Effects of anthropogenic disturbance on tree population structure and diversity of a rain forest biosphere reserve in Ghana, West Africa

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Abstract

We evaluated the impacts of anthropogenic disturbance on community structure and diversity along three management zones of the Bia biosphere reserve in Ghana. Sixty sample plots were distributed among the core, buffer and transition zones. We estimated the degree of disturbances from discernible indicators on the field and satellite images. All tree species ≥10 cm dbh (diameter at breast height) were identified and enumerated. Inventory data were compared across the zones and related to intensity of disturbances. A total of 1176 individual trees from 108 species and 33 families were encountered. Number of species varied from 27 in the highly disturbed (HD) to 61 in the least disturbed (LD) zone. Mean basal area (BA) varied from 11.71 in the HD to 28.26 in the LD. Both Margalef's species richness and Shannon-Weiner's α-diversity were highest in the moderately disturbed (MD) than either the least and most disturbed zones. Our study revealed significant differences in tree abundance, stem density, BA and species diversity, attributable to differences in degree of anthropogenic disturbances among zones. Given the different levels of anthropogenic disturbance and corresponding impacts across the reserve, we recommend an integrated management strategy for the conservation of biodiversity in the Bia biosphere reserve.

Key words: anthropogenic disturbances, Bia biosphere reserve, Ghana, intermediate disturbance hypothesis, tree structure, tropical forests

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Résumé

Nous avons évalué les impacts des perturbations anthropogènes sur la structure et la diversité de la communauté végétale dans trois zones de gestion de la Réserve de Biosphère de Bia, au Ghana. Soixante parcelles échantillons ont été réparties dans les zones centrale, tampon et de transition. Nous avons estimé le degré de perturbation au moyen d'indicateurs et d'images satellitaires. Toutes les espèces d'arbres d'un dbh ≥ à 10 cm ont été identifiées et dénombrées. Les données des inventaires ont été comparées entre les zones, et liées à l'intensité des perturbations. Nous avons compté un total de 1 176 arbres de 108 espèces et 33 familles. Le nombre d'espèces allait de 27 dans la zone la plus perturbée (HD) à 61 dans la moins perturbée (LD). La surface basale moyenne variait de 11,71 dans la zone HD à 28,26 dans la zone LD. Et l'indice de diversité de Margalef et la diversité-α de Shannon-Wiener étaient plus élevés dans les zones modérément perturbées que dans celles qui l'étaient plus, ou moins. Notre étude a révélé des différences significatives dans l'abondance des arbres, la densité des troncs, la surface basale et la diversité des espèces, que l'on peut attribuer aux différences de perturbations anthropogènes entre les zones. Étant donné ces différences de perturbations et les impacts correspondants dans toute la réserve, nous recommandons une stratégie de gestion intégrée pour la conservation de la biodiversité dans la Réserve de Biosphère de Bia.

Introduction

Prior to forest management activities, quantifying biophysical attributes, such as structure, species composition and diversity in response to disturbances, offers relevant information for restoring degraded landscapes (Defries *et al.*, 2005; Hansen & Defries, 2007). Rain forests hold the highest levels of species richness and endemism of any terrestrial biome (MEA, 2005). They are, therefore, usually the target of most biodiversity conservation initiatives (IUCN, 2010). In Africa, huge areas of rain forests and their resident biodiversity are decimated annually (FAO, 2010; Gardner *et al.*, 2010). This is on account of human disturbances through mainly agricultural conversions, lumbering, settlement development, road constructions and extraction of nontimber forest products (Malhi *et al.*, 2013). Despite the high disturbances, most protected rain forests conserve indigenous biodiversity better than other land uses on the continent (Struhsaker, Struhsaker & Siex, 2005). It is evident therefore, more than ever that the long-term sustainability of existing African rain forest reserves is greatly dependent on how disturbances are understood and effectively managed in protected and adjacent landscapes (Harvey *et al.*, 2008; Wittemyer *et al.*, 2008; Gardner *et al.*, 2009).

For many African countries, protected areas are essential elements of major intervention strategies to conserve biodiversity and, probably, the only means of conserving obligate forest species (Gardner *et al.*, 2009). An enhanced understanding of disturbance regimes and impacts on biodiversity is thus vital for the sustained management of these protected rain forests. Particularly in Ghana, although some studies are available on the subject (e.g. Hawthorne, 1993; Hall *et al.*, 2003; Addo-Fordjour *et al.*, 2009; Pappoe *et al.*, 2010), there is little agreement in knowledge for generalized application. This is for a number of reasons, including over-focusing on single disturbance events such as selective logging and fire (Hawthorne, 1993; Hall *et al.*, 2003; Bongers *et al.*, 2009; Wiafe, 2014) and differences in study scale and methodology. Moreover, notwithstanding the several studies on effect of disturbance on species diversity, there is no consensus yet on the diversity disturbance debate; thus requiring further work to explicate. For example, according to the refugia hypothesis, undisturbed habitats are of higher diversity compared to disturbed habitats because they serve as refugia for organisms (Townsend, 1989; Townsend & Hildrew, 1994). On the contrary, the intermediate disturbance hypothesis postulated by Connell (1978) suggests that diversity within communities is maximal at intermediate frequencies and intensities of disturbances.

