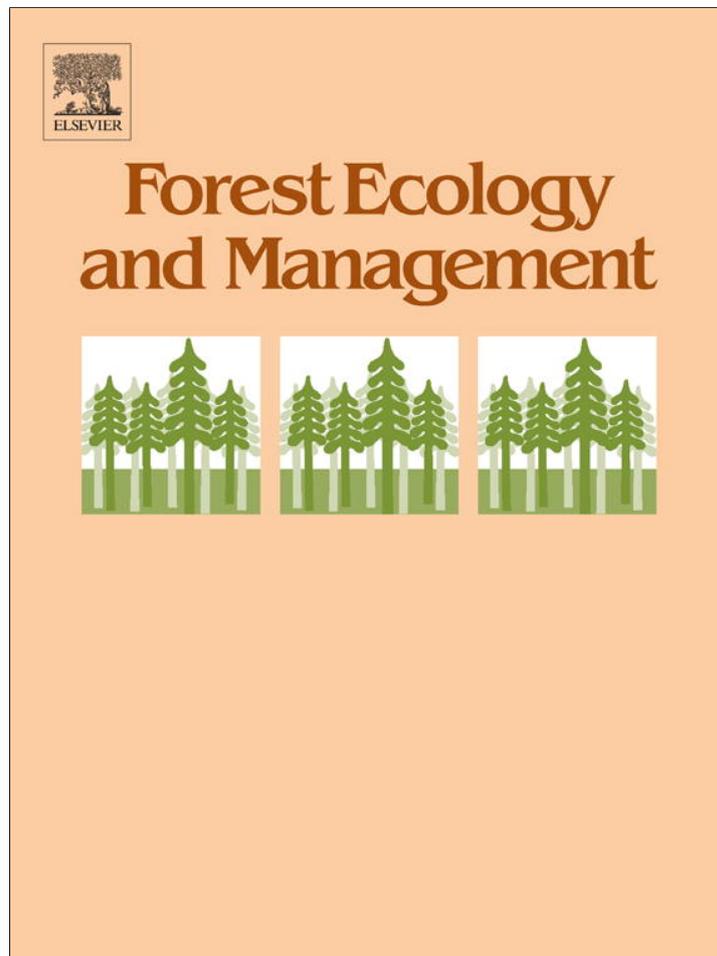


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# Forest Ecology and Management

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## Spatial and temporal variation of carbon stocks in a lowland tropical forest in West Africa

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### ABSTRACT

Understanding the nature and cause of spatial and temporal variation in forest carbon is critical for implementation of climate mitigation strategies such as REDD. Such knowledge is lacking and hard to acquire in resource poor regions such as West Africa's Upper Guinea where benefits of such schemes for forest conservation could have great impact.

We undertook a systematic and representative survey of an entire Upper Guinea forest – Gola Forest in southeast Sierra Leone – by measuring over 600 plots (0.125 ha) in order to quantify the level of spatial variation in C that might exist within a discrete forest type and relate this to historic and contemporary impacts on the forest. We modelled current C stocks and compared these with values calculated from historic surveys. Mean C content in above ground biomass was c. 160 Mg ha<sup>-1</sup>. The southern part of the forest which was subject to heavier logging in the 1980s had a lower C content (121–144 Mg ha<sup>-1</sup>) compared to the less disturbed central areas (186 Mg ha<sup>-1</sup>). Volumes of extracted timber and distance to settlements around the forest explained 42% of the variation in C content. Elevation, slope and other metrics of human impact such as distance to roads did not explain significant additional variation. A survey from the 1950s recorded much higher carbon content than currently found in the south of the forest. This accords with evidence that commercial logging in this area was destructively high. However, old surveys from the late 1960s/early 1970s in less disturbed areas recorded lower carbon content than present. Most of the past surveys were in areas that had not yet been commercially logged so the accumulation in biomass in the last 40 years implies recovery from a much older disturbance event, or a change in environmental conditions promoting growth.

As a typical Upper Guinean forest, our results from Gola demonstrate the long term impacts of disturbance events on carbon stocks and how these can vary greatly at small scales, highlighting the need for representative and regionally relevant empirical data to inform REDD type initiatives. Nonetheless these forests remain important for carbon sequestration and storage in the region despite this history and the parts of the forest with no recorded logging activity that increased in carbon in recent decades with levels now akin to undisturbed plots reported from elsewhere in the region demonstrate the sequestration potential these forests provide once adequately protected.

