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ORIGINAL ARTICLE

Termite diversity is resilient to land-use change along a forest-cocoa intensification gradient in Ghana, West Africa

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Abstract

Cocoa is an important crop for Ghana's economy, contributing 25% of Gross Domestic Product (GDP). The crop, however, is mainly cultivated on forest-derived soils and is a major cause of land-use change. Termites are an important biological component of tropical ecosystems providing numerous ecosystem services. Previous studies have indicated that termites are sensitive to forest disturbance and decrease in richness and abundance across land-use intensification gradients, with consequences for the essential services that they provide. Native shade trees are often used to improve cocoa cultivation and may reduce the detrimental effects of land-use change on some aspects of biodiversity. The aim of this study was therefore to explore how termites respond to land-use change along a shade-tree gradient in Kakum National Park and surrounding cocoa farms in Ghana (from forest at 80% tree cover to cocoa with no shade cover, to the extreme of cultivated arable crop land). It was predicted that termite richness and abundance would decrease with decreasing shade cover, and with increasing distance from the forest edge. Thirty-four species from 29 genera were sampled, with Ancistrotermes crucifer being found in all the locations (47% of all encounters). Species richness and abundance differed marginally across the land-use gradient, as well as the distance from the forest edge; however, species richness did not show any significance with distance. All the same, termite communities were robust to the disturbance. Our findings suggest that though site influenced species richness and abundance, cocoa trees can play a crucial role in maintaining biodiversity and environmental quality in an agricultural landscape by providing a habitat for forest species that are not found in pastures or farm fields. However, we caution that the relatively low forest baseline of existing forest diversity may inflate the value of cocoa land, with those forests no longer representing undisturbed natural habitats: this highlights that shifting baselines may need to be accounted for when interpreting findings in the Anthropocene.

KEYWORDS
cocoa agroforestry, feeding groups, forest reserve, shade trees, species richness

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1 | INTRODUCTION

The importance of tropical wet forests cannot be overstated. One of their critical roles is the provision of habitat to more than half of the world's terrestrial species (Kacholi, 2014; Pimm et al., 1988). The conversion of natural forest and its agricultural intensification are major causes of biodiversity loss globally, threatening ecosystem functioning as well as human well-being (Barnes et al., 2014; Tilman et al., 2012). In West Africa, about 90% of the rainforest has been transformed (Nix, 2019) with Ghana being one of the countries with the highest relative rate of deforestation globally, only exceeded by Togo and Nigeria (Ikpe, 2016). This is of great concern, especially to conservationists and environmentalists. However, traditional agroforestry systems in the tropics have some aspects that resemble natural rainforests and may be a promising land-use strategy to conserve a significant proportion of rainforest diversity (Perfecto et al., 2005; Schroth et al., 2004; Viswanath et al., 2018). The cultivation of cocoa (*Theobroma cacao*) in Ghana is a major economic activity and contributor to land-use change. Cocoa is cultivated in a range of management systems from shaded agroforests to open monocultures (Bisseleua et al., 2013; Perfecto et al., 1996). Traditionally, since it was first introduced from the Americas in 1870, it has been planted under native shade trees by removing the forest understory vegetation and thinning the forest canopy to form an agroforestry system (Anglaaere et al., 2011; Asare, 2005). Native shade trees are used as a strategy to keep cocoa production costs low as they reduce the need for agricultural inputs, and also maintain a substantial level of soil fertility (Abou Rajab et al., 2016; Braga et al., 2019; Saj et al., 2017). Additionally, shade trees can diversify production by providing, for example, oil, timber, seeds, or fruits (Cerda et al., 2014; Rice & Greenberg, 2000; Somarriba & Beer, 2011). Several research studies have shown that cocoa plantations have the capacity to conserve many animal species, possibly more than any other anthropogenic land-use system (Faria et al., 2007; Rice & Greenberg, 2000; Schroth & Harvey, 2007; van Bael et al., 2007). For example, in a study that surveyed an assemblage of migratory birds, the cocoa plantation had the most similar migrant assemblage to natural forest (Greenberg, 2004). Shaded cocoa agroforestry systems can also maintain beneficial ecosystem services and minimize potential ecosystem disservices through trophic and non-trophic interactions (Felicitas et al., 2018). Thus, cocoa farms maintaining substantial proportions of shade trees are seen as following a sustainable land-use practice with comparable ecosystem services to that provided by a primary or secondary forest (Vanhove et al., 2016). Additionally, they serve as faunal refuges because of the forest-like habitats they create (Griffith, 2000). Termites are critical components of tropical soil ecosystems constituting over 90% of the insect biomass in tropical forest soils (Eggleton, 2000; Jouquet et al., 2011; Khan & Ahmad, 2018; Nonoh, 2013). They play major roles in processes such as decomposition, and nutrient and carbon cycling (Ashton et al., 2019; Evans et al., 2011; Griffiths et al., 2019). Africa has the highest richness, biomass, and abundance of termites, particularly of soil-feeding termites of the Termitidae subfamilies Cubitermitinae and Apicotermitinae. The continent is also the center of origin, and has the highest abundance, of the widespread and dominant mound-building termites, the fungus growers (Aanen & Eggleton, 2005; Dahlsjö et al., 2014). Termite diversity is strongly influenced by a variety of local environmental factors such as vegetation type (Jones, 2000), habitat disturbance (Eggleton et al., 2002; DeBlauwe et al., 2008; Jones et al., 2003), and habitat fragmentation (Davies, Hernandez, et al., 2003b; DeSouza & Brown, 1994). Past studies have shown that termite diversity decreases strongly across disturbance gradients (Eggleton et al., 1995, 1997, 2002; Felicitas et al., 2018; Jones et al., 2003; Turner & Foster, 2008), as microclimate, nesting site, and food resources (e.g., dead wood) alter (Schyra & Korb, 2019). Disturbance is frequently accompanied also by selective loss of particular termite feeding groups, especially the soil feeders (DeSouza & Brown, 1994; Djuideu et al., 2020; Eggleton et al., 1997, 1998, 2002). The decline in soil feeders with land-use intensification can result in an increase in the relative abundance of fungus-growing termites, as fungus-growing termites are more resilient to habitat conversion (Eggleton et al., 1997, 2002; Jones et al., 2003). The decline in diversity may in part be related to distance from the forest (Fahrig, 2003; Fletcher, 2005; Laiolo & Rolando, 2005; Ries et al., 2004) and the related increase in temperature (and range) with increasing distance from the forest edge, which usually results in the loss of soil feeders. For example, ambient temperature monitored by The Nature Conservation Research Centre, Ghana (NCRC) in Kakum forest reserve and surrounding cocoa farms showed that the annual mean temperature inside the forest (24.9°C) was approximately 2.2°C lower than the temperature observed on cocoa farms (27.1°C) 5000 m from the forest edge (Unpublished, Table Supplementary information). Here, we determine the effect of cocoa shade cover and distance from forest edge on species richness, abundance, and composition of termites in the Kakum forest reserve, in Ghana, West Africa, and its surrounding cocoa agroforestry systems. We further investigate the influence of shade cover on the richness and relative abundance of pest termites and "deep forest" termite species to ascertain whether shade maintenance in cocoa agroforests reduces termite pest species while conserving deep forest termite species. We hypothesize that termite abundance and richness will decrease with decreasing shade cover and with increasing distance from the forest edge due to the local extinction of soil-feeding termites affected by disturbance. We also hypothesize that the abundance and richness of termite pest species will increase while non-pest species and deep forest termite species will decrease with decreasing shade cover. This is because soil-feeding termites (all of them are non-pest species) are vulnerable to low or no shade and are usually absent when there is limited canopy cover, while wood-feeding termites (many are pest species) are maintained due to their resilience under such environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Study area

