LETTER

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

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Abstract

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

Keywords

Drying climate, ecosystem functioning, plant traits, tropical forests, West Africa.

INTRODUCTION

The terrestrial biosphere is facing rapid changes as results of land-use and climate change with most ecosystems suffering alterations in their functioning by either the loss of species or shifts in species abundances (Pacifici *et al.* 2017). Nevertheless, methodological and data availability constraints hamper our ability to monitor both the distributions of species and ecosystem responses to climate change (Cayuela *et al.* 2009). These challenges are especially acute in high biodiversity areas such as the tropics (Malhi *et al.* 2014), for which there is not only greater uncertainty concerning the effects of climate on biodiversity, but also about current species distributions and their taxonomic identity (Cardoso *et al.* 2017). Tropical forest ecosystems are an especially key component of global biodiversity and have direct effects on human well-being through the varied set of ecosystem functions they provide (Lewis *et al.* 2015), including via their role as major global stocks and sources (Pan *et al.* 2013) and sinks (Pan *et al.* 2011) of carbon. Consequently, climate-driven forest disturbances may have large-scale feedbacks on climate via carbon dynamics (Fauset *et al.* 2015). However, tropical forest need not at all respond in the same

manner to environmental changes. Notably, it is possible that wetter tropical forests, that is those with intrinsically lower water deficits, may be either more sensitive or more resistant to climatic changes than tropical forest found in drier environments (Allen *et al.* 2017). Understanding how climate baselines may modify tropical forest responses to climate changes is of pivotal importance, not least because the different responses of tropical forests to a drying climate may in turn modify biodiversity composition in unexpected ways, including by accelerating or slowing tree mortality (Bonal *et al.* 2016).

There are many challenges associated with deciphering the impacts of climate change on forest ecosystems because of complex interactions between community composition and physiological responses of individual species to a given environmental change. For instance, over an elevational gradient in an Amazon to Andean forest transect, it was recently found that differences in tree community composition and associated traits offset the temperature response of individual species, leading to surprisingly modest spatial changes in productivity with elevation (Fyllas *et al.* 2017). Moreover, if communities respond to temporal environmental changes by shifting their species abundances and trait distributions

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towards more suitable ranges (Fauset *et al.* 2012), new dominant trait combinations may arise in the community. Changes in the community functional trait composition may also imply changes in key aspects of ecosystem functioning such as nutrient, carbon and water cycling. Therefore, understanding past and current responses of community-level traits has the potential to provide valuable insights into tropical forest resilience against environmental changes and offer a promising avenue for a better understanding of ecosystem functioning (Madani *et al.* 2018). While analysing biodiversity responses to environmental changes at the community level is clearly desirable, it is a challenging task for tropical forests in particular given their high diversity, relative paucity of trait data (e.g. Asner *et al.* 2015), and the difficulties with sustaining long-term monitoring.

In addition to the challenges associated with monitoring responses of tropical forests across climatic gradients to a drying environment, little is known about the effects of recent changes in climate on community-level trait composition. Analysing the precipitation anomaly over the last century, Fauset *et al.* (2012) have shown there has been a long-term drying trend in tropical Western Africa, which may had led to changes in forest composition and community level leaf phenology. However, there is an overall lack of integrated knowledge on how long-term droughts affect hydraulic, leaf and wood related community traits that are hypothesised to be tightly linked to how different tropical forest may respond to changes in climatic conditions. Here we coupled a unique combination of intensive plant traits collections together with a wider set of trait data to long-term forest inventories in a West African wet-dry forest gradient and explore if forests exposed to different water deficits show differential responses to a drying climate.

Given a drying trend across West Africa, we hypothesised that the tropical forest across the climatic gradient have shifted their trait distributions but that the magnitude of the trait shifts may be dependent on the forest type and the past and current climate conditions. Specifically, we hypothesised that forests with usually low water deficits, that is intrinsically wetter forests, may be more susceptible to a drying environment as their plant communities may be adapted to high levels of moisture and water availability. These wetter forests are therefore expected to show stronger trait shifts than drier forest. On the other hand, an increase in deciduousness may be a main strategy adopted by communities at the edge of their climatic suitability, for example drier forests, in order to adapt to a drying environment. Therefore, we expected to see an increase in the abundance of deciduous species in drier forests under this scenario. Investigating if and how plant communities have shifted their trait composition as a result of a drying climate will increase our understanding on how past climatic conditions have shaped current plant trait distributions and will render insights into how changes in climate may shape future tropical forest communities.

