

## LETTER

# Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana

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### Abstract

The future of tropical forests under global environmental change is uncertain, with biodiversity and carbon stocks at risk if precipitation regimes alter. Here, we assess changes in plant functional composition and biomass in 19 plots from a variety of forest types during two decades of long-term drought in Ghana. We find a consistent increase in dry forest, deciduous, canopy species with intermediate light demand and a concomitant decrease in wet forest, evergreen, sub-canopy and shade-tolerant species. These changes in composition are accompanied by an increase in above-ground biomass. Our results indicate that by altering composition in favour of drought-tolerant species, the biomass stocks of these forests may be more resilient to longer term drought than short-term studies of severe individual droughts suggest.

### Keywords

Biomass, climate change, dynamics, functional types, Ghana, long-term, permanent plot, plant traits, precipitation, species.

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## INTRODUCTION

The risk of longer or more intense drought is one of the most pervasive threats faced by tropical forests (Laurance & Peres 2006; Lewis 2006). Although future climate projections are uncertain, particularly with regard to West Africa (Christensen *et al.* 2007), many IPCC-AR4 models predict reduced precipitation and long-term soil moisture droughts in some tropical and sub-tropical areas (Sheffield & Wood 2008). Many forests may therefore be exposed to increased drought intensity, frequency or longevity. However, few studies have assessed the response of tropical forests to longer term drought. Here, we assess the effect of a decadal-scale drought on the composition and structure of Ghanaian forests.

The effects of long-term reductions in rainfall are more complex than the impact of short-term droughts, as patterns of mortality and recruitment may cause a shift in community composition over time. For example, studies of two large plots in Central America demonstrated that floristic composition altered to favour deciduous, compound-leaved, canopy species with high wood density over a time period which included an episode of low rainfall (Condit *et al.* 1996; Condit 1998; Enquist & Enquist 2011; Feeley *et al.* 2011). Key questions are whether such changes in composition are observed over larger spatial scales, and how they relate to changes in overall ecosystem function: if community composition shifts in favour of drought-tolerant species, forest carbon stocks may be more resilient to long-term drought than suggested by short-term studies of single, extreme droughts (Molen *et al.* 2011).

Monitoring forests over long periods that include droughts may be the only practical way to address these questions. Widespread

networks of small plots have been effective in demonstrating consistent changes to tropical forest dynamics and structure across multiple sites (e.g. Lewis *et al.* 2009a,b; Phillips *et al.* 2009a). If these plots suffer a drying trend, they can be used to examine how forest composition and structure change in response to a long-term reduction in rainfall.

The results of monitoring can, however, be difficult to interpret, as many factors may influence the dynamics of the system. In order to assess whether drought is the dominant process affecting the composition of tropical forests, it is necessary to consider other drivers of change, such as anthropogenic disturbance or other factors that may influence forest structure and composition. This can be achieved by comparing changes in the functional composition of communities to the changes that would be expected given different drivers (e.g. Parmesan & Yohe 2003; Lewis *et al.* 2009b). For example, if disturbances occurred during the monitoring period, increased light penetration would lead to an increase in the occurrence of pioneer species with low wood density (e.g. Verburg & Eijk-Bos 2003) and a decrease in the occurrence of shade-tolerant species (e.g. Kariuki *et al.* 2006). In contrast, if the forests under study were recovering from disturbances that occurred before monitoring began, high wood density, shade-tolerant trees would be expected to increase (e.g. Chave *et al.* 2008). Observations from plot networks have shown that many old growth tropical forests have increased in biomass in recent decades (Baker *et al.* 2004a; Lewis *et al.* 2009a). Increased atmospheric CO<sub>2</sub>, fallout of nutrients from biomass burning or Saharan dust, and changes in solar radiation have all been suggested as possible causes (Chave *et al.* 2008; Lewis *et al.* 2009b). Such increased resource availability has been hypothes-

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ised to affect species composition by favouring faster growing, canopy species that can capitalise on such resource increases (Laurance *et al.* 2004). In contrast, multi-decadal drought is likely to result in an increase in deciduous species that are associated with drier-forest types (Enquist & Enquist 2011; Feeley *et al.* 2011). Drought, current disturbance, past disturbance and increased resource availability are therefore predicted to have different effects on the functional composition of forests (Lewis *et al.* 2009b). By investigating changes in the functional composition of a network of forest plots undergoing drought, we aim to assess whether the reduction in rainfall is the major driver of change in this system.

Monitoring the long-term effects of drought requires a forest region that has experienced a decrease in precipitation, a long-term phytodemographic data set, and extensive ecological knowledge of the species. Ghanaian forests have these characteristics. West Africa has experienced drought since the 1970s (Dai 2011), perhaps linked to increasing sea surface temperatures (Shanahan *et al.* 2009; Dai 2011). In the forest zone of Ghana, there has been a step-change in mean annual precipitation: annual rainfall in Kumasi, located within the forest zone, shows a reduction of *c.* 250 mm for the period 1980–2000 compared with 1950–1970 (Owusu & Waylen 2009). In addition, the forest reserves of Ghana contain 600 one-ha permanent sample plots established in the early 1990s (Affum-Baffoe 1996). By continuing to sample a subset of these plots and using an extensive trait data for Ghanaian forest species (Hall & Swaine 1981; Hawthorne 1995), it is possible to assess two decades of species dynamics in a variety of forest types during an extended drought. Our results show that drought, rather than disturbance or increased resource availability, is most consistent with recent changes in the floristic and functional composition of these forests, and that this trend has been associated with an increase in above-ground biomass during the study period.

## MATERIAL AND METHODS

### Study sites

Data were collected from a network of 19 long-term permanent sample plots of 0.52–1 ha in size from ten forest reserves located within wet evergreen, moist evergreen and moist semi-deciduous forest types in Ghana (Table 1, Fig. 2b). Plots were established by the Forestry Commission of Ghana (FCG) during the early 1990s in unlogged forests and were re-censused between 2007 and 2010. Most plots remained undisturbed during the study period. However, in eight plots some subplots (covering 0.04–0.48 ha per plot) had been affected by tree felling; these subplots were removed from the data set. All plots were located at least 150 m from the nearest forest edge, with the majority  $\geq 1$  km within a reserve (Table 1); fragmentation effects on forest dynamics are greatest within 100 m of the forest edge (Laurance *et al.* 1998) and therefore should not influence our results. None of the plots included in the study were known to have been burnt, and at each site this was confirmed by examination of tree bases for evidence of fire scars. Although the precise long-term disturbance history of these plots is unknown, they all occur in old growth forest reserves, the majority of which were designated before 1940 (with the exceptions of Cape Three Points and Dadieso, which were established in 1950 and 1977, respectively). Data from two plots separated on the basis of soil type in other recent studies were combined to keep plot size as

consistent as possible (see Appendix S1, Supporting Information). These plots form part of the African Tropical Forest Observation Network (AfriTRON), and are stored in the ForestPlots.net data repository (Lopez-Gonzalez *et al.* 2011a).