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### 1. Introduction

Forests are of singular importance to global climate change because they may either emit or sequester significant volumes of carbon dioxide depending on how they are managed. Currently, forested regions are substantial contributors to atmospheric carbon dioxide with global annual emissions from deforestation and forest

*Abbreviations:* C, carbon; dbh, tree diameter in cm at 1.3 m above ground level; gbh, girth at breast height; REDD, Reduced Emissions from Degradation and Deforestation.

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degradation estimated to be 1.2 Pg (=10<sup>15</sup> g) between 1997–2006, equating to c. 12% of global man-made emissions in 2008 (van der Werf et al., 2009). However, tropical forests can also be an annual sink of carbon, as estimated from long term measurements on undisturbed plots, of around 1.3 Pg (Lewis et al., 2009). Both the temporal trend and the present-day distribution of carbon stocks will reflect disturbance history. Since the distribution and trends in carbon stocks in tropical forests are critical considerations for REDD at both local and regional scales, there is a pressing need for greater understanding of the impact of disturbance on carbon.

Disturbance caused by forest degradation is a poorly quantified component of the carbon balance partly because there is no agreed definition of degradation (Sasaki and Putz, 2009) and also because

it can be relatively complex to detect remotely (GOF-C-GOLD, 2010). The impact on carbon stocks from degradation will depend on the intensity and type of activity so removal of large trees selected for timber, for example, will have a disproportionate impact on carbon stocks since larger and denser wooded species contain the greater proportion of biomass in a forest. Generalised statements about the impact of degradation on forests will therefore always be hard to make, but all the more so in the absence of empirical studies that provide bench marks in particular circumstances.

Many forest landscapes now reflect a long history of human intervention including both forest conversion and degradation as well as land abandonment, as exemplified by the Upper Guinea forest block in West Africa. The distribution of biomass within this region reflects not only climatic and edaphic effects, but also the tree species composition – which has high levels of regional endemism – and a history of slash and burn agriculture and commercial timber exploitation. This has resulted in a landscape mosaic of varying-aged regrowth, and forests with varying levels of disturbance and recovery. This is also a region of high biological endemism in many taxa (Grubb et al., 1998; Stattersfield et al., 1998; Jongkind, 2004; Penner et al., 2011) but since these forests are under particular pressure from degradation and conversion to agriculture (Mittermeier et al., 2004) only remnant tracts of forest remain in all countries but Liberia (Christie et al., 2007) and many species in the region are now threatened with extinction as a result (BirdLife International, 2000; IUCN, 2011). Accounting for spatial variation in biomass and relating this to disturbance history is therefore important for this region, especially when assessing the value of REDD+ in funding conservation solutions for the region. Data from the region are rather few and we have little understanding of typical biomass stocking rates in Upper Guinea forests nor how a history of small scale and commercial exploitation can influence these stocks (Brown and Gaston, 1995; Clark et al., 2001; Lewis et al., 2009; Henry, 2010; Henry et al., 2010).

In order to understand the sequestration potential of Upper Guinean forests with this background of disturbance we identified three key questions, each with a management implication:

1. What is the current level of carbon stocks in the region's forest? This will determine the scale of contribution such forests can play in the carbon balance.
2. What accounts for the current distribution of carbon stocks in the forest? This will determine whether sequestration can be promoted by influencing these factors.
3. What historical changes has the forest experienced? This could indicate the extent to which these forests could change in the future.

We sought to address some of these questions in a typical Upper Guinean forest, Gola Forest, Sierra Leone (hereafter Gola). Although Gola is classified as largely one forest type (wet evergreen lowland forest, though see below), considerable variation in stand density, stature and species composition are apparent, partly due to past management and landuse, but presumably also due to ecological processes. Gola has a history of timber exploitation which has left a number of written records of past stock assessments and timber extraction. Such a site provides an ideal case in which to assess spatial and temporal variation in carbon stocks with respect to disturbance history.

## 2. Materials and methods

Gola lies along the border with Liberia between 7°18' and 7°51'N and 10°37' and 11°21'W. It is the largest remaining tract

of lowland moist evergreen high forest in Sierra Leone and lies at the western extremity of the Upper Guinea forest block. The woody vegetation is dominated by Leguminosae–Caesalpinoideae, Euphorbiaceae, Leguminosae–Mimosoideae and Sterculiaceae (Klop et al., 2008). Annual rainfall is 2500–3000 mm, mostly falling in a single wet season from May to October. Three forest reserves were gazetted from the 1930s onwards, consisting of four forest blocks (Fig. 1). Gola West (c. 67 km<sup>2</sup>) and Gola East (c. 205 km<sup>2</sup>) are low-lying and swampy in places (mean altitudes of 131 and 152 m). Gola North (c. 417 km<sup>2</sup>) and its Extension 2 (c. 61 km<sup>2</sup>) are more rugged and at a higher elevation than the surrounding landscape (mean altitude 303 m).