The Bia biosphere reserve of Southwestern Ghana is among the world's 25 biodiversity hotspots (Myers *et al.*, 2000) and also a World Heritage Site for UNESCO (Forestry Commission, 2010). Besides, it is the first biosphere reserve in Ghana, designated in 1983 by UNESCO. The reserve is therefore of both national and global conservation significance. Unfortunately, the latest assessment report on the management effectiveness of parks and reserves in Ghana revealed that the biosphere reserve was experiencing significant disturbances, largely from logging and agricultural activities (UICN/PACO, 2010). The need for effective management by the Wildlife Division of the Forestry Commission, to conserve the unique habitat and biodiversity of the biosphere reserve, is long overdue (Ministry of Environment and Science, 2002).

Although not regarded as formal protected areas, biosphere reserves have their origin from the protected area concept (Ishwaran, Persic & Tri, 2008; IUCN & UNEP-WCMC, 2014). Unlike 'classical' protected areas, however, the overall management of biosphere reserves encompasses both protected and nonprotected areas (Hansen & Defries, 2007). Lessons from study of biosphere reserves, therefore, have implications that go beyond the particular study area and can be applied to both managed and unmanaged landscapes (Batisse, 1993; German Commission for UNESCO, 2015). In this study, we sought to quantify the degree of disturbances and impacts on stand structure, tree composition and diversity in the Bia biosphere reserve. Specifically, we sought to: (i) comparatively analyse the degree of disturbances across the management zones of the reserve; (ii) determine the relationship between disturbance and forest stand structure, tree species composition and alpha diversity between zones; and (iii) proffer appropriate strategies on basis of findings from (i) and (ii), for better management of tree biodiversity in the reserve. In concurrence with the intermediate disturbance hypothesis, we posited that extreme anthropogenic disturbances in forest biosphere reserves eliminate sensitive tree species, but moderate levels of disturbances encourage more species to co-exist leading to high species richness and diversity in less disturbed areas.

Materials and methods

Study area description

The Bia biosphere reserve is situated in Southwestern Ghana, only about 5 km to the border with La Côte