In order to examine compositional changes since the onset of the drought (*c.* 1970), we also used data from two long-established one ha permanent sample plots at the University of Ghana Kade Agricultural Research Station (Swaine *et al.* 1987), where many censuses were completed between 1968 and 2010. The Kade data set was analysed separately for three reasons: first, to make use of the multiple censuses associated with these plots, second, because this data set extends to the beginning of the drought period and third, because the plots are located in a 12.4 km<sup>2</sup> fragment adjacent to a Forestry Commission reserve; the Kade plots have therefore been subject to higher anthropogenic disturbance than those in the plots in the main analysis.

### Precipitation trends

Using the WorldClim data set, recent long-term annual precipitation for each plot ranges from 1288 to 1928 mm (Hijmans *et al.* 2005; Fig. 2b). Rainfall is highest along the southwest coast and decreases inland. The rainfall pattern is bimodal; the main dry season (months <100 mm precipitation) begins in November or December and ends in February, with an additional dry month in all sites in August.

We evaluated the long-term change in precipitation since the early 20th century using the Climate Research Unit (CRU) 1901–2006 TS 3.0 data set (Mitchell & Jones 2005). To assess the accuracy of this global data set for Ghanaian forests, we compared it to monthly data from four weather stations within the forest zone: Axim (data available for years 1961–2007), Kumasi (1961–2007) and Sunyani (1970–2007) from the Ghana Meteorological Agency, and Kade (1980–2009) from the University of Ghana. Correlations of monthly precipitation between the weather stations and CRU data sets were high (Axim:  $r = 0.802$ , Kumasi:  $r = 0.797$ , Sunyani:  $r = 0.771$ , Kade:  $r = 0.630$ ), but wet season precipitation was underestimated by CRU, especially for Axim which is located on the very wet southern coast. The CRU data were therefore used only to assess temporal trends, rather than spatial patterns, in rainfall.

In all 10, 0.5 degree CRU grid cells containing the study sites, annual precipitation was significantly higher for years pre-1970 than post-1970 (Table S1), decreasing by 165 mm when averaged across all 10 grid cells. This value is lower than the reduction of 250 mm presented by Owusu & Waylen (2009). The calculations, however, are not directly comparable as Owusu & Waylen (2009) calculated their value for a different time period (excluding data from 1970 to 1980) and for a single location (Kumasi). The annual rainfall anomaly (averaged across all grid cells containing study sites) from the 1901–2006 mean clearly shows reduced rainfall after 1970 (Fig. 1). This decrease occurs all year round, with a higher absolute reduction during the wet season, but a proportionally higher reduction during the main dry season (22.8% reduction compared with average pre-1970 dry season precipitation, compared with a 10.2% reduction during the wet season). All sites experienced similar proportional reductions in precipitation.

### Measurements

Initial plot set-up and measurements were performed following Alder & Synnott (1992) and re-measurements followed similar standard

Table 1 Plot descriptions

Forest type	Forest reserve	Plot code	Latitude/ Longitude	Plot area (ha)	Distance to edge (km)	Census dates	Annual precipitation (mm)*	Consecutive dry months*	Stem density (Stems ha <sup>-1</sup> )		Basal Area (m <sup>2</sup> ha <sup>-1</sup> )		Biomass (Mg ha <sup>-1</sup> )		No. Species		Reference	
									Initial	Final	Initial	Final	Initial	Final	Initial	Final		
Moist Semi-deciduous	Asenanyo	ASN-02 <sup>a</sup>	6.56/-2.22	0.6	1.27	19/3/1993, 30/1/2007	1412	4	632	612	31.1	32.9	318	339	82	87	Lewis et al. 2009a	
		ASN-04 <sup>a</sup>	6.48/-2.17	0.88	1.8	26/3/1993, 30/1/2007	1432	4	486	478	28.6	31.0	270	299	101	105		
	Bobiri	BBR-14	6.71/-1.29	0.88	0.15	15/7/1990, 21/4/2010	1480	4	495	508	27.6	27.8	304	321	87	84	This study	
		BBR-16	6.70/-1.29	0.92	0.45	18/7/1990, 27/4/2010	1488	4	572	645	20.5	27.2	221	299	94	100		
		BBR-17	6.69/-1.28	0.96	2.3	23/7/1990, 1/12/2010	1493	4	458	501	30.7	31.2	345	351	78	73		
		ESU-18	5.86/-0.80	0.52	0.35	18/8/1993, 23/3/2010	1632	3	444	504	17.9	22.0	174	218	69	72	This study	
	Kade <sup>†</sup>	KAD-01	6.15/-0.92	1	0.78	9 censuses 1968–2010	1641	3	557	480	27.8	23.9	332	280	84	89	Swaine et al. 1987 & Lewis et al. 2009a	
		KAD-02	6.15/-0.92	1	1.1	8 censuses 1970–2010	1642	3	534	483	30.4	21.9	406	241	90	98		
	Tinte Bepo	TBE-05	7.01/-2.05	0.64	1.0	26/9/1990, 29/9/2010	1288	4	500	497	20.9	26.4	221	302	74	71	This study	
	Moist Evergreen	Bonsa River	BOR-05	5.35/-1.83	1	1.0	17/2/1993, 6/4/2009	1659	3	337	395	18.2	22.3	206	257	80	86	This study
			BOR-06	5.35/-1.84	1	2.0	25/2/1993, 30/1/2009	1660	3	430	486	20.4	22.0	241	256	87	91	
		Dadieso	DAD-03 <sup>§a</sup>	5.97/-3.03	1	2.3	15/3/1993, 27/5/2007	1658	3	412	245	16.5	13.9	154	138	80	72	Lewis et al. 2009a
			DAD-04 <sup>§a</sup>	5.99/-3.03	1	2.9	17/2/1993, 18/6/2007	1650	3	456	445	25.7	27.0	356	385	93	91	
		Tonton	TON-01	6.07/-2.12	1	1.15	14/2/1991, 17/2/2010	1461	4	458	394	28.7	28.1	378	385	62	63	This study
			TON-08	6.04/-2.10	1	2.2	12/5/1991, 25/2/2010	1457	3	483	464	28.6	29.5	315	327	88	92	
	Wet Evergreen	Cape Three Points	CAP-09 <sup>a</sup>	4.85/-2.10	1	1.4	14/2/1993, 6/2/2007	1733	3	485	497	31.2	34.5	428	487	64	69	Lewis et al. 2009a
			CAP-10 <sup>a</sup>	4.80/-2.05	1	1.1	17/2/1993, 17/2/2007	1689	4	427	449	20.1	23.1	194	248	97	97	
		Draw River	DRA-04	5.16/-2.38	1	1.15	28/4/1990, 31/3/2009	1921	3	425	489	23.7	25.3	291	284	86	84	This study
DRA-05			5.21/-2.44	1	1.0	28/4/1990, 26/3/2009	1928	3	422	447	24.3	27.1	273	306	82	83		
Fure Headwaters	FUR-07	5.56/-2.39	1	1.5	23/5/1990, 8/3/2009	1739	3	581	563	21.3	24.4	210	252	93	91	This study		
	FUR-08	5.58/-2.39	0.6	1.15	19/3/1990, 15/3/2009	1741	3	582	520	20.4	22.2	204	235	72	80			

