



**HAL**  
open science

## **Monitoring vegetation dynamics with open earth observation tools: the case of fire-modulated savanna to forest transitions in Central Africa**

Le Bienfaiteur Sagang Takougoum, Pierre Ploton, Gaëlle Viennois, Jean-Baptiste Féret, Bonaventure Sonké, Pierre Couteron, Nicolas Barbier

### ► **To cite this version:**

Le Bienfaiteur Sagang Takougoum, Pierre Ploton, Gaëlle Viennois, Jean-Baptiste Féret, Bonaventure Sonké, et al.. Monitoring vegetation dynamics with open earth observation tools: the case of fire-modulated savanna to forest transitions in Central Africa. *ISPRS Journal of Photogrammetry and Remote Sensing*, 2022, 188, pp.142-156. <10.1016/j.isprsjprs.2022.04.008>. <hal-03649011>

**HAL Id: hal-03649011**

**<https://hal.inrae.fr/hal-03649011v1>**

Submitted on 22 Jul 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY-NC 4.0 - Attribution - Non-commercial use - International License

1 Title:

2 Monitoring vegetation dynamics with open earth observation tools: the case of fire-modulated  
3 savanna to forest transitions in Central Africa

4 Authors:

5 Sagang Takougoum Le Bienfaiteur<sup>1,2,3,4</sup>, Ploton Pierre<sup>2</sup>, Viennois Gaëlle<sup>2</sup>, Féret Jean-Baptiste<sup>5</sup>,  
6 Sonké Bonaventure<sup>1,3</sup>, Couteron Pierre<sup>2</sup>, Nicolas Barbier<sup>2</sup>.

7 <sup>1</sup>Plant Systematics and Ecology Laboratory (LaBosystE), Department of Biology, Higher  
8 Teachers' Training College, University of Yaoundé I, Yaoundé. P.O. Box 047, Cameroon.

9 <sup>2</sup>AMAP, Univ Montpellier, IRD, CNRS, INRAE, CIRAD, 34394 Montpellier, France.

10 <sup>3</sup>International Joint Laboratory DYCOFAC, IRD-UYI-IRGM, Yaoundé. P.O. Box 1857,  
11 Cameroon.

12 <sup>4</sup>Institute of Agricultural Research for Development, Njombe, Cameroon.

13 <sup>5</sup>TETIS, Irstea, CIRAD, CNRS, Univ Montpellier, Montpellier, France.

14 Correspondence:

15 Sagang T. Le Bienfaiteur

16 [sangang.bienfaiteur@yahoo.fr](mailto:sangang.bienfaiteur@yahoo.fr)

17 Abstract

18 Woody encroachment and forest progression are widespread in forest-savanna transitional areas  
19 in Central Africa. Quantifying these dynamics and understanding their drivers at relevant spatial  
20 scales has long been a challenge. Recent progress in open access imagery sources with  
21 improved spatial, spectral and temporal resolution combined with cloud computing resources,  
22 and the advent of relatively cheap solutions to deploy laser sensors in the field, have  
23 transformed this domain of study. We present a study case in the Mpem & Djim National Park  
24 (MDNP), a 1,000 km<sup>2</sup> protected area in the Centre region of Cameroon. Using open source  
25 algorithms in Google Earth Engine (GEE), we characterized vegetation dynamics and the fire  
26 regime based on Landsat multispectral imagery archive (1975-2020). Current species  
27 assemblages were estimated from Sentinel 2 imagery and the open source `biodivMapR`  
28 package, using spectral dissimilarity. Vegetation structure (aboveground biomass; AGB) was  
29 characterized using Unmanned Aerial vehicle (UAV) LiDAR scanning data sampled over the  
30 study area. Savanna vegetation, which was initially dominant in the MDNP, lost about 50% of  
31 its initial cover in less than 50 years in favor of forest at an average rate of ca. 0.63%.year<sup>-1</sup> (6  
32 km<sup>2</sup>.year<sup>-1</sup>). Species assemblage computed from spectral dissimilarity in forest vegetation  
33 followed a successional gradient consistent with forest age. AGB accumulation rate was 3.2  
34 Mg.ha<sup>-1</sup>.year<sup>-1</sup> after 42 years of forest encroachment. In savannas, two modes could be  
35 identified along the gradient of spectral species assemblage, corresponding to distinct AGB  
36 levels, where woody savannas with low fire frequency store 40% more AGB than open grassy

37 savannas with high fire frequency. A fire occurrence every five year was found to be the fire  
38 regime threshold below which woody savannas start to dominate over grassy ones. A fire  
39 frequency below that threshold opens the way to young forest transitions. These results have  
40 implications for carbon sequestration and biodiversity conservation policies. Maintaining  
41 savanna ecosystems in the region would require active management actions to limit woody  
42 encroachment and forest progression, in contradiction with global reforestation goals.

43 Keywords: Forest-savanna transition, Google Earth Engine, fire, UAV-LiDAR, aboveground  
44 biomass, species assemblage.

## 45 1. Introduction

46 Understanding long term ecosystem dynamics, their drivers and effects on ecosystem state at a  
47 given point in time is a major challenge in ecology (Bastin et al., 2019; Estes et al., 2018;  
48 Valentini et al., 2014). Transitional areas between tropical forests and savannas form a  
49 widespread ecotone separating two of the most productive terrestrial ecosystems (Beer et al.,  
50 2010). Within a rather large domain of environmental conditions, both systems constitute  
51 alternative stable states (Hirota et al., 2011), each one generating the feedback loops ensuring  
52 its own maintenance. However, under all sufficiently wet climates where annual rainfall  
53 exceeds  $\approx 650$  mm, water availability is sufficient for woody canopy closure but disturbance  
54 mechanisms inherent to savannas, notably fire suppress trees and allow for their coexistence  
55 with grasses (Aleman et al., 2020; Sankaran et al., 2005; Staver et al., 2011b, 2011a). This  
56 balance has likely been shifted by ongoing climate change, as long term woody encroachment  
57 and forest progression into savannas have been described for forest-savanna ecotones (FSE) in  
58 Central Africa (Mitchard and Flintrop, 2013; Stevens et al., 2017, 2016; Youta-Happi et al.,  
59 2003).

60 These dynamics induce profound changes in ecosystem function and composition (Oliveras and  
61 Malhi, 2016; Zeng et al., 2013). Although tropical forests benefit from a good public image  
62 because of their high tree diversity (Sosef et al., 2017; Sullivan et al., 2017), aboveground  
63 carbon stocks (Mitchard et al., 2011; Santoro et al., 2021; Sullivan et al., 2017) and attributed  
64 aesthetic value (Niklas and Spatz, 2010; Panshin and De Zeeuw, 1980), they do not replace the  
65 specific fauna and flora of savannas, not to mention savanna's consequent belowground carbon  
66 stock (Blaum et al., 2007; Buisson et al., 2019; Sirami et al., 2009; Veldman et al., 2015).  
67 Moreover it will likely take centuries to attain a successional stage giving the newly formed  
68 forests a level of biomass and a floristic composition typical of old growth forests (Rüger et al.,  
69 2020). Conversely, recovering a typical grassland/savanna structure and composition, exempt

70 of invasive exotic species, may prove very difficult (Cava et al., 2020, 2018; Machida et al.,  
71 2021). Woody encroachment and forest progression at the expense of savannas is thus neither  
72 desirable from the viewpoint of climate change mitigation policies, like the Bonn Challenge  
73 and the Reducing Emissions from Deforestation and Degradation (REDD+) initiative nor from  
74 that of the biotope conservation or restoration agenda (Abreu et al., 2017; Dinerstein et al.,  
75 2020; Thomas et al., 2013). The main questions a manager needs to answer are therefore: 1/  
76 what are the tipping points for bush encroachment and forest transition in the current climatic  
77 conditions, considering the main mitigating tool at his disposal: the fire regime; 2/ what are the  
78 consequences of past ecosystem dynamics on the current distribution of carbon and  
79 biodiversity.

80 If field data provide an irreplaceable level of detail, notably for the characterization of  
81 vegetation structure and composition, they rarely provide the spatial and temporal hindsight  
82 necessary to understand ecosystem dynamics at a relevant scale. Currently available remote  
83 sensing approaches bring complementary and unique answers to the above questions. Thanks  
84 to its potential capacity for systematic observations at various scales, remote sensing (RS) offers  
85 practical and economical means to study vegetation cover changes over several decades,  
86 especially for large areas (Xie et al., 2019). Long term satellite imagery archives are now  
87 available globally, at a relatively high spatial and temporal resolution (Landsat, and now  
88 Sentinel 2) as well as open-access storage and computing facilities, such as the Google Earth  
89 Engine (GEE) computing platform (Gorelick et al., 2017). With these game-changing tools it  
90 is easy to monitor the transition from one biome to another, especially those with distinct  
91 spectral signatures as forest and savanna (DeVries et al., 2015; Dutrieux et al., 2015), at a  
92 meaningful spatiotemporal scale (Banskota et al., 2014). Mapping fire scars, which leave  
93 conspicuous and relatively long lasting marks in the landscape is also relatively easy (Daldegan  
94 et al., 2019, 2014; Liu et al., 2018) even using imagery with imperfect radiometric and  
95 atmospheric corrections.

96 Characterizing more subtle changes in species composition or vegetation structure (biomass),  
97 requires other data sources and algorithms. The Sentinel 2 constellation, carrying optical  
98 sensors of improved temporal, spectral and spatial resolutions have shown interesting prospects  
99 for detecting compositional gradients in the vegetation, notably in terms of the abundance of  
100 broad functional/optical plant types (Grabska et al., 2019; Ma et al., 2019). The unsupervised  
101 method for spectral species diversity analysis proposed by Féret and Asner (2014) for instance,  
102 provides preliminary assessment of such compositional gradients, loosely referred to as spectral

103 dissimilarity gradient (analogous to  $\beta$ -diversity), which could prove useful to detect sharp  
104 compositional changes occurring within transitioning pixels at the forest-savanna boundary,  
105 notably. However the capability of passive optical sensors to discriminate aboveground  
106 biomass (AGB) gradients is limited, especially in dense forests where AGB density frequently  
107 exceeds 200 Mg ha<sup>-1</sup> (Jha et al., 2020; Sagang et al., 2020). Airborne LiDAR has become the  
108 reference method for the characterization of vegetation structure (Duncanson et al., 2021), but  
109 cost can be prohibitive. The arrival on the market of low-cost LiDAR scanners, which can be  
110 carried on Unmanned Aerial Vehicles (UAV), is now democratizing this crucial tool for  
111 vegetation structure assessment in tropical countries.

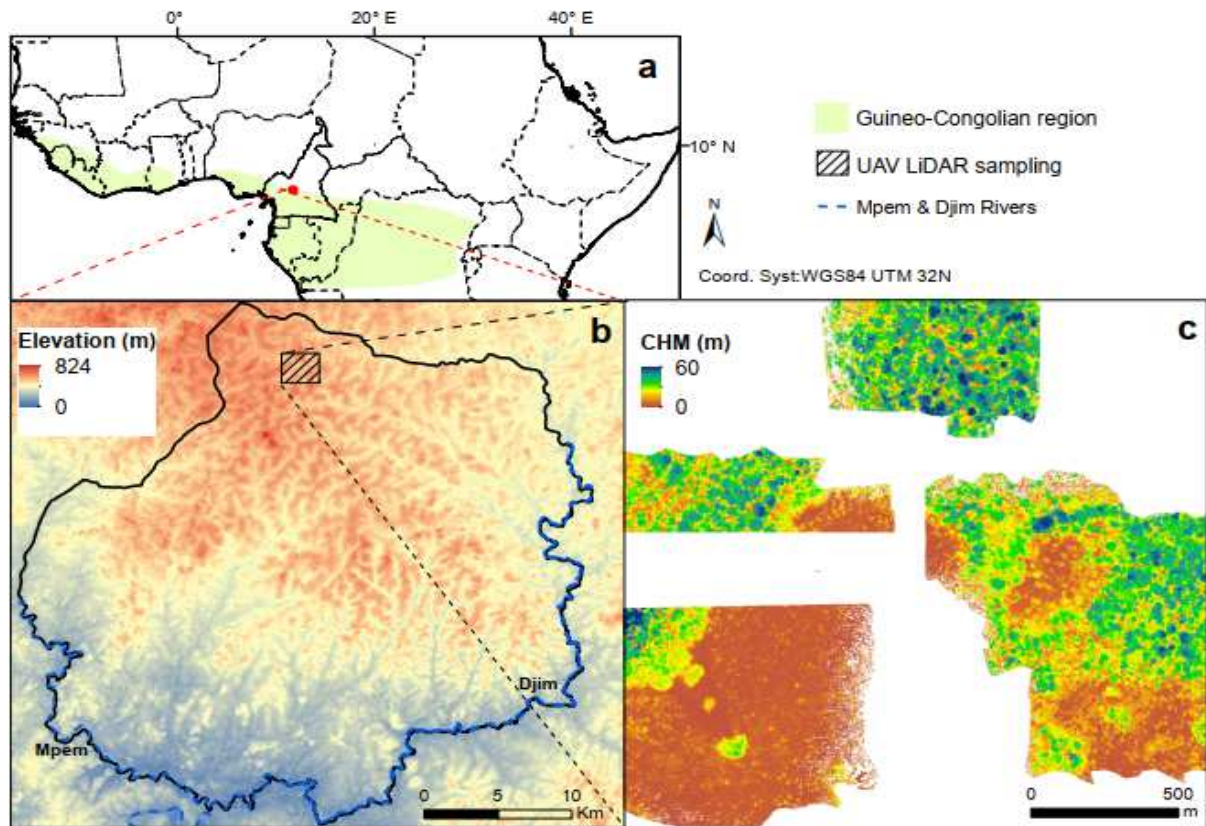
112 The objective of this study is twofold: the first aim is to advance our understanding of the  
113 dynamics and drivers of forest-savanna transitions, and their consequences in terms of above-  
114 ground carbon storage and tree species diversity. The second aim is to provide land managers  
115 (conservationists, as well as infrastructure investors in need for science-based compensation  
116 strategies) with reliable open tools allowing them to quantify the impact of different  
117 management strategies on ecosystem dynamics. To this end we combined the historical  
118 perspective on forest-savanna transition and fire regime provided by the Landsat archive to  
119 current day maps of spectral  $\beta$ -diversity and UAV-LiDAR derived AGB maps to obtain a  
120 coherent framework that could be generalized to similar transition areas for supporting and  
121 complementing traditional field campaigns. Our underlying hypotheses were the following: 1/  
122 changes in fire regimes induce woody encroachment and forest transition below a specific fire  
123 frequency threshold; 2/ forest transition age results in changes in species composition and AGB  
124 detectable using integrative remote sensing data.

## 125 2. Methods

### 126 2.1. Study area

127 The study was conducted within the Mpem & Djim National Park (MDNP) located in a forest  
128 savanna mosaic of the Guineo-Congolian transitional area in the Centre region of Cameroon  
129 (Fig. 1). The MDNP was established in 2004 and covers an area of ca. 1,000 km<sup>2</sup>. The area is  
130 under the influence of an equatorial climate of Guinean type (Djoufack, 2011), which is hot and  
131 humid with an average annual temperature of 25°C. Mean annual rainfall is 1,500 mm  
132 (Djoufack, 2011), with a rainfall distribution characterized by a five months dry season  
133 (November-March), during which the monthly rainfall is less than 70 mm per month. Soils are  
134 deep, mostly ferralitic red and yellow with a complete hydrolysis of minerals from granite-  
135 gneissic basement caused by warm rains (Santoir and Bopda, 1995). Savannas in the MDNP

136 are interspersed by semi-deciduous forests or gallery forests along watercourses (Letouzey,  
137 1985; Youta-Happi et al., 2003; Youta-Happi and Bonvallot, 1996).