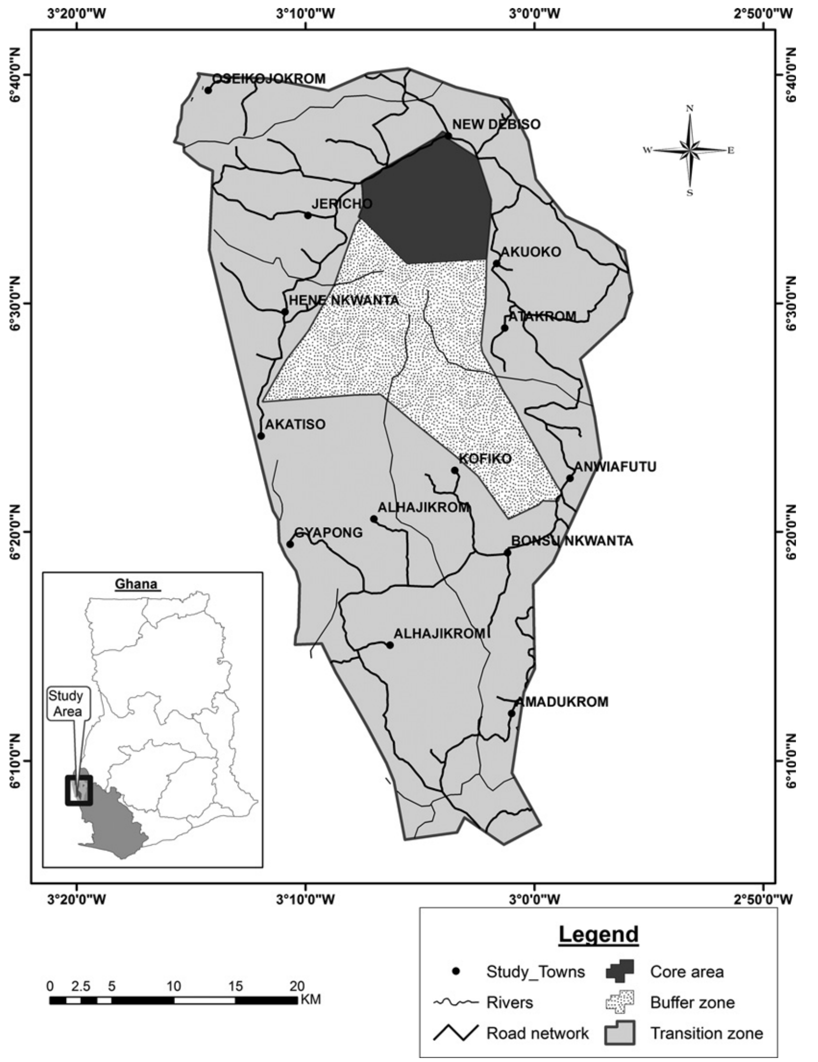

Fig 1 Location map of the Bia biosphere reserve in context of the Western Region of Ghana, showing management zones and road network linking major communities. [Colour figure can be viewed at wileyonlinelibrary.com]

d'Ivoire. Lying between latitudes 06°20′–06°39′N, and longitudes 02°58′–3°13′W (Fig. 1), the reserve covers an area of 355.6 km^2. It comprises a core area (also a National Park) of 77.7 km^2 to the north, a buffer area (also a Resource Reserve) of 227.9 km^2 to the south and a transition zone of 837 km^2. The transition area is dominated by large cocoa farms strewn with few trees and dotted with food crop farms (Forestry Commission, 2010). The area now corresponding to the buffer zone was excised from the National Park and opened up for timber exploitation until it was constituted as a Game Production Reserve in 1983 (Hawthorne *et al.*, 2001). The vegetation of the buffer (Resource Reserve) was disturbed by logging activities and wildfire up to 30 years ago (Hawthorne & Abu-Juam, 1995). On the other hand, the vegetation of the core (National Park) is generally undisturbed forest.

The Bia biosphere reserve forms part of the vulnerable upper Guinean rain forest, a strip of tropical forest that stretches from Sierra Leone to Ghana (Forestry Commission, 2010). It lies between the moist evergreen and semi-deciduous humid tropical forest of Ghana. The original vegetation was therefore characterized by tree species of both forest types. These included *Lophira alata* and *Scaphopetalum amoenum* which are characteristic species of the evergreen forest; and *Khaya ivorensis*, *Khaya anthotheca* and *Entandrophragma utile* which are unique to the semi-deciduous forest (Hall & Swaine, 1981). The reserve is also home to some 404 species of butterflies, 130 species of birds, the African elephant, chimpanzees and other primates (UICN/PACO, 2010).

The reserve lies in the wet semi-equatorial climatic zone and experiences alternating wet and dry seasons. The dry period is from December to March. Annual temperatures vary from a minimum of 20.5–22°C (February/March) to a maximum of 29–34°C (July/August), with mean temperatures between 24°C and 28°C (Forestry Commission, 2010). The area experiences a bimodal annual rainfall regime with two seasonal peaks in June and September. The annual mean precipitation is about 1500 mm. The topography is undulating and generally flat with elevation ranging between 168 and 238 m. The geology is mixed, with Lower Birimian to the east, granites to the west and Upper Birimian forming a north–south strip through the middle. The soils are acrisols, locally classified as forest ochrosols and are generally of red or reddish brown appearance. These soils are of moderate acidic reaction, with pH of between 6 and 7 (Dickson & Benneh, 1998). The human population is settled by over 40 communities, all in the transition zone and is largely agrarian, with majority being cocoa and subsistence food crop farmers.

Sampling and data collection

The sampling sites were the core, buffer and transition zones of the biosphere reserve. The field team (including the Principal author) used a sampling procedure of Hall & Swaine (1981), as modified by Hawthorne & Abu-Juam (1995). In brief, twenty sampling plots each 30 m × 50 m dimension were randomly distributed along three near-parallel 1 km transects in each site, avoiding only inaccessible areas such as highlands and large streams. Thus, in total 9 ha was sampled across the biosphere reserve. According to Lamprecht (1989), the minimum area needed to sufficiently sample a plant community is the point when increment in number of species levels off to below 10% of total species. About 3 ha was considered the minimum area for adequate enumeration of tree species at each site, as evident from species–area curves (Fig. 2).