MATERIAL AND METHODS

Study area and vegetation censuses

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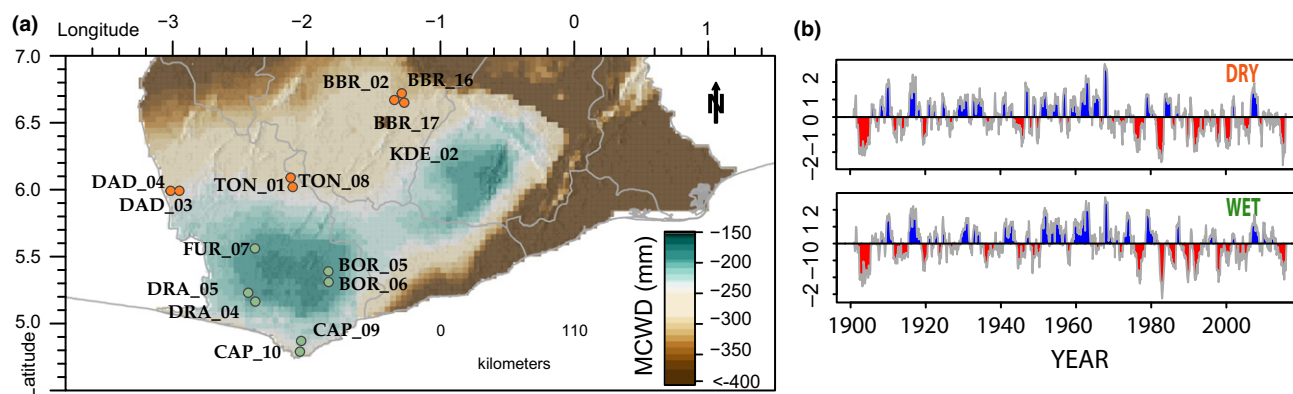

Figure 1 Geographic and climatic characteristics of the study area. (a) Map of the south of Ghana depicting the locations of vegetation plots collected and their corresponding maximum climatic water deficit (MCWD). Circles indicate location of vegetation census plots coloured as wetter (green) and drier (orange) forest types based on their MCWD (see methods). (b) The standardised 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 6-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.

Species functional traits

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

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

Community-level trait weighted mean

The mass ratio hypothesis states that the most dominant species drive the ecosystem processes by means of their traits (Grime 1998). We calculated for each of the traits t, and vegetation census plots, p, their community-level weighted mean (CWM) using the species basal area as the weighting factor as follows:

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 if 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}	$\mu mol\ m^{-2}\ s^{-1}$	Photosynthetic capacity at maximum carbon assimilation rates	
	A_{sat}	A_{sat}	$\mu mol\ m^{-2}\ s^{-1}$	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	

$CWM_{tp} = \sum_{i-1}^{s} BA_{ip} \times t_i$, where BA_{ip} is the basal area of species i in plot p and t_i is the average trait value of species i. There is a strong relationship between basal area and crown area as shown for old growth tropical forests (Shenkin *et al.* in review, Antin *et al.* 2013), and hence gives an indication of the amount of canopy area occupied by a specific trait. Hence the CWM is an indicator of mean canopy properties. In the case of categorical variables such as phenological strategy, nitrogen fixing capacity and guild we calculated the species abundance of each of their levels. We used the mean trait values per species. Species may show intraspecific trait variation, which we do not completely capture here; however, it has been shown such variation is relatively small in comparison to the trait variation found between tropical tree species and which is the focus of our study (Rozendaal *et al.* 2006). All analyses of CWM were carried out using the log10 transformed trait values and were carried out with the R package 'FD'.

