital as elephants have been suggested to be crucial for maintaining open savannas in the face of encroaching forests (Owen-Smith, 1987; Asner & Levick, 2012). However, the findings of this work highlighted the inability of forest elephants to do this, flagging potential issues with work that apply the behaviour of savanna elephants to all elephants across African landscapes. Furthermore, savanna elephants may also not be the most appropriate mega-herbivore to be using to predict the role that animals of the past played in structuring ecosystems (e.g. stegomastodons

in Pleistocene South America: Doughty *et al.*, 2015), and perhaps a more nuanced approach is needed.

Currently, consideration of the effects of animals is largely absent from some of the most influential research about fire and forest-savanna transitions, perhaps as a consequence of the prevailing framework having been developed in South America where mega-fauna are mostly extinct (Hoffmann *et al.*, 2012). The findings of this study showed how these frameworks on fire and transitions need to be amended for an African context, to incorporate the effects of abundant mega-fauna that still roam the savannas here, as has already been done for fire and the savanna interior (Archibald & Hempson, 2016).

This thesis presented a detailed study of one landscape, and although other tropical mosaics may well exhibit similar patterns, these findings remain to be tested. The methods used in this research are able to be readily replicated, the majority of them at minimal financial cost, and the findings of this work would be greatly enhanced if multi-site comparison could be made. Of particular interest would be to see if other tropical forest-savanna transitions are also intermediately fire-resistant and composed of a distinct suite of species, as is suggested to be the case in South America (Biddulph & Kellman, 1998) and southern Africa (Charles-Dominique *et al.*, 2018). If this was found to be the case, the evolutionary history of these species would be fascinating to explore, for example to clarify whether they are relics of previously expansive dry forests, or if

they the precursor to some of the more arid savanna tree species. It would also be interesting to assess whether the paths of other animal species are able to act as fire-breaks in the same way as forest elephant paths. This has been shown for leaf cutter ants in Brazil (Carvalho *et al.*, 2012) however remains to be explored for non-elephant mammal species across the tropics. A better understanding of the distinct roles that different animals play in structuring tropical landscapes through evolutionary time could be established through comparison between sites where megafauna are long extinct (e.g. South America) vs sites where the extinction is relatively recent and only local (e.g. in Africa).

8.3 References

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