On each plot, we tagged and measured diameter of all trees ≥10 cm at breast height (dbh) over-bark and at 1.37 m above ground and identified to species. Diameter of trees with buttresses was measured 50 cm above the buttresses. Forked trees were recorded as separate individuals if branching occurred below 1.37 m above ground otherwise were counted as single individuals. Because the same sampling approach was used on all plots and as

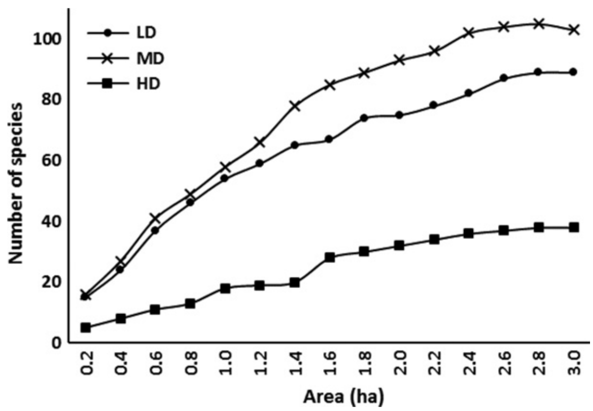

Fig 2 Species–area curves for all sample trees ≥10 cm dbh in the Bia biosphere reserve, Ghana

species density and richness are both not linearly related to plot size, we did not adjust calculations for size, but all data were used directly. Species were identified on the field and where this was impossible, botanical specimens were collected, taken to the National Herbarium at the University of Ghana, for later identification. The names of all species were standardized using the Taxonomic Name Resolution Service (tnrs.iplantcollaborative.org/TNRSapp.html), the Plant List (www. theplantlist.org) and the literature (Taylor, 1952; Hutchison *et al.*, 1957-1972; Hawthorne, 1990). All nomenclature followed the International Plant Nomenclature Index (IPNI, 2008).

Estimation of disturbance levels and index

The three management zones of the biosphere reserve were sampled separately. They were ranked according to the degree of anthropogenic disturbance, using a hybrid method introduced by Sagar, Raghubanshi & Singh (2003) and Kumar & Shahabuddin (2005). Prior to tree inventorying, all major disturbance regimes and their severity were discussed with managers of the reserve and selected farmers. From satellite images, we were able to estimate three indicators of disturbance: degree of agricultural activities (represented as proportion of cultivated area to total area), proportion of human settlements to total area and number of roads/footpaths in each zone. Four additional indicators were assessed on sampling plots, namely proportion of trees cut or lopped (from logging and other wood harvesting activities), degree of lopping (on a scale of 0–5 for each tree: 0 = no lopping; 1 = rudimentary signs of lopping; 2 = up to a quarter of

Table 1 Estimated relative disturbance intensities in the Bia biosphere reserve of Southwestern Ghana

Indicators of disturbance	Relative impacts of disturbance LD	MD	HD
Agricultural activities	0	0	5
Human settlements	0	0	5
Cutting/Lopping	0	1	5
Tree canopy openness	1	2	5
Ground vegetation cover	1	2	4
Disturbed soil/bare	1	2	4
Footpaths/skid trails/roads	1	2	4
Total	4	9	32

main branches lopped; 3 = up to half of main branches lopped; 4 = more than half of main branches lopped; and 5 = nearly all main branches lopped or tree reduced to a stump by lopping or harvesting; the total lopping score was then divided by the total number of trees present), extent of tree canopy openness, proportion of ground vegetation cover and per cent bare ground/disturbed soil cover. We calculated the relative impacts of disturbance in each management zone by finding the total score of all plots. As per the computations, the core, buffer and transition zones were designated as least disturbed (LD), moderately disturbed (MD) and highly disturbed (HD), hereafter referred to as LD, MD and HD respectively (Table 1).

Also, for each sample plot, a disturbance index (DI) was calculated as the percentage of trees in the plot that are pioneers (Bongers *et al.*, 2009), taking into account all pioneer species ≥10 cm dbh. This index was used because it reflects disturbance history at different scales in Ghanaian forests (Bongers *et al.*, 2009).

Data analysis

Adequacy of sampling was determined from constructed species–area curves (Lamprecht, 1989; Brose, Martinez & Williams, 2003; Gotelli & Chao, 2013). Following, we analysed community composition at species, genera and family levels, using inventory data. Species richness (number of species per sample plot), evenness (distribution of abundances among species) and α-diversity (level of species heterogeneity) were calculated using Margalef's index (SR), Shannon-Weiner α-diversity index (H') and Simpson's α-diversity index (D). These were computed from standard formulae within PAST 3 (a PAlaeontological Statistics) software (Hammer, Harper & Yan, 2001) as follows (Kent & Coker, 2002):

$$\mathrm{SR} = \frac{S-1}{\ln(N)} \tag{1}$$

$$\mathrm{E}_w = \frac{S}{\ln Ni - \ln Ns} \tag{2}$$

$$H' = \sum_{i=1}^{s} pi \ln pi \tag{3}$$

$$D = 1 - \left(\sum_{i=1}^{s} p_i^2\right). \tag{4}$$

Whittaker's β-diversity index (β_w) was calculated based on the twenty 30 m × 50 m sample plots of each site. The values, therefore, reflect habitat diversity within a zone and were calculated as (Whittaker 1972; cited in Kent & Coker, 2002):