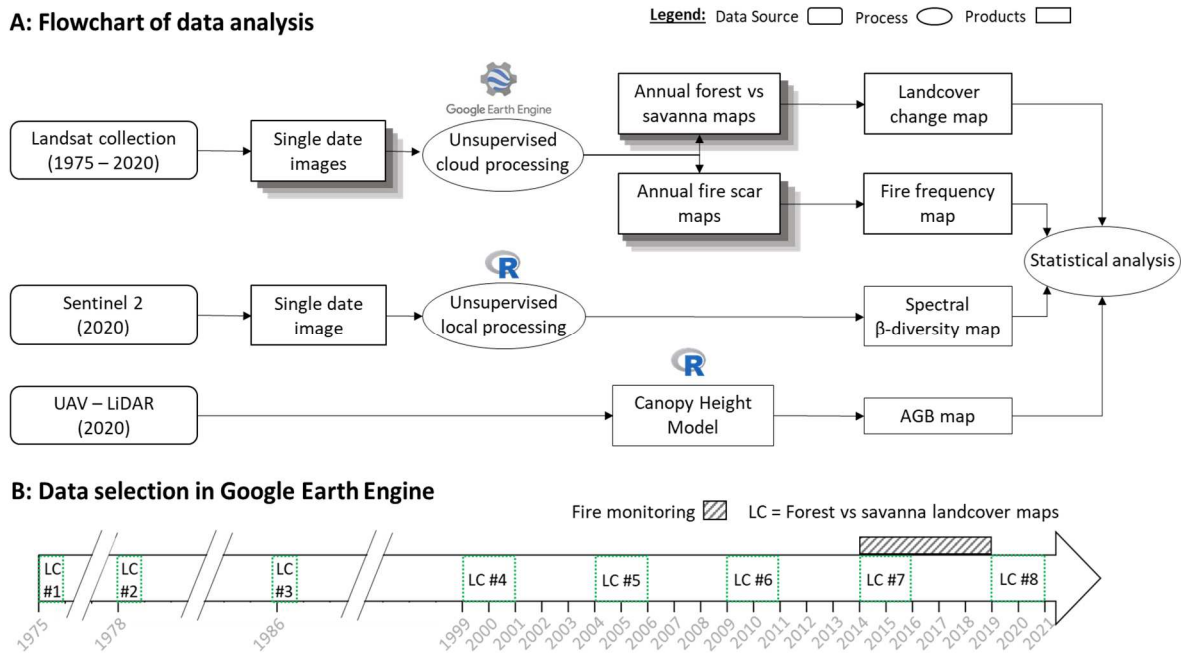


138 Fig. 1: Study area. (a) Location (red point) within the Guineo-Congolian transitional area (light  
139 green) and (b) boundaries of the Mpem & Djim National Park (full black polygon) following  
140 Mpem and Djim rivers (overlapping blue dashed lines). (c) UAV LiDAR-derived Canopy  
141 Height Model (CHM) at a 1m spatial resolution collected in the area (low areas in orange and  
142 higher ones in dark blue).  
143

144 Tree species dominating young colonizing forests in direct contact with savanna are *Alchornea*  
145 *cordifolia* (Schumach. & Thonn.) Müll.Arg., *Albizia zygia* (DC.) J.F.Macbr., *Albizia*  
146 *adianthifolia* (Schumach.) W.Wight and *Albizia ferruginea* (Guill. & Perr.) Benth., *Macaranga*  
147 *spinosa* Müll. Arg., while emergent trees species such as *Mansonia altissima* (A.Chev.)  
148 A.Chev., *Terminalia superba* Engl. & Diels. and *Triplochiton scleroxylon* K. Schum., dominate  
149 in older forest successions. A distinct set of mostly pyrophilous tree species characterizes the  
150 savanna, mainly: *Annona senegalensis* Pers., *Bridelia ferruginea* Benth., *Crossopterix*  
151 *febrifuga* (Afzel. ex G.Don) Benth., *Hymenocardia lyrata* Tul., *Lannea kerstingii* (Enql.) K.  
152 Krause., *Terminalia glaucescens* Planch. ex Benth., *Piliostigma thonningii* (Schumach.) Milne-  
153 Redh., *Psorospermum febrifugum* Spach.. The grass cover is dominated by species of the  
154 Poaceae family: *Hyparrhenia diplandra* (Hack.) Stapf., *Hyparrhenia rufa* (Nees.) Stapf.,  
155 *Pennisetum purpureum* Schumach. and *Andropogon spp.* (Youta-Happi, 1998).

156 2.2. Workflow of the analysis

157 The general workflow of the analysis is shown in Fig. 2 and can be grouped into three chunks.



158  
159 Fig. 2: Methodological workflow used in this study (A) and temporal domains covered by  
160 spaceborne data for vegetation and fire monitoring (B).

161 The first chunk includes the mapping of historical forest-savanna dynamics over the study area.  
162 The second chunk includes the mapping of the spatial distribution of fire frequency, and the  
163 third chunk includes the mapping of present-day vegetation diversity and biomass levels  
164 (Section A of Fig. 2). We used the GEE platform to access and preprocess (i.e., clouds and  
165 cloud shadows filtering) all spaceborne optical data. To map the historical forest-savanna  
166 dynamics, we leveraged Landsat archives from 1975 to 2020 and used automated  
167 (unsupervised) processing routines in GEE to generate a landcover change map (Section B of  
168 Fig. 2; see section 2.3 for a full description of the method). To assess the effect of fire on forest-  
169 savanna dynamics, a fire frequency map based on Landsat archives from 2014 to 2019 was  
170 generated using a semi-automated classification (see section 2.4). Fire regimes derived from  
171 Landsat were also compared to those derived from the MODIS burned area product. The  
172 assessment of present-day vegetation diversity gradients in the MDNP vegetation was based on  
173 a Sentinel 2 image from 2020, following the unsupervised spectral diversity analysis described  
174 in Féret and Boissieu (2020, see section 2.5.1). Last, we used UAV-borne LiDAR scanning  
175 (UAV-LS) data acquired in 2019 to map present-day vegetation biomass stocks (see section  
176 2.5.2).

## 177 2.3. Mapping landcover changes

### 178 2.3.1. Temporal aggregation

179 There are three common strategies to process archive imagery collections for landcover  
180 monitoring (Banskota et al., 2014; Gómez et al., 2016; Nguyen et al., 2020). The simplest one  
181 consists in using individual, high quality cloud free scenes. In tropical, frequently cloudy  
182 conditions, this approach can prove difficult. The second alternative, where sufficient archive  
183 is available, is to generate temporal aggregates around pivot dates, allowing the use of  
184 information contained in partially cloudy images, at the expense of a reduced precision on the  
185 timing of detected changes (Hansen et al., 2013). Finally for dense temporal time series, pixel-  
186 level temporal analysis can be performed (Hermosilla et al., 2015) to optimize the use of the  
187 available data and the temporal precision of event detections. In this study, we were interested  
188 in the temporal hindsight, and therefore had to deal with very sparse series prior to the launch  
189 of Landsat 7 and 8 (and due to the long absence of ground stations in Africa). The third approach  
190 was thus excluded. Moreover, a major difficulty lies in inter-image heterogeneity induced by  
191 directional and atmospheric effects, although correction models are now routinely applied to  
192 recover bottom-of-atmosphere reflectance (such as the LEDAPS algorithm for Landsat 5 to 8  
193 TM, ETM and OLI data collections produced by USGS, 2020). To work around the spectral  
194 stability issue, different approaches can be taken for image classification, mirroring the  
195 temporal aggregation choices summarized above: (i) train a classifier for each image, either  
196 manually, or automatically, if the landcover classes are sufficiently distinct, (ii) use the time  
197 redundancy (i.e. the similarity between successive temporal version of the pixels) to stabilize  
198 the signal at the scene level by time-aggregating a sufficient number of images or classifications  
199 (Souverijns et al., 2020), (iii) use the time redundancy to stabilize the signal at pixel level, to  
200 classify stable landcover classes between major breakpoint events (Verbesselt et al., 2010).

### 201 2.3.2. Automated-unsupervised landcover mapping

202 We developed an automated-unsupervised landcover mapping pipeline in GEE. Performing  
203 landcover classification directly on GEE is appealing in that it alleviates data transfer between  
204 the GEE platform and the operator. Besides, the use of unsupervised classification - which does  
205 not require human inputs for the processing of each single image - together with the massive  
206 computational capabilities of GEE, offers prospects for large-scale landcover mapping,  
207 provided that the unsupervised algorithm can accurately predict the landcover classes of  
208 interest. In the very convenient case of forest-savanna mosaics, the spectral contrast between

209 the two classes is so important, with highly bi-modal radiometric distribution in most spectral  
210 bands (see Appendix A). Therefore landcover classification can easily be performed  
211 automatically at the individual image level. This is true as long as clouds, cloud shadows and  
212 strong haze can be masked, as well as very distinct landcover classes such as water bodies and  
213 urban areas. Preliminary testing suggested that a simple k-means algorithm with two clusters  
214 successfully separated the two classes. On each image passing through the pipeline, we thus  
215 randomly selected 10,000 pixels to train a k-means algorithm and predicted the class of each  
216 remaining pixel using the NDVI. K-means classification was applied on single date images  
217 acquired before 1999 to generate the first three landcover maps (LC # 1 to 3 in section B of Fig.  
218 2). For images acquired after 1999, K-means classifications of individual images were  
219 aggregated within the same 2-years intervals as in section 2.3.2 (LC # 4 to 8), by keeping the  
220 modal class of each pixel across images within time intervals. This resulted into eight binary  
221 forest (value of 1) and savanna (value of 0) maps.

### 222 2.3.3. Generating landcover change map

223 The eight forest-savanna maps were stacked to generate a transition map representing landcover  
224 change (or vegetation dynamics) between the years 1975 and 2020. Forests pre-existing in 1975  
225 were grouped in a single class of forests older than 45 years (stable forests). Pixels that  
226 witnessed a permanent change from savanna (0) to forest (1) or the opposite were classified as  
227 “forest gain” or “forest loss” respectively and the year of detected transition was recorded.  
228 Pixels that underwent more than one transition throughout the monitoring period (i.e., 4% of  
229 the cases) were classified as “unstable dynamics” and discarded from the analysis.

### 230 2.3.4. Validation of landcover and landcover change maps and estimation of the area of 231 land change

232 To assess the accuracy of landcover and landcover change maps and estimate the area of land  
233 change, we followed good practices guidelines detailed in Olofsson et al. (2014). In particular,  
234 the estimation of landcover maps accuracy was made using reference samples selected by  
235 stratified random sampling. For each binary forest-savanna map, 50 pixels were randomly  
236 drawn from each stratum and pixels’ label (i.e. forest or savanna) was assigned by visual  
237 interpretation using the Landsat image of the year corresponding to the classification. The set  
238 of reference samples was then used to generate a confusion matrix and derive accuracy statistics  
239 (i.e. producer, user and overall accuracy), as described in section 4.3 of Olofsson et al. (2014).

240 The landcover change map was evaluated by assessing the accuracy of the dominant classes  
241 throughout the study period, namely stable forests (i.e., 2020's forests existing since 1975 or  
242 earlier), stable savannas, and forest gain (i.e., forests that appeared between 1975-2020). While  
243 forest loss (i.e., forests that transitioned to savannas between 1975-2020) was also observed in  
244 the landcover change map, it only concerned 0.2% of the pixels and was therefore discarded  
245 from the analysis. We randomly drew 100 pixels from each stable class and 200 pixels in the  
246 forest gain class, and followed the same procedure as for the binary maps to compute accuracy  
247 statistics.

248 To estimate the area of forest gain, we used two methodological approaches. The first approach  
249 consisted in simply counting pixels classified as "forest gain" in the landcover change map (i.e.,  
250 so-called pixel-counting method, Waldner and Defourny, 2017) from which an area estimate  
251 could be derived. To warrant the unbiasedness of the estimate and assess the uncertainty around  
252 this estimate, we also followed the approach prescribed in Olofsson et al. (2014), namely using  
253 a probability sample and invoking design-based inference. In practice, the set of reference  
254 samples used to assess the accuracy of the landcover change map, together with the landcover  
255 change map itself, was used to estimate the area of forest gain from the samples.

#### 256 2.4. Mapping fire frequency

257 The unsupervised 2-class clustering approach used to discriminate between forest and savanna  
258 could not be used to map fire scars, despite the conspicuous spectral signature of recent burns.  
259 Although the burn scars remain visible for weeks or more through time, their signature is  
260 progressively attenuating (Appendix B) and many images may not display scars. For the same  
261 reason, temporal image aggregates are useless, as fire scars are too transitory. We therefore  
262 needed to turn to a more traditional approach, based on a fixed spectral threshold applied to  
263 each image in the collection. Due to the sparsity of image series acquired before 1999 and the  
264 failure in the scan line corrector of Landsat 7 we limited the fire frequency analysis to Landsat  
265 8 as from jan. 2014 to dec. 2018 before LC #8 (5 years; see Fig. 2B).

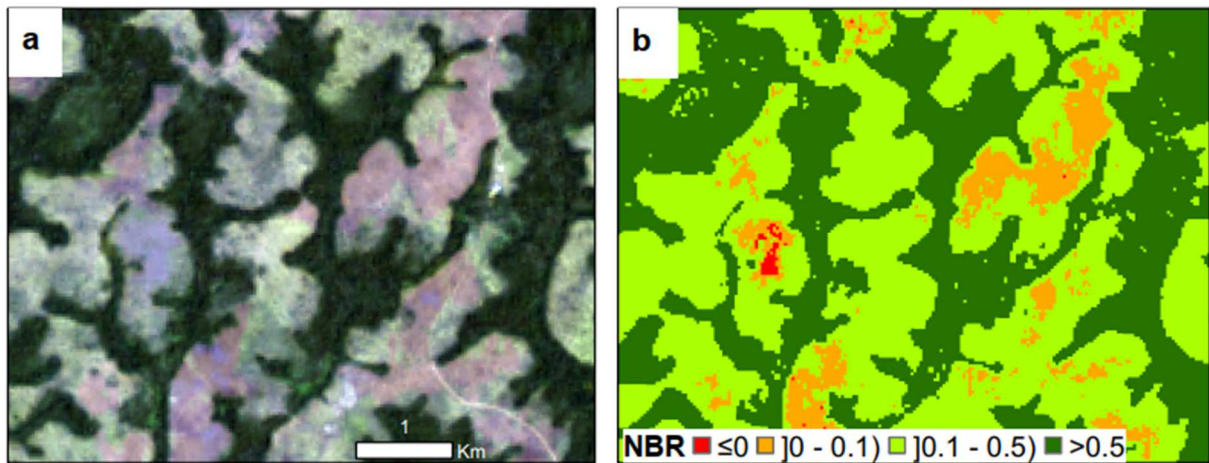
##### 266 2.4.1. Mapping fires scars

267 Amongst the numerous vegetation indices used to characterize fire occurrence, the Normalized  
268 Burn Ratio (NBR, Key and Benson, 2003; Fig. 3) has gained consideration for detecting burn  
269 scars left after a fire (Escuin et al., 2008; Kane et al., 2014; Miller and Thode, 2007; Sunderman  
270 and Weisberg, 2011). The NBR index (equation 1) is calculated using reflectance data from

271 passive optical sensors, especially the near infrared (NIR) and Shortwave infrared (SWIR)  
272 bands:

273 
$$NBR = \frac{(NIR-SWIR)}{(NIR+SWIR)} \quad (\text{eq. 1})$$

274 NBR was computed for each pixel and each observation in their respective time series in GEE.  
275 We then adopted a semi-automated approach to map fire scars from the NBR time series. First,  
276 we haphazardly selected one Landsat 8 image with apparent fire scars and visually delineated  
277 polygons on burned and unburned areas in each image. Based on a visual assessment of NBR  
278 distributions in burned and unburned polygons, we fixed an NBR cut-off value of 0.1 to separate  
279 burned ( $NBR < 0.1$ ) and unburned ( $NBR \geq 0.1$ ) pixels in the entire image collection (see  
280 Appendix B-a). This threshold of 0.1 was confirmed when observing the NBR variation with  
281 time (i.e. on other Landsat 8 images) for frequently and rarely burned pixels (Appendix B-b),  
282 which showed the progressive fading of fire scars' influence on pixel spectral properties. For  
283 each pixel, the result of this classification process was thus a time series - hereafter referred to  
284 as the fire scar time series - with observations classified as burned (presence of fire scar) or  
285 unburned (absence of fire scar) and featuring, for each observation, the associated image  
286 acquisition date.



287  
288 Fig. 3: Example of fire scar discrimination from the Normalized burn ratio (NBR). (a) RGB  
289 true colour composite of a forest-savanna landscape from Landsat 8  
290 (LC08\_186056\_20191130). (b) NBR of the same area highlighting burn scars in red and orange  
291 with photosynthetically active savanna in light green and forest vegetation in darkgreen.