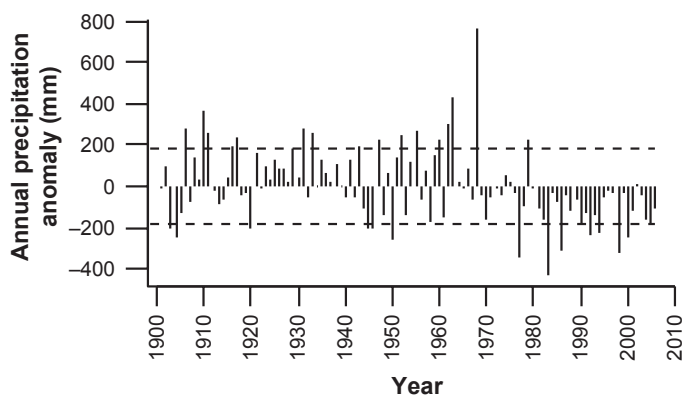
\*Annual Precipitation and consecutive dry months (<100 mm precipitation) taken from WorldClim (Hijmans et al. 2005). All plots have one additional dry month in August.

†Data set from the University of Ghana Agricultural Research Station at Kade, not part of the FCG plot network.

<sup>a</sup>From ForestPlots.net (Lopez-Gonzalez et al. 2011a).

<sup>§</sup>Plots DAD-31 and DAD-32 combined, see Appendix S1.

<sup>¶</sup>Plots DAD-41 and DAD-42 combined, see Appendix S1.



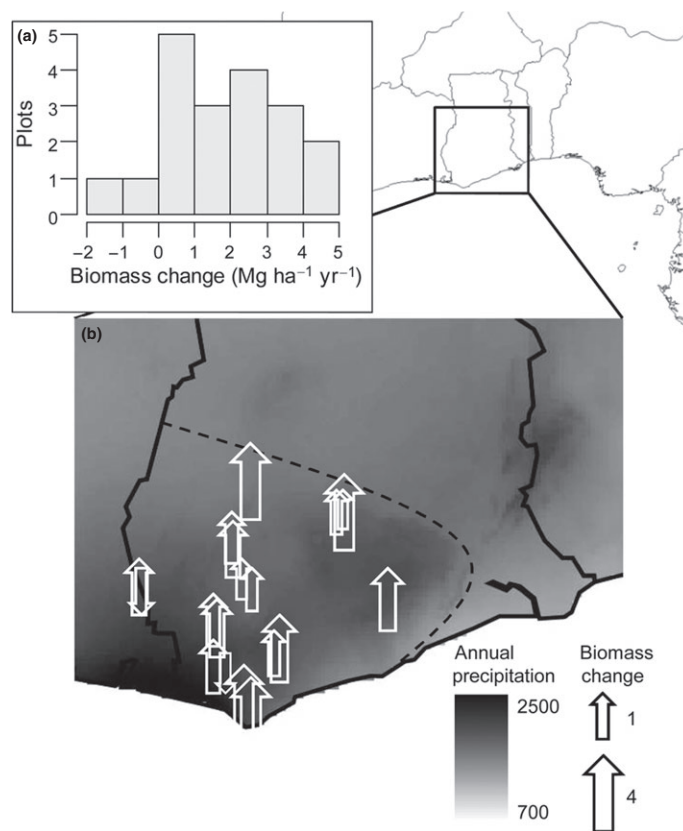
**Figure 1** Annual precipitation anomaly (mm) from the 1901–2006 mean for the average annual rainfall across all grid squares containing plot locations (1901–2006 mean 1386 mm). Dashed lines represent one standard deviation from the mean. Data from CRU (Mitchell & Jones 2005).

protocols (Lewis *et al.* 2009a; Phillips *et al.* 2009b). Each stem  $\geq 10$  cm  $D$  (diameter at breast height; 1.3 m or above buttresses) was given a metal reference tag, and  $D$  and species identity were recorded. Of 10 224 recorded stems, 97.3% of trees were identified to species-level, 2.04% to genus-level only, 0.03% to family-level only and 0.58% were unidentified. Identification was carried out by employees of FCG for the initial census and by K.P. Duah and Y. Nkrumah (FCG), supplemented by J. Dabo of the Forestry Research Institute of Ghana (FORIG) and the use of the FORIG herbarium for the recent census. Species names follow Hawthorne (1995) and were checked against the African Plant Database (CJB & SANBI 2011).

### Functional trait data set

We collated data on species' habitat preferences, wood density, leaf phenology, adult canopy position and successional status. Habitat score was based on a detrended correspondence analysis (DCA, with rare species down-weighted) of an extensive independent data set on 1550 vascular plant species found in 155, 0.0625 ha plots (Hall & Swaine 1976, 1981) and 552 inventory lists (Hawthorne & Abu Juan 1995) from across the forest zone of Ghana. The first axis of this ordination (eigenvalue = 0.36, gradient length = 4.38, total inertia = 6.68) shows a clear relationship with the wet to dry gradient across the forest zone ( $t = -37.6$ , d.f. = 701,  $r = -0.82$ ,  $P < 0.0001$ , Pearson's correlation; Fig. S1). Soil fertility covaries with rainfall due to a long history of leaching under higher precipitation regimes. However, overall the first axis scores are more strongly correlated with rainfall than soil fertility (see Swaine 1996 for further details). The value for each species along this axis was used as the habitat score for that species, with higher numbers referring to drier-forest species. The full range of species scores from the original ordination was  $-259$  to  $687$ , and for species included in the plot network the range was  $-166$  to  $503$ . A habitat score was available for 97.1% of species and 99.1% of stems.

Wood density,  $\rho$ , was taken from the ForestPlots.net database (Zanne *et al.* 2009; Lopez-Gonzalez *et al.* 2011a,b), assigned to stems at species level where possible, or given the genus- or family-level mean as appropriate (Baker *et al.* 2004b; Flores & Coomes 2011).