$$\beta w = \frac{S}{\hat{S}}. \tag{5}$$

In Eqs 1–5 above, S = total number of species; N = total number of individuals of all species; n_i = number of individuals of the ith species; $p_i = n_i/N$ = the proportion of individuals belonging to the ith species; Ni = number of individuals of most important species; $\hat{S}$ = average number of species per sample plot; ln = natural log (i.e. 2.718). We also estimated stand structure of each site on basis of BA and diameter class distribution data. Basal area of an individual tree was estimated as (Kent & Coker, 2002):

$$\mathrm{BA} = \pi r^2 = 3.14x\left(\frac{\mathrm{dbh}}{200}\right)^2 \tag{6}$$

where BA (in m^2) is BA, and r is radius of tree (in cm).

For analysis, we used one-way analysis of variance (ANOVA) to establish significant differences in tree density and BA among the three disturbance zones. Also, we grouped all sampled trees into four diameter classes, following Swaine and Hall (1988): poles (10–19.9 cm dbh), small trees (20–39.9 cm dbh), medium trees (40–69.9 cm dbh) and large trees (≥70 cm dbh). For each diameter class, we calculated stem density and BA and subjected the results to ANOVA to determine significant differences in these values among the diameter classes. We applied Tukey's honest significant difference (HSD) comparison test at a 5% probability significance threshold to compare all means that exhibited differences. All data used for statistical analyses were tested for normality and homogeneity of variance assumptions, and where necessary appropriate data transformations were carried out. Species richness data were square-root transformed to meet the above-mentioned assumptions. Nonetheless, data on tree abundances and stem density could not be normalized, and, therefore, non-parametric Kruskal–Wallis test (*H*) test was used to compare their differences among zones. Significance level was set at $P = 0.05$ (two-tailed) for all tests. Relationship between level of disturbance and stand structure was determined by running Pearson's correlation analysis between the following parameters: (i) DI versus BA and (ii) DI versus square-root of species richness ($\sqrt{S}$R).

Results

Effects of disturbance on tree abundance

Across the three zones, inventories yielded a total of 1176 individual trees comprising 108 species belonging to 91 genera and 33 families (Table S1). The highest number of individual trees and species was encountered in MD (556 individuals; 102 species – from 91 genera and 32 families) followed by LD (471 individuals; 87 species – from 77 genera and 28 families) and the least in HD (149 individuals; 42 species – from 27 genera and 18 families). The most abundant species encountered belonged to the Fabaceae (seventeen species), Malvaceae (fourteen species) and Meliaceae (thirteen species) families. Among the zones, species belonging to the Fabaceae family were preponderant in both LD and MD (fifteen species each). However, in HD, the Malvaceae were the most represented (seven species) followed by Fabaceae (six species) and Moraceae (five species). Number of species per study plot ranged from 42 in HD to 102 in MD. Similarly, number of genera varied from 27 in HD to 91 in MD. A number of unique species were identical between sites; being between 4 and 5. A number of species with more than ten individual trees were few and ranged between 1 and 3, indicating codominance of species in the vegetation (Table 2).

Overall, *Ceiba pentandra*, *Antiaris toxicaria*, *Terminalia superba*, *Erythroxylum mannii* and *Celtis mildbraedii* were the five most abundant species in all zones (see Table S1). The three most abundant tree species in the LD zone were *C. pentandra*, *A. toxicaria* and *E. mannii*, constituting 10.19% of total individuals. In the MD forest, *C. pentandra*, *A. toxicaria* and *Nesogordonia papaverifera* were the three most abundant species, constituting 10.25% of all trees in the zone. In the HD zone, *Elaeis guineensis*, *Mangifera indica* and *C. pentandra* were the three most abundant tree species, making up 26.85% of all standing trees in the HD part of the biosphere.

The most disturbed zone had significantly fewer trees than either the least or MD zones. A Kruskal–Wallis test

Table 2 Pattern of tree stand composition and structure in Bia biosphere reserve grouped by level of disturbance

	LD	MD	HD
a. Stand composition and structure			
Number of species	87	102	42
Number of genera	77	91	27
Number of families	28	32	18
Number of unique species	4	5	4
Number of species with >10 individuals	3	3	1
Mean stem density (≥10 cm dbh)	107 ± 49	171 ± 53	69 ± 29
Mean basal area (m^2 $plot^{-1}$)	28 ± 7.70	21 ± 7.94	11 ± 9.62
b. Species richness and diversity			
Species richness (Margalef's index)	11 ± 0.72	13 ± 3.91	4 ± 2.62
Evenness (Whittaker's index)	4.73 ± 1.28	4.67 ± 1.14	1.85 ± 0.72
Shannon-Weiner's α-diversity	4.22 ± 0.63	4.61 ± 1.15	1.08 ± 0.87
Simpson's α-diversity (1-*D*)	0.94 ± 0.25	0.97 ± 0.21	0.64 ± 0.13
Whittaker's β-diversity	1.69	1.71	1.72

(*H*) revealed that there was a significant effect of anthropogenic disturbances on tree abundances in the three zones of the biosphere reserve ($H = 45.19$; $\chi^2 = 5.99$; df = 2; $P < 0.05$). The order of tree abundance among the zones was: HD < LD < MD).

