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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-03649011>

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1 Title:

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

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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 km² 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⁻¹ (6
32 km².year⁻¹). 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⁻¹.year⁻¹ 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 ≈ 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 β -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⁻¹ (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.

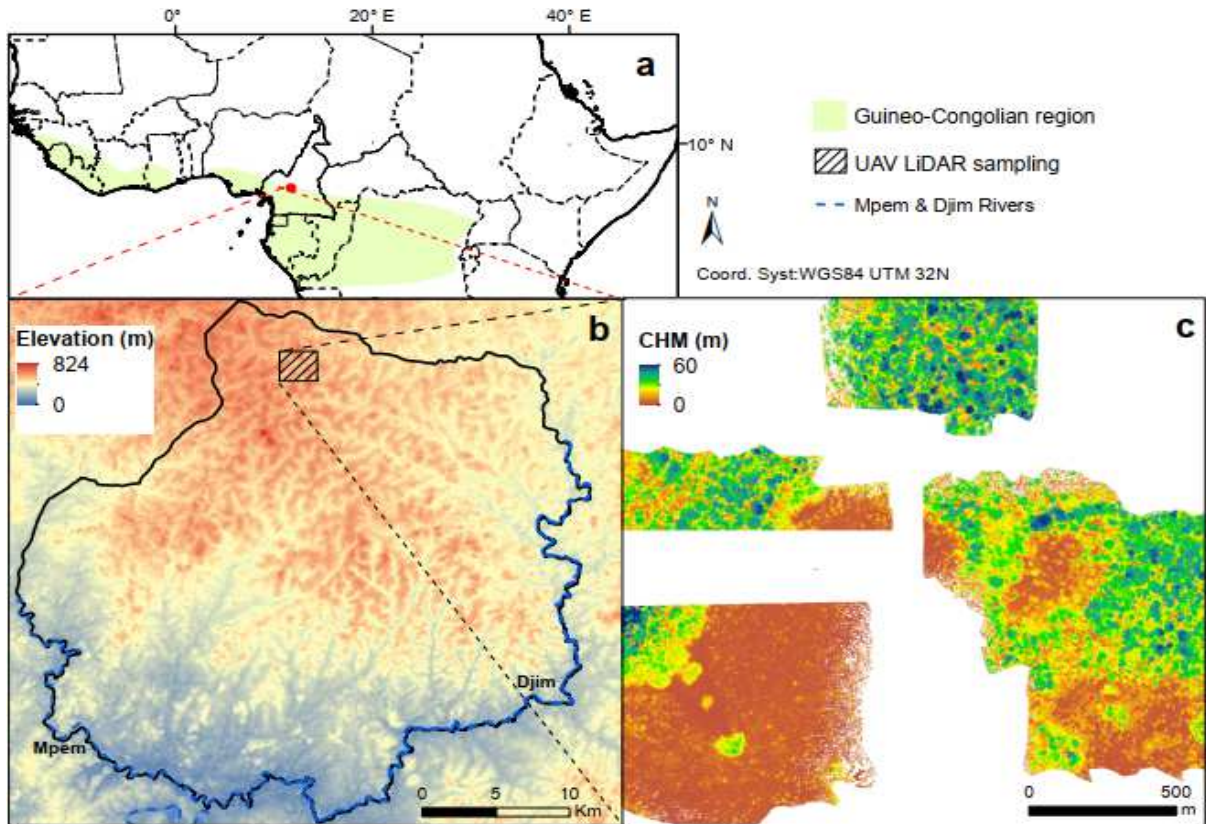
112 The objective of this study is twofold: the first aim is to advance our understanding of the
113 dynamics and drivers of forest-savanna transitions, and their consequences in terms of above-
114 ground carbon storage and tree species diversity. The second aim is to provide land managers
115 (conservationists, 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 β -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 km². 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).

