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Drier tropical forests are susceptible to functional changes in response to a long-term drought

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Contributions

J.A.G, Y.M. and B.E. conceived the idea of the study. Y.M. conceived and funded the traits field campaign, I.O., A.G., T.P. collected trait data, I.O. K.Z., A.G. processed laboratory samples and cleaned and parsed the GEM trait data, S.M., S.F., S.L., T.F., W.H., M.S., S.A., T.P. and K.A. collected the plant census data, and O.P., Y.M., and S.L. funded their collection. J.A.G. designed and carried out the analysis. J.A.G. led the writing with substantial input from Y.M. and I.O. All co-authors commented on and approved the manuscript.

Data availability

The vegetation census data and part of the traits data that support the findings of this study are available from their sources. The processed data, maps and code created or used in this study will be archived in a public

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56 repository and will be available from the corresponding author upon request. The data DOI will be included at
57 the end of the article.

For Review Only

58 **Abstract**

59 Climatic changes have profound effects on the distribution of biodiversity, but untangling the links
60 between climatic change and ecosystem functioning is challenging, particularly in high diversity
61 systems such as tropical forests. Tropical forests may also show different responses to a changing
62 climate, with baseline climatic conditions potentially inducing differences in the strength and timing
63 of responses to droughts. Trait-based approaches provide an opportunity to link functional
64 composition, ecosystem function and environmental changes. We demonstrate the power of such
65 approaches by presenting a novel analysis of long-term responses of different tropical forest to
66 climatic changes along a rainfall gradient. We explore how key ecosystem biogeochemical properties
67 have shifted over time as a consequence of multi-decadal drying. Notably, we find that drier tropical
68 forests have increased their deciduous species abundance and generally changed more functionally
69 than forests growing in wetter conditions, suggesting an enhanced ability to adapt ecologically to a
70 drying environment.

For Review Only

71 Introduction

72 The terrestrial biosphere is facing rapid changes as results of land-use and climate change with most
73 ecosystems suffering alterations in their functioning by either the loss of species or shifts in species
74 abundances (Pacifi et al. 2017). Nevertheless, methodological and data availability constraints
75 hamper our ability to monitor both the distributions of species and ecosystem responses to climate
76 change (Cayuela et al. 2009). These challenges are especially acute in high biodiversity areas such as
77 the tropics (Malhi et al. 2014), for which there is not only greater uncertainty concerning the effects
78 of climate on biodiversity, but also about current species distributions and their taxonomic identity
79 (Cardoso et al. 2017). Tropical forest ecosystems are an especially key component of global
80 biodiversity and have direct effects on human well-being through the varied set of ecosystem
81 functions they provide (Lewis et al. 2015), including via their role as major global stocks and sources
82 (Pan et al. 2013) and sinks (Pan et al. 2011) of carbon. Consequently, climate-driven forest
83 disturbances may have large-scale feedbacks on climate via carbon dynamics (Fauset et al. 2015).
84 However, tropical forest need not all respond in the same manner to environmental changes.
85 Notably, it is possible that wetter tropical forests, i.e. those with intrinsically lower water deficits,
86 may be either more sensitive, or more resistant, to climatic changes than tropical forest found in
87 drier environments (Allen et al. 2017). Understanding how climate baselines may modify tropical
88 forest responses to climate changes is of pivotal importance, not least because the different
89 responses of tropical forests to a drying climate may in turn modify biodiversity composition in
90 unexpected ways, including by accelerating or slowing tree mortality (Bonaf et al. 2016).

91 There are many challenges associated with deciphering the impacts of climate change on
92 forest ecosystems because of complex interactions between community composition and
93 physiological responses of individual species to a given environmental change. For instance, over an
94 elevational gradient in an Amazon to Andean forest transect, it was recently found that differences
95 in tree community composition and associated traits offset the temperature response of individual
96 species, leading to surprisingly modest spatial changes in productivity with elevation (Fyllas et al.
97 2017). Moreover, if communities respond to temporal environmental changes by shifting their
98 species abundances and trait distributions towards more suitable ranges (Fauset et al. 2012), new
99 dominant trait combinations may arise in the community. Changes in the community functional trait
100 composition may also imply changes in key aspects of ecosystem functioning such as nutrient,
101 carbon and water cycling. Therefore, understanding past and current responses of community level
102 traits has the potential to provide valuable insights into tropical forest resilience against
103 environmental changes and offer a promising avenue for a better understanding of ecosystem
104 functioning (Madani et al. 2018). While analysing biodiversity responses to environmental changes
105 at the community level is clearly desirable, it is a challenging task for tropical forests in particular
106 given their high diversity, relative paucity of trait data (e.g. Asner et al. 2015), and the difficulties
107 with sustaining long-term monitoring.

108 In addition to the challenges associated with monitoring responses of tropical forests across
109 climatic gradients to a drying environment, little is known about the effects of recent changes in
110 climate on community level trait composition. Analysing the precipitation anomaly over the last
111 century Fauset et al. (2012) have shown there has been a long term drying trend in tropical Western
112 Africa, which may had led to changes in forest composition and community level leaf phenology.
113 However, there is an overall lack of integrated knowledge on how long-term droughts affect

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3 114 hydraulic, leaf and wood related community traits that are hypothesised to be tightly linked to how
4 115 different tropical forest may respond to changes in climatic conditions. Here we coupled a unique
5 116 combination of intensive plant traits collections together with a wider set of trait data to long-term
6 117 forest inventories in a West African wet-dry forest gradient and explore if forests exposed to
7 118 different water deficits show differential responses to a drying climate.