### 2.1. Contemporary data collection

Trees were surveyed between October 2005 and May 2007 in 609 circular plots (radius 19.95 m = 0.125 ha) at 200 m intervals along 43 transects of up to 4 km length. Plot positions were established along transects using a compass and tape measure and locations determined using a GPS (Garmin Map 60). The transects were distributed over the entire forest, using a systematic segmented grid (Buckland et al., 2004) randomly superimposed onto the area. All trees > 30 cm diameter at breast height (1.3 m) were identified, measured and tagged whilst trees 10–30 cm dbh were surveyed in a sub-plot (radius 6.31 m = 0.0125 ha). Species identifications were undertaken by Sierra Leone Department of Forestry experts. Tree height was estimated from a log:log regression of height on dbh with a correction factor (Baskerville, 1972) using a dataset of 354 trees in Gola where height was measured with a clinometer (Small, 1953; this study) (see Appendix A). Wood specific gravity data were gathered from published databases (Chave et al., 2009; Zanne et al., 2009; Henry et al., 2010) and were available for 65.2% of trees in the dataset (see Appendix A).

### 2.2. Calculation of total carbon stock and spatial variation

The aboveground carbon content of individual trees was estimated using an allometric equation for moist tropical forest based on dbh + height + wood specific gravity (Chave et al., 2005) and a carbon fraction of 0.47 (Aalde et al., 2006) (see Appendix A). The C stock in each contemporary plot was calculated as:

$$Mg_{\text{total}} = \sum Mg_n + 10^* \sum Mg_m \quad (1)$$

where  $n$  was trees > 30 cm dbh and  $m$  was trees 10–30 cm dbh. The total C stock in the plot was adjusted to account for sloping ground using clinometer data from the plot ( $n = 354$  plots) or a global digital elevation model ( $n = 75$  plots; Aster: METI and NASA, 2009) (see Appendix B).

### 2.3. Scaling up to the whole forest – spatial prediction model

The overall carbon stocks in Gola were initially estimated from an average C density from all plots. To provide information on spatial variation in carbon stocks and to account for this variation a linear model was developed in which transect mean C density was modelled on a range of available explanatory variables using R software (v 2.13.1: R 2.13, 2011). The variables were measured in a GIS by extracting values for each plot and calculating the mean of these for each transect. The variables were elevation, slope, distance to nearest stream, distance to forest reserve boundary, distance to nearest road, distance to nearest settlement, recorded logging offtake (cubic m/ha). See Appendix C for further details. Although soil type and geology are important determinants of forest ecology (though their influence on biomass is less certain – Paoli et al., 2008) no maps were available for soils in Gola, and



Fig. 1. Location of Gola Forest, Sierra Leone and position of the four forest management blocks. Only chiefdom and district headquarters are shown.

geology maps remain undigitised, so neither could be included in the analysis. A visual inspection of paper geology maps suggested a low level of differentiation within Gola.

All explanatory variables were included in an average model including all models with a  $\Delta AIC$  less than 4 (R procedure Dredge). In addition, variables were selected in a conventional stepwise manner according to AIC (R procedure stepAIC). The parameter estimates for the selected variables were then used in a GIS to predict C stock in each hectare cell for the whole of Gola. Overall C stock for Gola was then derived by summing all hectare cells together. The impact of individual variables on the total C stock in Gola was assessed by reversing their effect at the prediction stage and examining the resulting change in C stocks predicted for the forest. This allowed us to ascertain the extent that improved forest management could influence C stocks in the forest.

Spatial variation in C stocks may also be explained in terms of the ecological characteristics of tree species. For example, pioneer species typically have low wood density whereas shade-bearing species have denser wood. Since pioneer species predominate in disturbed forests stand-level wood density has been used to quantify levels of disturbance in tropical forests (Slik et al., 2008). We assigned tree species to key guilds (Hawthorne, 1995; Hawthorne and Jongkind, 2006; W. Hawthorne pers. comm.) and tested whether guild could account for variation in C stocking rates in Gola.

#### 2.4. Calculation of historical change

Gola was subject to commercial selective logging between 1960 and 1989 (Iles et al., 1993) with operations covering c. 30% of the reserves concentrated in Gola West and East and the western parts

of Gola North. Some official figures of logging offtake by compartment survive (Iles et al., 1993), although are regarded as unreliable for some compartments. Forestry surveys have been conducted in Gola all of which predated commercial logging operations in the area they covered. We used these surveys to estimate past carbon stocks in Gola for comparison with contemporary stocks (Table 1).