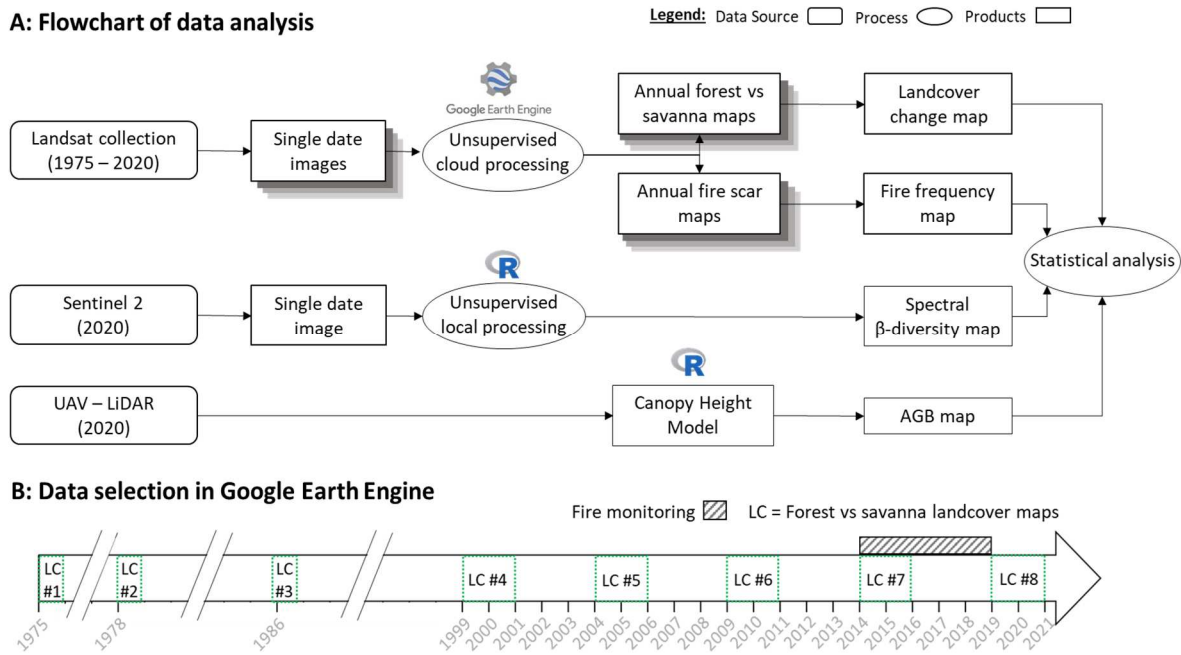


138
 139 Fig. 1: Study area. (a) Location (red point) within the Guineo-Congolian transitional area (light
 140 green) and (b) boundaries of the Mpem & Djim National Park (full black polygon) following
 141 Mpem and Djim rivers (overlapping blue dashed lines). (c) UAV LiDAR-derived Canopy
 142 Height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

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

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).