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10 119 Given a drying trend across West Africa, we hypothesised that the tropical forest across the
11 120 climatic gradient have shifted their trait distributions but that the magnitude of the trait shifts may
12 121 be dependent on the forest type and the past and current climate conditions. Specifically, we
13 122 hypothesised that forests with usually low water deficits, i.e. intrinsically wetter forests, may be
14 123 more susceptible to a drying environment as their plant communities may be adapted to high levels
15 124 of moisture and water availability. These wetter forests are therefore expected to show stronger
16 125 trait shifts than drier forest. On the other hand, an increase in deciduousness may be a main strategy
17 126 adopted by communities at the edge of their climatic suitability, e.g. drier forests, in order to adapt
18 127 to a drying environment. Therefore, we expected to see an increase in the abundance of deciduous
19 128 species in drier forests under this scenario. Investigating if and how plant communities have shifted
20 129 their trait composition as a result of a drying climate will increase our understanding on how past
21 130 climatic conditions have shaped current plant trait distributions and will render insights into how
22 131 changes in climate may shape future tropical forest communities.

23 132 **Material and Methods**

24 133 *Study area and vegetation censuses*

25 134 The study focuses on the forest zone of Ghana, West Africa (Fig. 1a). We obtained vegetation census
26 135 data for 15 unique 1ha permanent plots with no signs of fire events or large logging actions and with
27 136 at least two censuses recorded from the African Tropical Rainforest Observation Network (AfriTRON;
28 137 www.afritron.org) (see Table S1 in supporting Information). Only four of the selected plots were
29 138 minimally affected by logging actions (≤ 0.08 ha) between the two censuses selected, of which the
30 139 affected area was left out from our analysis. The plots have their tree records databased and curated
31 140 at www.ForestPlots.net (Lopez-Gonzalez et al. 2009; Lopez-Gonzalez et al. 2011). In each plot, all
32 141 individuals with a diameter ≥ 10 cm at breast height (DBH) or above buttress were recorded, 7041
33 142 in the first census and 7170 during the second census. The individuals belonged to 330 different taxa,
34 143 which were identified to the species (93.2%) or genus level (6.8%) and their DBH was recorded.

35 144 *Species functional traits*

36 145 In 2015 and 2016 we collected the species traits data at seven permanent 1ha plots along a rainfall
37 146 gradient (Fig. S1), as part of the Global Ecosystems Monitoring campaign (GEM;
38 147 <http://gem.tropicalforests.ox.ac.uk/>). The selected traits characterise part of the species hydraulics,
39 148 leaf and wood economics spectrum (see Table 1 for their description and SI for their relevance). The
40 149 sites sampled were Ankasa (two plots) in the humid forest zone (latitude: 5.26, longitude: -2.69),
41 150 Bobiri (two plots) in the semi-deciduous forest zone (lat: 6.69, long: -1.33) and Kogyae (3 plots) on
42 151 the dry forest zone (lat: 7.26, long: -1.15). Further site details and description of the carbon cycle are
43 152 given in Moore et al (2018) and in full details of trait data collection are given in the extended
44 153 methods section in the Supplementary Information. The GEM traits database forms the main trait
45 154 input data and when needed was complemented with data from the BIEN (Enquist et al. 2009) and

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3 155 the TRY (Kattge et al. 2011) databases. We aimed to account for at least 60% of the plot's basal area
4 156 covered by trait information at the genus level. Reaching more than ~60% representation was often
5 157 possible but not always. In order to fill missing information we applied a Bayesian Hierarchical
6 158 Probabilistic Matrix Factorization approach (BHPMF, Schrodte et al. 2015). For extended details in the
7 159 BHPMF method see the SI. Our final gap-filled trait matrix used in subsequent analysis covered ~90%
8 160 of the plots' basal area with trait data (Fig. S2).

11 161 *Community level trait weighted mean*

12 162 The mass ratio hypothesis states that the most dominant species drive the ecosystem processes by
13 163 means of their traits (Grime 1998). We calculated for each of the traits t , and vegetation census
14 164 plots, p , their community level weighted mean (CWM) using the species basal area as the weighting
15 165 factor as follows: $CWM_{tp} = \sum_{i=1}^S BA_{ip} \times t_i$, where BA_{ip} is the basal area of species i in plot p and t_i is
16 166 the average trait value of species i . There is a strong relationship between basal area and crown area
17 167 as shown for old growth tropical forests (Shenkin et al. in review, Antin et al. 2013), and hence gives
18 168 an indication of the amount of canopy area occupied by a specific trait. Hence the CWM is an
19 169 indicator of mean canopy properties. In the case of categorical variables such as phenological
20 170 strategy, nitrogen fixing capacity and guild we calculated the species abundance of each of their
21 171 levels. We used the mean trait values per species. Species may show intraspecific trait variation,
22 172 which we do not completely capture here, however, it has been shown such variation is relatively
23 173 small in comparison to the trait variation found between tropical tree species and which is the focus
24 174 of our study (Rozendaal et al. 2006). All analyses of CWM were carried out using the log10
25 175 transformed trait values and were carried out with the R package "FD".

33 176 *Climatic data*

34 177 For each vegetation plot we calculated the maximum climatological water deficit (MCWD; Fig. 1b
35 178 and Fig. S3), a measure of drought intensity (Malhi et al. 2009). MCWD was defined as the most
36 179 negative value of the climatological water deficit (CWD) over a year. CWD is defined as precipitation
37 180 (P) (mm/month) – potential evapotranspiration (PET) (mm/month) with a minimum deficit of 0. To
38 181 calculate the MCWD for a time period representative of the vegetation census we obtained long-
39 182 term precipitation and evapotranspiration data from the TerraClimate dataset (Abatzoglou et al.
40 183 2018) which covers the period 1958 to 2017 at a spatial resolution of ~4x4 km. This dataset was
41 184 selected given its high spatial and temporal resolution and its greater accuracy when compared to
42 185 other historical dataset as the Climatic Research Unit data (Harris & Jones 2017). The current climate
43 186 products underestimate precipitation at the coast in Ghana where two of our plots (CAP_09 and
44 187 CAP_10) are located. Thus for these plots we averaged the MCWD of a radius of ten grid cells around
45 188 the plot locations and used this value to characterise their MCWD.