#### 292 2.4.2. Quantifying fire frequency

293 We quantified the fire frequency by computing a Fire Frequency Index (FFI) from the fire scar  
294 time series. To account for the irregular distribution of spaceborne observations within and  
295 among years resulting from the filtering of cloudy or shadowed observations, we first

306 aggregated the information contained in pixels' fire scars time series into yearly observations.  
307 For a given pixel a year was considered as a "burned year" when the pixel was classified as fire  
308 scar for at least two consecutive observations. The FFI for a pixel was then computed as the  
309 ratio between the numbers of "burned years" over the total number of years in the fire  
300 monitoring period.

#### 301 - Comparing Landsat- and MODIS-derived fire frequencies

302 The MODIS burned area monthly product (MCD64A1.006 Collection 6) at 500 m resolution  
303 (Boschetti et al., 2019) is a reference data source that we used for the sake of comparison with  
304 fire frequencies derived from Landsat. We computed FFI values of all burned pixels from  
305 MODIS burned area monthly product in the 2014-2018 fire monitoring period, and compared  
306 the distribution of areas (in km<sup>2</sup>) in each FFI class to the distribution derived from Landsat. The  
307 comparison aimed at assessing the interest of increased spatial resolution (i.e., 30 vs 500 m) for  
308 our understanding of forest-savanna dynamics.

### 309 2.5. Mapping current vegetation diversity and structure

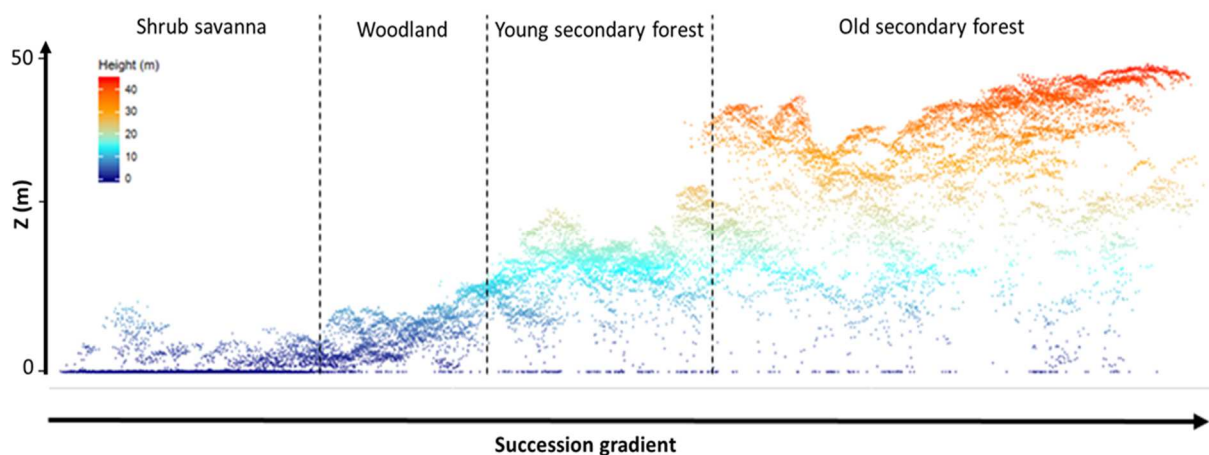
#### 310 2.5.1. Spectral composition gradients

311 The increase in spatial and spectral resolutions of open-access spaceborne images offers  
312 interesting prospects for the monitoring of biodiversity from space. The link between remotely  
313 sensed spectral information and ecological indicators of diversity was formulated by Palmer et  
314 al., (2002) and referred to as the spectral variation hypothesis (SVH). This hypothesis initially  
315 related the spatial variability in spectral information to environmental heterogeneity, and was  
316 used in various contexts in order to provide an estimation of species diversity (Rocchini et al.,  
317 2016, 2010). Féret and Asner (2014) developed a method aiming at computing diversity  
318 indicators directly from spectral information in order to compare them to the same diversity  
319 indicators derived from species field inventories, and used dissimilarity metrics as a proxy for  
320 tree taxonomic turnover. This methodology implemented in the biodivMapR R package (Féret  
321 and Boissieu, 2020) relies on the assumption that discrimination among species, or groups of  
322 species, can be obtained from the clustering of spectral information. The resulting clusters,  
323 named 'spectral species' by the authors, aim at defining optical types (Ustin and Gamon, 2010)  
324 with an unsupervised procedure. These optical types provide combined information on  
325 functional and taxonomic properties of vegetation. Here, we used this method to assess and map  
326 spectral composition gradients on a cloud free Sentinel 2 image of the dry season (27-01-2020;  
327 T32NQL & T32NRL). Although the analysis was performed on a local computer after

328 retrieving the Sentinel 2 image composite from Google Earth Engine, it is worth noting that  
329 biodivMapR can as well be implemented on the fly using an R interface on the Google cloud  
330 platform, thus alleviating the need for any local image data processing. We processed forest  
331 and savanna pixels separately, using the previously derived 2019-2020 landcover classification  
332 as a mask. Within a given landcover subset (i.e., forest or savanna) an unsupervised k-means  
333 clustering was used to assign individual pixels to spectral species based on their spectral  
334 signatures. Féret and Boissieu (2020) suggested using 40 - 50 spectral species to accommodate  
335 for the high diversity of tropical forests. However, using a large number of spectral species did  
336 not change the overall pattern of spectral composition gradients in our study area, and we thus  
337 set the number of spectral species to 10. The image was then gridded into 30 x 30 m windows  
338 (to match the spatial resolution of the Landsat-derived landcover change map) and the  
339 dissimilarity between each pair of windows was computed using the Bray-Curtis dissimilarity  
340 metric. Principal Coordinate Analysis (PCoA; Legendre and Legendre, 1998) was then applied  
341 on the resulting dissimilarity matrix and the first axis was retained to reflect turn-over in  
342 (spectral) species composition, for either savanna or forest ecosystems.

#### 343 2.5.2. Aboveground biomass

344 LiDAR scanning technology has emerged as the reference approach for mapping variation of  
345 vegetation AGB at landscape scale (Colgan and Asner, 2014; Jha et al., 2020; Sagang et al.,  
346 2020) due to its ability to accurately characterize the vegetation's three-dimensional structure.



347 Fig. 4: Three-dimensional profile of the vegetation structure along a savanna to forest  
348 transitional gradient extracted from the UAV-borne LiDAR scanning data available in the study  
349 area. The profile corresponds to a 14 m thick extract.  
350

351 We used a DJI Matrice 600 UAV to mount a Riegl mini VUX-1 UAV scanner encased in a  
352 YellowScan Vx-20 device and acquired 3D data of the vegetation in 2019. The scanner works  
353 at 100 kHz over 360 degrees, yielding a point location accuracy of 2.5 cm vertically, thanks to

354 differentially corrected DGNS (post-processing with local base station) positions and readings  
355 from an Applanix 20 inertial station (IMU). Flight height was set to 70 m above ground (SRTM;  
356 DTM) level with an average ground speed of 8 m.s<sup>-1</sup>. The scan angle was filtered down to ±  
357 60°, yielding a band swath of 121 m and a 50% overlap between two adjacent flight lines, which  
358 resulted in an average point density of 10.5 points.m<sup>-2</sup>. The UAV-borne sampling was collected  
359 over ≈ 300 ha and was designed to cover a transitional gradient from savannas to the oldest  
360 forest patches of the landscape (Fig. 4). Points were classified into ground and vegetation  
361 returns using progressive morphological filter (pmf) algorithm (Zhang et al., 2003) as  
362 implemented in the classify\_ground() function of the lidR R package (Roussel et al., 2021). To  
363 filter non-ground returns, we ran the pmf algorithm using a sequence of window sizes (from 3  
364 to 12 pixels every 3 pixels) and elevation difference thresholds (from 0.1 to 1.5 every 0.35, see  
365 Zhang et al., 2003 and Roussel et al., 2021 for details on the pmf algorithm and its  
366 implementation in lidR). We applied a continuous normalization of the non-ground point cloud  
367 through the interpolation of the elevation of every single point location using ground points  
368 with the normalize\_height() function of the lidR R package. Interpolation was done using a k-  
369 nearest neighbor approach with an inverse-distance weighting (see Roussel et al., 2021). The  
370 normalized point cloud was used to generate a 1-m canopy height model (CHM), from which  
371 we predicted vegetation AGB at 40-m spatial resolution using a model calibrated in a forest-  
372 savanna mosaic of the same region (equation 2, from Sagang et al., 2020).

$$373 \quad \text{AGB} = 6.27 + 8.52 \times \text{CHM} \quad (\text{eq. 2})$$

374 with AGB in Mg.ha<sup>-1</sup> and CHM in m.

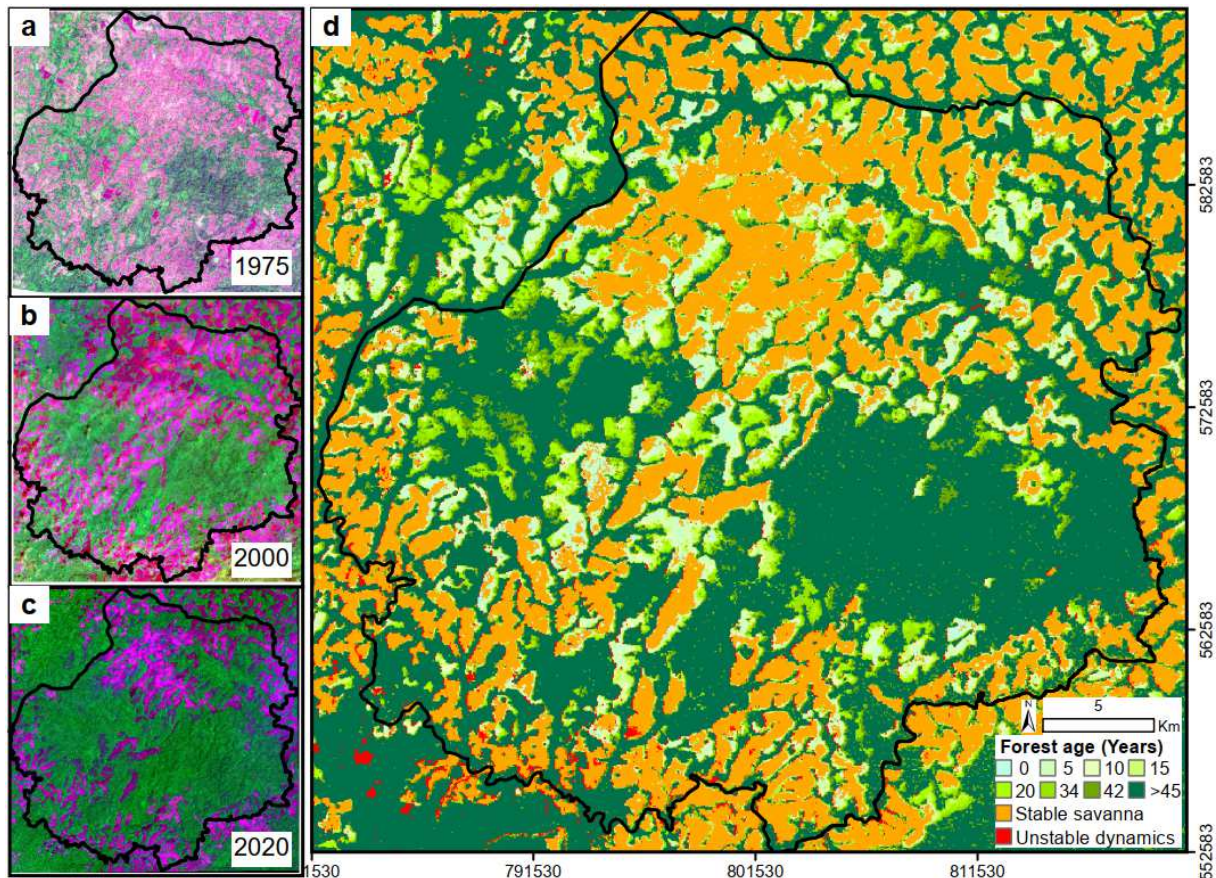
375 Further, we evaluated the rate of AGB uptake for young secondary forests (≤ 20 years; IPCC,  
376 2006) and all the transitory forests (< 45 years; forest that appeared between 1975 and 2020)  
377 by (i) resampling the AGB map from 40-m to the 30-m resolution at which vegetation dynamics  
378 was assessed, and (ii) adjusting a simple linear relationship between predicted AGB and forest  
379 age derived from the forest transition map. All the statistical analyses were done using the R  
380 statistical software (R Core Team, 2018).

### 381 3. Results

#### 382 3.1. Tracking four decades of landcover change trajectory

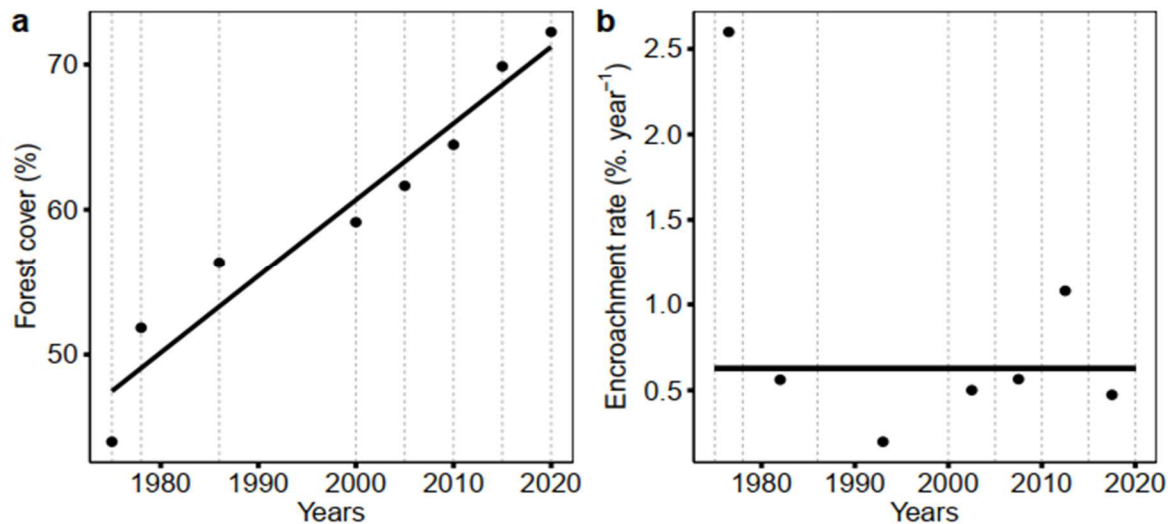
383 Overall accuracies of automated forest-savanna classifications ranged from 85.78% (± 6.26) to  
384 96.85% (± 3.57) with an average of 92.54% (± 4.72, Appendix C). The Landsat 2 acquisition  
385 of dec. 1975 (Fig. 5-a) shows that the MDNP was at that time dominated by savannas (c. 54%

386 of the park area; Fig. 6-a). After four decades of vegetation dynamics (see illustrative panels b  
 387 and c in Fig. 5), the MDNP was, in 2020, dominated by forest (c. 72% of the park area; Fig. 6-  
 388 a). Using binary forest-savanna classifications to assess landcover changes, the automated GEE  
 389 routine suggested a 275 km<sup>2</sup> increase of forest area during the study period, which is consistent  
 390 with the area estimate obtained from reference samples in a design-based inferential framework  
 391 (i.e., 266 km<sup>2</sup> ± 26, Appendix D).