Tree data from the contemporary survey were filtered and summarised to create datasets (e.g. stand tables of stem counts in size classes) equivalent to the historic data to ensure meaningful comparison. C stocks were calculated from stand tables by converting each stem size class to a dbh using the middle value of the class and converting dbh to biomass using an allometric equation from West Africa based on dbh only (Henry et al., 2010). We used a simpler equation in these analyses because difficulties assigning wood density values to the historic data negated the value of a more complex equation (see Appendix A). Only contemporary plots that fell within the same management compartments as the historic data were included in historic comparisons and each plot was treated as a replicate within each compartment being compared.

In order to relate current biomass estimates and changes to records of past timber volumes extracted we used a default biomass expansion and conversion factor (1.3; from Table 4.5, Aalde et al., 2006) to convert volumes of timber to above ground biomass.

### 3. Results

Of 7721 trees recorded, 7099 were identified to species level (229 species of 179 genera), 468 were identified only to genus level (60 genera) and 154 were unidentified. 14 of 609 plots had no stems over 10 cm dbh because they had been recently cleared for

**Table 1**  
Details of historic forestry surveys in Gola Forest, Sierra Leone, from the 1950s to 1970s.

Surveyor	Date	Location	Sampling	Sampling limits	Data available	Reference
D. Small, Assistant Conservator of Forests, Sierra Leone.	Early 1950s	Gola East Block III	Belt transects for 5% enumeration of one compartment (c. 3100 ha)	All species Minimum dbh = 58.2 cm (5 feet girth)	Stems counts in girth classes for each species	Small (1953)
D. Small	Early 1950s	Gola East	3 Square plots 0.5 and 1 ha each	All species Minimum dbh = 9.7 cm (1 foot girth)		Small (1953)
D. Small	Early 1950s	Gola East	3 Belt transects 1 acre each	All species Minimum dbh = 4.85 cm (7 inches girth)		Small (1953)
J.A. White FAO Forestry Officer	1969–1972	16 Compartments in Gola East and North	8891 Plots of 0.25 acres each	All species Minimum dbh = 38.8 cm (4 feet girth)	Stems counts by species in c. 30 cm (1 foot) girth classes for each compartment. Non commercial species pooled.	White (1972)

**Table 2**  
Mean carbon content (Mg C ha<sup>-1</sup>) and confidence intervals in the four historic forestry management units of Gola Forest, Sierra Leone derived from field surveys in 2006–2007. The West and East blocks were (heavily) commercially logged in the past whilst the North was only logged in part of its area and Extension 2 had no commercial logging.

	West	East	North	Extension 2
Mean Mg C ha <sup>-1</sup>	121.7	144.1	186.2	111.4
±95% CI	15.3	14.7	14.2	26.4
n	75	174	312	34

agriculture or were located in open swamps or had experienced recent wind-throw.

### 3.1. Total carbon content and spatial variation in Gola

The mean from all plots of above ground living C stocks in Gola was 161.4 Mg C ha<sup>-1</sup> (95% CI: 152.2–170.5) giving a total C stock in Gola of 11,472,700 Mg C (95% CI: 10,828,605–12,121,795). There was considerable spatial variation in C biomass with the highest levels being found in Gola North and the lowest levels in Extension 2 (Table 2). Maximum and mean dbh and stem density all varied significantly between the forest blocks (Fig. 2), but wood density did not ( $F_{3,599} = 0.33, p = 0.80$ ).

The ecological characteristics of the tree species in the plots had little influence on the overall C stock of the plot despite clear differences in C content of individual species due to variation in wood density. Of 7415 trees that were assigned to guilds, 6.5% were pioneers, 35.2% were non-pioneer light demanders, 38% were shade bearing and 11.9% were swamp forest species. The remainder (8.4%) were a mix of savannah and cultivated species indicating Gola's history of disturbance. C stocks were higher in plots with higher tree diversity even after controlling for the positive effect of tree density on diversity ( $F_{2,584} = 148.3, p < 0.0001$ ). Trees