46 189 We characterise the climatic conditions across each of the two time periods with vegetation
47 190 census data, for the first period we captured the average MCWD between the years 1958 and 1992
48 191 and for the second between 1979 and 2013. Then the absolute ($\Delta MCWD_{Abs}$) and relative ($\Delta MCWD_{Rel}$)
49 192 changes in the MCWD between censuses was calculated by subtracting the $\Delta MCWD_{Abs}$ and
50 193 $\Delta MCWD_{Rel}$ of the first periods from that of the second. We also calculate the standardized
51 194 precipitation and evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010) using a 12 month

195 windows to explore the water deficit or surplus conditions over the past century using CRU TS data
196 (Harris & Jones 2017).

197 *Data analysis*

198 We conducted all statistical analysis in R (v. 3.4.1; www.r-project.org). We analysed the water
199 balance across each of the vegetation plots using the SPEI. After this we first investigated changes at
200 the plot level in the species basal area, number of individuals and number of species between
201 censuses. Second, we mapped the species distributions in trait space with a Principal Component
202 Analysis (PCA) using the NIPALS function with a maximum of 500 iterations in the “ade4” package to
203 infer species associations to the traits used. Third, we calculated the Δ CWM by subtracting the CWM
204 of census 1 from the CWM of census 2 for each trait and plot. We then grouped the plots based on
205 their MCWD, where plots with a MCWD \leq 250 were classified as “wetter” sites, thus with lower
206 water deficits and the rest as “drier” sites. We chose this threshold as it may represent a transition
207 from tropical wet forest towards a more seasonal and savanna like vegetation (Malhi et al. 2009).
208 Based on the above mentioned protocol, eight plots were classified as plots in “wetter” and seven as
209 in “drier” locations (Table S1). We investigated if there were significant changes in trait CWM by
210 means of Bayesian estimation (Kruschke 2013) for each one of the plot groups separately (“wetter”
211 and “drier”). Here we computed posterior distributions to compare the CWM change trait values of
212 between the two censuses, resulting in probability change estimates. We used normal priors with
213 large standard deviation for μ , broad uniform priors for σ , and a shifted-exponential prior for the
214 normality parameter ν , using the “BEST” package.

215 Lastly, we investigated if the community level trait changes were related to climatic
216 conditions, i.e. the absolute and relative changes in MCWD and the long-term MCWD, by means of
217 linear regression modelling under a Bayesian framework. We built a set of different models to
218 explain the Δ CWM: 1) a model using the Δ CWM as a function of the long-term MCWD; 2) we further
219 modelled the Δ CWM as a function of the Δ MCWD_{Abs}; 3) of the Δ MCWD_{Rel}; 4) also as a function of
220 changes in the abundance of deciduous species and its interaction with the forest type (“Dry” or
221 “Wet”); and 5) against a model which had no covariates, referred to as a null model. We compared
222 the five models described above and selected the best by means of leave one out cross-validation
223 (LOO). We fitted the models only for those traits that experienced an important change in their
224 CWM trait value. All models were built using the “rstanarm” and “loo” packages.

225 **Results**

226 *Long-term drought*

227 Our results with the SPEI confirm the presence of a long-term drought (Fig. 1b and Fig. S3). We
228 observed the onset of the drought starting between the 1970’s and 1980’s across the study sites
229 (negative SPEI values), becoming stronger in the 1990’s and becoming milder for most locations
230 after the year 2005 (positive SPEI values in Fig. 1b).

231 *Species dynamics*

232 There were 330 tree species present in the 15 study plots, which accounted for a total basal area
233 (BA) of 362 m² in the first vegetation census and 382 m² in the last vegetation census. From the total
234 species pool, 6 % experienced landscape-level changes in BA of between \pm 1 to \pm 5 m² (summed

235 across all 15 plots), which may strongly impact plot and landscape level trait composition (Fig. S4a).
 236 Of the 20 species changing more strongly in basal area seven accounted for a total decrease in BA of
 237 12 m² and 13 species for an increase of 24 m². Of these species, two (*Antiaris toxicaria* and
 238 *Strombosia pustulata*) showed the most extreme BA declines (>2.9 m²) in drier plots; in contrast,
 239 *Celtis midbraedii* and *Ceiba pentandra* showed the largest BA increases (>3m²), also in drier plots.
 240 Most vegetation plots presented absolute Δ BA <5 m² (Fig. S5) and on average wetter plots increased
 241 by 28 individuals ha⁻¹ more than drier plots (probability 75.2%; Highest Posterior Density Interval =
 242 62, 122).

243 *Distribution of species in traits space*

244 We extracted the first two main axes describing the species distributions in hydraulic, leaf and wood
 245 trait space (Fig. 2). The first was mainly loaded by hydraulic and to a lesser extent by wood economic
 246 traits (PC1; 39% of variance) separating species with high vessel density (ρ V), higher leaf area-
 247 sapwood area ratios (LA:SA) and high wood density (WD), from species with wider vessels, high
 248 potential stem specific conductivity (Kp) and higher lumen fraction (VLF; Fig. 2). Notably, there was a
 249 strong correlation between VLF, Kp and vessel diameter (VD). The second main axis (26% of variance)
 250 was dominated by the contrast between species with high photosynthetic capacity (A_{\max} and A_{sat})
 251 and high leaf nutrient content, which appear to be also taller and fast growers in our dataset, against
 252 shorter species with lower photosynthetic capacity (Fig. 2). The climate affiliation of species (wet or
 253 dry habitat species, and broad range species) did not show a particular distribution in trait space
 254 (Fig. 2a). Of the 13 species showing large increases in basal area, eight were drought-deciduous
 255 species and only three evergreen species (the phenology classification was not available for two
 256 species; Fig. S4a).