Climatic data

For each vegetation plot, we calculated the maximum climatological water deficit (MCWD; Fig. 1b and Fig. S3), a measure of drought intensity (Malhi *et al.* 2009). MCWD was defined as the most negative value of the climatological water deficit (CWD) over a year. CWD is defined as precipitation (P) (mm/month) – potential evapotranspiration (PET) (mm/month) with a minimum deficit of 0. To calculate the MCWD for a time period representative of the vegetation census, we obtained long-term precipitation and evapotranspiration data from the TerraClimate data set (Abatzoglou *et al.* 2018) which covers the period 1958–2017 at a spatial resolution of *c.* 4×4 km. This data set was selected given its high spatial and temporal resolution and its greater accuracy when compared to other historical data set as the Climatic Research Unit data (University of East Anglia Climatic Research Unit, Harris & Jones 2017). The current climate products underestimate the precipitation at the coast in Ghana where two of our plots (CAP_09 and CAP_10) are located. Thus for these plots, we averaged the MCWD of a radius of ten grid cells around the plot locations and used this value to characterise their MCWD.

We characterise the climatic conditions across each of the two time periods with vegetation census data, for the first period we captured the average MCWD between the years 1958 and 1992 and for the second between 1979 and 2013. Then the absolute ($\Delta MCWD_{Abs}$) and relative ($\Delta MCWD_{Rel}$) changes in the MCWD between censuses was calculated by subtracting the $\Delta MCWD_{Abs}$ and $\Delta MCWD_{Rel}$ of the first periods from that of the second. We also calculated the standardised precipitation and evapotranspiration index (SPEI) (Vicente-Serrano *et al.* 2010) using a 12-month windows to explore the water deficit or surplus conditions over the past century using CRU TS data (University of East Anglia Climatic Research Unit, Harris & Jones 2017).

Data analysis

We conducted all statistical analysis in R (v. 3.4.1; www.r-project.org). We analysed the water balance across each of the

vegetation plots using the SPEI. Then we first investigated the changes at the plot level in the species basal area, number of individuals and number of species between censuses. Second, we mapped the species distributions in trait space with a Principal Component Analysis (PCA) using the NIPALS function with a maximum of 500 iterations in the 'ade4' package to infer species associations to the traits used. Third, we calculated the ΔCWM by subtracting the CWM of census 1 from the CWM of census 2 for each trait and plot. We then grouped the plots based on their MCWD, where plots with a MCWD ≤ 250 were classified as 'wetter' sites, thus with lower water deficits and the rest as 'drier' sites. We chose this threshold as it may represent a transition from tropical wet forest towards a more seasonal and savannah like vegetation (Malhi *et al.* 2009). Based on the above mentioned protocol, eight plots were classified as plots in 'wetter' and seven as in 'drier' locations (Table S1). We investigated if there were significant changes in trait CWM by means of Bayesian estimation (Kruschke 2013) for each one of the plot groups separately ('wetter' and 'drier'). Here we computed posterior distributions to compare the CWM change trait values of between the two censuses, resulting in probability change estimates. We used normal priors with large standard deviation for μ, broad uniform priors for σ and a shifted-exponential prior for the normality parameter ν, using the 'BEST' package.