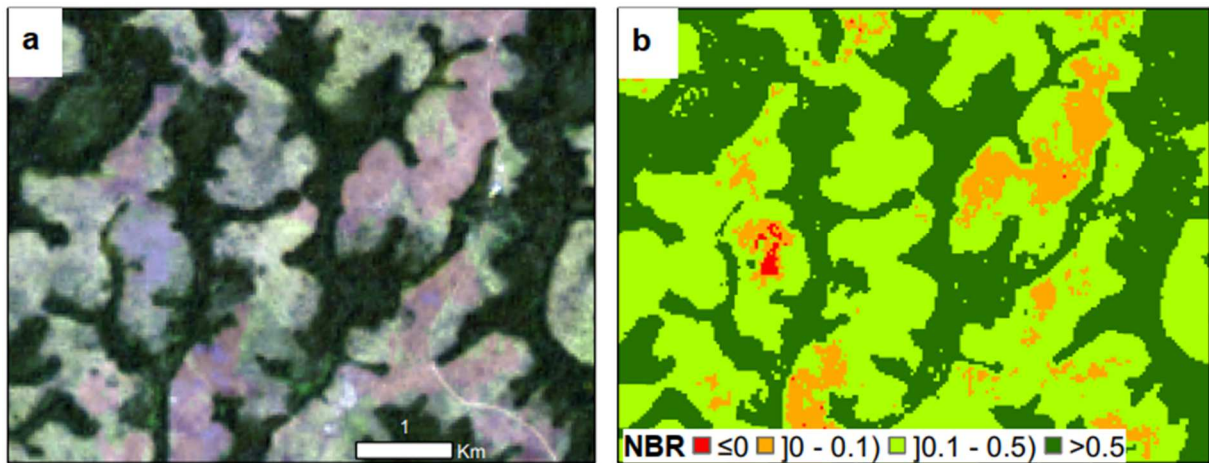
266 2.4.1. Mapping fires scars

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

296 aggregated the information contained in pixels' fire scars time series into yearly observations.
297 For a given pixel a year was considered as a "burned year" when the pixel was classified as fire
298 scar for at least two consecutive observations. The FFI for a pixel was then computed as the
299 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 km²) 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

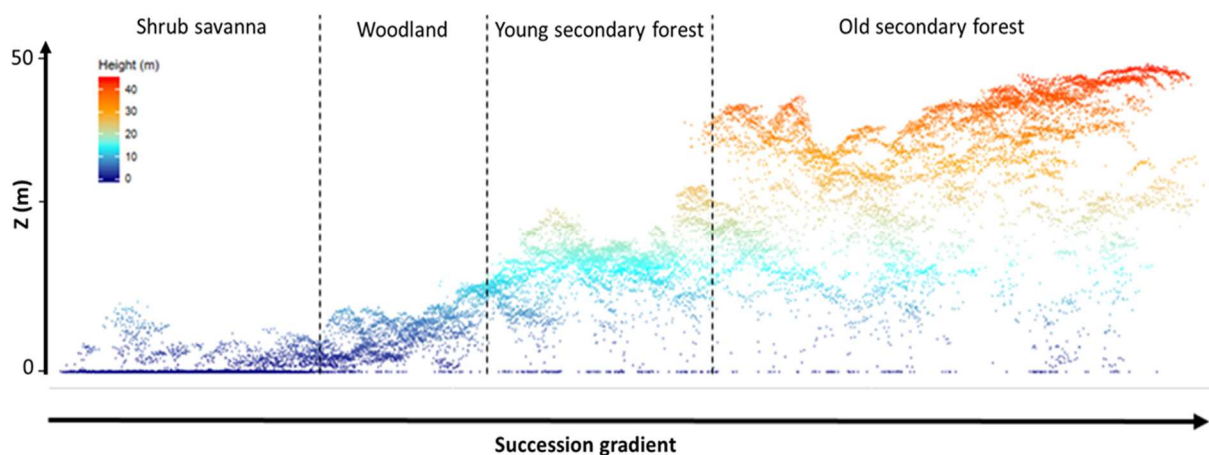
310 2.5.1. Spectral composition gradients

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⁻¹. 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⁻². 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⁻¹ and CHM in m.