257 Deciduous species with stronger changes in basal area showed lower ρ V, LA:SA and being taller with
 258 higher photosynthetic investment and lower WD (Fig. S4b). Evergreen species with large basal area
 259 changes usually had lower Kp, narrower vessels and tended to have smaller VLF, however they were
 260 more widely distributed in the second PC axis than deciduous species. Potential nitrogen fixing
 261 species were more associated with higher nutrient (N_L , P_L) concentrations in taller trees with higher
 262 photosynthetic capacity but could also be found across the central parts of the traits space (Fig. 2b).
 263 Overall taller deciduous species tended to have higher N_L and P_L , higher photosynthetic capacity but
 264 smaller SLA and lower WD than evergreen species (Fig. 2c).

265 *Changes in community level traits*

266 We next examined how changes in community species abundances manifest as changes in
 267 community mean traits. Almost always only plots classified as being at the drier end of the MCWD
 268 range, i.e. "Dry" plots, showed important (most above 92% highest posterior density interval, *HPDI*)
 269 shifts in their CWM trait values (Fig. 3; Table S2), thus we mainly focus on this group of plots. For
 270 hydraulics related traits, the LA:SA ratio on average decreased 3.5%. For the leaf economics, leaves
 271 increased 1.6% on average and up to 6% in N_L content in "wetter" locations and up to 3% in "drier"
 272 sites. Drier sites also showed increased A_{\max} of up to 2.8%. The maximum height (Height_{\max}) of the
 273 species increased on average 4.7% and up to 15%, and an increase in non-pioneer light demanders
 274 (NPLD) of on average 8.6% was detected, accompanied by a marginal decrease in shade bearers (SB)
 275 of 8.4% in drier plots. Deciduous species abundance (DE) increased up to 10% ($\mu = 4.2\%$) in drier
 276 sites, with a similar decrease in evergreens. Nitrogen fixers increased on average by 0.8% and up to

277 3% (92% HPDI) but only in wetter locations, with no important change in the drier sites. Other traits
 278 did not present important changes (>92% HPDI) in either dry or wet plots (Fig. 3; Table S2).

279 Overall, the drier plots in our study transect have developed taller trees with canopies that are rich
 280 in nitrogen with higher A_{\max} and lower LA:SA, and are more abundant in deciduous, non-pioneer
 281 light-demanding species.

282 *MCWD and Phenology as drivers of changes in trait CWM*

283 We examined whether the change in canopy properties can be explained by the MCWD, the
 284 absolute and the relative change in MCWD between censuses or by the interaction between forest
 285 type ("Dry" or "Wet") and the deciduous species abundance (see Table S3). The results below focus
 286 on those traits with important shifts in their CWM and on the best model selected (Table S4). The
 287 MCWD was the best parameter explaining the increase in deciduous species abundance, of up to
 288 10% ($R^2=0.29$; Fig. 4a), also explaining a linear trend increment in non-pioneer light demanders
 289 ($R^2=0.14$; Fig. 4b). The slight increase in nitrogen fixers (NF), was best explained by the change in
 290 $MCWD_{Abs}$ (Fig. 4c). The model accounting for changes in abundance of deciduous species and their
 291 interaction with forest type was the best explaining the changes in LA:SA in wetter and drier
 292 locations with further decreases in LA:SA as deciduous species abundance increased (Fig. 4d;
 293 $R^2=0.63$). This model further explained the increases in A_{\max} (Fig. 4e; $R^2=0.43$), with a steeper positive
 294 slope in drier than wetter sites, and stronger increases in N_L in wetter sites with less deciduous
 295 species (Fig. 4f; $R^2=0.54$). This model explained the larger increases in $Height_{t_{\max}}$ (Fig. 4g; $R^2=0.81$) at
 296 drier locations compared to wetter ones. The interaction between the forest type and deciduous
 297 species abundance explained the declines in evergreen species (Fig. 4h; $R^2=0.86$) and shade bearers
 298 (Fig. 4i; $R^2=0.50$) of close to 9% at drier plots with increases of close to 10% of deciduous species.

299 Overall, the MCWD and the shift towards deciduous species largely explain why the canopies are
 300 increasing in photosynthetic rate, decreasing their leaf-sap wood area ratio and becoming taller.

301 **Discussion**

302 Gradients in fundamental abiotic conditions (e.g. temperature, rainfall) shape the distribution of
 303 biodiversity by driving the assemblage of species and their traits, and dictating the functioning of
 304 ecosystems. Climate change is altering these gradients, with consequent impacts on ecosystem
 305 functioning. Here we show how by combining extensive plant traits data collection with long-term
 306 inventory records it is possible to derive new insights into how complex ecosystems respond to a
 307 changing climate. This study shows that the tropical forests in West Africa respond in different ways
 308 to a drying climate by modifications of their trait composition. We show that the changes in
 309 deciduous species abundance, which are more accentuated in drier than in wetter forests, are
 310 mediated by the climatic water deficit across the different forest types and may modify the
 311 community level trait composition.

312 *Changing forests: differences along the climatic gradient*

313 Trait composition changed across time and across the precipitation gradient. For most traits the
 314 long-term climatic water deficit, and not its absolute or relative changes, adequately described
 315 changes in trait composition as a possible response to climate changes. The observed trait
 316 compositional changes are not likely to be the result of a successional process taking place (see also

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3 317 Fauset et al. 2012) given the absence of increase in wood density and pioneers and the lack of
4 318 significant increases in SLA as expected in such scenario (Carreño-Rocabado et al. 2012; Lohbeck et
5 319 al. 2013). Esquivel et al. (2018) argue that Amazonian forest communities may be shifting towards
6 320 communities more adapted to drier conditions, with large stature taxa becoming more dominant.
7 321 Our results are in contrast to findings from a study of Neotropical forests (Sande et al. 2016), which
8 322 proposed that changes in the CWM of some leaf and wood traits in their plots are not the result of
9 323 drought but more from successional processes. Sande et al. (2016) reported an increase in wood
10 324 density but no evidence of changes in percentage of deciduous trees in drier sites and no increase in
11 325 nitrogen fixers such as Fabaceae. We did find slight increases in nitrogen fixing species and a clear
12 326 increase in deciduous, non-pioneer light demanders, supporting our hypothesis of adaptations to a
13 327 changing climate. However, the drying trend in West Africa is much stronger than any observed in
14 328 recent decades in most Amazonian regions (Malhi & Wright 2004). The fact that the climate
15 329 affiliation of species did not show a particular distribution in the PCA space (Fig. 2a), is likely the
16 330 result of the PCA focusing on the species taxonomic identity and not on the basal area the species
17 331 cover, which may differ across the climatic gradient.