**Figure 2** Location of plots and biomass changes. (a) Histogram of annual rates of above-ground biomass change ( $\text{Mg ha}^{-1} \text{yr}^{-1}$ ). (b) Mean annual precipitation (mm) of southern Ghana from WorldClim (Hijmans *et al.* 2005) with plot locations (approximate) and annual rates above-ground biomass changes (arrows, size determines rate of biomass change, direction increasing or decreasing biomass,  $\text{Mg ha}^{-1} \text{yr}^{-1}$ ), dashed line shows approximate edge of the forest zone.

Species-, genus- and family-level values were used for 65.4, 23.5 and 8.3% of stems, respectively; in total, 97.2% of stems were allocated a wood density value. Data on leaf phenology, adult canopy position and successional guild were collated from Hawthorne (1995), Hall & Swaine (1981) and Poorter *et al.* (2004). Leaf phenology was classified as deciduous or evergreen (classification possible for 78.2% of species and 91.8% of stems). Where deciduousness was ambiguous (for instance where a species was stated as 'sometimes deciduous'), it was classified as deciduous (17 species). Adult tree canopy position was classified as understorey ( $<10$  m), sub-canopy (10–30 m) or canopy ( $>30$  m) (classification possible for 92.2% of species and 97.8% of stems). Successional guilds were defined as pioneer (unable to establish in closed forest shade), shade-tolerant (able to establish in closed forest shade) or non-pioneer light demander (NPLD – seedlings are present in the shaded understorey but require higher light environments to reach adult size) following Hawthorne (1995) (classification possible for 91.5% of species and 97.4% of stems).

### Changes in biomass

To investigate changes in biomass stocks, annualised rates of biomass change were calculated using the moist forest allometric equation based on diameter and species wood density from Chave *et al.* (2005):

$$\text{Aboveground biomass} = \rho \times \exp\{-1.499 + 2.148\ln(D) + 0.207[\ln(D)]^2 - 0.0281[\ln(D)]^3\}$$

to calculate biomass at each census. Of the tropical biomass equations available, the Chave *et al.* (2005) moist forest equation was most suitable; further justification and methods to calculate biomass change are provided in Appendix S1.

### Plot-level trait shifts

To assess changes over time in the plot-level trait values, we used a similar bootstrapping method to Feeley *et al.* (2011). This method involved three steps: calculating plot-level trait values for each plot at each census, calculating the rate of change in each trait for each plot and finally determining if the mean rate of change across all plots was significantly different from zero. First, for each continuous trait (habitat score, wood density) the plot-level trait score,  $x_j$ , for each census,  $j$ , was calculated as  $x_j = \sum_{i=1}^S p_i \cdot q_i$  where  $S$  is the total number of species in the plot,  $p_i$  is the abundance of species  $i$  (based on stems or biomass) and  $q_i$  is the trait score of species  $i$ . For categorical variables (leaf phenology, adult canopy position and guild),  $x_j$  was simply calculated as the percentage of stems or biomass in each category. For example, for successional guild, the percentage of pioneers was calculated, followed by the percentage of non-pioneer light demanders and then the percentage of shade-tolerant. Thus, each category was treated separately. Species with a missing trait value were excluded from the analysis of that trait. Second, the annual rate of change of each trait was calculated as  $(x_2 - x_1)/t$ , where  $x_1$  is the initial plot-level trait score,  $x_2$  is the final plot-level trait score and  $t$  is the census interval (years). Third, to test if the mean rate of change of a trait across the 19 sampled plots was significantly different from zero, we randomly selected, with replacement, 19 plots 5000 times, and calculated the mean rate of change of the trait, weighted linearly by plot size (Appendix S1), for each bootstrap. If the 95% confidence intervals (CI) from the distribution derived from the bootstrapped data (125 and 4875th ranked mean rate of change) did not overlap zero, we considered that the change in that trait was significant (at the  $P < 0.05$  level). For categorical variables, the method was performed twice, the second time using change in absolute numbers of stems or biomass in each category rather than change in percentage.

We also assessed which species significantly increased or decreased in abundance across the plot network to assess whether species that showed similar changes in abundance also shared similar functional traits (Appendix S1).

## RESULTS

### Changes in forest structure

Above-ground live biomass of plots increased significantly during the census interval (mean interval 17.1 years; Fig. 2, Table S2) with a plot-size weighted mean increase of 1.78 Mg dry mass  $\text{ha}^{-1} \text{yr}^{-1}$  (bootstrapped 95% CI = 1.09–2.48). Basal area also increased significantly during the census interval (Table S2) with a plot-size weighted mean increase of 0.12  $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$  (bootstrapped 95% CI = 0.063–0.18). Changes in stem density differed markedly among plots and did not change significantly overall (plot-size weighted

mean 0.032 stems  $\text{ha}^{-1} \text{yr}^{-1}$ , bootstrapped 95% CI = -1.81–1.49, Table S2). The increase in biomass observed is therefore likely due to the increase in basal area.

### Plot-level trait shifts

Community composition shifted in favour of drought-tolerant, deciduous, non-pioneer light demanding species. On a stem basis and using change in percentage for the categorical variables (Fig. 3, Table S3), plot mean habitat score increased significantly (with higher scores reflecting drier species composition) during the study period (0.387 units  $\text{yr}^{-1}$ , 95% CI = 0.203–0.565), as did the percentage of deciduous trees (0.108 pp  $\text{yr}^{-1}$ , 95% CI = 0.031–0.197, pp is percentage point) and the percentage of non-pioneer light demanders (0.113 pp  $\text{yr}^{-1}$ , 95% CI = 0.038–0.189). The percentage of shade-tolerant trees significantly decreased (-0.141 pp  $\text{yr}^{-1}$ , 95% CI = -0.247 to -0.045). The percentage of canopy and sub-canopy trees did not change significantly. Based on absolute rates of stem change, deciduous trees significantly increased but changes in successional guild and canopy position were not significant (Table S3).

On a biomass basis and using change in percentage for the categorical variables (Table S4), patterns were similar to those based on stems. Significant increases were found for habitat score (0.429 units  $\text{yr}^{-1}$ , 95% CI = 0.067–0.770), percentage of deciduous trees (0.120 pp  $\text{yr}^{-1}$ , 95% CI = 0.025–0.223), percentage of NPLDs (0.206 pp  $\text{yr}^{-1}$ , 95% CI = 0.100–0.318) and percentage of canopy trees (0.190 pp  $\text{yr}^{-1}$ , 95% CI = 0.095–0.290). Shade-tolerant (-0.138 pp  $\text{yr}^{-1}$ , 95% CI = -0.262 to -0.022) and sub-canopy trees (-0.153 pp  $\text{yr}^{-1}$ , 95% CI = -0.230 to -0.079) significantly decreased. Based on absolute biomass, increases in deciduous trees, NPLDs and canopy trees were significant but other changes were not.