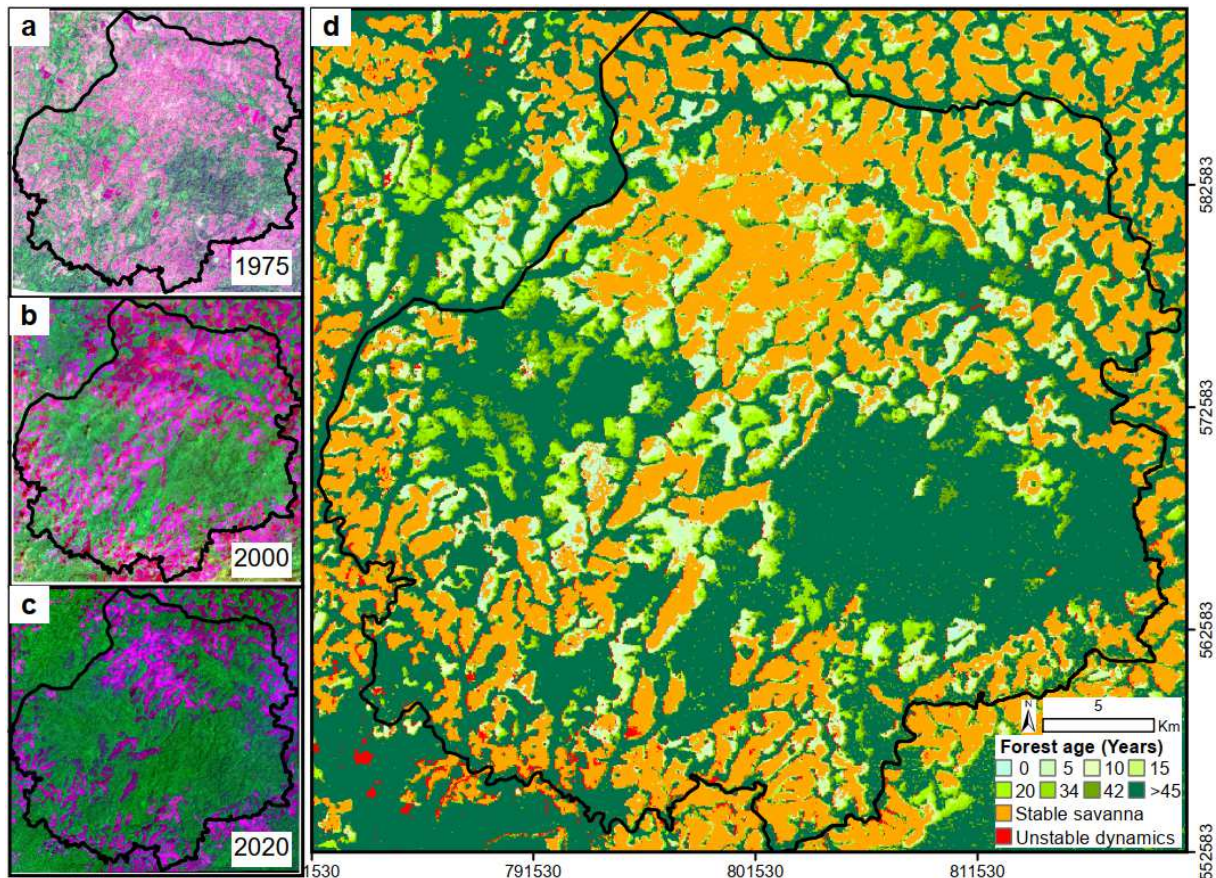
375 Further, we evaluated the rate of AGB uptake for young secondary forests (≤ 20 years; IPCC,
376 2006) and all the transitory forests (< 45 years; forest that appeared between 1975 and 2020)
377 by (i) resampling the AGB map from 40-m to the 30-m resolution at which vegetation dynamics
378 was assessed, 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

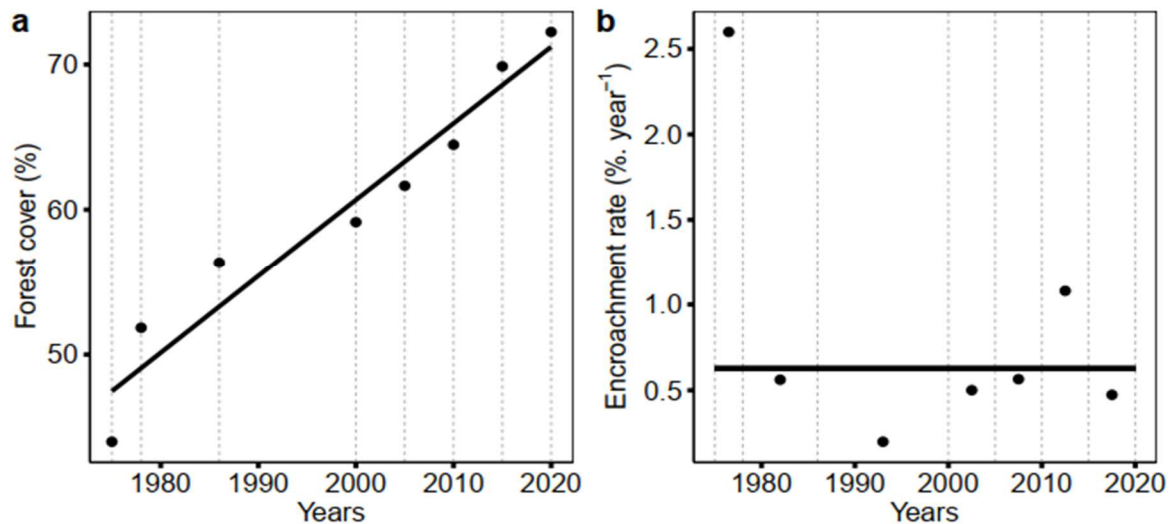
383 Overall accuracies of automated forest-savanna classifications ranged from 85.78% (± 6.26) to
384 96.85% (± 3.57) with an average of 92.54% (± 4.72, Appendix C). The Landsat 2 acquisition
385 of dec. 1975 (Fig. 5-a) shows that the MDNP was at that time dominated by savannas (c. 54%