23 332 We hypothesised that forests would respond to changes in climatic conditions by modifying
24 333 their trait composition. We expected such changes to be more prominent in wetter forests as these
25 334 could be thought to suffer most from a drying environment given that their species are better
26 335 adapted to high levels of moisture and water availability (Feeley et al. 2011). Contrary to our
27 336 expectations, we found that drier forests are responding more to changes in climate than wetter
28 337 forests. A potential explanation is that drier forests are already under high ecophysiological stress
29 338 because of limited water resources, and therefore a drier environment would push them closer to
30 339 their climatic threshold (Allen et al. 2017). In contrast to drier forests with high water deficits, forest
31 340 found in regions with high precipitation and low water deficits tend to have high soil water
32 341 potentials that can be especially exploited during periods of droughts by taller trees with more
33 342 expansive and deeper rooting systems (Giardina et al. 2018). The higher soil water availability may
34 343 thus explain the higher resilience from these wetter forests to the ongoing drying trend in contrast
35 344 to forests located in drier environments. An important point that remains unanswered is whether
36 345 there is a tipping point that if exceeded can cause significant shifts in the community and trait
37 346 composition of the wetter forest communities in tropical Africa.

43 347 ***Changing traits***

45 348 Community level traits are changing. Changes in environmental conditions could trigger structural
46 349 trait changes as an adaptation measure when simpler physiological mechanisms, e.g. stomata
47 350 opening frequency, are not enough to deal with such environmental changes (Magnani et al. 2002).
48 351 Here we show that for West African tropical forests, community-level trait structural changes have
49 352 taken place, likely as a response to a drying environment, leading to large shifts in the community
50 353 trait composition. Moreover, the increase of deciduous species abundance in drier locations
51 354 suggests a direct response to the changing environmental conditions. Tropical deciduous species are
52 355 in general physiologically and structurally different and tend to be better adapted to dry
53 356 environments than evergreen species (Álvarez-Yépez et al. 2017).

58 357 Tropical evergreen species are exposed to stressful hot and dry periods during the dry
59 358 season when they still invest water resources to maintain photosynthesis and to cool leaves by
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3 359 means of transpiration, increasing the possibility of xylem cavitation during long periods of drought
4 360 (Hasselquist et al. 2010; Tomlinson et al. 2013). Deciduous species, in contrast, avoid water loss
5 361 during the periods of drought by dropping their leaves, but at the cost of no photosynthesis during
6 362 the dormant season. The drying and warming trend appears to be shifting this trade-off in favour of
7 363 deciduous species (Vico et al. 2017). Deciduous trees with smaller leaf lifespans and efficient
8 364 vascular system (Sobrado 1993) make high investment in fast resources acquisition, a behaviour that
9 365 could explain the observed increase in mean A_{\max} for carbon allocation in drier forests (Ishida et al.
10 366 2013). Moreover, we show that the increase in A_{\max} can be directly related to the increase in
11 367 abundance of deciduous trees and may be facilitated in cases where nutrient availability is not a
12 368 limiting factor (Turner et al. 2018). In fact, higher levels of A_{\max} have been shown to be related to
13 369 higher levels of total foliar N_L and P_L in forests across the globe (Walker et al. 2014) and our results
14 370 showed an increase in both N_L and P_L (but only nitrogen significantly), in drier forests. Surprisingly,
15 371 the increased N_L was not reflected in the increase in the abundance of nitrogen fixing species in
16 372 deciduous forests, suggesting that nitrogen limitation may not play a role in the observed nutrient
17 373 trait shifts. Moreover, besides the increase in leaf nutrients, drier locations also experienced
18 374 decreases in LA:SA, which we argue may be a compensatory response to decreases in water
19 375 availability and possible increases in leaf transpiration (McDowell et al. 2002). In summary, the
20 376 above mentioned trait characteristics may allow deciduous species to overcome the effects of water
21 377 deficits during the drier periods of the year, with their higher leaf nutrients (P_L and N_L) allowing them
22 378 to maximize growth during wetter periods (Tomlinson et al. 2013).

379 ***Climate and phenology as predictors of community trait shifts***

380 As a consequence of changing environmental conditions across time and space, the CWM that
381 reflects the trait values of the most dominant species at the community level may also shift,
382 modifying the local functional diversity and impacting on ecosystem functioning (e.g. Fauset et al.
383 2015). Besides the local climatic characteristics also soil conditions may contribute determining
384 vegetation distributions in tropical forests (Poorter et al. 2015). Our analysis includes vegetation
385 plots distributed across a climatic gradient, which also encompasses different soil characteristics
386 (Moore et al. 2018). The focus of this study was to investigate the extent to which climatic factors by
387 their own determine shifts in plant trait composition. However, given the importance of soil nutrient
388 characteristics for plant distributions, and possibly for community level trait composition, future
389 studies that incorporate their interacting effects with climatic conditions in tropical forests would be
390 highly valuable.