In all stem and biomass analyses, changes in wood density, pioneer and understorey trees were not significant.

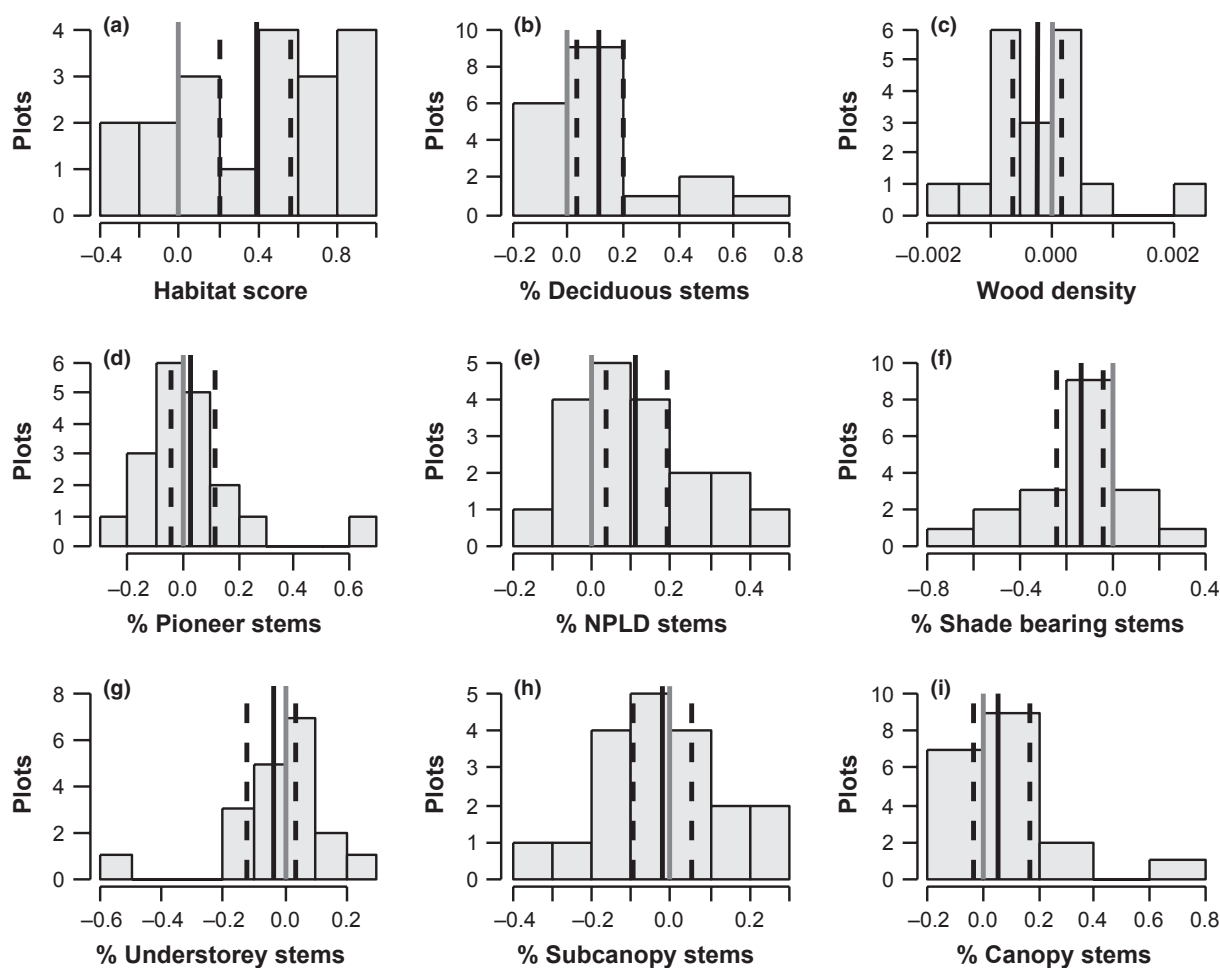
Species significantly increasing in abundance and species significantly decreasing in abundance showed significant differences in traits, with the increasing species group comprised of significantly more deciduous, NPLD, canopy species than the decreasing species group (Appendix S1).

### Trait shifts at Kade

The data set spanning 1968–2010 of two, one ha plots showed very similar shifts in species composition to the plot network (Fig. 4). Most functional traits showed significant changes over time. Habitat score, percentage of deciduous, NPLD (KAD-01 only) and canopy trees increased, whilst the percentage of shade-tolerant and sub-canopy trees decreased ( $P < 0.003$ ,  $r^2 = 0.606$ –0.979, Fig. 4). However, in contrast to the plot network, understorey trees significantly increased over time in KAD-01 (but not KAD-02). Pioneer trees and wood density, which showed no significant change in the plot network, significantly increased and decreased, respectively, in both Kade plots.

## DISCUSSION

This is the first report from tropical forests of concerted species compositional shifts in response to drought across a range of sites and habitat types. Over the past two decades, species composition