392 Fig. 5: Vegetation transition map of the Mpem & Djim National Park from 1975 to 2020. (a, b,  
 393 c) illustrative Landsat images (RGB composition: Red-NIR-Green) for the years 1975, 2000  
 394 and 2020. Under this RGB composition, forests appear in green and savannas in purple. (d)  
 395 Forest age map derived from the landcover classification at different dates.  
 396

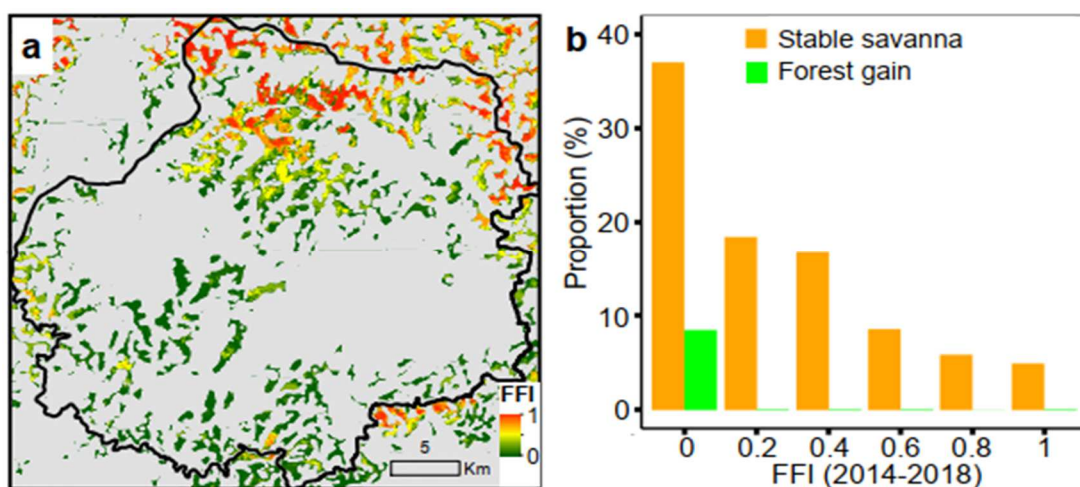
397 The landcover change map depicted a consistent and regular pattern of forest progression into  
 398 savanna (Fig. 6-a) and allowed deducing current forest age (displayed in Fig. 5-d) and average  
 399 rate of forest progression. For instance, a weighted mean of forest encroachment rates obtained  
 400 from successive classifications - using the length of monitoring periods as weights (vertical  
 401 dashed bar in Fig. 6) - yield an average rate of 0.63%.year<sup>-1</sup> or equivalently c. 6 km<sup>2</sup>.year<sup>-1</sup> (Fig.  
 402 6-b). Since 1975, the MDNP has thus lost about 50% of its initial savanna area, and linear  
 403 extrapolation of forest cover change suggests that savannas will completely disappear from the  
 404 park within the next 30 years.



405  
 406 Fig. 6: Landcover change throughout the study period. (a) Variation of the proportion of forest  
 407 cover over the years. Vertical gray dashed lines represent landcover classification dates and full  
 408 black circles the forest cover estimate on each landcover map. The full black line represents the  
 409 fit of a linear model. (b) Variation of forest encroachment rate between consecutive landcover  
 410 classifications. The full black line represents a weighted mean of forest encroachment rates  
 411 throughout the study period, using the time lengths between consecutive landcover  
 412 classifications as weights.

### 413 3.2. Relationships between fire frequency and landcover change

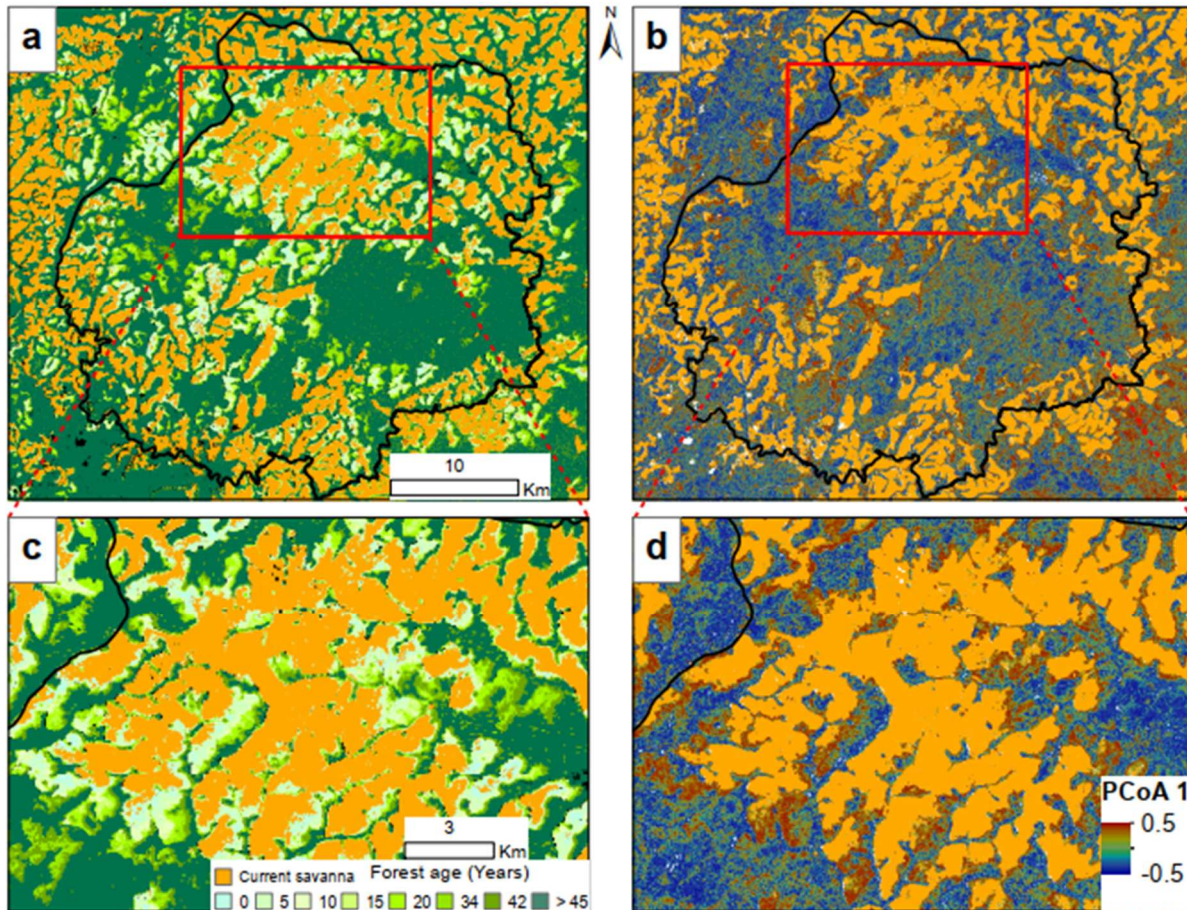
414 Based on a visual interpretation we noticed that savannas surrounding the park principally in  
 415 the northern part underwent higher fire frequencies as compared to the southern savannas (Fig.  
 416 7-a). Most of the savanna that transitioned to forest between two consecutive dates had an average  
 417 Fire Frequency Index (FFI) of 0 in the 5 previous years (Fig. 7-b), meaning that no fire was  
 418 detected. Persisting savanna that did not undergo any forest transition had a FFI presenting a  
 419 broad range of FFI values.



420  
 421 Fig. 7: Maps of the Fire Frequency Index (FFI) derived from Landsat 8 between 2014-2018 (a)  
 422 with existing forests at the beginning of the monitoring period displayed in grey. (b) Associated  
 423 barplots showing the distribution of FFI classes for stable savanna (orange) and forest gains  
 424 (green) in consecutive landcover classifications.

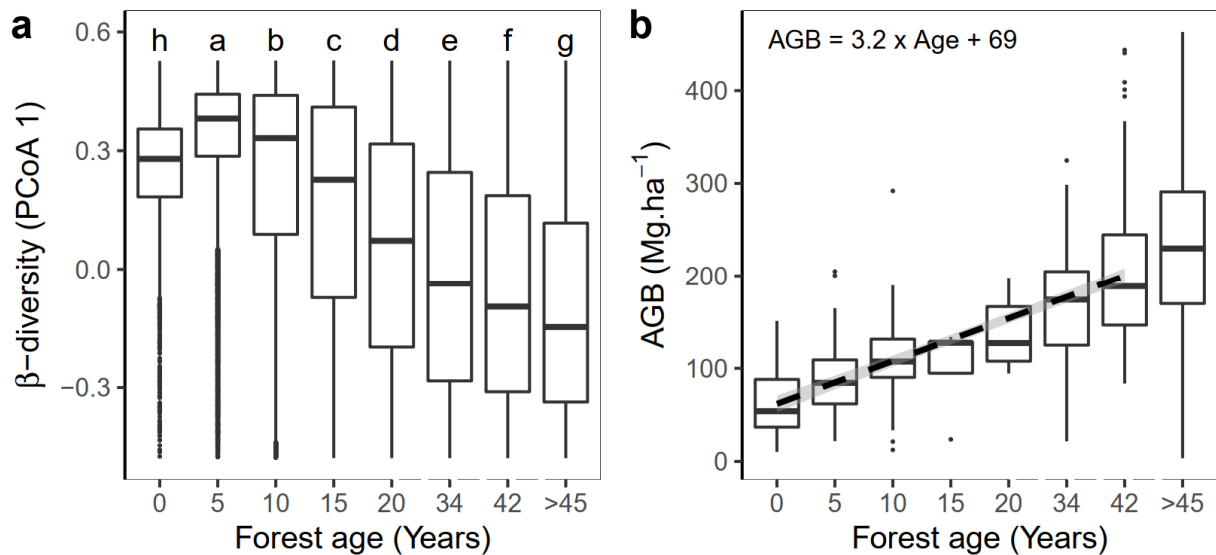
425 3.3. Change in forest composition and structure with age

426 We assessed the relationships between forest age and (1) forest composition, indirectly  
427 characterized through spectral composition gradient analysis of 30 x 30 m windows spectral  
428 response and (2) forest structure, quantified by AGB estimates.



429 Fig. 8: Gradient of forest transition and the spatial distribution of the spectral composition over  
430 the study area. Forest age map (a) and (b) the spatial distribution of pixel scores along the first  
431 axis of a Principal Coordinate Analysis (PCoA 1 see section 2.5.1 for details). Negative PCoA  
432 values correspond to old growth forests while positive values correspond to young regrowth.  
433 (c) and (d) are subsets illustrating the area where the patterns are marked.  
434

435 The first axis of the PCoA (PCoA 1) applied on the dissimilarity matrix computed from spectral  
436 species composition depicted a gradual change in forest composition from the forest-savanna  
437 edges (young forests in light green in Fig. 8-a & c with brown tone in Fig. 8-b & d) to the forest  
438 interior (old forests in dark green in Fig. 8-a & c with blue tone in Fig. 8-b & d). The spatial  
439 structure of forest spectral composition gradients matched the pattern of forest progression,  
440 with younger and older stands found on the positive and negative sides of PCoA 1 (Fig. 9-a),  
441 respectively.

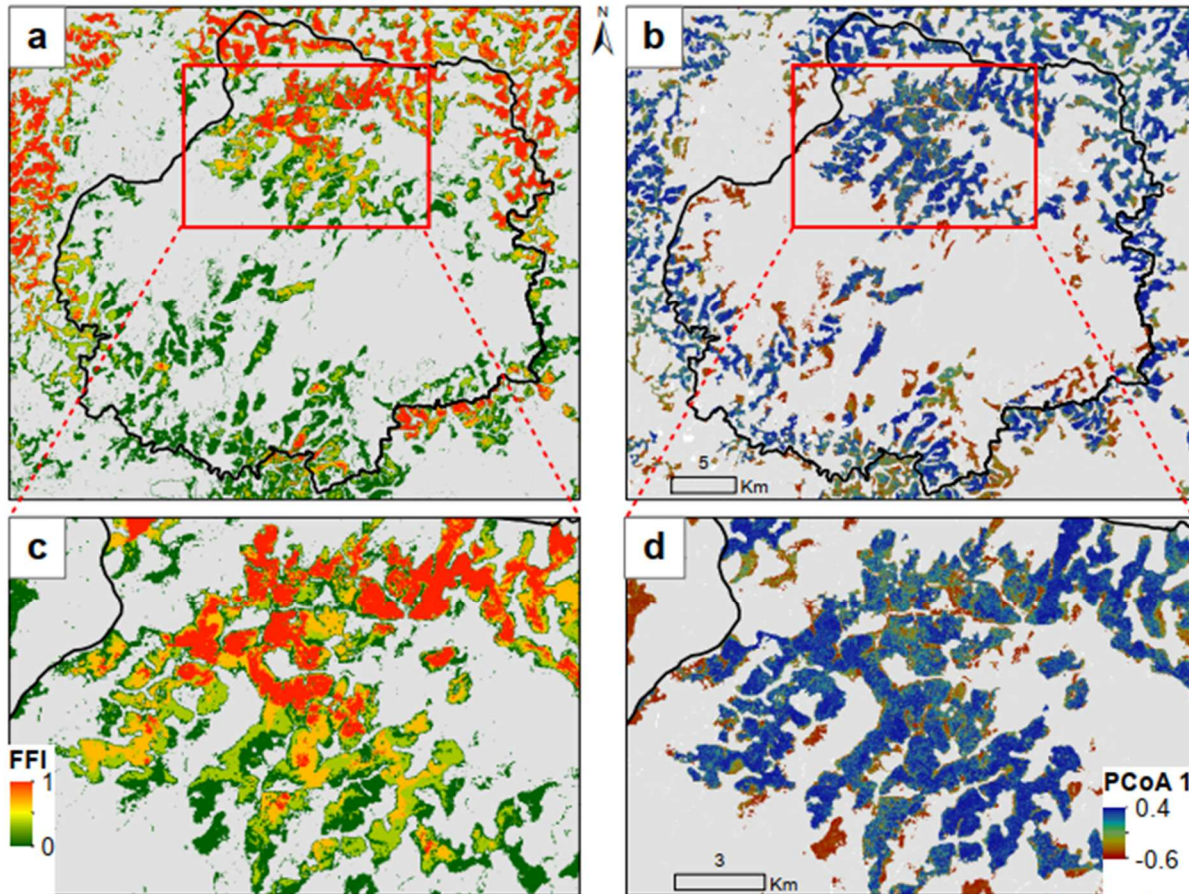


442 Fig. 9: Relationships between forest age, spectral composition and structure. (a) Boxplot of  
 443 spectral composition derived from PCoA 1 (see section 2.5.1 for details), by forest age bins.  
 444 Labelled letters represent the results of a Tukey honest significant difference (HSD) test, with  
 445 different letters for boxes having different means at the probability cut-off value of  $p < 0.05$ .  
 446 (b) Boxplot of pixels' aboveground biomass (AGB) by forest age bins. Dotted line represents  
 447 the fit of a simple linear model between forest age and AGB for transitory forests ( $< 45$  years)  
 448 with its 95% confidence interval (grey ribbon). Note that in panels a and b, x axes after year 20  
 449 are represented with broken lines to mark a change in the interval between age bins.  
 450

451 It is worth noting that the variability (cf. e.g. the interquartile range in box plots) of spectral  
 452 composition seemed to increase with age. We also observed consistent changes in forest  
 453 structure (Fig. 9-b), with an increase in forest AGB from  $61 \pm 33 \text{ Mg.ha}^{-1}$  for younger forests  
 454 (less than 5 years since afforestation) up to  $230 \pm 80 \text{ Mg.ha}^{-1}$  for the oldest forests ( $> 45$  years).  
 455 The transition map thus suggested an average linear increase of about  $3.2 \text{ Mg.ha}^{-1}.\text{year}^{-1}$  in  
 456 MDNP forests since 1975 (Fig. 9-b). Young regenerating forests ( $\leq 20$  years) seemed to show  
 457 a higher AGB accumulation rate of  $4.1 \text{ Mg.ha}^{-1}.\text{year}^{-1}$  (not shown).