Effects of disturbance on species richness and diversity

Generally, increasing disturbance decreased evenness in distribution of species (Table 2). Whittaker's evenness index was identical in LD and MD but was very low in HD. Both species richness and α-diversity (both Shannon-Weiner's and Simpson's) were highest at intermediate disturbance. Species richness was highest in MD and lowest in the HD. A similar trend was seen for both Shannon-Weiner's α-diversity and Simpson's α-diversity. Surprisingly, β-diversity was identical across all sites and seems not to respond to degree of anthropogenic disturbance.

Effect of disturbance on stand structure

Due to differences in disturbance, mean BA varied from 11.71 m^2 ha^{-1} in HD to 28.26 m^2 $plot^{-1}$ in LD (Table 2). There were significant differences in BA among all the pairs of the zones ($F_{2,3} = 3.27$, $P = 0.002$). For each pair, the less disturbed zone had significantly higher BA than the more disturbed zone (i.e. LD > MD, LD > HD, MD > HD). BA of trees in MD and HD was 24% and 59% less than that of LD respectively. Large standard errors in variables suggest marked stand variability between the zones. Stem density of tree ≥10 cm dbh differed across zones with mean ranging between 69 in HD and 171 in MD (Table 2). There were significant differences in stem density ($H = 14.92$; $\chi^2 = 5.99$; df = 2; $P < 0.05$) among all the pairs of zones due to anthropogenic disturbances in the reserve. For each pair, the MD zone recorded significantly higher stem density than the LD zone (i.e. MD > LD, MD > HD and LD > HD).

The density of all diameter classes significantly varied between zones: poles ($F_{2,3} = 5.02$; $P < 0.001$); small trees ($F_{2,3} = 7.52$; $P < 0.004$), medium trees ($F_{2,3} = 11.41$; $P < 0.009$) and large trees ($F_{2,3} = 6.83$; $P < 0.000$). At $P < 0.05$ significance, Turkey's test revealed that there were significant differences in density of both poles and small trees, between LD and HD and between LD and MD. Nonetheless, the difference between HD and MD was insignificant (Tukey HSD; $P = 0.085$). Density of medium trees differed significantly between LD and HD and between MD and HD but not between LD and MD (Tukey HSD; $P = 0.117$). Differences in density of large trees between LD and HD and between MD and HD were both significant. Nonetheless, no significant difference was found between LD and MD (Tukey HSD; $P = 0.381$). Generally, numbers of both medium and large trees declined with increasing level of disturbance.

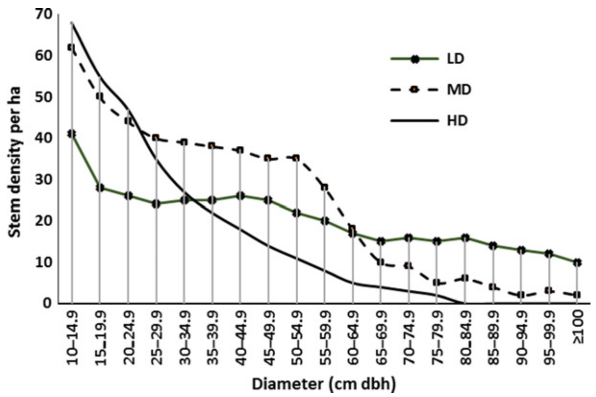

Fig. 3 Distribution of stem diameter sizes by levels of disturbance in the Bia biosphere reserve of Southwestern Ghana

Generally, all diameter distributions were positively skewed (Fig. 3) towards the small diameter cohort. However, tree population by diameter size varied greatly between the zones. In HD, nearly 75% of the trees were either poles or small trees compared to about 23% medium and 2% large trees, none above 80 cm dbh. In MD, about 58% trees were either poles or small trees, 35% medium trees and 7% large trees. In LD, about 47% trees were either poles or small trees, 37% medium-size trees and 16% large trees. Broadly, increasing disturbance corresponded to decreasing population of large-size trees.

A negative linear relationship was also observed when DI was regressed on BA and species richness (Fig. 4). Thus, increasing forest disturbance consistently led to a decline in BA and species richness in all zones. Comparatively, the strength of relationships (R^2) was in the order: LD > MD > HD.