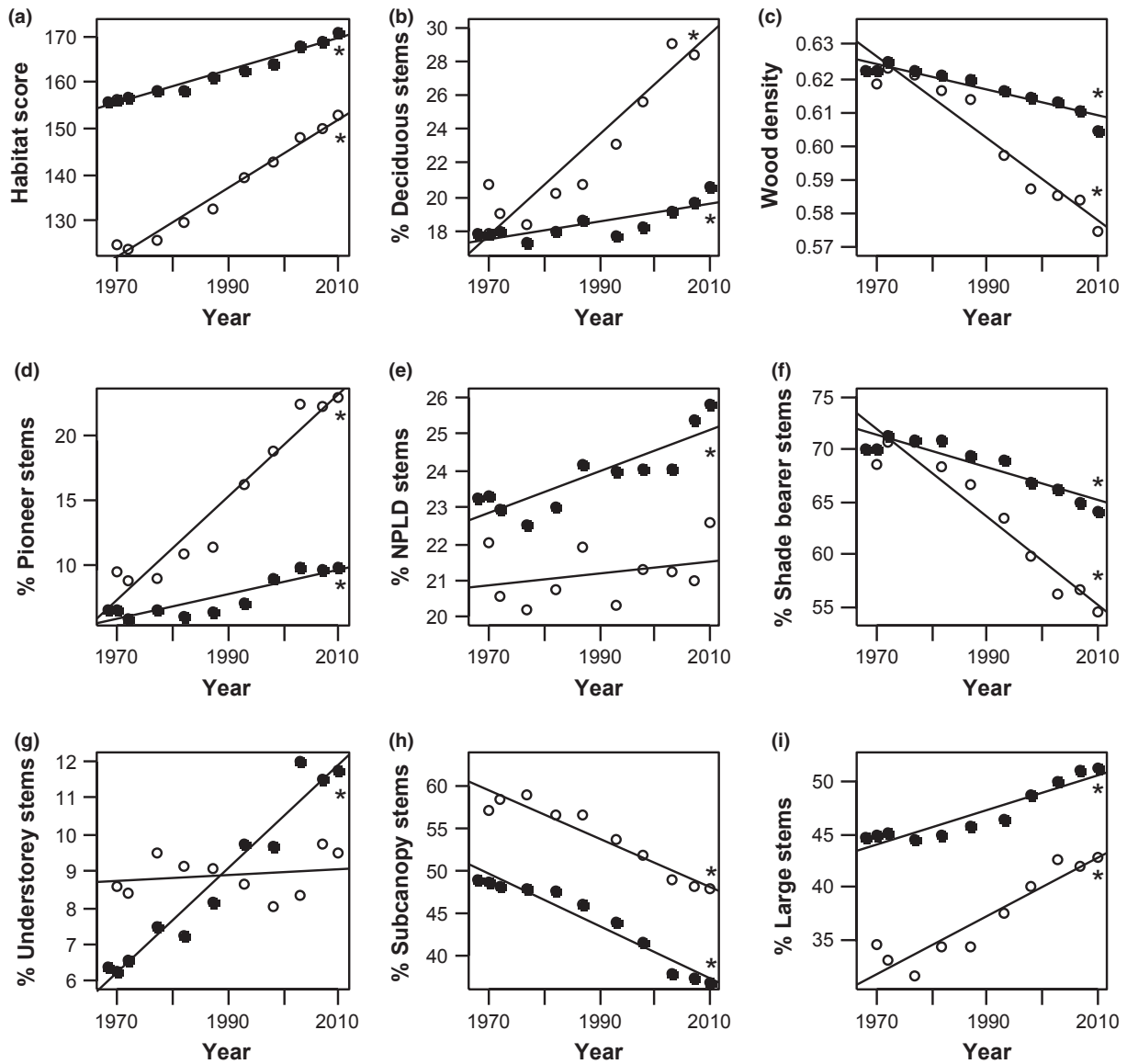
**Figure 3** Histogram of annual rates of change in functional traits, based on stems. (a) change in plot mean habitat score (where higher values relate to drier habitat species), (b) change in % of deciduous stems, (c) change in plot mean wood density, (d) change in % of pioneer stems, (e) change in % of non-pioneer light demanding (NPLD) stems, (f) change in % of shade bearing stems, (g) change in % of understorey stems, (h) change in % of sub-canopy stems, (i) change in % of canopy stems. Black lines – bootstrapped mean annual rate of change, dashed – 95% confidence intervals and dark grey lines – zero change. Habitat score, deciduous, NPLD and shade-tolerant traits show significant directional change.

in Ghanaian forests has shifted to favour deciduous, drier-forest affiliated, canopy species with intermediate light requirements, over wetter-forest affiliated, evergreen, shade-tolerant, sub-canopy species. This suggests that changes to the rainfall regime are important in structuring these communities. In addition, the long-term data set at Kade provides evidence that these functional changes have been occurring since the onset of the West African drought.

#### Are widespread compositional changes likely to be caused by drought or other drivers?

We need to carefully assess the multiple drivers that may have led to the significant directional shifts in forest composition that we observed. For example, we hypothesised that disturbance during the study period would increase the abundance of pioneer and reduce the abundance of shade-tolerant species, while recovery from disturbance prior to monitoring would lead to an increase in shade-tolerant and a reduction in pioneer species (Chave *et al.* 2008). However, although we found a reduction in shade-tolerant species, there was no change in the abundance of pioneer species, suggest-

ing that neither current disturbance patterns nor recovery from past disturbance are the dominant drivers of compositional change in this data set. A second potential explanation is related to increased resource availability, which has been hypothesised to favour fast growing, canopy species (Laurance *et al.* 2004). In our data set, canopy species did increase in abundance but there was no trend in mean wood density, a proxy for diameter growth rate (King *et al.* 2006). These patterns are partially consistent with this hypothesis, as is the overall rise in above-ground biomass, suggesting that increased resource availability may be having a detectable effect on functional composition. Finally, we hypothesised that the drought would lead to an increase in both deciduous species and species associated with drier-forest types. Both of these patterns were found within our data set (Fig. 3). Overall, considering the consistent trends in habitat score and deciduous species found across the plot network, drought, rather than disturbance or resource availability, appears to have been the dominant driver of compositional change. Furthermore, the case for drought as the driving force of changes in functional traits during the census period is supported by the finding that the traits that increased or decreased over time



**Figure 4** Changes in functional composition of KAD-01 (closed circles) and KAD-02 (open circles) from 1968 to 2010. (a) Change in plot mean habitat score, (b) change in % of deciduous stems, (c) change in plot mean wood density, (d) change in % of pioneer stems, (e) change in % of non-pioneer light demanding stems, (f) change in % of shade bearing stems, (g) change in % of understorey stems, (h) change in % of sub-canopy stems, (i) change in % of canopy stems. \* denotes a significant change in trait over time.

reflect the changes that occur spatially from wetter to drier forests (Appendix S2). For example, habitat score and the abundance of canopy trees increase in drier sites, whilst shade-tolerant and sub-canopy trees increase in wetter sites (Appendix S2).

Despite these broad trends in compositional change across the plot network, some individual plots show patterns which reflect the importance of other drivers at smaller scales. For instance, DAD-03 exhibits a large increase in the percentage of pioneer trees ( $0.54 \text{ pp yr}^{-1}$ ) and reductions in biomass and stem density (Tables S2–4). These result from a strong disturbance during the census period. Surveying the site, it was considered that the most likely cause of disturbance was an anomalous flood (S. L. Lewis, pers. obs.). The plot also shows large increases in drought-tolerant trees, with an increase in habitat score and one of the largest increases in the percentage of deciduous trees ( $0.54 \text{ pp yr}^{-1}$ ). One explanation

may be that the mortality event has allowed the changes seen in the other plots to be accelerated, as a greater proportion of trees in DAD-03 were replaced in the 20-year study period.