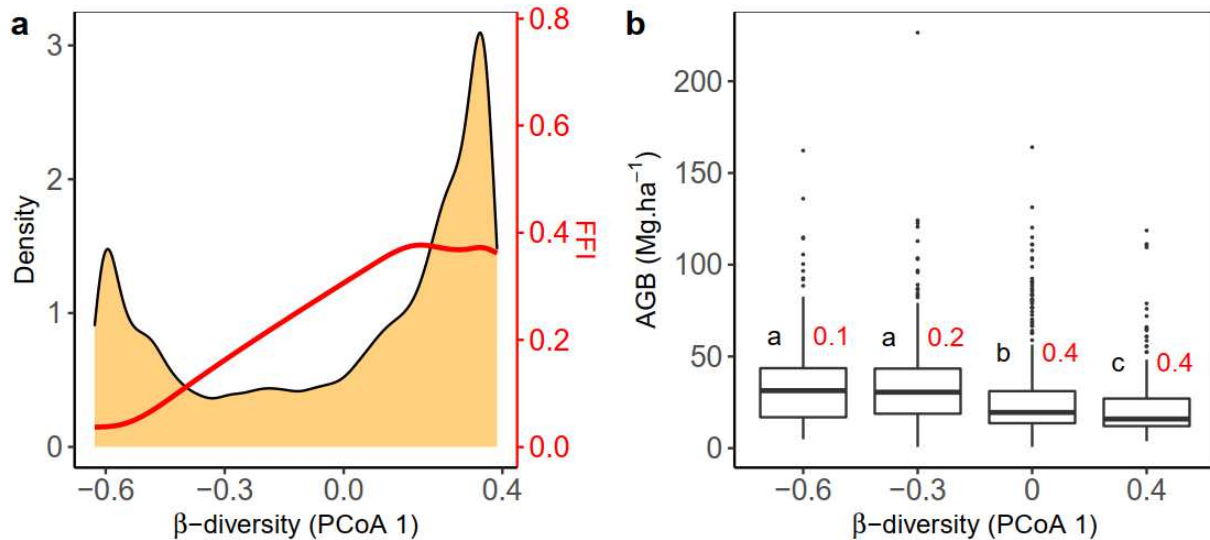
#### 458 3.4. Change in savanna composition and structure with fire frequency

459 We investigated the relationships between the fire frequency of the past 5 years and the  
 460 composition and structure of stable savannas (2020). Savanna spectral composition was  
 461 consistent with the fire frequency (Fig. 10) and showed a marked bimodality along PCoA 1  
 462 with a clear segregation between the two extreme states (Fig. 11).



463  
 464 Fig. 10: Gradient of fire frequency and the spatial distribution of the spectral composition over  
 465 persisting savannas the study area pixels from 1975 to 2020. Fire frequency map (a) and (b) the  
 466 spatial distribution of pixel scores along the first axis of a Principal Coordinate Analysis (PCoA  
 467 1) over savannas. Negative PCoA values correspond to woody savanna while positive values  
 468 correspond to grassy savanna. Forest pixels in 2020 are masked out (grey). (c) and (d) are  
 469 subsets illustrating the area where the patterns are marked.

470 The spatial distribution of FFI was congruent with distribution patterns of spectral species  
 471 composition opposing woody savanna (negative scores on PCoA 1 with a mode around ca.-0.6;  
 472 Fig. 11-a) with higher AGB (c.  $36 \pm 27 \text{ Mg}\cdot\text{ha}^{-1}$  for leftmost box in Fig. 11-b) and grassy  
 473 savanna (positive scores on PCoA 1 with a mode around ca. 0.4; Fig. 11-a) with lower AGB  
 474 ( $22 \pm 18 \text{ Mg}\cdot\text{ha}^{-1}$  for the rightmost box; Fig. 11-b). Woody savannas had rare fire events (FFI  
 475 close to 0) while grassy savannas had higher fire frequencies (FFI close to 0.4).



476  
 477 Fig. 11: Relationships between savanna spectral composition, fire frequency and savanna  
 478 structure. **(a)** Density plot of spectral composition score on PCoA 1 and associated recent  
 479 (2014-2018) fire frequency, represented by a smooth average of Fire Frequency Index (FFI; red  
 480 line). **(b)** Boxplot of AGB variation by PCoA 1 bins. The labelled letters represent the results  
 481 of a Tukey honest significant difference (HSD) test, with different letters for boxes having  
 482 different means at the probability cut-off value of  $p < 0.05$ . Red numbers above the plots  
 483 represent the average FFI for each PCoA 1 bin.

#### 484 4. Discussion

##### 485 4.1. Forest expansion

486 The FSE of northern hemisphere tropical Africa are currently experiencing woody  
 487 encroachment and forest progression over savannas. Several studies, scattered from Guinea to  
 488 the Central African Republic (Boulvert, 1990; Mitchard et al., 2011; Mitchard and Flintrop,  
 489 2013; Youta-Happi, 1998) and even central Gabon (Cardoso et al., 2020; Jeffery et al., 2014)  
 490 have illustrated this trend, while referring to time windows of variable lengths within the last  
 491 six decades (Aleman et al., 2017). However, in all documented sites, no methodologically  
 492 consistent picture was available over more than 30 years. We show in the present study that  
 493 simple principles for distinguishing contrasted vegetation types and fire occurrence regimes  
 494 allow benefitting from massive high spatial resolution image series and cloud computing to  
 495 consistently document the dynamics of forest-savanna boundaries. We indeed achieved an  
 496 integrated picture of vegetation changes in a protected area in Central Cameroon (MDNP, ca.  
 497 1,000 km<sup>2</sup>) from 1975 to present, which is all over the timeframe covered by the Landsat series.  
 498 Our characterization of forest progression qualitatively agrees with previous studies in nearby  
 499 areas of the Guineo-Congolian region in Central Africa that stretched over either an early time  
 500 window (50s – 90s, Youta-Happi, 2003) or a more recent one (1986 – 2006, Mitchard et al.,  
 501 2009). Youta-Happi (2003) measured a forest encroachment rate of 0.74%.year<sup>-1</sup> after 39 years

502 (1950-1989) of monitoring in a nearby area in Cameroon (Mbam et Kim confluent) using air  
503 photographs. Mitchard et al. (2009) expressed woody encroachment qualitatively as increases  
504 in canopy area index (CAI) computed using 3 images (1986, 2000, 2006), and observed a  
505 shrinking of low CAI areas ( $0.2 \text{ m}^2/\text{m}^2$  area, interpreted as “grassy savanna”) by 43% over 20  
506 years ( $0.9\% \text{ y}^{-1}$  for 1986-2000 and  $1.29\%$  for 2000-2006). This trend was reported benefiting  
507 mostly to intermediate CAI classes (interpretable as both dense savanna and young forest) with  
508 a marginal increase of upper CAI class ( $>1 \text{ m}^2/\text{m}^2$  which unequivocally relates to close canopy  
509 forest) (Mitchard et al., 2009). Hence their results suggest both forest expansion and woody  
510 biomass built-up in perpetuating savannas.

511 After forest transition, differences in the functional composition of plant communities are  
512 apparent in the spectral reflectance of forest canopies captured by Sentinel 2 satellite data.  
513 Spectral species composition appeared structured along a forest-age gradient. This reflects the  
514 successional gradient of floristic assemblages where fast growing pioneer species with low  
515 aboveground biomass yet strong photosynthetic activity dominate recent transitions and are  
516 then gradually replaced by long-lived species in old regenerating forests (Cuni-Sanchez et al.,  
517 2016; Deklerck et al., 2019; Ibanez et al., 2013; Youta-Happi et al., 2003). The fact that spectral  
518 variability increased with forest ages in our study area apparently contradicts findings by  
519 (Réjou-Méchain et al., 2014) in another context of Central African forests, where floristic  
520 variability assessed from field inventory data was found to be higher at the initial stages of  
521 succession. It may well be that the spectral signature, especially with a relatively low spectral  
522 resolution (compared to hyperspectral data at least) tends to group a number of similar species  
523 into broader functional groups (e.g. early pioneers; Laurin et al., 2016).

524 Thanks to the comparison between spaceborne image series and local UAV-borne LiDAR data  
525 we were able to quantify the pace of AGB increment from recent forest transitions to older  
526 forests. AGB was found to steadily increase with a hint of leveling-off after 20 years. Our rate  
527 of AGB increase of  $4.1 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  found for young secondary forests ( $\leq 20$  years as defined  
528 by IPCC) is 59% lower than the IPCC (2006) default AGB accumulation rate for young tropical  
529 rainforest in Africa ( $\approx 10 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ; Suarez et al., 2019). Refined IPCC 2006 default AGB  
530 accumulation rate proposed by Suarez et al. (2019) is still above our own estimate by 46% ( $7.6$   
531  $\pm 5.9 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ). This would reflect a contrasted scenario of AGB uptake depending on  
532 whether the forest recovers after disturbances (reforestation) or encroaches over grassy and  
533 woody savanna (afforestation). The former regeneration process would imply an average AGB  
534 uptake 2-fold greater than in the latter scenario as compared to the Suarez et al. (2019)

535 estimates. The type of previous landcover or disturbance has been found elsewhere to  
536 significantly influence the carbon accumulation rate (Cook-Patton et al., 2020; Moran et al.,  
537 2000). Reforestation actually occurs on previously forested soils (Janzen, 2016), keeping  
538 characteristics (soil fertility and structural properties) favorable to forest seedlings  
539 establishment and growth (Viani et al., 2011). Afforestation on the other hand generally occurs  
540 on nutrient-poor savanna soils leading to a slower forest gain (Moran et al., 2000). This study  
541 focused on aboveground carbon stocks and no consideration was made to the carbon stored in  
542 soils which can be higher in grassy and woody savannas as compared to forests (Buisson et al.,  
543 2019; Silveira et al., 2020).

#### 544 4.2. The role of fire in shaping savanna structure and dynamics

545 Mesic savannas represent alternative stable states to forest (Hirota et al., 2011; Staver et al.,  
546 2011a) in areas of intermediate rainfall (between 700 and 1900 mm/year for Africa; Aleman et  
547 al., 2020; Staver et al., 2011a), where savannas are maintained thanks to regular disturbances,  
548 notably by fire (Langevelde et al., 2003; Veenendaal et al., 2018; Venter et al., 2018). The  
549 MDNP being in the intermediate rainfall area, the observed forest progression might either be  
550 the result of a reduction of fire disturbances or to global climate change inducing locally wetter  
551 climatic conditions. As observed elsewhere, such as in La Lopé National Park (LLNP) in Gabon  
552 (Jeffery et al., 2014), fire frequency is not homogeneous across the landscape, because of  
553 variation in ignition sources or natural breaks. This heterogeneity translates in differential rates  
554 for woody encroachment and forest progression. In most cases, no fire occurrence was recorded  
555 during at least five years for pixels of woody savanna that transited to forest between the last  
556 two consecutive monitoring periods. Fire-free intervals facilitate tree recruitment and growth  
557 and allow trees to approach canopy closure which suppresses fire by excluding grasses (Bond  
558 and Midgley, 2000; Hirota et al., 2011; Staver et al., 2011b; Veenendaal et al., 2018, 2015). In  
559 LLNP savannas newly protected from fire can sufficiently thicken up over a 15 year period to  
560 reach a structure comparable to a colonizing forest (Jeffery et al., 2014). In the absence of fire,  
561 the system switches from a state of co-occurrence of fire-adapted trees and heliophytic grasses  
562 to a state with fire impervious, shade-bearing giant herbs (*Aframomum spp.*) and forbs  
563 (*Chromolaena odorata*, a well-known invasive woody weed; Youta-Happi, 1998; Oliveras and  
564 Malhi, 2016) along with saplings of light-demanding forest tree species such as *Albizia spp.*,  
565 *Macaranga spp.* (Ibanez et al., 2013; Youta-Happi, 1998; Youta-Happi et al., 2003; Youta-  
566 Happi and Bonvallot, 1996). Cardoso et al., (2020) evidenced the presence of an ecotone  
567 community in LLNP that occupies a narrow belt between savanna and forest and prevents fire

568 progression within the forest when savanna burn regularly. According to our floristic data from  
569 61 0.16-ha field plots which analysis is beyond the scope of the present paper, the  
570 aforementioned community is also frequent in the ecotones of the MDNP and a similar role can  
571 be hypothesized.

572 The spectral diversity in the (currently remaining) savannas of our study site evidenced two  
573 contrasting dominant states either related to low (FFI  $\approx$  0) or high (FFI  $\approx$  0.4) fire frequencies.  
574 Interestingly, we observed a decreasing relationship between AGB and the fire frequency that  
575 led from high AGB (mean of ca. 36 Mg.ha<sup>-1</sup>) with low fire frequencies (corresponding to woody  
576 savanna) to low AGB (ca. 22 Mg.ha<sup>-1</sup>) with high fire frequency situations (corresponding to  
577 grassy savanna). This suggests that savannas with low fire frequency (FFI  $\leq$  0.2) accumulate  $\approx$   
578 40% more AGB than those with high fire frequency. We may here note that we observed very  
579 few savannas displaying intermediate fire frequency (0.2-0.3.year<sup>-1</sup>) and intermediate AGB ( $\approx$   
580 27 Mg/ha<sup>-1</sup>). Analogously, Mitchard et al. (2009) found that savannas of intermediate CAI were  
581 relatively scarce in the nearby Mbam-Djerem region. Our results suggest that humid savannas  
582 seem to be the most unstable/prone to forest transition under a low fire frequency as the latter  
583 is not sufficient to prevent woody biomass build-up. Inversely, increased woody biomass and  
584 cover is known to depress grass production (Hoffmann et al., 2012; Veenendaal et al., 2018)  
585 that is the main fire fuel after drying-up, thereby indirectly limiting fire intensity and  
586 propagation (Lehmann et al., 2011). The shift towards woody savanna and associated  
587 ineffective fire regimes seems here to occur for AGB values around 27 Mg.ha<sup>-1</sup>. Once this  
588 threshold is exceeded, the AGB build-up towards 36 Mg.ha<sup>-1</sup> (i.e. towards a woody savanna)  
589 seems inexorable and prefigures the progressive floristic shift towards stands dominated by  
590 forest pioneer species that displayed AGB values in the range 60 - 100 Mg.ha<sup>-1</sup>. Field  
591 prospection allowed us to frequently observe dense woody savanna characterized by tall  
592 savanna trees (mainly *Terminalia glaucescens*) frequently fringing young forests dominated by  
593 species such as *Albizia adianthifolia* and *Macaranga spp.* that overtopped surviving *T.*  
594 *glaucescens* engulfed in dense thickets of *C. odorata*. All this strongly suggests recent  
595 afforestation. During the five years of fire monitoring (2014-2018) we noticed some persistent  
596 savannas (for which no forest transition was detected) with low fire frequency (FFI < 0.2).  
597 While not documented in this study, other factors may explain this savanna stability under low  
598 fire frequencies, such as topo-edaphic controls (Colgan et al., 2012), or fire characteristics  
599 (Jeffery et al., 2014; Walters, 2012).

600 4.3. Implications for conservation and management

601 The creation of the MDNP in 2004 may have hindered anthropogenic activities principally at  
602 its less accessible savanna core where we observed intense forest expansion. A lower proportion  
603 of forest transitions is observed in peripheral savannas, which are more accessible especially in  
604 the northern part of the MDNP where natural boundaries constituted by Mpem and Djim rivers  
605 are absent. From the various observations made during field campaigns conducted between  
606 2019 and 2020; we noticed that those savannas were subject to substantial livestock  
607 transhumance during the dry season (Nov. - Mar.). During that period shepherds regularly burn  
608 the savanna to favor grass flush (Youta-Happi and Bonvallot, 1996; Mitchard et al., 2009).  
609 Poachers also set fire for the same reason, as well as to increase visibility or drive the game (as  
610 described by Walters, 2010). Frequent fires limit the growth of woody savanna species and  
611 woody build-up in savannas which makes the establishment of forest species unlikely (Dantas  
612 et al., 2013; Venter et al., 2018) and delays forest expansion. On the other hand, cattle grazing  
613 and trampling limit the accumulation of grass fuel and are liable to depress both fire frequency  
614 and intensity. Our results suggest that a quinquennial fire frequency (i.e., a fire event every five  
615 years) could constitute a tipping point between grassy savanna and woody savanna. Considering  
616 the dramatic forest expansion we evidenced, the current, unplanned fire regimes seem unable  
617 to preserve the mosaic landscape.