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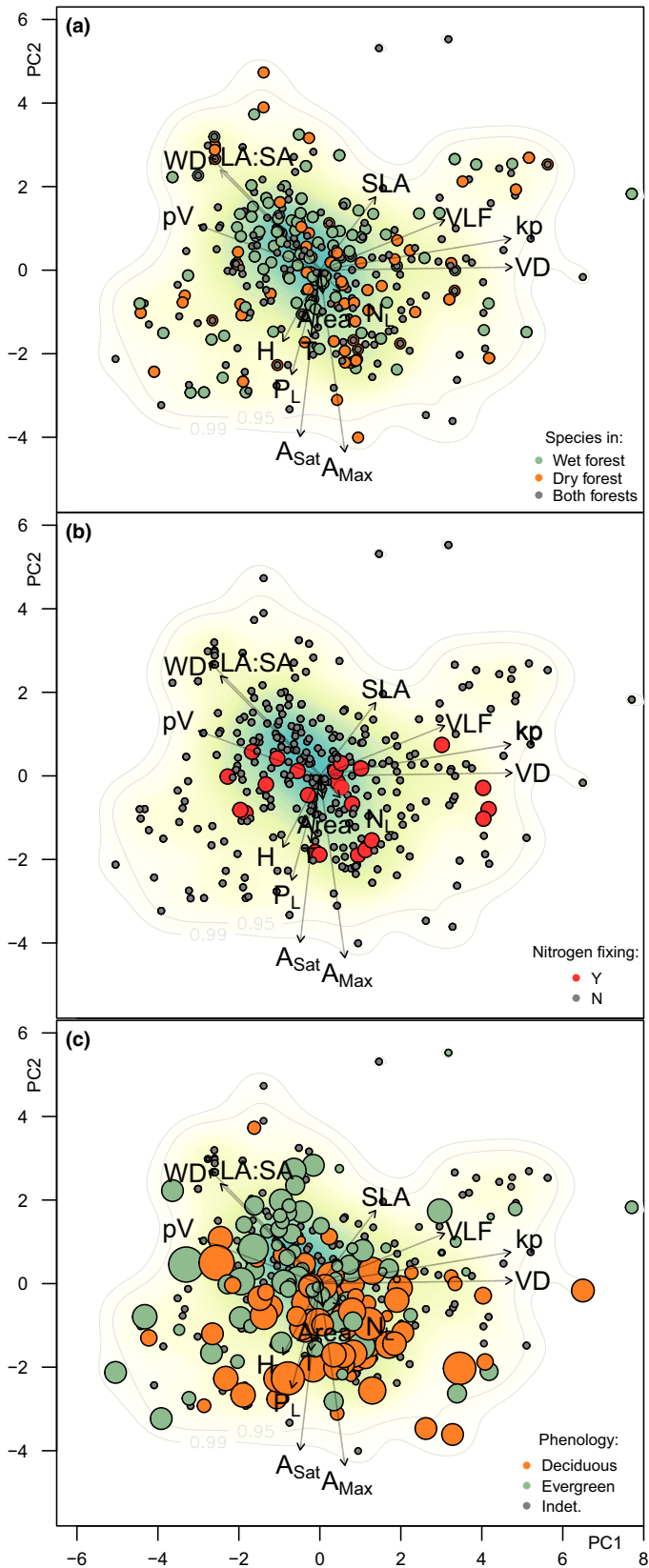
RESULTS

Long-term drought

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

Species dynamics

There were 330 tree species present in the 15 study plots, which accounted for a total basal area (BA) of 362 m^2 in the first vegetation census and 382 m^2 in the last vegetation

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 (≥ 5 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 (Kg m^{-1} s^{-1} MPa^{-1}), ρV: vessel density (vessels per mm^2), SLA: Specific leaf area (m^2 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 (μmol m^{-2} s^{-1}), A$_{max}$: photosynthetic capacity at maximum carbon assimilation rates (μmol m^{-2} s^{-1}), WD: wood density (g/cm^3), H: adult maximum height (m).

and landscape level trait composition (Fig. S4a). Of the 20 species changing more strongly in basal area, seven accounted for a total decrease in BA of 12 m^2 and 13 species for an increase of 24 m^2. Of these species, two (*Antiaris toxicaria* and *Strombosia pustulata*) showed the most extreme BA declines (> 2.9 m^2) in drier plots; in contrast, *Celtis mildbraedii* and *Ceiba pentandra* showed the largest BA increases (> 3 m^2), also in drier plots. Most vegetation plots presented absolute ΔBA <5 m^2 (Fig. S5) and on average wetter plots increased by 28 individuals ha^{-1} more than drier plots (probability 75.2%; Highest Posterior Density Interval = −62, 122).