#### Longer term change at Kade

The 40-year data set from Kade shows very similar results to the plot network: habitat score, deciduous trees, NPLDs and canopy trees all increased, with a concurrent reduction in shade-tolerant and sub-canopy trees (Fig. 4). These changes occurred consistently over time, suggesting that the shifts seen since 1990 across the plot network have been ongoing since the onset of the West African drought and steadily continued throughout the census period to 2010. Pioneer species significantly increased and mean wood density significantly decreased over time suggesting that the Kade plots

have experienced more disturbance than the majority of sites in the plot network. This trend is likely to be due to the small fragment size and possibly higher anthropogenic pressure on the Kade forest. In contrast to the plot network, understorey trees also increased over time in KAD-01. This is due to two tree species, *Diospyros canaliculata* and *Microdesmis puberula*, increasing in abundance. Other understorey species remained rare or decreased throughout the study period. These two species have relatively high habitat scores, above the 70th percentile of all shade-tolerant species present in the plot. It is possible that the high drought-tolerance of these particular species may be allowing them to increase in abundance at this site.

### Effects of long-term and short-term drought

The results presented here and from other long-term drought studies differ from those focusing solely on short-term, extreme droughts. Many studies of the impact of short-term droughts on mortality, typically linked to El Niño Southern Oscillation (ENSO) events, find that large trees suffer greater mortality than small understorey trees (Condit *et al.* 1995; Nieuwstadt & Sheil 2005; Phillips *et al.* 2010). In addition, results from throughfall exclusion (TFE) experiments have also reported increased mortality of large trees (Nepstad *et al.* 2007; da Costa *et al.* 2010). In contrast, this study and those from Panama (Condit *et al.* 1996; Feeley *et al.* 2011) and Costa Rica (Enquist & Enquist 2011) show an increase in abundance of canopy trees and often a decrease in small trees. One explanation for this may lie in the types of drought that these studies cover. In TFE experiments, 50% of rainfall may be excluded (Nepstad *et al.* 2007; da Costa *et al.* 2010) and ENSO events characteristically reduce pan-tropical rainfall by approximately 30% (Malhi & Wright 2004 p. 321) and often with much greater reductions at individual sites. Long-term droughts, however, can be more complex, with long-term reductions in precipitation which may or may not also be punctuated by stronger drought events. For example, the average decrease in annual rainfall in this study is 11%, with some years experiencing especially low rainfall (Fig. 1). Precipitation at the site studied by Enquist & Enquist (2011) gradually decreased over the 20th century and included nine years of extremely low rainfall during the census period. At the study site in Panama, annual precipitation declined by 11% from 1965 to 1996 compared with pre-1965 precipitation (Condit *et al.* 1996), with a particularly strong drought during the 1982/83 ENSO event which the forest may still be responding to (Feeley *et al.* 2011). Although, over extended time periods drought strength is likely to vary, rainfall declines in the long-term data sets are usually weaker than those in short-term studies of individual extreme natural or experimental droughts. Increased mortality of large trees may occur when soil water levels fall below a critical threshold (Nepstad *et al.* 2007) due to the high transpiration demand of canopy trees and the distance over which water must be transported (da Costa *et al.* 2010), resulting in hydraulic failure (Phillips *et al.* 2010). Smaller trees might be susceptible to drought-induced mortality at less severe reductions in soil water than canopy trees, possibly due to the higher likelihood of carbon starvation in a low light environment, or their shorter rooting depths (Condit *et al.* 1996). Longer term but less extreme droughts may result in weaker soil water deficits, sufficient to affect small trees but not reaching the threshold at which canopy trees face physiological difficulties. Consistent with this, Phillips *et al.* (2010) found that the relative risk of mortality for large trees was lower where droughts were less severe.

Recent evidence shows that intact tropical forests have increased in biomass over decadal timescales (Baker *et al.* 2004a; Lewis *et al.* 2009a) and a variety of potential drivers have been proposed: increased resource availability from atmospheric CO<sub>2</sub>, nutrient enrichment and solar radiation (Lewis *et al.* 2009b). In contrast, studies of anomalous short droughts and TFE studies have found rapid biomass loss over short periods (Nieuwstadt & Sheil 2005; Phillips *et al.* 2009a; da Costa *et al.* 2010) showing that these extreme droughts can temporarily reverse the processes leading to increased biomass. Despite the long-term drought, this study found an increase in biomass of a similar magnitude to other African (Lewis *et al.* 2009a) and Amazonian (Phillips *et al.* 2009a) forests over recent decades. We hypothesise that the shift in composition in favour of drought-tolerant species that we detected may play a key role in allowing the carbon stocks of these forests to be maintained during this long-term, low-intensity drought. As the forest structure is maintained, the driver(s) of widespread biomass increase may still be able to act on the system, whereas only during extreme droughts do increases in tree mortality dominate and cause substantial decreases in above-ground biomass.

The results presented here show species compositional change in response to drought in conjunction with an increase in biomass. However, scaling-up these results requires extreme caution. This study only assessed old growth sites and avoided areas with direct anthropogenic impacts or that had been subject to wildfires; thus, these sites are not representative of Ghanaian forests which are typically subject to high levels of human activity and in which disturbance, or in some areas fire, are likely to play an important role. Furthermore, extrapolating results to other parts of the tropics should be done with care. The West African species pool may contain a particularly large proportion of disturbance- and drought-adapted taxa compared with other tropical forests for three reasons. First, West African forests may have experienced such droughts as part of an approximately 40-year wet–dry cycle operating over the past several thousand years (Shanahan *et al.* 2009). Second, forests generally occur in Africa under lower precipitation than in other tropical areas and have experienced dry periods during glacial-interglacial cycles (Anhuf *et al.* 2006). Third, though forests globally have been subject to some level of human activity for thousands of years, humans have been present in Africa for a greater time than other areas of the tropics (Barnosky *et al.* 2004) and West African forests have been fragmented and exposed to high levels of anthropogenic disturbance (Fairhead & Leach 1998). Other tropical forest regions may not be so well-stocked with species adapted to such changes in the environment.

In conclusion, this study shows the importance of changes in species composition within a forest stand in determining the response of tropical forests to long-term drought. While highlighting the sensitivity of tropical forest composition to environmental change we also demonstrate that the range of strategies represented within species-rich forests means that low-intensity droughts may not necessarily reduce forest carbon stocks.

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## AUTHOR CONTRIBUTIONS

SF, TRB, SLL, MDS, TRF and KCH designed the study; SF, TRF and EGF collected data; KAB, SLL and MDS provided data; SF analysed data and wrote the paper; all authors contributed to revisions.