618 Our findings have important management implications as they provide insight into the  
619 ecological challenge associated with woody and forest encroachment, which is a pervasive  
620 phenomenon and a growing concern for managers of African savannas (Stevens et al., 2017;  
621 Venter et al., 2018). Fire frequency in the MDNP is generally the product of non-managed fires  
622 as the park still lacks an effective fire management program. Therefore, managers in the MDNP  
623 have little influence on how much of the park burns on an annual basis, and that area burned is  
624 largely dictated by uncontrolled actions from transhumant shepherds and poachers. Maintaining  
625 at least one or more fires every five years is necessary to ensure the maintenance of an open  
626 canopy cover. Forest expansion appeared indeed as a continuous and steady process in the  
627 MDNP and if we extrapolate the observed fairly constant rate of forest gain into savanna, the  
628 area may lose all its savanna in less than 30 years. This is even more certain when we consider  
629 the rise in CO<sub>2</sub> concentration and climate change predictions for tropical Africa that expect an  
630 increase in precipitation over the next decades (Pachauri and Meyer, 2014). Both events can  
631 influence the growth rate of juvenile plants, thereby affecting tree recruitment and the  
632 conversion of open savannas to woodlands (Bond and Midgley, 2012) favoring forest expansion  
633 (Bond and Midgley, 2012; Staver et al., 2011b; Stevens et al., 2017). Local factors including

634 fire management, soil fertility or hydromorphy and herbivory pressure are expected to mediate  
635 this general prediction. Although carbon mitigation programs such as REDD+ scheme tend to  
636 encourage forest expansion, the loss of savanna ecosystems in the area will drastically modify  
637 landscape-level diversity (Bond, 2016; Veldman, 2016) and ecosystem services, including  
638 hydrology (Acharya et al., 2018) and soil nutrient cycles (Berthrong et al., 2009), including soil  
639 carbon storage (Chiti et al., 2018; Cuni-Sanchez et al., 2016), and it would markedly alter  
640 community assemblages (Abreu et al., 2017; Bremer and Farley, 2010) especially those of  
641 savanna plant and animal specialists, including iconic large mammals and big cats. That is the  
642 reason why park authorities should aim at maintaining the mosaic of forest and humid savannas  
643 that pre-existed gazettement of the protected areas they are in charge of (Jeffery et al., 2014).

#### 644 4.4. Progress in modelling landscape dynamics

645 We here demonstrated the potential of approaches based on open source imagery and cloud-  
646 based platforms such as Google Earth Engine for landcover change monitoring. This offer  
647 prospects for an improved measurement of national level aboveground carbon stocks (Sagang  
648 et al., 2020) and stock changes in forest-savanna transitional landscapes (in relation to Tier 2  
649 and Tier 3 accuracy levels), in compliance with the United Nations Framework Convention on  
650 Climate Change (UNFCCC) and IPCC requirements for countries still reporting at Tier 1 level,  
651 as it is the case in Central Africa (Romijn et al., 2015). Localized airborne LiDAR data provide  
652 a good reference to map AGB variation over sufficiently large regions (Wulder et al., 2012) to  
653 allow upscaling using spaceborne data (Sagang et al., 2020). The FFI obtained in this study  
654 using 30 m Landsat was shown to better retrieve the variability of fire frequencies than the 500  
655 m MODIS fire product. The latter indeed estimated FFI 28% lower than the former on average,  
656 and totally failed to detect areas with the highest frequency (yearly) of fire regime. This finding  
657 accords with Chuvieco et al. (2019) and Ramo et al. (2021) who found that recent BA products  
658 covering Africa with Sentinel-2 images (at 20 m spatial resolution) over a single year reached  
659 estimates 1.8 and 3.2 times higher, respectively, than the estimates from MODIS products. This  
660 strong discrepancy is mostly caused by insufficient spatial resolution leading to the omission  
661 of small fires (< 100 ha) (Roteta et al., 2019) as the study area is likely dominated by small low-  
662 intensity fires (Mitchard et al., 2009), in accordance with the fire biomes typology (Archibald  
663 et al., 2013). This raises a caveat considering that several studies (Axelsson and Hanan, 2018;  
664 Diouf et al., 2012; Staver et al., 2011b, 2011a; Venter et al., 2018) fully relied on MODIS to  
665 assess fire frequency influence on the vegetation structure. A limitation that needs to be pointed  
666 out in this study is that fire monitoring was restricted to yearly fire statistics, ignoring the

667 seasonality of fire within the year (early or late fires) despite known influence on savanna  
668 structure (Bucini and Lambin, 2002; Diouf et al., 2012). Subsequent efforts are therefore needed  
669 to temporally disaggregate annual FFI products. Another obvious perspective is to extend our  
670 approaches to other forest-savanna transition zones. Preliminary tests show that the open source  
671 algorithms proposed along with this publication should allow a smooth transposition, as long  
672 as the studied areas present vegetation mosaics having sufficiently distinct radiometric  
673 signatures.

## 674 5. Conclusion

675 We leveraged on the potential offered by open access satellite imagery and cloud computing  
676 facilities (GEE), as well as UAV-LiDAR data, to monitor complex forest-savanna biomass and  
677 compositional dynamics at a meaningful scale in the MDNP. Landsat image archives recorded  
678 a long-term (> 42 years) forest spread into savanna at a rate of ca. 0.63%.year<sup>-1</sup>. The spectral  
679 assemblages of the forest cover characterized using Sentinel 2 multispectral imagery and AGB  
680 variations quantified using UAV-LiDAR data allowed map compositional and structural  
681 changes along the forest succession gradient and quantify rates of biomass accumulation. Fire  
682 occurrence, as recorded via the Landsat archive, modulated bush encroachment and forest  
683 expansion, with a five-year fire frequency found to be the threshold below which woody plants  
684 dominate and open the way to forest transition. These results highlight the importance of fire in  
685 maintaining savanna ecosystem in the area. These findings allow providing detailed  
686 information to support decision makers in charge of carbon sequestration and biodiversity  
687 conservation policies.

## 688 Acknowledgements

689 This work was financially supported by the Nachtigal Hydropower Company (Contract n°  
690 C006C007-DES-2017) under the environmental impact study associated to the construction of  
691 a hydroelectric dam on the Sanaga river in the Centre region of Cameroon. This study is also  
692 part of the 3DForMod project (ANR-17-EGAS-0002-01) funded by the framework of the JPI  
693 FACCE ERA-GAS call under the European Union's Horizon 2020 research and innovation  
694 program (grant agreement no. 696356). L.B.T.S. benefited from the "Allocations de recherche  
695 pour une thèse au Sud (ARTS)" grant program to fund research stays in France. J.B.F.  
696 acknowledges financial support from Agence Nationale de la Recherche (BioCop project-  
697 ANR-17-CE32-0001). We thank Clément Aubert for assistance in UAV-LiDAR data  
698 acquisition. We are grateful to Imma Tchefferi, Amélie Kunito and the MDNP staff officers for

699 assistance during field data collection. We thank the anonymous reviewers for their significant  
700 comments and contributions to the manuscript.

#### 701 Authors' contributions

702 L.B.T.S., and N.B. conceived and designed the experiments. L.B.T.S., P.P. and N.B. edited the  
703 different GEE scripts. G.V. and J.B.F. helped with image processing using BiodivMapR.  
704 L.B.T.S. performed the experiments and analysed the results, with the help of P.P., N.B. and  
705 P.C. L.B.T.S. wrote the first drafts of the paper and N.B., P.C., P.P., G.V., B.S. and J.B.F.  
706 contributed edits and advice on content. All authors have read and agreed to the published  
707 version of the manuscript.

#### 708 Data Accessibility

709 Data that support the findings of this study are available from the corresponding author upon  
710 request. The forest transition and fire frequency raster and Google Earth Engine codes are  
711 available [here](#) .

#### 712 Orcid

713 Sagang Takougoum Le Bienfaiteur <https://orcid.org/0000-0001-8778-3121>

714 Ploton Pierre <https://orcid.org/0000-0002-8800-3593>

715 Viennois Gaëlle <https://orcid.org/0000-0001-9772-343X>

716 Jean-Baptiste Féret <https://orcid.org/0000-0002-0151-1334>

717 Sonké Bonaventure <https://orcid.org/0000-0002-4310-3603>

718 Couteron Pierre <https://orcid.org/0000-0002-4627-1696>

719 Nicolas Barbier <https://orcid.org/0000-0002-5323-3866>

720 References

- 721 Abreu, R.C.R., Hoffmann, W.A., Vasconcelos, H.L., Pilon, N.A., Rossatto, D.R., Durigan,  
722 G., 2017. The biodiversity cost of carbon sequestration in tropical savanna. *Sci. Adv.* 3,  
723 1–8.
- 724 Acharya, B.S., Kharel, G., Zou, C.B., Wilcox, B.P., Halihan, T., 2018. Woody plant  
725 encroachment impacts on groundwater recharge: A review. *Water*.  
726 <https://doi.org/10.3390/w10101466>
- 727 Aleman, J.C., Fayolle, A., Favier, C., Staver, A.C., Dexter, K.G., Ryan, C.M., Azihou, A.F.,  
728 Bauman, D., Te Beest, M., Chidumayo, E.N., Comiskey, J.A., Crowsigt, J.P.G.M.,  
729 Dessard, H., Doucet, J.-L., Finckh, M., Gillet, J.-F., Gourlet-Fleury, S., Hempson, G.P.,  
730 Holdo, R.M., Kirunda, B., Kouame, F.N., Mahy, G., Gonçalves, F.M.P., McNicol, I.,  
731 Quintano, P.N., Plumptre, A.J., Pritchard, R.C., Revermann, R., Schmitt, C.B.,  
732 Swemmer, A.M., Talila, H., Woollen, E., Swaine, M.D., 2020. Floristic evidence for  
733 alternative biome states in tropical Africa. *Proc. Natl. Acad. Sci. U. S. A.* 1–8.  
734 <https://doi.org/10.1073/pnas.2011515117>
- 735 Aleman, J.C., Jarzyna, M.A., Staver, A.C., 2017. Forest extent and deforestation in tropical  
736 Africa since 1900. *Nat. Ecol. Evol.* 2, 26–33. <https://doi.org/10.1038/s41559-017-0406-1>
- 737 Archibald, S., Lehmann, C.E.R., Gomez-Dans, J.L., Bradstock, R. a, 2013. Defining pyromes  
738 and global syndromes of fire regimes. *Proc. Natl. Acad. Sci.* 110, 6442–6447.  
739 <https://doi.org/10.1073/pnas.1211466110>
- 740 Axelsson, C.R., Hanan, N.P., 2018. Rates of woody encroachment in African savannas reflect  
741 water constraints and fire disturbance. *J. Biogeogr.* 45, 1209–1218.  
742 <https://doi.org/10.1111/jbi.13221>
- 743 Banskota, A., Kayastha, N., Falkowski, M.J., Wulder, M.A., Froese, R.E., White, J.C., 2014.  
744 Forest Monitoring Using Landsat Time Series Data: A Review. *Can. J. Remote Sens.* 40,  
745 362–384. <https://doi.org/10.1080/07038992.2014.987376>
- 746 Bastin, J.F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M.,  
747 Crowther, T.W., 2019. The global tree restoration potential. *Science (80-. )*. 364, 76–79.  
748 <https://doi.org/10.1126/science.aax0848>
- 749 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C.,  
750 Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G.,

751 Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Roupsard, O.,  
752 Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D., 2010. Terrestrial  
753 gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*  
754 (80-. ). 329, 834–838. <https://doi.org/10.1126/science.1184984>

755 Berthrong, S.T., Jobbágy, E.G., Jackson, R.B., 2009. A global meta-analysis of soil  
756 exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecol. Appl.* 19, 2228–  
757 2241. <https://doi.org/10.1890/08-1730.1>

758 Blaum, N., Rossmannith, E., Popp, A., Jeltsch, F., 2007. Shrub encroachment affects  
759 mammalian carnivore abundance and species richness in semiarid rangelands. *Acta*  
760 *Oecologica* 31, 86–92. <https://doi.org/10.1016/J.ACTAO.2006.10.004>

761 Bond, W.J., 2016. Ancient grasslands at risk. *Science* (80-. ). 351, 120–122.  
762 <https://doi.org/10.1126/science.aad5132>

763 Bond, W.J., Midgley, G.F., 2012. Carbon dioxide and the uneasy interactions of trees and  
764 savannah grasses. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 601–612.  
765 <https://doi.org/10.1098/rstb.2011.0182>

766 Bond, W.J., Midgley, G.F., 2000. A proposed CO<sub>2</sub>-controlled mechanism of woody plant  
767 invasion in grasslands and savannas. *Glob. Chang. Biol.* 6, 865–869.

768 Boschetti, L., Roy, D.P., Giglio, L., Huang, H., Zubkova, M., Humber, M.L., 2019. Global  
769 validation of the collection 6 MODIS burned area product. *Remote Sens. Environ.* 235,  
770 111490. <https://doi.org/10.1016/j.rse.2019.111490>

771 Boulvert, Y., 1990. Avancée ou recul de la forêt centrafricaine : changements climatiques,  
772 influence de l’homme et notamment des feux, in: *Paysages Quaternaires de l’Afrique*  
773 *Centrale Atlantique*. Paris, pp. 353–366.

774 Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green  
775 deserts? A synthesis of the effects of land-use transitions on plant species richness.  
776 *Biodivers. Conserv.* 19, 3893–3915. <https://doi.org/10.1007/s10531-010-9936-4>

777 Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A.,  
778 Fernandes, G.W., Bond, W.J., Hermann, J.M., Mahy, G., Alvarado, S.T., Zaloumis, N.P.,  
779 Veldman, J.W., 2019. Resilience and restoration of tropical and subtropical grasslands,  
780 savannas, and grassy woodlands. *Biol. Rev.* 94, 590–609.

781 <https://doi.org/10.1111/brv.12470>

782 Cardoso, A.W., Oliveras, I., Abernethy, K.A., Jeffery, K.J., Glover, S., Lehmann, D., Edzang  
783 Ndong, J., White, L.J.T., Bond, W.J., Malhi, Y., 2020. A distinct ecotonal tree  
784 community exists at central African forest–savanna transitions. *J. Ecol.* 00, 1–14.  
785 <https://doi.org/10.1111/1365-2745.13549>

786 Cava, M.G.B., Pilon, N.A.L., Priante, C.F., Ribeiro, M.C., Durigan, G., 2020. The recovery  
787 rates of secondary savannas in abandoned pastures are poorly explained by  
788 environmental and landscape factors. *Appl. Veg. Sci.* 23, 14–25.  
789 <https://doi.org/10.1111/avsc.12457>

790 Cava, M.G.B., Pilon, N.A.L., Ribeiro, M.C., Durigan, G., 2018. Abandoned pastures cannot  
791 spontaneously recover the attributes of old-growth savannas. *J. Appl. Ecol.* 55, 1164–  
792 1172.

793 Chiti, T., Rey, A., Jeffery, K., Lauteri, M., Mihindou, V., Malhi, Y., Marzaioli, F., White,  
794 L.J.T., Valentini, R., 2018. Contribution and stability of forest-derived soil organic  
795 carbon during woody encroachment in a tropical savanna. A case study in Gabon. *Biol.*  
796 *Fertil. Soils* 54, 897–907. <https://doi.org/10.1007/s00374-018-1313-6>

797 Chuvieco, E., Mouillot, F., van der Werf, G.R., San Miguel, J., Tanasse, M., Koutsias, N.,  
798 García, M., Yebra, M., Padilla, M., Gitas, I., Heil, A., Hawbaker, T.J., Giglio, L., 2019.  
799 Historical background and current developments for mapping burned area from satellite  
800 Earth observation. *Remote Sens. Environ.* 225, 45–64.  
801 <https://doi.org/10.1016/j.rse.2019.02.013>

802 Colgan, M.S., Asner, G.P., 2014. Coexistence and environmental filtering of species-specific  
803 biomass in an African savanna. *Ecology* 95, 1579–1590. [https://doi.org/10.1890/13-](https://doi.org/10.1890/13-1160.1)  
804 1160.1

805 Colgan, M.S., Asner, G.P., Levick, S.R., Martin, R.E., 2012. Topo-edaphic controls over  
806 woody plant biomass in South African savannas. *Biogeosciences* 9, 1809–1821.  
807 <https://doi.org/10.5194/bg-9-1809-2012>

808 Cook-Patton, S.C., Leavitt, S.M., Gibbs, D., Harris, N.L., Lister, K., Anderson-Teixeira, K.J.,  
809 Briggs, R.D., Chazdon, R.L., Crowther, T.W., Ellis, P.W., Griscom, H.P., Herrmann, V.,  
810 Holl, K.D., Houghton, R.A., Larrosa, C., Lomax, G., Lucas, R., Madsen, P., Malhi, Y.,  
811 Paquette, A., Parker, J.D., Paul, K., Routh, D., Roxburgh, S., Saatchi, S., van den

812 Hoogen, J., Walker, W.S., Wheeler, C.E., Wood, S.A., Xu, L., Griscom, B.W., 2020.  
813 Mapping carbon accumulation potential from global natural forest regrowth. *Nature* 585,  
814 545–550. <https://doi.org/10.1038/s41586-020-2686-x>

815 Cuni-Sanchez, A., White, L.J.T., Calders, K., Jeffery, K.J., Abernethy, K., Burt, A., Disney,  
816 M., Gilpin, M., Gomez-Dans, J.L., Lewis, S.L., 2016. African savanna-forest boundary  
817 dynamics: A 20-year study. *PLoS One* 11, 1–23.  
818 <https://doi.org/10.1371/journal.pone.0156934>

819 Daldegan, G.A., de Carvalho Júnior, O.A., Guimarães, R.F., Gomes, R.A.T., Ribeiro, F. de F.,  
820 McManus, C., 2014. Spatial patterns of fire recurrence using remote sensing and GIS in  
821 the Brazilian savanna: Serra do Tombador Nature Reserve, Brazil. *Remote Sens.* 6,  
822 9873–9894. <https://doi.org/10.3390/rs6109873>

823 Daldegan, G.A., Roberts, D.A., Ribeiro, F. de F., 2019. Spectral mixture analysis in Google  
824 Earth Engine to model and delineate fire scars over a large extent and a long time-series  
825 in a rainforest-savanna transition zone. *Remote Sens. Environ.* 232, 15pp.  
826 <https://doi.org/10.1016/j.rse.2019.111340>

827 Dantas, V. de L., Batalha, M.A., Pausas, J., 2013. Fire drives functional thresholds on the  
828 savanna – forest transition. *Ecology* 94, 2454–2463.