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 km² 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 km² ± 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

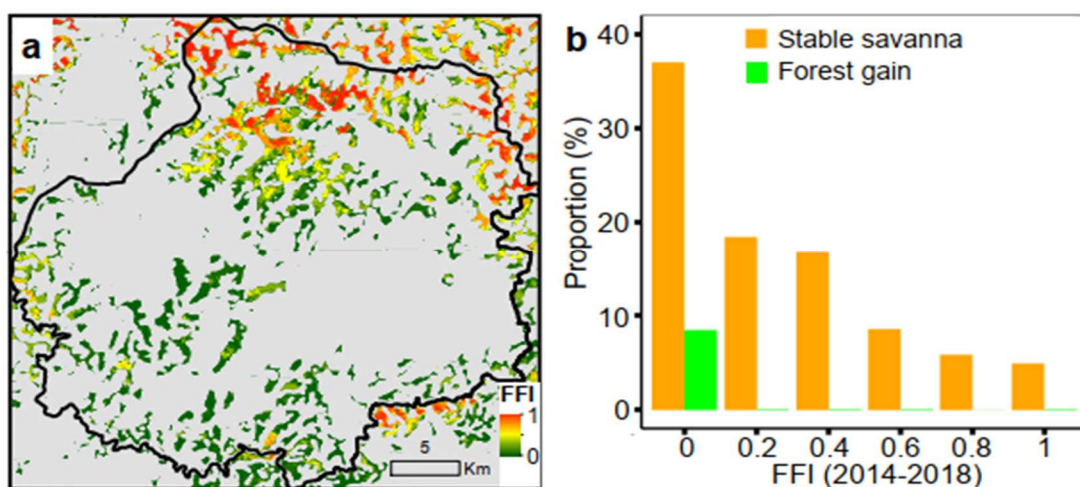
397 The landcover change map depicted a consistent and regular pattern of forest progression into
 398 savanna (Fig. 6-a) and allowed deducing current forest age (displayed in Fig. 5-d) and average
 399 rate of forest progression. For instance, a weighted mean of forest encroachment rates obtained
 400 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⁻¹ or equivalently c. 6 km².year⁻¹ (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