391 In summary, we find that the response of the plant communities to a drying climate in
392 Western African forests appears to be mediated by the increases in deciduousness across time. We
393 find that once the abundance of deciduous species increases, these species would determine the
394 characteristics of other relevant functional traits in the community. The new functional trait
395 composition is expected to confer advantages to the communities in face of new environmental
396 conditions (Enquist et al. 2015). Although we show that forest communities are not being “resilient”
397 *per se* (see Hodgson et al. 2015) and have shifted their trait composition across time, such shifts may
398 actually enhance the resilience of ecosystem functions, e.g. reduce the likelihood of the forest
399 shifting into a savanna. Given the expected changes in climatic conditions in the near future,
400 especially in Western Africa where the average rainy season length is expected to decline (Weber et
401 al. 2018), it is imperative we are able to predict how different forest types may respond to these

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3 402 modifications (e.g. by being resilient or resistant to such changes). This is of especial importance for
4 403 drier deciduous forests, as those here analysed, which may be thought to be highly vulnerable to
5 404 even further small variations in climatic conditions (Zelazowski et al. 2011).

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8 405 The long term history of tropical African forests and the effects of past and recent climate
9 406 changes on their plant community have been largely debated (Malhi 2018). However, these forests
10 407 have received less research attention in regard to environmental change effects on their structure,
11 408 composition and function than their Amazon and SE Asian counterparts (but see Lewis et al. 2009;
12 409 Lewis et al. 2013). African tropical forests are in general different in diversity (Richards 1973;
13 410 Parmentier et al. 2007), soil (Moore et al. 2018), baseline climate conditions (Malhi et al. 2013), and
14 411 El Niño impacts (e.g., Rifai et al. 2018) than other tropical forests, and may thus respond to
15 412 environmental changes in unforeseen manner. These characteristics highlight the need of more
16 413 research efforts focused in the African tropical forests. We acknowledge that the tropical forests in
17 414 Africa have a legacy of human impact since the Stone Age (ca. 40,000 years BP) (Malhi et al. 2013),
18 415 with relatively recent recovery from past agricultural impacts (Morin-Rivat et al. 2017). This human-
19 416 forest history could still have an impact on the current distribution of its species and traits.

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24 417 Overall, the observed responses of our different forest types across the climatic gradient,
25 418 their relationship with the abundance of deciduous species and, subsequently, of other community
26 419 level traits, can aid when investigating past to present and in understanding future possible impact
27 420 of changes in climatic conditions in tropical rain forests. These results open new opportunities for
28 421 monitoring different tropical forests across climatic gradients and time by linking phenological
29 422 fluctuations that are potentially observable by means of remote sensing techniques (Jetz et al. 2016)
30 423 (e.g. deciduousness) to infer the characteristics of other canopy level traits.
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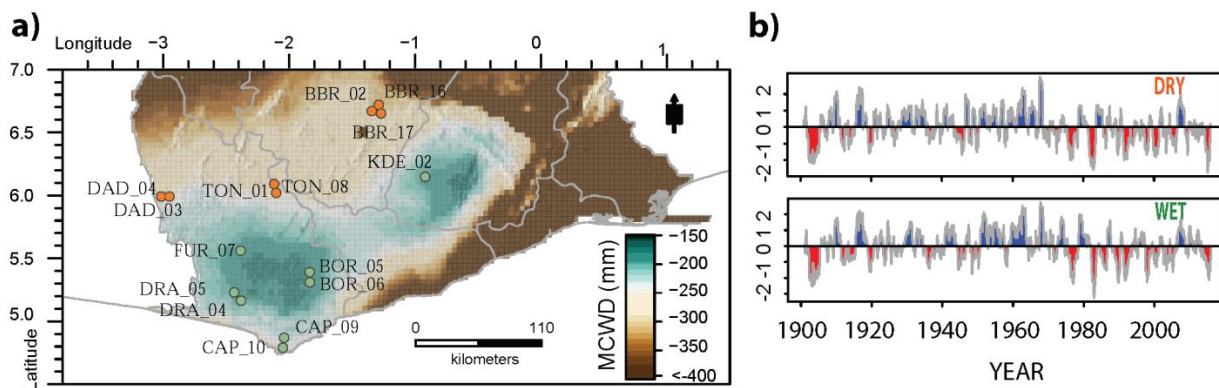


Figure 1. Geographic and climatic characteristics of the study area. a) Map of the south of Ghana depicting the locations of vegetation plots collected and their corresponding maximum climatic water deficit (MCWD). Circles indicate location of vegetation census plots coloured as wetter (green) and drier (orange) forest types based on their MCWD (see methods). **b)** The standardized precipitation and evapotranspiration index (SPEI), a drought index that determines the magnitude and strength of drought conditions; here we show the drought conditions by plotting continuous six month windows over the past century. Red colours represent drought periods and blue wet periods. All census plots have experienced droughts, especially during the 1970-2000 period compared to the preceding decades; with monitoring beginning ca. 1990 (cf. Table S1). Only a representative set of SPEI from a wet (BOR_05) and a dry (BBR2) plot are shown, for the SPEI for all plots see Fig. S3.