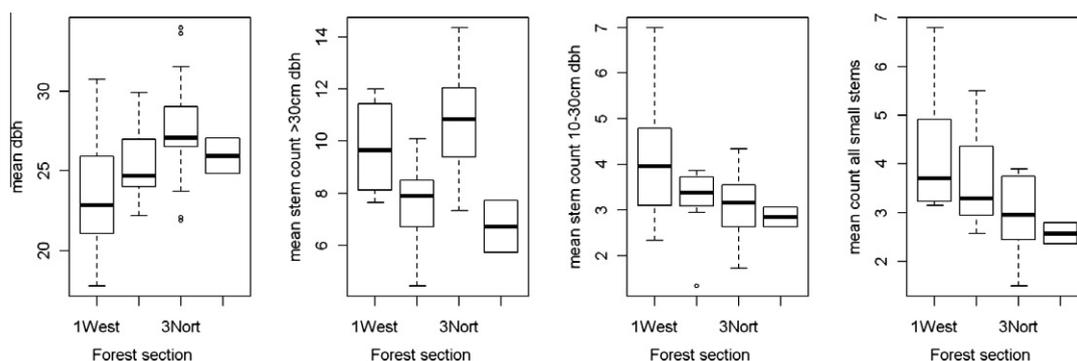
classed as pioneers had significantly lower wood density than other species ( $F_{1,6839} = 97.22, p < 0.0001$ ) and plots with lower C stocks had a higher proportion of large trees (>30 cm dbh) classed as pioneers, but this effect was marginally insignificant after controlling for stem density ( $t = -1.90, p = 0.06$ ). C stocks did not vary according to the dominance on the plot by any particular guild ( $t = -1.11, p = 0.27$ ).

A GLM of mean C values for each transect using a model averaging procedure highlighted the importance of forest block, settlement distance and past logging volumes. The average coefficients tended to predict a somewhat higher mean C value for the whole forest of 178.5 Mg C ha<sup>-1</sup> compared with the mean of the plots (Fig. 3).

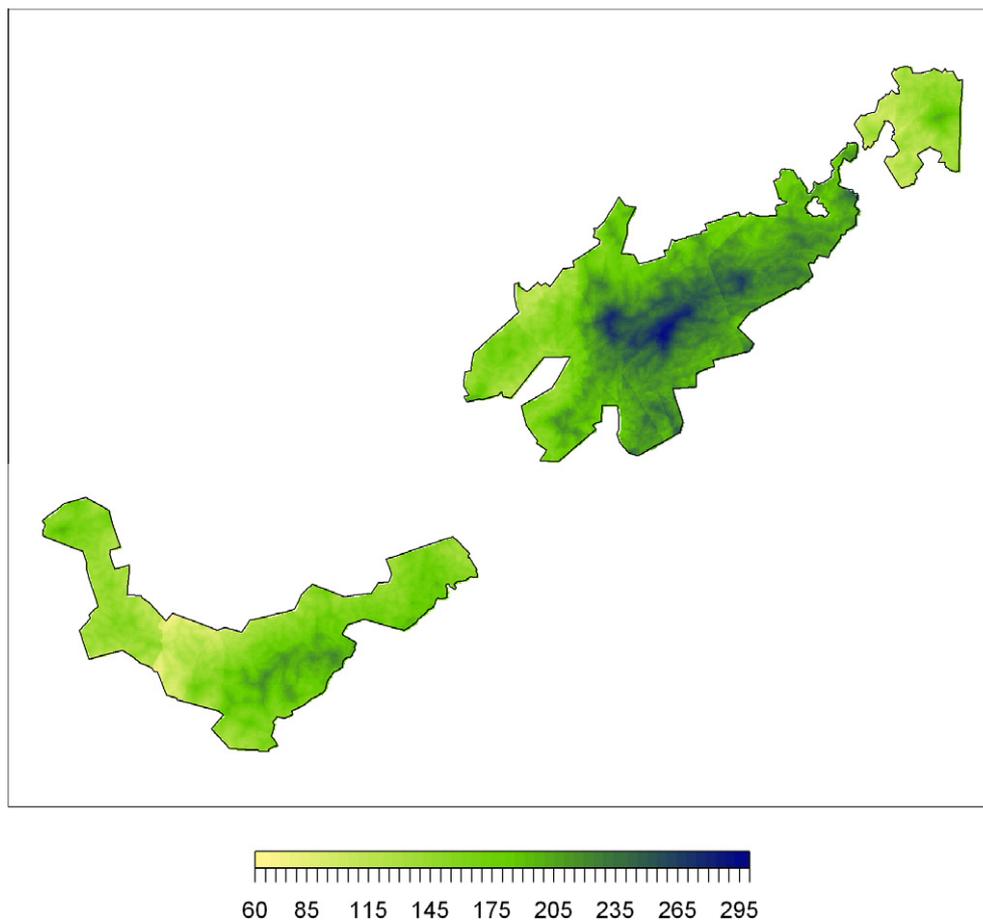
A stepwise selection found that distance from settlement and past logging volumes explained 42.1% of the variation in C content ( $F_{5,39} = 7.39, p < 0.0001$ ). Forest block was also retained in the model suggesting that there were unaccounted for factors associated with geographic locality over and above those measured (Table 3). This simpler model predicted mean C density of 159 Mg C ha<sup>-1</sup> in Gola equating to an overall site estimate of 11,327,666 Mg C (95% CI: 10,579,498–12,075,834), similar to the plot mean. When parameter values for the explanatory variables were reversed in the prediction (volume of past logging = 0 and distance to settlement = maximum recorded in Gola) the estimate of C in Gola increased to 15,815,847 Mg C, a potential gain of 4,488,181 Mg C. Logging alone accounted for 1,437,814 Mg C and the settlement effect alone for 3,050,366 Mg C.