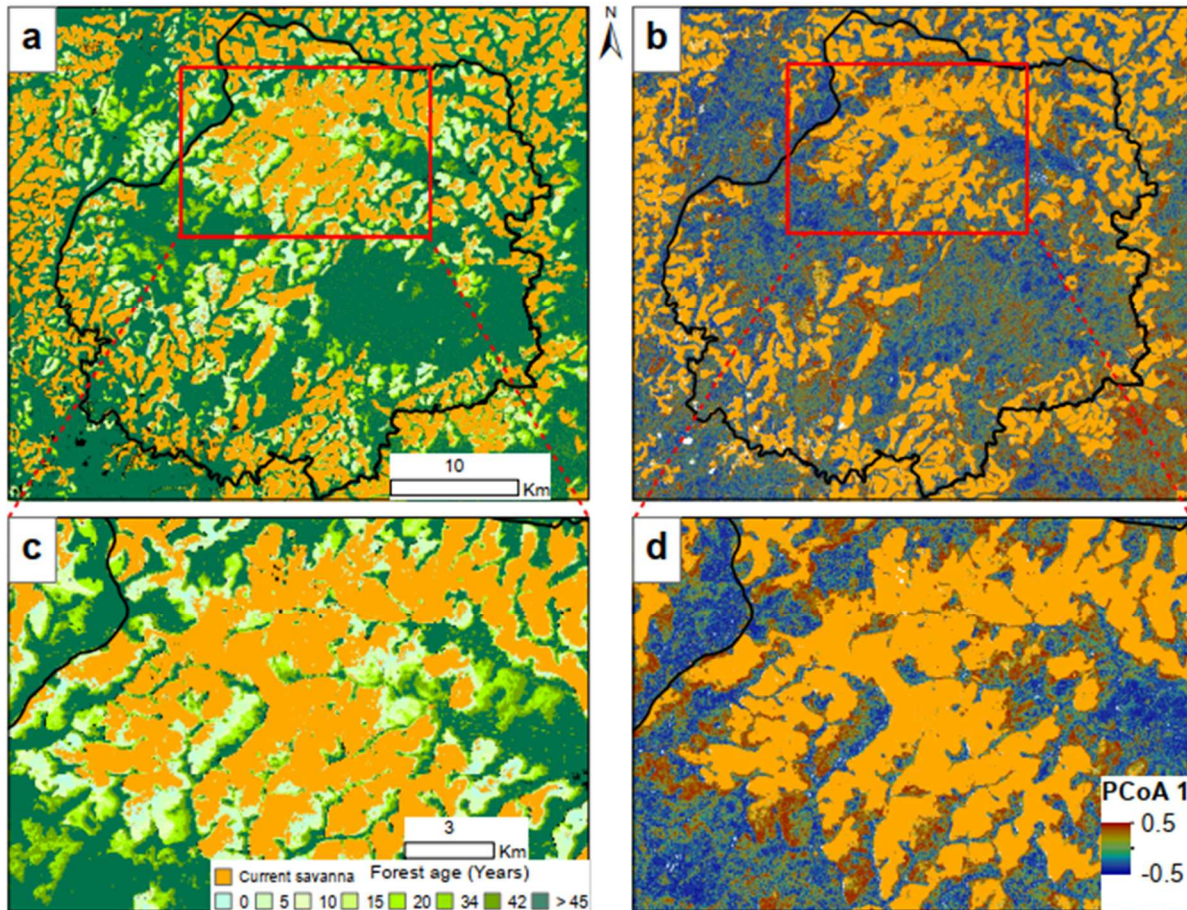
414 Based on a visual interpretation we noticed that savannas surrounding the park principally in
 415 the northern part underwent higher fire frequencies as compared to the southern savannas (Fig.
 416 7-a). Most of the savanna that transitioned to forest between two consecutive dates had an average
 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.

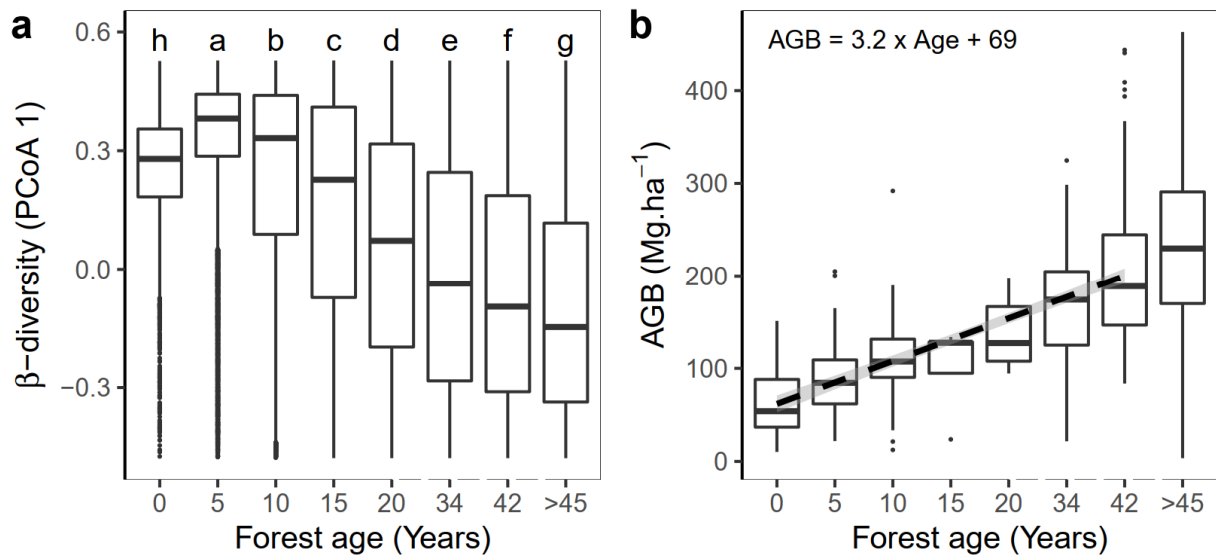
425 3.3. Change in forest composition and structure with age