829 Deklerck, V., De Mil, T., Ilondea, B.A., Nsenga, L., De Caluwé, C., Van den Bulcke, J., Van  
830 Acker, J., Beeckman, H., Hubau, W., 2019. Rate of forest recovery after fire exclusion  
831 on anthropogenic savannas in the Democratic Republic of Congo. *Biol. Conserv.* 233,  
832 118–130. <https://doi.org/10.1016/j.biocon.2019.02.027>

833 DeVries, B., Verbesselt, J., Kooistra, L., Herold, M., 2015. Robust monitoring of small-scale  
834 forest disturbances in a tropical montane forest using Landsat time series. *Remote Sens.*  
835 *Environ.* 161, 107–121. <https://doi.org/10.1016/j.rse.2015.02.012>

836 Dinerstein, E., Joshi, A.R., Vynne, C., Lee, A.T.L., Pharand-Deschênes, F., França, M.,  
837 Fernando, S., Birch, T., Burkart, K., Asner, G.P., Olson, D., 2020. A “global safety net”  
838 to reverse biodiversity loss and stabilize earth’s climate. *Sci. Adv.* 6, 13pp.  
839 <https://doi.org/10.1126/sciadv.abb2824>

840 Diouf, A., Barbier, N., Lykke, A.M., Couteron, P., Deblauwe, V., Mahamane, A., Saadou, M.,  
841 Bogaert, J., 2012. Relationships between fire history , edaphic factors and woody  
842 vegetation structure and composition in a semi-arid savanna landscape ( Niger , West

843 Africa ). *Appl. Veg. Sci.* 15, 488–500. <https://doi.org/10.1111/j.1654->  
844 109X.2012.01187.x

845 Djoufack, M.V., 2011. Étude multi-échelles des précipitations et du couvert végétal au  
846 Cameroun : Analyses spatiales, tendances temporelles, facteurs climatiques et  
847 anthropiques de variabilité du NDVI. PhD Thesis. Université de Bourgogne et Université  
848 de Yaoundé I. 321pp. Thesis. Université de Bourgogne et Université de Yaoundé I.

849 Duncanson, E.L., Disney, M., Armston, J., Nickeson, J., Minor, D., 2021. Committee on  
850 Earth Observation Satellites Working Group on Calibration and Validation Land Product  
851 Validation Subgroup Aboveground Woody Biomass Product Validation Good Practices  
852 Protocol 0–236. <https://doi.org/10.5067/doc/ceoswgcv/lpv/agb.001>

853 Dutrieux, L.P., Verbesselt, J., Kooistra, L., Herold, M., 2015. Monitoring forest cover loss  
854 using multiple data streams, a case study of a tropical dry forest in Bolivia. *ISPRS J.*  
855 *Photogramm. Remote Sens.* 107, 112–125.  
856 <https://doi.org/10.1016/j.isprsjprs.2015.03.015>

857 Escuin, S., Navarro, R., Fernández, P., 2008. Fire severity assessment by using NBR  
858 (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) derived  
859 from LANDSAT TM/ETM images. *Int. J. Remote Sens.* 29, 1053–1073.  
860 <https://doi.org/10.1080/01431160701281072>

861 Estes, L., Elsen, P.R., Treuer, T., Ahmed, L., 2018. The spatial and temporal domains of  
862 modern ecology. *Nat. Ecol. Evol.* · 2, 819–826. <https://doi.org/10.1038/s41559-018->  
863 0524-4

864 Féret, J.-B., Asner, G.P., 2014. Mapping tropical forest canopy diversity using high-fidelity  
865 imaging spectroscopy. *Ecol. Appl.* 24, 1289–1296.

866 Féret, J., Boissieu, F. de, 2020. biodivMapR: An r package for  $\alpha$ - and  $\beta$ -diversity mapping  
867 using remotely sensed images. *Methods Ecol. Evol.* 11, 64–70.  
868 <https://doi.org/10.1111/2041-210X.13310>

869 Gómez, C., White, J.C., Wulder, M.A., 2016. Optical remotely sensed time series data for  
870 land cover classification : A review. *ISPRS J. Photogramm. Remote Sens.* 116, 55–72.  
871 <https://doi.org/10.1016/j.isprsjprs.2016.03.008>

872 Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google

873 Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.*  
874 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>

875 Grabska, E., Hostert, P., Pflugmacher, D., Ostapowicz, K., 2019. Forest stand species  
876 mapping using the sentinel-2 time series. *Remote Sens.* 11, 1–24.  
877 <https://doi.org/10.3390/rs11101197>

878 Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A.,  
879 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* (80-  
880 ). 342, 850–854.

881 Hermosilla, T., Wulder, M.A., White, J.C., Coops, N.C., Hobart, G.W., 2015. An integrated  
882 Landsat time series protocol for change detection and generation of annual gap-free  
883 surface reflectance composites. *Remote Sens. Environ.* 158, 220–234.  
884 <https://doi.org/10.1016/j.rse.2014.11.005>

885 Hirota, M., Holmgren, M., Nes, E.H. Van, Scheffer, M., 2011. Global Resilience of Tropical  
886 Forest and Savanna to Critical Transitions. *Science* (80- ). 334, 232–235.  
887 <https://doi.org/10.1126/SCIENCE.1210657>

888 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,  
889 Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest  
890 boundary: How plant traits, resources and fire govern the distribution of tropical biomes.  
891 *Ecol. Lett.* 15, 759–768. <https://doi.org/10.1111/j.1461-0248.2012.01789.x>

892 Ibanez, T., Munzinger, J., Gaucherel, C., Curt, T., Hély, C., 2013. Inferring savannah-  
893 rainforest boundary dynamics from vegetation structure and composition: A case study  
894 in New Caledonia. *Aust. J. Bot.* 61, 128–138. <https://doi.org/10.1071/BT12255>

895 Ippc, 2006. 2006 IPCC Guidelines for National Greenhouse Gas Inventories, Prepared by the  
896 National Greenhouse Gas Inventories Programme, Eggleston H.S., Buendia L., Miwa K.,  
897 Ngara T. and Tanabe K. (eds). Hayama, Japan.

898 Janzen, H.H., 2016. The Soil Remembers. *Soil Sci. Soc. Am. J.* 80, 1429–1432.  
899 <https://doi.org/10.2136/sssaj2016.05.0143>

900 Jeffery, K.J., Korte, L., Palla, F., Walters, G., White, L.J.T., Abernethy, K.A., 2014. Fire  
901 management in a changing landscape: A case study from Lopé national park, Gabon.  
902 *Parks* 20, 39–52. <https://doi.org/10.2305/IUCN.CH.2014.PARKS-20-1.KJJ.en>

903 Jha, N., Tripathi, N.K., Chanthorn, W., Brockelman, W., Nathalang, A., Pélissier, R.,  
904 Pimmasarn, S., Ploton, P., Sasaki, N., Virdis, S.G.P., Réjou-Méchain, M., 2020. Forest  
905 aboveground biomass stock and resilience in a tropical landscape of Thailand.  
906 *Biogeosciences* 17, 121–134. <https://doi.org/https://doi.org/10.5194/bg-17-121-2020>

907 Kane, V.R., North, M.P., Lutz, J.A., Churchill, D.J., Roberts, S.L., Smith, D.F., McGaughey,  
908 R.J., Kane, J.T., Brooks, M.L., 2014. Assessing fire effects on forest spatial structure  
909 using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. *Remote*  
910 *Sens. Environ.* 151, 89–101. <https://doi.org/https://doi.org/10.1016/j.rse.2013.07.041>

911 Key, C.H., Benson, N.C., 2003. The Normalized Burn Ratio (NBR): A Landsat TM  
912 radiometric measure of burn severity. *US Geol. Surv. North. Rocky Mt. Sci. Center. U.S.*  
913 *Dep. Inter. U.S. Geol. Surv. North. Rocky Mt. Sci. Center.*

914 Langevelde, V.F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N.,  
915 Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins,  
916 H.H.T., Rietkerk, M., 2003. Effects of fire and herbivory on the stability of savanna  
917 ecosystems. *Ecology* 84, 337–350.

918 Laurin, V.G., Puletti, N., Hawthorne, W., Liesenberg, V., Corona, P., Papale, D., Chen, Q.,  
919 Valentini, R., 2016. Discrimination of tropical forest types, dominant species, and  
920 mapping of functional guilds by hyperspectral and simulated multispectral Sentinel-2  
921 data. *Remote Sens. Environ.* 176, 163–176. <https://doi.org/10.1016/j.rse.2016.01.017>

922 Legendre, P., Legendre, L.F.J., 1998. *Numerical ecology*. Elsevier.

923 Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A., Bond, W.J., 2011. Deciphering the  
924 distribution of the savanna biome. *New Phytol.* 191, 197–209.  
925 <https://doi.org/10.1111/j.1469-8137.2011.03689.x>

926 Letouzey, R., 1985. *Carte phytogéographique du Cameroun, 1:500 000, 8 feuillets + 5*  
927 *notices*. Institut de la Carte Internationale de la Végétation, Toulouse, France.

928 Liu, J., Heiskanen, J., Maeda, E.E., Pellikka, P.K.E., 2018. Burned area detection based on  
929 Landsat time series in savannas of southern Burkina Faso. *Int. J. Appl. Earth Obs.*  
930 *Geoinf.* 64, 210–220. <https://doi.org/https://doi.org/10.1016/j.jag.2017.09.011>

931 Ma, X., Mahecha, M.D., Migliavacca, M., van der Plas, F., Benavides, R., Ratcliffe, S.,  
932 Kattge, J., Richter, R., Musavi, T., Baeten, L., Barnoiaea, I., Bohn, F.J., Bouriaud, O.,

933 Bussotti, F., Coppi, A., Domisch, T., Huth, A., Jaroszewicz, B., Joswig, J., Pabon-  
934 Moreno, D.E., Papale, D., Selvi, F., Laurin, G.V., Valladares, F., Reichstein, M., Wirth,  
935 C., 2019. Inferring plant functional diversity from space: the potential of Sentinel-2.  
936 *Remote Sens. Environ.* 233, 111368. <https://doi.org/10.1016/j.rse.2019.111368>

937 Machida, W.S., Gomes, L., Moser, P., Castro, I.B., Miranda, S.C., da Silva-Júnior, M.C.,  
938 Bustamante, M.M.C., 2021. Long term post-fire recovery of woody plants in savannas of  
939 central Brazil. *For. Ecol. Manage.* 493, 119255.  
940 <https://doi.org/10.1016/j.foreco.2021.119255>

941 Miller, J.D., Thode, A.E., 2007. Quantifying burn severity in a heterogeneous landscape with  
942 a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sens. Environ.*  
943 109, 66–80. <https://doi.org/https://doi.org/10.1016/j.rse.2006.12.006>

944 Mitchard, E.T.A., Flintrop, C.M., 2013. Woody encroachment and forest degradation in sub-  
945 Saharan Africa ' s woodlands and savannas 1982 – 2006. *Philos. Trans. R. Soc. B Biol.*  
946 *Sci.* 368, 1–7. <https://doi.org/http://dx.doi.org/10.1098/rstb.2012.0406>

947 Mitchard, E.T.A., Saatchi, S.S., Gerard, F.F., Lewis, S.L., Meir, P., 2009. Measuring woody  
948 encroachment along a forest-savanna boundary in Central Africa. *Earth Interact.* 13,  
949 29pp. <https://doi.org/10.1175/2009EI278.1>

950 Mitchard, E.T.A., Saatchi, S.S., Lewis, S.L., Feldpausch, T.R., Woodhouse, I.H., Sonké, B.,  
951 Rowland, C., Meir, P., 2011. Measuring biomass changes due to woody encroachment  
952 and deforestation / degradation in a forest – savanna boundary region of central Africa  
953 using multi-temporal L-band radar backscatter. *Remote Sens. Environ.* 115, 2861–2873.  
954 <https://doi.org/10.1016/j.rse.2010.02.022>

955 Moran, E.F., Brondizio, E.S., Tucker, J.M., da Silva-Forsberg, M.C., McCracken, S., Falesi,  
956 I., 2000. Effects of soil fertility and land-use on forest succession in Amazônia. *For.*  
957 *Ecol. Manage.* 139, 93–108. [https://doi.org/10.1016/S0378-1127\(99\)00337-0](https://doi.org/10.1016/S0378-1127(99)00337-0)

958 Nguyen, T.H., Jones, S., Soto-Berelov, M., Haywood, A., Hislop, S., 2020. Landsat time-  
959 series for estimating forest aboveground biomass and its dynamics across space and  
960 time: A review. *Remote Sens.* 12, 1–25. <https://doi.org/10.3390/RS12010098>

961 Niklas, K.J., Spatz, H.C., 2010. Worldwide correlations of mechanical properties and green  
962 wood density. *Am. J. Bot.* 97, 1587–1594. <https://doi.org/10.3732/ajb.1000150>

963 Oliveras, I., Malhi, Y., 2016. Many shades of green: the dynamic tropical forest–savannah  
964 transition zones. *Philos. Trans. R. Soc. Biol. Sci.* 371, 15pp.  
965 <https://doi.org/10.1098/rstb.2015.0308>

966 Olofsson, P., Foody, G.M., Herold, M., Stehman, S. V., Woodcock, C.E., Wulder, M.A.,  
967 2014. Good practices for estimating area and assessing accuracy of land change. *Remote*  
968 *Sens. Environ.* 148, 42–57. <https://doi.org/10.1016/j.rse.2014.02.015>

969 Pachauri, R., Meyer, L.A., 2014. *Climate Change 2014: Synthesis Report. Contribution of*  
970 *Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental*  
971 *Panel on Climate Change.* Geneva, Switzerland.

972 Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S., Wohlgemuth, T., 2002. Quantitative  
973 tools for perfecting species lists, in: *Environmetrics.* John Wiley & Sons, Ltd, pp. 121–  
974 137. <https://doi.org/10.1002/env.516>

975 Panshin, A.J., De Zeeuw, C., 1980. *Textbook of wood technology : structure, identification,*  
976 *properties, and uses of the commercial woods of the United States and Canada.* McGraw-  
977 Hill.

978 R Core Team, 2018. *R: A language and environment for statistical computing.* R Foundation  
979 for Statistical Computing.