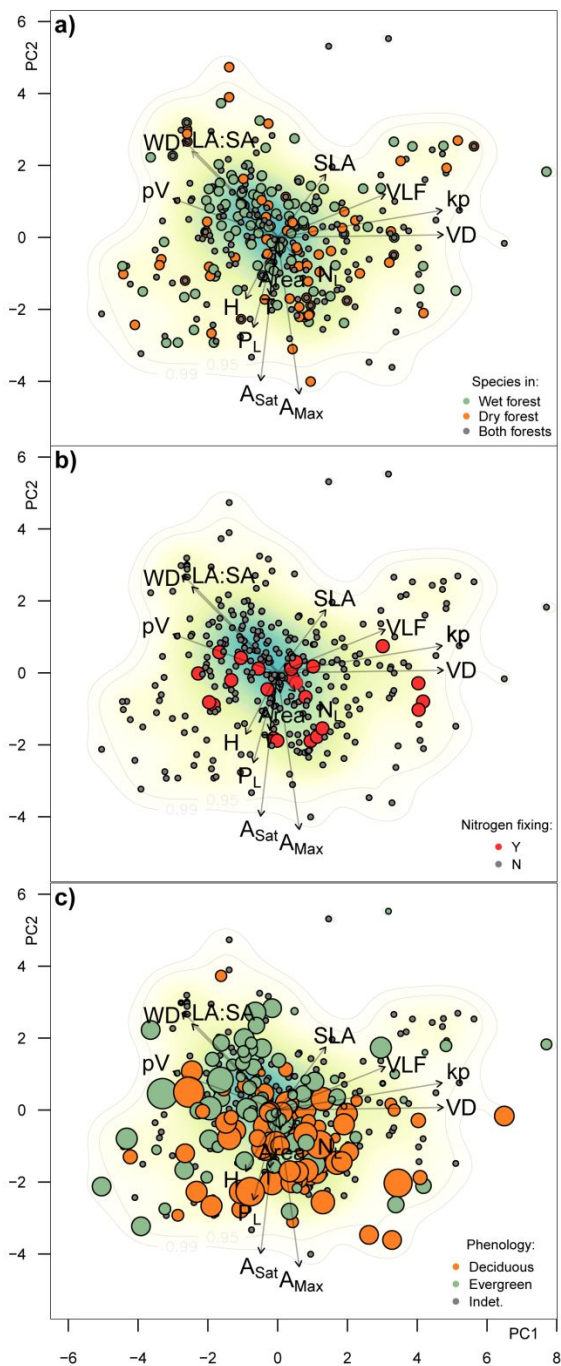


Figure 2. Principal component analysis results showing the distribution of the species in hydraulics-leaf-wood economics trait space. PC1 accounts for 39% of variance, and PC2 accounts for 26%. In a) the species are separated by their presence in the different forest types (wet, dry or both); b) the species that experienced the strongest absolute changes in basal area ($\geq 5 \text{ m}^2$) are highlighted showing their distribution in trait space and their phenology; c) highlights the distribution of nitrogen fixing species and d) shows the distribution of the phenology in trait space with bigger symbols representing species with taller maximum heights. LA:SA: leaf area to sapwood area ratio (m^2/mm^2), VLF: vessel lumen fraction (mm^2/mm^2), VD: vessels diameter (μm), Kp: potential stem specific conductivity ($\text{Kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), ρV : vessel density (vessels per mm^2), SLA: Specific leaf area ($\text{m}^2 \text{g}^{-1}$), Area: leaf area (cm^2), T: leaf thickness (mm), N_L : leaf nitrogen content (g Kg^{-1}), P_L : leaf phosphorus content (g Kg^{-1}), A_{sat} : photosynthetic capacity at light saturated carbon assimilation rates ($\mu\text{mol m}^{-2} \text{s}^{-1}$), A_{max} : photosynthetic capacity at maximum carbon assimilation rates ($\mu\text{mol m}^{-2} \text{s}^{-1}$), WD: wood density (g/cm^3), H: adult maximum height (m).

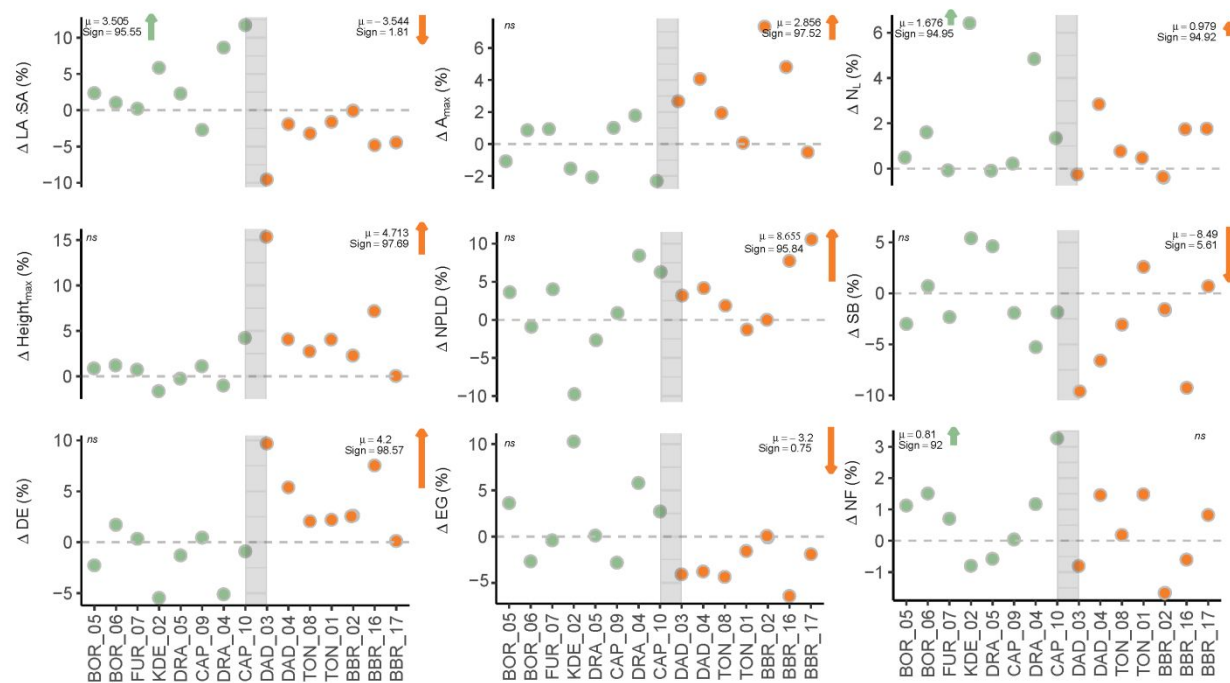


Figure 3. Changes in CWM of traits between census and forest types (green: wetter plots; orange: drier plots). The X-axis shows the vegetation plots ($n=15$) ranked wettest to driest based on the MCWD, and the Y-axis the observed changes in trait community-weighted mean. The grey vertical line separates the forest types by their MCWD into wetter (green) and drier (orange) plots. The wet plot with highest climatic deficit is CAP_10 with a MCWD of -227 mm and the dry plot with lowest MCWD is DAD_03 with a MCWD of -270.5 mm; hence the wet-dry transition in our analysis corresponds to an MCWD of roughly -250 mm. μ : mean change value, *Sign*: importance of the changes in CWM, *ns*: not significant. The arrows on top of each graph represent the magnitude of change in the CWM of the trait so that larger arrows represent larger CWM changes. Only traits with at least marginally important changes in CWM are shown (>92% or <8% High Density Intervals). See Fig. S6 for all other traits and full statistical details of models in Table S2. LA:SA: leaf area to sapwood area ratio, A_{max} : photosynthetic capacity at maximum carbon assimilation rates, N_L : leaf nitrogen content, $Height_{max}$: adult maximum height, NPLD: fractional change in non-pioneer light demanders, SB: shade bearers trees, DE: deciduous trees, EG: evergreen trees, NF: nitrogen fixers.