### 3.2. Historical changes

Six plots and transects in one compartment surveyed in the 1950s (Table 1) had a mean C density of 266.2 Mg C ha<sup>-1</sup> which was twice the current figure in the same area, whilst a fully repre-



**Fig. 2.** Variation in tree dbh and stem density of different size classes in the four forest blocks of Gola Forest, Sierra Leone. The forest sections in each graph are ordered left to right as Gola West, Gola East, Gola North and Extension 2.



**Fig. 3.** Interpolation of carbon biomass ( $\text{Mg C ha}^{-1}$ ) in Gola Forest, Sierra Leone from modelled distribution of carbon biomass based on a model average of eight variables (Appendix C).

**Table 3**

Results of a GLM of carbon density with respect to human settlements (distance to settlement) and past logging history (volume of logging) in Gola Forest, Sierra Leone. Each sample unit was an aggregated value from all plots located along a transect with  $n = 43$  transects. Model:  $\text{agbC} = a + \text{distance} + \text{volume} + \text{block}$ .

	Estimate	Std. error	<i>t</i> Value	<i>p</i>
(Intercept)	156.08	19.06	8.19	<0.001
Distance to settlement	-6.23	2.43	-2.57	0.01
Volume of logging	-37.93	19.46	-1.95	0.06
Block - East	21.01	16.94	1.24	0.22
Block - North	-68.38	31.19	-2.19	0.03
Block - Extension 2	156.08	19.06	8.19	<0.001

representative 5% enumeration of the same compartment had 70.3% higher C density than current levels. The reduction in C since the 1950s was  $40 \text{ Mg C ha}^{-1}$  which equated to a volume of timber of c.  $30.8 \text{ m}^3 \text{ ha}^{-1}$ , whilst the recorded extraction from this compartment was just  $11.4 \text{ m}^3 \text{ ha}^{-1}$  (Iles et al., 1993), disregarding any growth since logging ceased. In 14 unlogged forest compartments surveyed in the early 1970s (White, 1972), the contemporary data showed 47.8% higher C levels (mean increase =  $36.8 \text{ Mg C ha}^{-1}$ ,  $t_{19,i} = -3.82$ ,  $p < 0.002$ ) which represented a mean rate of increase of  $1.02 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  (Fig. 4).