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.

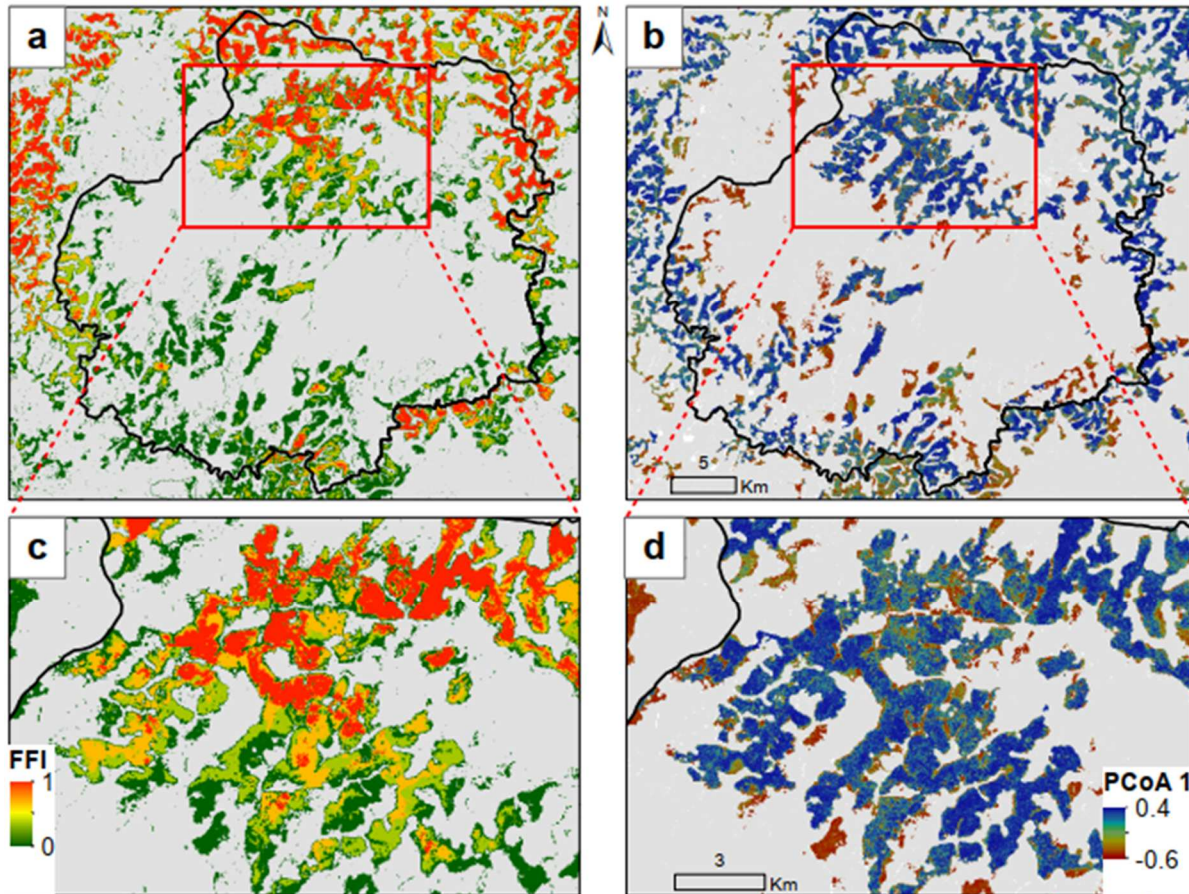


442
 443 Fig. 9: Relationships between forest age, spectral composition and structure. (a) Boxplot of
 444 spectral composition derived from PCoA 1 (see section 2.5.1 for details), by forest age bins.
 445 Labelled letters represent the results of a Tukey honest significant difference (HSD) test, with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

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 $61 \pm 33 \text{ Mg}\cdot\text{ha}^{-1}$ for younger forests
 454 (less than 5 years since afforestation) up to $230 \pm 80 \text{ Mg}\cdot\text{ha}^{-1}$ for the oldest forests (> 45 years).
 455 The transition map thus suggested an average linear increase of about $3.2 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ in
 456 MDNP forests since 1975 (Fig. 9-b). Young regenerating forests (≤ 20 years) seemed to show
 457 a higher AGB accumulation rate of $4.1 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (not shown).