Distribution of species in traits space

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

Deciduous species with stronger changes in basal area showed lower ρV, LA:SA and being taller with higher photosynthetic investment and lower WD (Fig. S4b). Evergreen species with large basal area changes usually had lower Kp, narrower vessels and tended to have smaller VLF; however they were more widely distributed in the second PC axis than

census. From the total species pool, 6% experienced landscape-level changes in BA of between ± 1 to ± 5 m^2 (summed across all 15 plots), which may strongly impact plot

deciduous species. Potential nitrogen fixing species were more associated with higher nutrient (N_L, P_L) concentrations in taller trees with higher photosynthetic capacity but could also be found across the central parts of the traits space (Fig. 2b). Overall taller deciduous species tended to have higher N_L and P_L, higher photosynthetic capacity but smaller SLA and lower WD than evergreen species (Fig. 2c).

Changes in community-level traits

We next examined how changes in community species abundances manifest as changes in community mean traits. Almost always only plots classified as being at the drier end of the MCWD range, that is 'Dry' plots, showed important (most above 92% highest posterior density interval, *HPDI*) shifts in their CWM trait values (Fig. 3; Table S2), thus we mainly focus on this group of plots. For hydraulics-related traits, the LA:SA ratio on average decreased 3.5%. For the leaf economics, leaves increased 1.6% on average and up to 6% in N_L content in 'wetter' locations and up to 3% in 'drier' sites. Drier sites also showed increased A_{max} of up to 2.8%. The maximum height (Height$_{max}$) of the species increased on average 4.7% and up to 15%, and an increase in non-pioneer light demanders (NPLD) of on average 8.6% was detected, accompanied by a marginal decrease in shade bearers (SB) of 8.4%

in drier plots. Deciduous species abundance (DE) increased up to 10% ($\mu = 4.2\%$) in drier sites, with a similar decrease in evergreens. Nitrogen fixers increased on average by 0.8% and up to 3% (92% *HPDI*) but only in wetter locations, with no important change in the drier sites. Other traits did not present important changes (> 92% *HPDI*) in either dry or wet plots (Fig. 3; Table S2).

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

MCWD and phenology as drivers of changes in trait CWM

We examined whether the change in canopy properties can be explained by the MCWD, the absolute and the relative change in MCWD between censuses or by the interaction between forest type ('Dry or 'Wet') and the deciduous species abundance (see Table S3). The results below focus on those traits with important shifts in their CWM and on the best model selected (Table S4). The MCWD was the best parameter explaining the increase in deciduous species abundance, of up to 10% ($R^2 = 0.29$; Fig. 4a), also explaining a linear trend increment in non-pioneer light demanders ($R^2 = 0.14$; Fig. 4b). The slight increase in nitrogen fixers (NF) was the
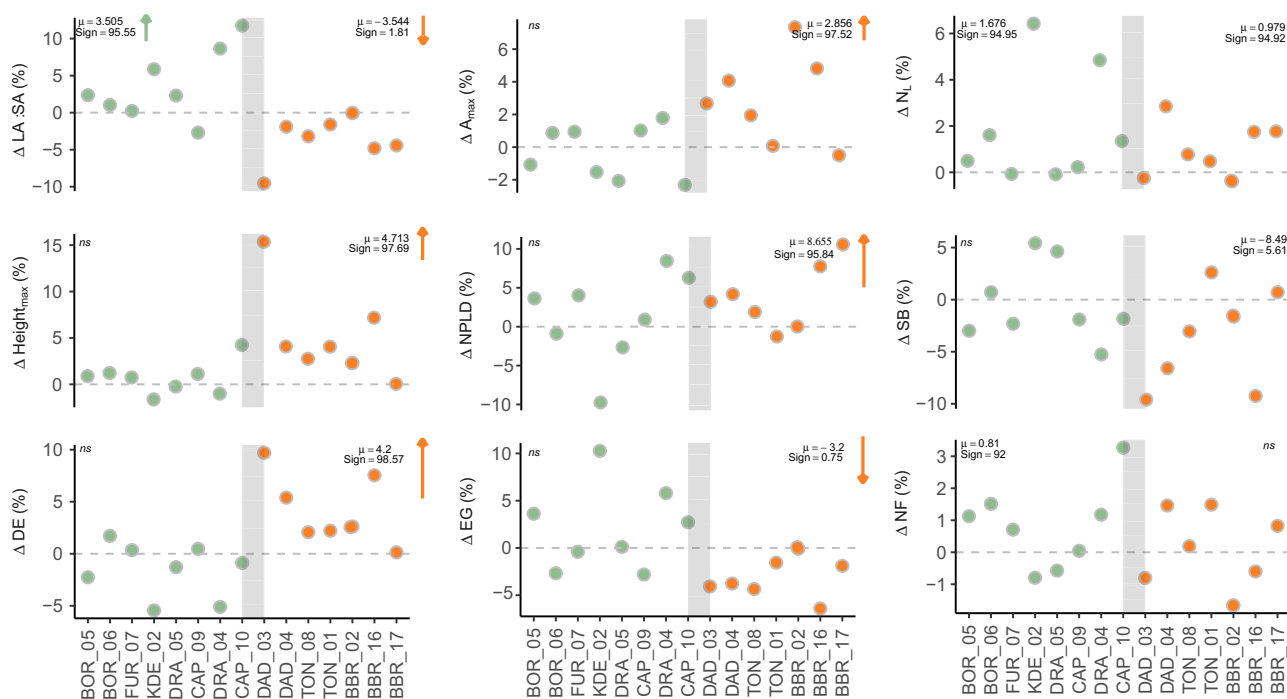