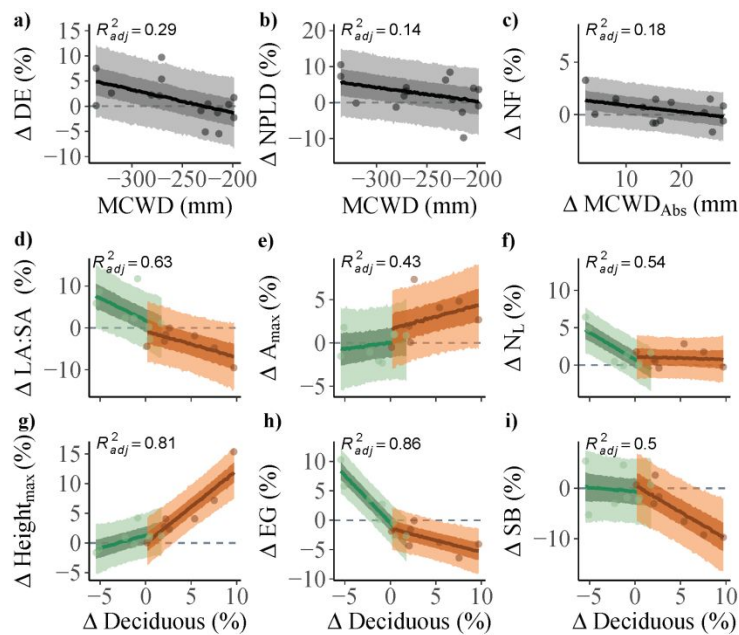


Figure 4. Changes in community weighted mean values of traits explained by the (a-b) maximum climatic water deficit (MCWD), c) the absolute change in MCWD or (d-i) changes in abundance of deciduous species and its interaction with forest type (wet= green; dry=orange). Only the traits with important changes in CWM over time are presented. The solid line represents the Bayesian median posterior distribution, dark shading colours shows the 50% posterior predictive density intervals (PPD) and light shading colours the 90% PPD. The horizontal grey dotted line shows the no change limit. For full statistical model details see Table S4. DE: deciduous, NPLD: non-pioneer light demanders, NF: Nitrogen fixer, LA:SA: leaf area to sapwood area ratio, A_{\max} : photosynthetic capacity at maximum carbon assimilation rates, N_L : leaf nitrogen content, $Height_{\max}$: adult maximum height, EG: evergreen, SB: shade bearers.

Table 1. Characteristics of functional traits selected, description and main references.

Economics spectrum	Trait	Abbreviation	Units	Description	References
Hydraulics	Leaf area to sapwood area ratio	LA:SA	m ² mm ²	Leaf area of a species per unit cross-section of sapwood	(Maseda & Fernández 2006; Poorter et al. 2010; Fan et al. 2012; Perez-Harguindeguy et al. 2013; Gleason et al. 2016)
	Vessel lumen fraction	VLF	mm ² mm ⁻²	Ratio of total vessel lumen area to xylem area	
	Vessels density	ρV	number mm ²	Number of vessels per unit wood area	
	Vessels mean diameter	VD	μm	Mean vessel diameter	
	Potential stem specific conductivity	Kp	Kg m ⁻¹ s ⁻¹ MPa ⁻¹	Hydraulic potential conductivity	
Leaf economics spectrum	Leaf area	Area _L	cm ²	Area of the leaf	(Wright et al. 2004; Juneau & Tarasoff 2012; Walker et al. 2014; Díaz et al. 2016)
	Specific leaf area	SLA	m ² g ⁻¹	One-sided area of a leaf divided by dry mass	
	Leaf nitrogen content	N _L	g Kg ⁻¹	Leaf nitrogen content per unit dry leaf mass	
	Leaf phosphorus content	P _L	g Kg ⁻¹	Leaf phosphorus content per unit dry leaf mass	
	Leaf thickness	Thickness _L	mm	Thickness of a fresh leaf	
	A _{max}	A _{max}	μmol m ⁻² s ⁻¹	Photosynthetic capacity at maximum carbon assimilation rates	
	A _{sat}	A _{sat}	μmol m ⁻² s ⁻¹	Photosynthetic capacity at light saturated carbon assimilation rates	
Wood economics spectrum	Maximum height	Height _{max}	m	Adult maximum adult height	(Hawthorne 1995; Chave et al. 2006)
	Wood density	WD	g cm ³	Wood oven dry mass divided by its fresh volume	
Timing, succession and fixing capacity	Phenology	DE: Deciduous EG: Evergreen	Phenology class	Phenology of the species. If sometimes deciduous but mostly evergreen, this was classified as evergreen and if sometimes evergreen but mostly deciduous it was classified as deciduous	(Hawthorne 1995; Sprent 2009; Sprent et al. 2017)
	Guild	PI: Pioneer NPLD: non-pioneer light demanders SB: shade bearer SW: swamp	Guild class	Guild class of the species	
	Nitrogen fixing capacity	Nitrogen class	NF: Fixer NNF: non-fixer	Classified as nitrogen fixers or non-fixers	