Discussion

Effect of disturbance on tree species richness and diversity

Local species richness and diversity can be markedly influenced by disturbances, and depending on type of

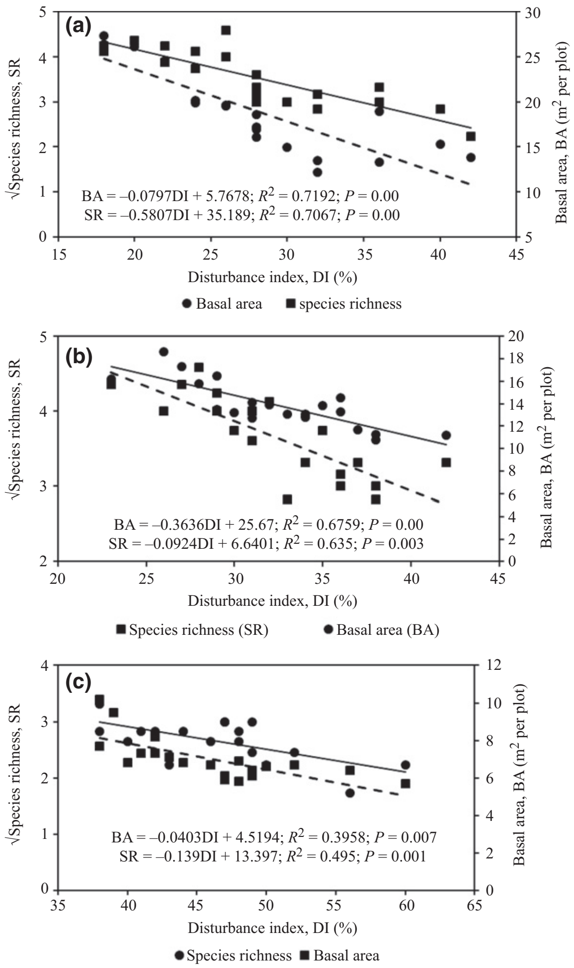

Fig 4 Relationship between disturbance index and species richness and basal area at the different management zones of the Bia biosphere reserve, Ghana; (n=20): (a) LD (core zone); (b) MD (buffer zone); and (c) HD (transition zone)

forests and extent of disturbance, may vary significantly (Hall *et al.*, 2012). Our study estimated the lowest species richness in the HD portion of the biosphere reserve, corresponding to the transition zone. This could be attributed to frequent disturbances from human activities, such as farming, logging and settlement development, known to occur in nearly all agroecological zones of Ghana (Antwi *et al.*, 2014) and especially outside protected forests (Ardayfio-Schandorf *et al.*, 2007; UICN/PACO, 2010).

In this study, a linear relationship was found between DI and species richness at all sites. Generally, species richness was maximum when forest disturbance was only moderate but declined with increasing anthropogenic disturbance. Our observation concurs with other studies in other tropical forests outside Africa (Sheil, 1999; Zhu *et al.*, 2007) and in Ghana as well (Addo-Fordjour *et al.*, 2009). Our findings also lend credence to the intermediate disturbance hypothesis which posits that extreme disturbances usually eliminate sensitive species, but moderate levels of disturbances allow more species to co-exist (Tilman, 1982; Sheil, 1999; Wilkinson, 1999).

Our study also documented that disturbance caused a significant decline in tree species diversity as revealed by Shannon-Weiner and Shannon indices. Nonetheless, a study of the effects of disturbance on tree species diversity along a wet–dry climatic gradient in Ghana's forests revealed that disturbance contributed significantly to the maintenance of tree species diversity in dry forest but played only a minor role in moist and wet forests (Bongers *et al.*, 2009). A combination of factors related to local differences in land-use intensification, biodiversity management and on-site history (Hawthorne, 1993; Forestry Commission, 2010) as well as study scale (Bongers *et al.*, 2009) could be responsible for the discordant outcomes. Indeed, in most tropical regions, conversion of forests to farmlands involves the removal of a substantial number of forest trees (Makana & Thomas, 2006). Agricultural land-use intensification, usually involving slash-and-burn cultivation, is rather pervasive and a major cause of tree species loss in Ghana's agroecological zones (Antwi *et al.*, 2014). In the Bia biosphere reserve, differences in approach to biodiversity management in the different zones might have exacerbated tree species loss as observed in some protected tropical rain forests (Defries *et al.*, 2005; Hansen & Defries, 2007).

Effects of disturbance on tree stand structure

Our evidence that mean densities of trees varied significantly between sites indicates high spatial variability in tree distribution in the biosphere reserve. Our observation concurs with many other studies elsewhere in the tropical region (Whitmore & Burslem, 1998; Burslem & Whitmore, 1999; Sheil, 1999; Ramirez-Marcial, Gonzalez-Espinosa & Williams-Linera, 2001; Sagar, Raghubanshi & Singh, 2003; Sahu, Sagar & Singh, 2008).