Figure 3 Changes in CWM of traits between census and forest types (green: wetter plots; orange: drier plots). The *X*-axis shows the vegetation plots ($n = 15$) ranked wettest to driest based on the MCWD, and the *Y*-axis, the observed changes in trait community-weighted mean. The grey vertical line 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.
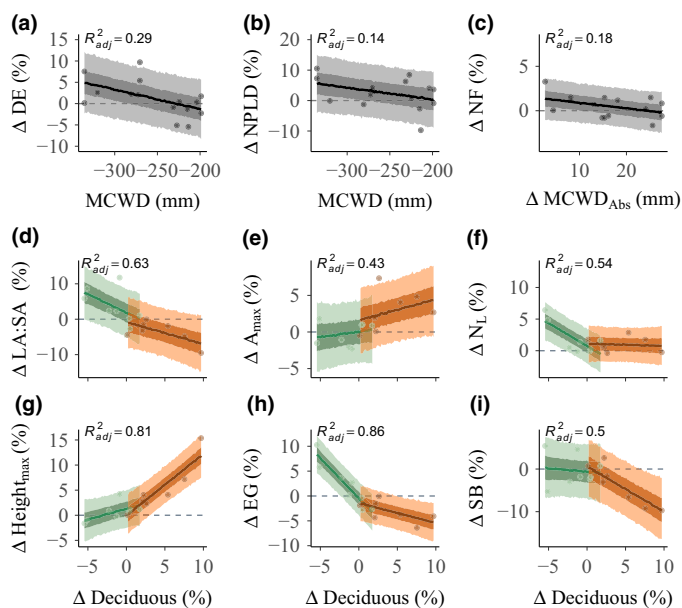
Figure 4 Changes in community weighted mean values of traits explained by the (a and b) maximum climatic water deficit (MCWD), (c) the absolute change in MCWD or (d–i) changes in abundance of deciduous species and its interaction with forest type (wet= green; dry=orange). Only the traits with important 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.

best explained by the change in MCWD$_{Abs}$ (Fig. 4c). The model accounting for changes in abundance of deciduous species and their interaction with forest type was the best explaining the changes in LA:SA in wetter and drier locations with further decreases in LA:SA as deciduous species abundance increased (Fig. 4d; $R^2 = 0.63$). This model further explained the increases in A_{max} (Fig. 4e; $R^2 = 0.43$), with a steeper positive slope in drier than wetter sites, and stronger increases in N_L in wetter sites with less deciduous species (Fig. 4f; $R^2 = 0.54$). This model explained the larger increases in Height$_{max}$ (Fig. 4g; $R^2 = 0.81$) at drier locations compared to wetter ones. The interaction between the forest type and deciduous species abundance explained the declines in evergreen species (Fig. 4h; $R^2 = 0.86$) and shade bearers (Fig. 4i; $R^2 = 0.50$) of close to 9% at drier plots with increases of close to 10% of deciduous species.