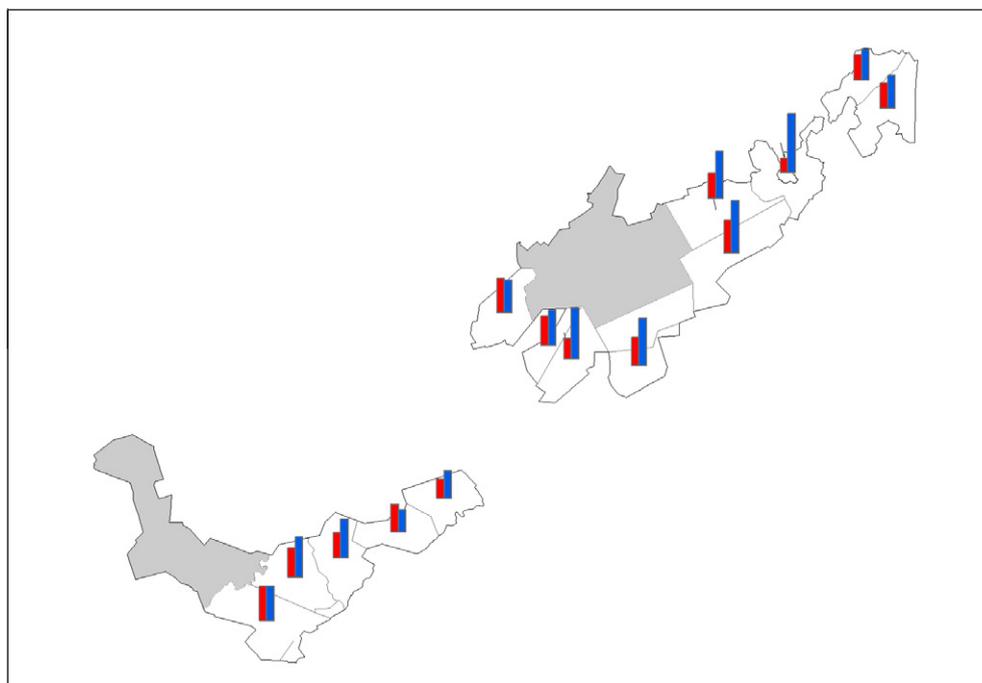
#### 4. Discussion

We have provided the first estimate of above ground C content in an entire Upper Guinean forest based on representative field

sampling across the whole forest. This has not only demonstrated the extent to which C density can vary across a site even within a relatively uniform forest type, but also with respect to past human activities. We have also demonstrated that even relatively coarse covariates in a simple linear model can have significant power in explaining the distribution of C within a site, offering the possibility of mapping C over far larger areas than can be realistically sampled by fieldwork. Such models can then be used to investigate likely changes in C under alternative management scenarios. Patterns of biomass largely reflected past logging history – demonstrating a lasting impact of disturbance history on forest biomass as has been noted elsewhere (Blanc et al., 2009) – but despite past disturbance this type of forest still retains substantial carbon stocks and can accumulate further if left undisturbed.

##### 4.1. Current carbon stocks

The site-wide estimates of overall C content of c. 160 t per ha included all above ground biomass of living trees over 10 cm dbh, but excluded standing dead wood, coarse woody debris and leaf litter. The figure accords well with published values for Afrotropical forests (Table 4). Regionally-specific data reported by Lewis et al. (2009) included 33 plots from undisturbed forest in the Upper Guinea zone. C content was assessed in the same carbon pool and using very similar allometry as the current study. The mean of these plots was  $195.3 \text{ Mg C ha}^{-1} (\pm 15.9)$ , which is statistically indistinguishable from the mean value for Gola North ( $186 \text{ Mg C ha}^{-1} \pm 14$ ). Given that this part of Gola was far from



**Fig. 4.** Comparison of past and current mean stocking levels of carbon within each compartment in Gola Forest, Sierra Leone. 1972 data in grey are from White (1972) and black bars are contemporary data from plots in the same compartments. The shaded areas shows compartments which the 1970s survey omitted, presumably because logging was already underway in these areas by that time.

**Table 4**

Default values (IPCC and EC) and other published C values for forests in the Upper Guinea region of West Africa where Gola Forest is located.

Description	Mg C ha <sup>-1</sup>	Source
Wet tropical forest IPCC default value	155	Penman et al. (2003)
Moist tropical forest IPCC default value	130	Penman et al. (2003)
Tropical rain forest in Africa > 30% canopy cover EC default value	204	European Commission (2010)
Tropical moist deciduous forest EC default value	156	European Commission (2010)
Mean of 833 × 1 km <sup>2</sup> cells overlapping Gola Forest extracted from GIS dataset	122.3	Baccini et al. (2008)
Mean of 33 plots in undisturbed Upper Guinea forest	195.3	Lewis et al. (2009)

undisturbed, this suggests that finding indisputably undisturbed lowland forests in the Upper Guinea region may now be very hard. Forest plots from the central Congolian forest block in Africa, by contrast, averaged a much higher 250 Mg C ha<sup>-1</sup> (±16.5) (Lewis et al., 2009). Nonetheless these forests hold substantial carbon stocks of importance for global climate mitigation.

#### 4.2. Spatial variation in carbon

The importance of spatial representativeness in forest sampling is clear from the variation demonstrated in this study and has been noted for other tropical forest regions (Laumonier et al., 2010). This large scale heterogeneity shows that a failure to locate even large plots in a truly representative way could have resulted in a twofold error in assessing the overall C stocks in Gola. Local spatial variation in C levels has rarely been investigated in Afrotropical forests beyond characterising C content of discrete forest types (Glenday, 2006, 2008). The current distribution of C in Gola broadly reflected the recent history of commercial logging. The model also highlighted the impact of the human population living around the forest with a mean 8.8 Mg C ha<sup>-1</sup> increase in C levels per kilometre from a settlement. It is probable that logging was responsible for a larger component of the variation than revealed here since the well-logged southern areas still had lower C stocks even after accounting for recorded logging history and distance to settle-

ments. This would be consistent with the suspected under-reporting of timber extraction in the southern parts of Gola compared with the central areas (Iles et al., 1993). The difference between observed changes in C content and recorded timber extraction volumes suggested at least a threefold under-reporting of volumes from one particular compartment and this discrepancy would be greater if growth since logging ceased was taken into account. Although data from forestry operations can have valuable applications for forest carbon assessment (Maniatis et al., 2011) it is clear that an uncritical acceptance of some types of data – especially figures that might prejudice forestry operations – is unwise. In spite of these limitations in prediction our results demonstrate the extent to which management actions to limit timber extraction and other forms of degradation can lead to improved sequestration.