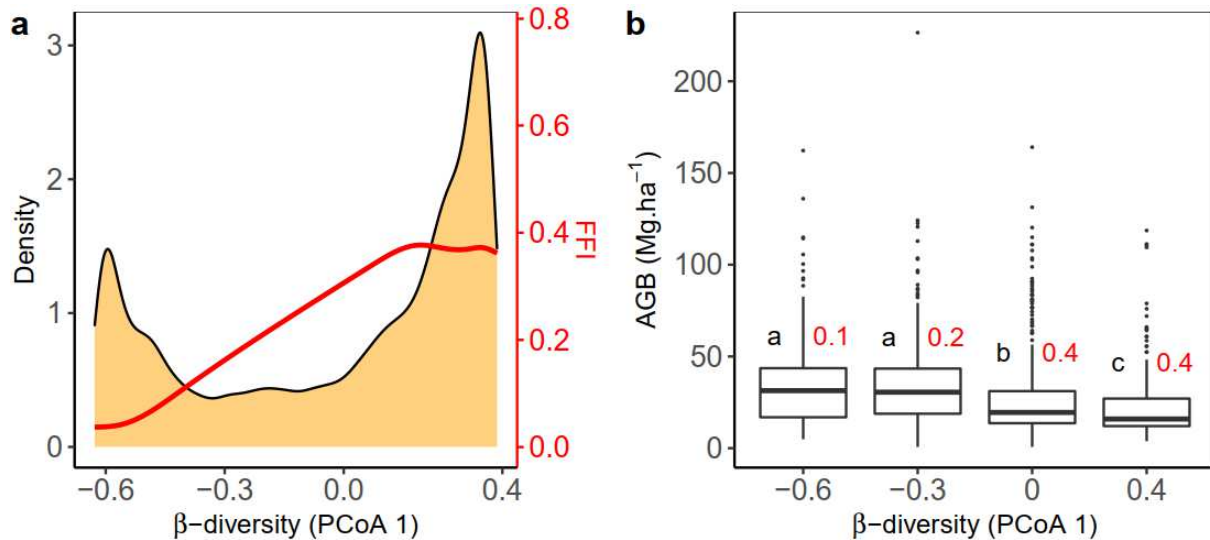
458 3.4. Change in savanna composition and structure with fire frequency

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 km²) 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⁻¹ 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 (≤ 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⁻¹) with low fire frequencies (corresponding to woody
576 savanna) to low AGB (ca. 22 Mg.ha⁻¹) 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⁻¹) and intermediate AGB (\approx
580 27 Mg/ha⁻¹). 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⁻¹. Once this
588 threshold is exceeded, the AGB build-up towards 36 Mg.ha⁻¹ (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⁻¹. 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 CO₂ 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. $0.63\% \cdot \text{year}^{-1}$. 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](#) .

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