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

DISCUSSION

Gradients in fundamental abiotic conditions (e.g. temperature, rainfall) shape the distribution of biodiversity by driving the

assemblage of species and their traits, and dictating the functioning of ecosystems. Climate change is altering these gradients, with consequent impacts on ecosystem functioning. Here we show how by combining extensive plant traits data collection with long-term inventory records is possible to derive new insights into how complex ecosystems respond to a changing climate. This study shows that the tropical forests in West Africa respond in different ways to a drying climate by modifications of their trait composition. We show that the changes in deciduous species abundance, which are more accentuated in drier than in wetter forests, are mediated by the climatic water deficit across the different forest types and may modify the community-level trait composition.

Changing forests: differences along the climatic gradient

Trait composition changed across time and across the precipitation gradient. For most traits the long-term climatic water deficit, and not its absolute or relative changes, adequately described changes in trait composition as a possible response to climate changes. The observed trait compositional changes are not likely to be the result of a successional process taking place (see also Fauset et al. 2012) given the absence of increase in wood density and pioneers and the lack of significant increases in SLA as expected in such scenario (Carreño-Roca-bado et al. 2012; Lohbeck et al. 2013). Esquivel et al. (2018) argue that Amazonian forest communities may be shifting towards communities more adapted to drier conditions, with large stature taxa becoming more dominant. Our results are in contrast to findings from a study of Neotropical forests (Sande et al. 2016), which proposed that changes in the CWM of some leaf and wood traits in their plots are not the result of drought but more from successional processes. Sande et al. (2016) reported an increase in wood density but no evidence of changes in percentage of deciduous trees in drier sites and no increase in nitrogen fixers such as Fabaceae. We did find slight increases in nitrogen fixing species and a clear increase in deciduous, non-pioneer light demanders, supporting our hypothesis of adaptations to a changing climate. However, the drying trend in West Africa is much stronger than any observed in recent decades in most Amazonian regions (Malhi & Wright 2004). The fact that the climate affiliation of species did not show a particular distribution in the PCA space (Fig. 2a) is likely the result of the PCA focusing on the species taxonomic identity and not on the basal area the species cover, which may differ across the climatic gradient.

We hypothesised that forests would respond to changes in climatic conditions by modifying their trait composition. We expected such changes to be more prominent in wetter forests as these could be thought to suffer most from a drying environment given that their species are better adapted to high levels of moisture and water availability (Feeley et al. 2011). Contrary to our expectations, we found that drier forests are responding more to changes in climate than wetter forests. A potential explanation is that drier forests are already under high ecophysiological stress because of limited water resources, and therefore a drier environment would push them closer to their climatic threshold (Allen et al. 2017). In contrast to drier forests with high water deficits, forest found in

regions with high precipitation and low water deficits tend to have high soil water potentials that can be especially exploited during periods of droughts by taller trees with more expansive and deeper rooting systems (Giardina *et al.* 2018). The higher soil water availability may thus explain the higher resilience from these wetter forests to the ongoing drying trend in contrast to forests located in drier environments. An important point that remains unanswered is whether there is a tipping point that if exceeded can cause significant shifts in the community and trait composition of the wetter forest communities in tropical Africa.

Changing traits

Community-level traits are changing. Changes in environmental conditions could trigger structural trait changes as an adaptation measure when simpler physiological mechanisms, for example stomata opening frequency, are not enough to deal with such environmental changes (Magnani *et al.* 2002). Here we show that for West African tropical forests, community-level trait structural changes have taken place, likely as a response to a drying environment, leading to large shifts in the community trait composition. Moreover, the increase of deciduous species abundance in drier locations suggests a direct response to the changing environmental conditions. Tropical deciduous species are in general physiologically and structurally different and tend to be better adapted to dry environments than evergreen species (Álvarez-Yépiz *et al.* 2017).