#### 4.3. Historical changes

Analysis of C stock change in Gola in the last few decades showed C levels in the more heavily logged areas remained significantly lower than levels that were found prior to logging, whilst C levels in areas that escaped commercial logging have nonetheless increased. Current C stocks in one heavily logged compartment were 69% of those observed in the 1950s, despite at least 15 years of regrowth since logging ceased, and so were presumably lower still on cessation of logging. It is known that forest biomass can

continue to decline after logging ceases (for up to 10 years) because of a delayed effect on tree mortality (Blanc et al., 2009), so it may be only relatively recently that this compartment has started to experience net annual accumulation of C. Prior to logging, C levels in this compartment were c. 28% higher than those found in other unlogged areas of Gola 20 years later (White, 1972), but they were still lower than are found currently in many undisturbed areas of the forest. So regardless of the relatively recent impacts of logging and subsequent recovery, these figures suggest there is an underlying signal of C accumulation in Gola, probably as a response to an earlier disturbance history though possibly also due other effects such as CO<sub>2</sub> fertilisation.

Most of the areas surveyed in the 1960s and 1970s now hold relatively high stocks compared with the rest of the forest. These areas may have been avoided by loggers because of low initial levels of timber because they had been subject to earlier episodes of disturbance. Although the Gola region was more heavily populated in past centuries, there is no compelling evidence to suggest that the forest was ever completely cleared. Indeed, herpetological data imply some persistence in forest cover in the Gola region over millennia (Penner et al., 2011) and a hundred years ago Gola was intact enough to be identified as an important forest in Sierra Leone. However, even at that date it was clearly disturbed in many areas and thought then to have been recovering from prior clearance (Unwin, 1909). Based on our analysis, the rate of C accumulation in Gola over the last c. 40 years is approximately 60% higher than the continental average for undisturbed forest (Lewis et al., 2009) and the evidence suggests that this forest has considerable potential to sequester greater amounts of carbon into the future.

The importance of human history for explaining current forest distribution is increasingly recognised (White and Oates, 1999). Far from being long term stable environments many African forests are now regarded as relatively dynamic, with this impression being underlined further by reconstructions of historical climate in the region (Vincens et al., 1999; Cowling et al., 2008) as well as recent climate change (Fauset et al., 2012). This has important implications for our understanding of forest resilience to both climatic and anthropogenic impacts. Although the extent and intensity of past disturbance in Gola Forest remains unknown it is clear that the forest has had an unstable past pre-dating commercial logging activity. But in spite of this history, Gola continues to function as a priority site for West African forest conservation (Klop et al., 2010; Lindsell et al., 2011; Monticelli et al., 2011) besides serving as a substantial carbon sink.

## 5. Conclusions

Our results show a clear lasting impact of disturbance history on the distribution of carbon stocks within a typical West African forest and give some indication of the scale of such an effect. Accounting for disturbance history is therefore a key consideration in any assessment of temporal changes in carbon stocks. Current accumulation in carbon may be as much due to recovery from past disturbance as to any environmental shifts that may be causing ecological change. As it becomes increasingly hard to identify forest with an undisturbed past – and in West Africa this is largely the case – disturbance history will assume increased importance.

This is of some significance in the context of REDD-type schemes for forests like Gola where credits for enhanced carbon stocks can supplement those calculated from avoidance of anticipated deforestation rates. Using the linear model it was possible to predict the quantities that might be involved in such sequestration should adequate protection be achieved. Further increases may be achieved if natural regeneration and site protection also

served to reduce some of the unexplained variation associated with the four main forest blocks.

These results provide a significant new dataset on C in Afrotropical forests, and how C varies spatially and has changed historically. This will significantly improve our ability to both estimate and account for C stocks in forests in Africa, especially in the Upper Guinean region. Such progress is essential for the development of effective funding mechanisms, such as REDD+, to ensure the protection of Upper Guinean forests which are increasingly threatened by encroachment and degradation.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.09.045>.

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