This study found a higher number of unique species in the HD zone of the biosphere reserve. This can be attributed to introduction of species through cultivation or invasion by opportunistic species (Hawthorne, 1993; Addo-Fordjour *et al.*, 2009). Another key observation was that many species found in the LD core and MD buffer zones of the biosphere reserve were absent in the HD transition zone. According to Lamprecht (1989), high utilization pressure could be responsible. Generally, in many forests of Ghana, adult population of many economic trees is of low densities; averaging one tree per hectare (Hawthorne & Abu-Juam, 1995; Lauma-Aho, 2003; Appiah, 2013), sometimes even less than one commercial tree per 10 ha (Lamprecht (1989). With rapid increases in human population, recurrent activities of shifting cultivation, timber extraction and fuelwood harvesting could alter the habitat suitability for most tree species (Hawthorne, 1993).

Usually, ecologists interpret large numbers of juveniles relative to adults as indicative of a stable community, perhaps growing; but a few juveniles relative to adults depict a declining population (Condit *et al.*, 1998). The particularly high population of poles and small trees in the transition zone suggests active tree regeneration (Hall *et al.*, 2012), probably, facilitated by germination and development of pioneer species because of enhanced light penetration (Hawthorne *et al.*, 2001). However, the fact that both species richness and diversity were low in this zone suggests that any biodiversity intervention strategy should aim at replacing lost species.

Management options for biodiversity conservation

Evidently, anthropogenic disturbance has disproportionately influenced tree species composition, structure and diversity pattern in the various management zones of the Bia biosphere reserve. Considering that tree species composition, structure and diversity varied greatly along the different levels of forest disturbance, an integrated management strategy will be required to achieve effective biodiversity conservation in the biosphere reserve. With careful application, likely restorative actions could include (i) protection of intact native forests; (ii) tree canopy management; (iii) natural regeneration; (iv) enrichment planting; and (v) agroforestry.

Our study reveals that extreme anthropogenic disturbances led to loss of species diversity in the Bia biosphere reserve, particularly in the transition zone. It is therefore reasonable that natural forest protection remains an integral part of the conservation strategy of the biosphere reserve. Notwithstanding, forest protection alone is unlikely to succeed, especially under conditions of increasing land-use pressure (Defries *et al.*, 2005). Selective logging as a management strategy has been applied to increase species richness and diversity (Ola-Adams, 1987; Hawthorne, 1993; Verburg & Van Eijk-Bos, 2003; Edwards & Lawrance, 2013). This may be encouraged in the buffer zone to enhance light penetration for natural regeneration of pioneer and light-demanding obligate species, especially rare and endemic species (van der Werff & Consiglio, 2004).

In the HD transition zone, agroforestry practices on and around farms as an alternative to more extensive and less sustainable land-use practices may improve biodiversity conservation (Garrity, 2004; Makundi & Sathaye, 2004; Schroth *et al.*, 2004). This can also help minimize the quest of local people to deforest more land for agriculture, in addition to coping with limited availability of forest land and resources (Schroth *et al.*, 2004). Enrichment planting (Lamprecht, 1989; Doucet *et al.*, 2009) could be encouraged as well to replace lost species. However, given the inappropriateness of exotic species for replanting degraded lands in Ghana (McCullough, Decher & Kpelle, 2005), selective use of native species will be preferred to exotic species (Appiah, 2011). Selective use of native species will be in concordance with the Forestry and Wildlife policy of Ghana (Ministry of Land and Forestry, 1994).

The realization of any of the above biodiversity management objectives in the Bia biosphere reserve will entail respecting the ecological integrity of the core conservation area and managing the environment within which adjoining areas are established for biodiversity conservation. This will ensure that the fundamental principles of the biosphere reserve concept remain honoured. Also, strengthening any existing community-based forest management structures and promotion of alternative livelihood programmes could help maintain forest structure and tree species richness in the long term.

Conclusion

This study has demonstrated that forest structure, tree species richness and diversity are all influenced along a disturbance gradient. The management zones of the biosphere reserve experienced variability in floristics in response to disturbances. An integrated biodiversity management is therefore recommended for rehabilitation of disturbed areas of the biosphere reserve.

Acknowledgements

We are thankful to the Ghana-MAB committee, under the auspices of the Ghana Environmental Protection Agency (EPA) for permission to use inventory data collected as part of the 'Green Economy Project' for the analysis. We are also grateful to the Manager and local mangement team of the Bia biosphere reserve for assistance in Table S1 collection.

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(*Manuscript accepted 27 March 2017*)

doi: 10.1111/aje.12427

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Tree species, their families and abundance at three levels of anthropogenic disturbance in the Bia biosphere reserve of southwestern Ghana.