Tropical evergreen species are exposed to stressful hot and dry periods during the dry season when they still invest water resources to maintain photosynthesis and to cool leaves by means of transpiration, increasing the possibility of xylem cavitation during long periods of drought (Hasselquist *et al.* 2010; Tomlinson *et al.* 2013). Deciduous species, in contrast, avoid water loss during the periods of drought by dropping their leaves, but at the cost of no photosynthesis during the dormant season. The drying and warming trend appears to be shifting this trade-off in favour of deciduous species (Vico *et al.* 2017). Deciduous trees with smaller leaf lifespans and efficient vascular system (Sobrado 1993) make high investment in fast resources acquisition, a behaviour that could explain the observed increase in mean A_{max} for carbon allocation in drier forests (Ishida *et al.* 2013). Moreover, we show that the increase in A_{max} can be directly related to the increase in abundance of deciduous trees and may be facilitated in cases where nutrient availability is not a limiting factor (Turner *et al.* 2018). In fact, higher levels of A_{max} have been shown to be related to higher levels of total foliar N_L and P_L in forests across the globe (Walker *et al.* 2014) and our results showed an increase in both N_L and P_L (but only nitrogen significantly), in drier forests. Surprisingly, the increased N_L was not reflected in the increase in the abundance of nitrogen fixing species in deciduous forests, suggesting that nitrogen limitation may not play a role in the observed nutrient trait shifts. Moreover, besides the increase in leaf nutrients, drier locations also experienced decreases in LA:SA, which we argue may be a compensatory response to decreases in water availability and possible increases in leaf transpiration (McDowell *et al.* 2002). In summary, the above mentioned

trait characteristics may allow deciduous species to overcome the effects of water deficits during the drier periods of the year, with their higher leaf nutrients (P_L and N_L) allowing them to maximise growth during wetter periods (Tomlinson *et al.* 2013).

Climate and phenology as predictors of community trait shifts

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

In summary, we find that the response of the plant communities to a drying climate in Western African forests appears to be mediated by the increases in deciduousness across time. We find that once the abundance of deciduous species increases, these species would determine the characteristics of other relevant functional traits in the community. The new functional trait composition is expected to confer advantages to the communities in face of new environmental conditions (Enquist *et al.* 2015). Although we show that forest communities are not being 'resilient' *per se* (see Hodgson *et al.* 2015) and have shifted their trait composition across time, such shifts may actually enhance the resilience of ecosystem functions, for example reduce the likelihood of the forest shifting into a savannah. Given the expected changes in climatic conditions in the near future, especially in Western Africa where the average rainy season length is expected to decline (Weber *et al.* 2018), it is imperative we are able to predict how different forest types may respond to these modifications (e.g. by being resilient or resistant to such changes). This is of special importance for drier deciduous forests, as those here analysed, which may be thought to be highly vulnerable to even further small variations in climatic conditions (Zelazowski *et al.* 2011).

The long-term history of tropical African forests and the effects of past and recent climate changes on their plant community have been largely debated (Malhi 2018). However, these forests have received less research attention in regard to environmental change effects on their structure, composition and function than their Amazon and SE Asian counterparts (but see Lewis *et al.* 2009, 2013). African tropical forests are in general different in diversity (Richards 1973; Parmentier *et al.* 2007), soil (Moore *et al.* 2018), baseline climate conditions (Malhi *et al.* 2013) and El Niño impacts (e.g., Rifai *et al.* 2018) than other tropical forests, and may thus respond to environmental changes in unforeseen manner. These

characteristics highlight the need of more research efforts focused in the African tropical forests. We acknowledge that the tropical forests in Africa have a legacy of human impact since the Stone Age (*c.* 40 000 years BP) (Malhi *et al.* 2013), with relatively recent recovery from past agricultural impacts (Morin-Rivat *et al.* 2017). This human-forest history could still have an impact on the current distribution of its species and traits.

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

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. and T.P. collected trait data. I.O. K.Z. and A.G. processed the laboratory samples, 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 ACCESSIBILITY STATEMENT

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 https://hal.archives-ouvertes.fr/hal-02008154 and will be available from the corresponding author upon request.

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