## REFERENCES

- Affum-Baffoe, K. (1996). Revised permanent sample plot procedures in Ghana. In: *IUFRO Conference on Growth Studies in Moist Tropical Forests in Africa* (eds Foli, E.G., Vanclay, J.K. & Ofosu-Asiedu, A.). Forestry Research Institute of Ghana, Kumasi, pp. 35–42.
- Alder, D. & Synnott, T.J. (1992). *Permanent Sample Plot Techniques for Mixed Tropical Forests*. Oxford Forestry Institute, Oxford.
- Anhuf, D., Ledru, M.-P., Behling, H., Da Cruz, F.W. Jr, Cordeiro, R.C., Van der Hammen, T. *et al.* (2006). Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeogr. Palaeoclimatol.*, 239, 510–527.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A. *et al.* (2004a). Increasing biomass in Amazonian forest plots. *Philos. T. Roy. Soc. B*, 359, 353–365.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A. *et al.* (2004b). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Change Biol.*, 10, 545–562.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. & Shabel, A.B. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science*, 306, 70–75.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D. *et al.* (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99.
- Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S. *et al.* (2008). Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol.*, 6, 455–462.
- Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I. *et al.* (2007). Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M. & Averyt, K.B. *et al.*). Cambridge University Press, Cambridge, UK, pp. 848–940.
- Condit, R. (1998). Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change*, 39, 413–427.
- Condit, R., Hubbell, S.P. & Forster, R.B. (1995). Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.*, 65, 419–439.
- Condit, R., Hubbell, S.P. & Forster, R.B. (1996). Changes in tree species abundance in a neotropical forest: impact of climate change. *J. Trop. Ecol.*, 12, 231–256.
- Conservatoire et Jardin Botaniques de la Ville de Genève & South African National Biodiversity Institute (2011). African Plant Database. Available at: <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>. Last accessed 15 September 2011.
- da Costa, A.C.L., Galbraith, D., Almeida, S., Portela, B.T.T., da Costa, M., de Athaydes Silva Junior, J. *et al.* (2010). Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazon rainforest. *New Phytol.*, 187, 579–591.
- Dai, A. (2011). Drought under global warming: a review. *Wiley Interdiscip. Rev. Clim. Change*, 2, 45–65.
- Enquist, B.J. & Enquist, C.A. (2011). Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Glob. Change Biol.*, 17, 1408–1424.
- Fairhead, J. & Leach, M. (1998). *Reframing Deforestation: Global Analyses and Local Realities*. Routledge, London.
- Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S. & Foster, R.B. (2011). Directional changes in the species composition of a tropical forest. *Ecology*, 92, 871–882.
- Flores, O. & Coomes, D.A. (2011). Estimating the wood density of species for carbon stock assessments. *Method. Ecol. Evol.*, 2, 214–220.
- Hall, J.B. & Swaine, M.D. (1976). Classification and ecology of closed-canopy forest in Ghana. *J. Ecol.*, 64, 913–951.
- Hall, J.B. & Swaine, M.D. (1981). *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana*. Dr W Junk publishers, The Hague.
- Hawthorne, W.D. (1995). *Ecological Profiles of Ghanaian Forest Trees*. Oxford Forestry Institute, Oxford.
- Hawthorne, W.D. & Abu Juam, M. (1995). *Forest Protection in Ghana*. IUCN, Gland, Switzerland and Cambridge.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.
- Kariuki, M., Kooyman, R.M., Smith, R.G.B., Wardell-Johnson, G. & Vanclay, J. K. (2006). Regeneration changes in tree species abundance, diversity and structure in logged and unlogged subtropical rainforest over a 36-year period. *Forest Ecol. Manag.*, 236, 162–176.
- King, D.A., Davies, S.J., Tan, S. & Noor, N.S.M.D. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *J. Ecol.*, 94, 670–680.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M. & Laurance, S.G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, 79, 2032–2040.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C. *et al.* (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171–175.
- Laurance, W.F. & Peres, C.A. (eds) (2006). *Emerging Threats to Tropical Forests*. The University of Chicago Press, Chicago.
- Lewis, S.L. (2006). Tropical forests and the changing earth system. *Philos. T. Roy. Soc. B*, 361, 195–210.
- Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O. *et al.* (2009a). Increasing carbon storage in intact African tropical forests. *Nature*, 457, 1003–1006.
- Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A. & Laurance, W.F. (2009b). Changing ecology of tropical forests: Evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.*, 40, 529–549.
- Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M. & Phillips, O.L. (2011a). ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *J. Veg. Sci.*, 22, 610–613.
- Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M. & Phillips, O.L. (2011b). *Forest Plots Database*. Available at: <http://www.forestplots.net>. Last accessed 15 September 2011.
- Malhi, Y. & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos. T. Roy. Soc. B*, 359, 311–329.
- Mitchell, T.D. & Jones, P.D. (2005). An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.*, 25, 693–712.
- van der Molen, M.K., Dolman, A.J., Ciais, P., Eglin, T., Gobron, N., Law, B.E. *et al.* (2011). Drought and ecosystem carbon cycling. *Agr. Forest Meteorol.*, 151, 765–773.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, 88, 2259–2269.
- van Nieuwstadt, M.G.L. & Sheil, D. (2005). Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *J. Ecol.*, 93, 191–201.

- Owusu, K. & Waylen, P. (2009). Trends in spatio-temporal variability in annual rainfall in Ghana (1951–2000). *Weather*, 64, 115–120.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G. *et al.* (2009a). Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344–1347.
- Phillips, O.L., Baker, T.R., Feldpausch, T.R. & Brien, R. (2009b). RAINFOR Field Manual for Plot Establishment and Remeasurement. Available at: [http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals\\_eng.html](http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals_eng.html). Last accessed 15 September 2011.
- Phillips, O.L., van der Heijden, G., Lewis, S.L., Lopez-Gonzalez, G., Aragao, L. E.O.C., Lloyd, J. *et al.* (2010). Drought-mortality relationships for tropical forests. *New Phytol.*, 187, 631–646.
- Poorter, L., Bongers, F., Kouame, F.N. & Hawthorne, W.D. (eds) (2004). *Biodiversity of West African Forests: An Ecological Atlas of Woody Plant Species*. CABI Publishing, Wallingford.
- Shanahan, T.M., Overpeck, J.T., Anchukaitos, K.J., Beck, J.W., Cole, J.E., Dettman, D.L. *et al.* (2009). Atlantic forcing of persistent drought in West Africa. *Science*, 74, 377–380.
- Sheffield, J. & Wood, E.F. (2008). Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Clim. Dynam.*, 31, 79–105.
- Swaine, M.D. (1996). Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *J. Ecol.*, 84, 419–428.
- Swaine, M.D., Hall, J.B. & Alexander, I.J. (1987). Tree population dynamics at Kade, Ghana (1968–1982). *J. Trop. Ecol.*, 3, 331–345.
- Verburg, R. & van Eijk-Bos, C. (2003). Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *J. Veg. Sci.*, 14, 99–110.
- Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L. *et al.* (2009). Global Wood Density Database. Available at: <http://hdl.handle.net/10255/dryad.235>. Last accessed 15 September 2011.

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