980 Ramo, R., Roteta, E., Bistinas, I., van Wees, D., Bastarrika, A., Chuvieco, E., van der Werf,  
981 G.R., 2021. African burned area and fire carbon emissions are strongly impacted by  
982 small fires undetected by coarse resolution satellite data. *Proc. Natl. Acad. Sci.* 118,  
983 e2011160118. <https://doi.org/10.1073/pnas.2011160118>

984 Réjou-Méchain, M., Flores, O., Péliissier, R., Fayolle, A., Fauvet, N., Gourlet-Fleury, S.,  
985 2014. Tropical tree assembly depends on the interactions between successional and soil  
986 filtering processes. *Glob. Ecol. Biogeogr.* 23, 1440–1449.  
987 <https://doi.org/10.1111/geb.12222>

988 Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S., Kark, S.,  
989 Levin, N., Lucas, K., Luoto, M., Nagendra, H., Oldeland, J., Ricotta, C., Southworth, J.,  
990 Neteler, M., 2010. Remotely sensed spectral heterogeneity as a proxy of species  
991 diversity: Recent advances and open challenges. *Ecol. Inform.* 5, 318–329.  
992 <https://doi.org/10.1016/j.ecoinf.2010.06.001>

993 Rocchini, D., Boyd, D.S., Féret, J.B., Foody, G.M., He, K.S., Lausch, A., Nagendra, H.,  
994 Wegmann, M., Pettorelli, N., 2016. Satellite remote sensing to monitor species diversity:  
995 potential and pitfalls. *Remote Sens. Ecol. Conserv.* 2, 25–36.  
996 <https://doi.org/10.1002/rse2.9>

997 Romijn, E., Lantican, C.B., Herold, M., Lindquist, E., Ochieng, R., Wijaya, A., Murdiyarso,  
998 D., Verchot, L., 2015. Assessing change in national forest monitoring capacities of 99  
999 tropical countries. *For. Ecol. Manage.* 352, 109–123.  
1000 <https://doi.org/10.1016/j.foreco.2015.06.003>

1001 Roteta, E., Bastarrika, A., Padilla, M., Storm, T., Chuvieco, E., 2019. Development of a  
1002 Sentinel-2 burned area algorithm: Generation of a small fire database for sub-Saharan  
1003 Africa. *Remote Sens. Environ.* 222, 1–17. <https://doi.org/10.1016/j.rse.2018.12.011>

1004 Roussel, J.-R., David, A., Florian, D.B., Anderw, S.M., Jean-François, B., Demetrios, G.,  
1005 Steinmeier, L., Stanislaw Adaszewski, 2021. Package ‘lidR.’

1006 Rüger, N., Condit, R., Dent, D.H., DeWalt, S.J., Hubbell, S.P., Lichstein, J.W., Lopez, O.R.,  
1007 Wirth, C., Fariior, C.E., 2020. Demographic trade-offs predict tropical forest dynamics.  
1008 *Science (80- )*. 368, 165–168. <https://doi.org/10.1126/science.aaz4797>

1009 Sagang, L.B.T., Ploton, P., Sonké, B., Poilvé, H., Couteron, P., Barbier, N., 2020. Airborne  
1010 Lidar Sampling Pivotal for Accurate Regional AGB Predictions from Multispectral  
1011 Images in Forest-Savanna Landscapes. *Remote Sens.* 12, 20pp.  
1012 <https://doi.org/doi:10.3390/rs12101637>

1013 Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux,  
1014 J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G.,  
1015 Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C.,  
1016 Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea,  
1017 W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African  
1018 savannas. *Nature* 438, 846–849. <https://doi.org/10.1038/nature04070>

1019 Santoir, C., Bopda, A., 1995. Atlas régional Sud-Cameroun.

1020 Santoro, M., Cartus, O., Carvalhais, N., Rozendaal, D., Avitabile, V., Araza, A., De Bruin, S.,  
1021 Herold, M., Quegan, S., Rodr\`iguez-Veiga, P., others, 2021. The global forest above-  
1022 ground biomass pool for 2010 estimated from high-resolution satellite observations.  
1023 *Earth Syst. Sci. Data* 13, 3927–3950.

- 1024 Silveira, F.A.O., Arruda, A.J., Bond, W., Durigan, G., Fidelis, A., Kirkman, K., Oliveira,  
1025 R.S., Overbeck, G.E., Sansevero, J.B.B., Siebert, F., Siebert, S.J., Young, T.P., Buisson,  
1026 E., 2020. Myth-busting tropical grassy biome restoration. *Restor. Ecol.* 28, 1067–1073.  
1027 <https://doi.org/10.1111/REC.13202>
- 1028 Sirami, C., Seymour, C., Midgley, G., Barnard, P., 2009. The impact of shrub encroachment  
1029 on savanna bird diversity from local to regional scale. *Divers. Distrib.* 15, 948–957.  
1030 <https://doi.org/10.1111/J.1472-4642.2009.00612.X>
- 1031 Sosef, M.S.M., Dauby, G., Blach-Overgaard, A., van der Burgt, X., Catarino, L., Damen, T.,  
1032 Deblauwe, V., Dessein, S., Dransfield, J., Droissart, V., Duarte, M.C., Engledow, H.,  
1033 Fadeur, G., Figueira, R., Gereau, R.E., Hardy, O.J., Harris, D.J., de Heij, J., Janssens, S.,  
1034 Klomberg, Y., Ley, A.C., Mackinder, B.A., Meerts, P., van de Poel, J.L., Sonké, B.,  
1035 Stévert, T., Stoffelen, P., Svenning, J.C., Sepulchre, P., Zaiss, R., Wieringa, J.J.,  
1036 Couvreur, T.L.P., 2017. Exploring the floristic diversity of tropical Africa. *BMC Biol.*  
1037 15, 1–23. <https://doi.org/10.1186/s12915-017-0356-8>
- 1038 Souverijns, N., Buchhorn, M., Horion, S., Fensholt, R., Verbeeck, H., Verbesselt, J., Herold,  
1039 M., Tsendbazar, N.-E., Bernardino, P.N., Somers, B., Van De Kerchove, R., 2020. Thirty  
1040 Years of Land Cover and Fraction Cover Changes over the Sudano-Sahel Using Landsat  
1041 Time Series. *Remote Sens.* 12. <https://doi.org/10.3390/rs12223817>
- 1042 Staver, A.C., Archibald, S., Levin, S., 2011a. Tree cover in sub-Saharan Africa : Rainfall and  
1043 fire constrain forest and savanna as alternative stable states. *Ecol. Stud.* 92, 1063–1072.
- 1044 Staver, A.C., Archibald, S., Levin, S.A., 2011b. The Global Extent and Determinants of  
1045 Savanna and Forest as Alternative Biome States. *Science* (80-. ). 334, 230–232.  
1046 <https://doi.org/10.1126/science.1210465>
- 1047 Stevens, N., Erasmus, B.F.N., Archibald, S., Bond, W.J., 2016. Woody encroachment over 70  
1048 years in South African savannahs: Overgrazing, global change or extinction aftershock?  
1049 *Philos. Trans. R. Soc. Biol. Sci.* 371, 9pp. <https://doi.org/10.1098/rstb.2015.0437>
- 1050 Stevens, N., Lehmann, C.E.R., Murphy, B.P., Durigan, G., 2017. Savanna woody  
1051 encroachment is widespread across three continents. *Glob. Chang. Biol.* 23, 235–244.  
1052 <https://doi.org/10.1111/gcb.13409>
- 1053 Suarez, D.R., Phillips, O.L., Rozendaal, D.M.A., Sy, V. De, Dávila, E.A., Teixeira, K.A.,  
1054 Araujo, A., Luzmila, M., Timothy, A., Frans, R.B., Griscom, B.W., Carter, S., Cook,

1055 S.C., Ted, P., Harris, N., Hérault, B., Leavitt, S.M., Lewis, S.L., N, J.K., Guessan,  
1056 A.E.N., Sist, P., Mendoza, A.M., Sonké, B., Sullivan, M.J.P., Wang, M.M.H., Martius,  
1057 C., Vilanova, E., Herold, M., 2019. Estimating aboveground net biomass change for  
1058 tropical and subtropical forests : Refinement of IPCC default rates using forest plot data.  
1059 *Glob. Chang. Biol.* 3609–3624. <https://doi.org/10.1111/gcb.14767>

1060 Sullivan, M.J.P., TalbDiversity and carbon storage across the tropical forest biomeot, J.,  
1061 Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau,  
1062 W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland,  
1063 T., Ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S.I., De Almeida, E.C., De  
1064 Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C.,  
1065 Ashton, P., Aymard, G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin,  
1066 J.F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R., Camargo, J.L.C., Cerón,  
1067 C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde,  
1068 F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, M.N.,  
1069 Doucet, J.L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R.,  
1070 Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K.,  
1071 Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F., Leal, M.E., Lovejoy, T.,  
1072 Lovett, J.C., Lukasu, F.M., Makana, J.R., Malhi, Y., Maracahipes, L., Marimon, B.S.,  
1073 Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R.,  
1074 Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance,  
1075 G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma,  
1076 J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P.,  
1077 Samsedin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoung, H.,  
1078 Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umunay, P.M., Gamarra, L.V.,  
1079 Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and  
1080 carbon storage across the tropical forest biome. *Sci. Rep.* 7.  
1081 <https://doi.org/10.1038/srep39102>

1082 Sunderman, S.O., Weisberg, P.J., 2011. Remote sensing approaches for reconstructing fire  
1083 perimeters and burn severity mosaics in desert spring ecosystems. *Remote Sens.*  
1084 *Environ.* 115, 2384–2389. <https://doi.org/10.1016/j.rse.2011.05.001>

1085 Thomas, C.D., Anderson, B.J., Moilanen, A., Eigenbrod, F., Heinemeyer, A., Quaipe, T., Roy,  
1086 D.B., Gillings, S., Armsworth, P.R., Gaston, K.J., 2013. Reconciling biodiversity and  
1087 carbon conservation. *Ecol. Lett.* 16, 39–47. <https://doi.org/10.1111/ele.12054>

1088 USGS, 2020. United States Geological Survey. Science for a changing world [WWW  
1089 Document]. URL <https://earthexplorer.usgs.gov/>

1090 Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. *New Phytol.*  
1091 <https://doi.org/10.1111/j.1469-8137.2010.03284.x>

1092 Valentini, R., Arneeth, A., Bombelli, A., Castaldi, S., Cazzolla Gatti, R., Chevallier, F., Ciais,  
1093 P., Grieco, E., Hartmann, J., Henry, M., Houghton, R.A., Jung, M., Kutsch, W.L., Malhi,  
1094 Y., Mayorga, E., Merbold, L., Murray-Tortarolo, G., Papale, D., Peylin, P., Poulter, B.,  
1095 Raymond, P.A., Santini, M., Sitch, S., Vaglio Laurin, G., van der Werf, G.R., Williams,  
1096 C.A., Scholes, R.J., 2014. A full greenhouse gases budget of Africa: synthesis,  
1097 uncertainties, and vulnerabilities. *Biogeosciences* 11, 381–407.  
1098 <https://doi.org/10.5194/bg-11-381-2014>

1099 Veenendaal, E.M., Feldpausch, T.R., Domingues, T.F., Gerard, F., Schrodtt, F., Saiz, G.,  
1100 Quesada, C.A., Djangbletey, G., Ford, A., Kemp, J., Marimon, B.S., Lenza, E., Ratter,  
1101 J.A., Maracahipes, L., Sasaki, D., Zapfack, L., Villarroel, D., Schwarz, M., Ishida, F.Y.,  
1102 Gilpin, M., Nardoto, G.B., Arroyo, L., Bloomfield, K., Ceca, G., Compaore, H., Davies,  
1103 K., Diallo, A., Fyllas, N.M., Gignoux, J., Hien, F., Johnson, M., Mouglin, E., Hiernaux,  
1104 P., Killeen, T., Metcalfe, D., Miranda, H.S., Steininger, M., Sykora, K., Bird, M.I.,  
1105 Grace, J., Lewis, S., Phillips, O.L., Lloyd, J., 2015. Structural , physiognomic and above-  
1106 ground biomass variation in savanna – forest transition zones on three continents – how  
1107 different are co-occurring savanna and forest formations ? *Biogeosciences* 12, 2927–  
1108 2951. <https://doi.org/10.5194/bg-12-2927-2015>

1109 Veenendaal, E.M., Torello-Raventos, M., Miranda, H.S., Sato, N.M., Oliveras, I., Langevelde,  
1110 F., Asner, G.P., Lloyd, J., 2018. On the relationship between fire regime and vegetation  
1111 structure in the tropics. *New Phytol.* 218, 153–166. <https://doi.org/10.1111/NPH.14940>

1112 Veldman, J.W., 2016. Clarifying the confusion : old-growth savannahs and tropical ecosystem  
1113 degradation. *Philos. Trans. R. Soc. B Biol. Sci.* 371, 11.

1114 Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W.,  
1115 Durigan, G., Buisson, E., Putz, F.E., Bond, W.J., 2015. Where Tree Planting and Forest  
1116 Expansion are Bad for Biodiversity and Ecosystem Services. *Bioscience* 65, 1011–1018.  
1117 <https://doi.org/10.1093/biosci/biv118>

1118 Venter, Z.S., Cramer, M.D., Hawkins, H.J., 2018. Drivers of woody plant encroachment over

- 1119 Africa. Nat. Commun. 9, 1–7. <https://doi.org/10.1038/s41467-018-04616-8>
- 1120 Verbesselt, J., Hyndman, R., Newnham, G., Culvenor, D., 2010. Detecting trend and seasonal  
1121 changes in satellite image time series. *Remote Sens. Environ.* 114, 106–115.  
1122 <https://doi.org/10.1016/j.rse.2009.08.014>
- 1123 Viani, R.A.G., Rodrigues, R.R., Dawson, T.E., Oliveira, R.S., 2011. Savanna soil fertility  
1124 limits growth but not survival of tropical forest tree seedlings. *Plant Soil* 349, 341–353.  
1125 <https://doi.org/10.1007/s11104-011-0879-7>
- 1126 Waldner, F., Defourny, P., 2017. Where can pixel counting area estimates meet user-defined  
1127 accuracy requirements? *Int. J. Appl. Earth Obs. Geoinf.* 60, 1–10.  
1128 <https://doi.org/https://doi.org/10.1016/j.jag.2017.03.014>
- 1129 Walters, G., 2012. Customary Fire Regimes and Vegetation Structure in Gabon’s Bateke  
1130 Plateaux. *Hum. Ecol.* 40, 943–955. <https://doi.org/10.1007/s10745-012-9536-x>
- 1131 Wulder, M.A., White, J.C., Nelson, R.F., Næsset, E., Ørka, H.O., Coops, N.C., Hilker, T.,  
1132 Bater, C.W., Gobakken, T., 2012. Lidar sampling for large-area forest characterization:  
1133 A review. *Remote Sens. Environ.* 121, 196–209.  
1134 <https://doi.org/10.1016/j.rse.2012.02.001>
- 1135 Xie, Z., Phinn, S.R., Game, E.T., Pannell, D.J., Hobbs, R.J., Briggs, P.R., McDonald-Madden,  
1136 E., 2019. Using Landsat observations (1988–2017) and Google Earth Engine to detect  
1137 vegetation cover changes in rangelands - A first step towards identifying degraded lands  
1138 for conservation. *Remote Sens. Environ.* 232, 111317.  
1139 <https://doi.org/10.1016/j.rse.2019.111317>
- 1140 Youta-Happi, J., 1998. Arbres contre graminées : la lente invasion de la savane par la forêt au  
1141 Centre-Cameroun. PhD Thesis. Université De Paris-Sorbone (PARIS IV). 241 p. Thesis.  
1142 Université De Paris-Sorbone (PARIS IV).
- 1143 Youta-Happi, J., Bonvallet, J., 1996. La disparition des savanes au Centre Cameroun entre  
1144 1950 et 1990, in: CNRS-ORSTOM (Ed.), *Dynamique à Long Terme Des Écosystèmes*  
1145 *Forestiers Intertropicaux*. Paris, France, p. 3.
- 1146 Youta-Happi, J., Bonvallet, J., Hotyat, M., Guillet, B., Peltre, P., Schwartz, D., Servant, M.,  
1147 Simonneaux, V., 2003. Bilan de la dynamique du contact forêt-savane en quarante ans (  
1148 1950-1990 ) Dans la région du confluent du Mbam et du Kim, Centre-Cameroun, in:

- 1149 IRD, É. (Ed.), *Peuplements Anciens et Actuels Des Forêts Tropicales*. p. 380 p.  
1150 <https://doi.org/10.4000/books.irdeditions.1486>
- 1151 Zeng, Z., Piao, S., Chen, A., Lin, X., Nan, H., Li, J., Ciais, P., 2013. Committed changes in  
1152 tropical tree cover under the projected 21st century climate change. *Sci. Rep.* 3, 1951.  
1153 <https://doi.org/10.1038/srep01951>
- 1154 Zhang, K., Chen, S., Whitman, D., Shyu, M., Yan, J., 2003. A Progressive Morphological  
1155 Filter for Removing Nonground Measurements From Airborne LIDAR Data 41, 872–  
1156 882.