The study site was the Kakum National Park and the Assin-Attandanso Resource Reserve, within the Kakum Conservation Area, Ajueso shelter belt and surrounding cocoa farms in southern Ghana at latitude

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5°35′26.88″N to 5°29′23.75″W and longitude 1°14′50.34″N to 1°17′51.11″W (Figure 1). The Kakum and Assin Attandanso forests were demarcated between 1925 and 1926 and put into reserve and managed as forest reserves in 1931 and 1937, respectively, for timber production and for the protection of the watersheds of the Kakum and other rivers that supply water to Cape Coast city and the surrounding areas. The reserve was made into a National Park in 1992. The reserve has gone through a long period of disturbance as a result of commercial and subsistence hunting and logging (Wiafe, 2016). Logging operations were prevalent in the park between 1975 and 1989. The cocoa farms are located in two surrounding communities of Homaho, close to the adjacent Assin-Attandanso Resource Reserve, and Kwame Amoabeng, close to the Ajueso shelter belt (Morel et al., 2019). The study area has two peak rainy seasons, a major wet season from March/April to July and a minor one from September to November, with two dry seasons in between the rainy seasons (August, and January to February) (Hall & Swaine, 1981; Mensah-Ntiamoah, 1989). Overall, mean annual rainfall is 1500 mm and the average temperature is 25°C (Morel et al., 2019). The natural vegetation is moist semi-deciduous forest, although large areas have been converted to agriculture, where food crops (cassava and maize) and cocoa are grown. The soils are predominantly weathered oxisols with high sand content.

2.2 | Field sampling

Fourteen locations were sampled along a land-use gradient of decreasing shade influence, that is, from 80% shade cover in the forest to no shade cover in the full-sun cocoa and arable cropland (Table 1). The locations included six plots established in the Kakum forest, Assin-Attandanso Resource Reserves represent natural forest habitat of varied distances from forest edge (100–3000 m). The forest plots had tall canopy trees (>15–59.9 m), dominated by the tree families Fabaceae, Malvaceae, Meliaceae, Ebenaceae, Euphorbiaceae, and Cannabaceae, with some species particularly abundant: Carapa procera, Parkia bicolor, Cola gigantea, and Diospyros gabanensis. Tree density was between 317 and 478 trees ha^{-1} with majority of trees in 0–29 and 30–59 diameter classes. Leaf litter and deadwood biomass on forest plots ranged from 0.886 to 1.816 Mg ha^{-1} and 2.310 to 16.545 Mg ha^{-1}, respectively. We sampled six cocoa agroforests (27%–75% shade cover) situated from 100 to 5000 m from forest edge with shade trees providing shade cover over the cocoa trees. The 75% cocoa agroforest plot had several mature timber trees maintained above the cocoa canopy such that the farm seemed managed more as a timber plantation than a farm intended to maximize cocoa production. The number of shade trees maintained on

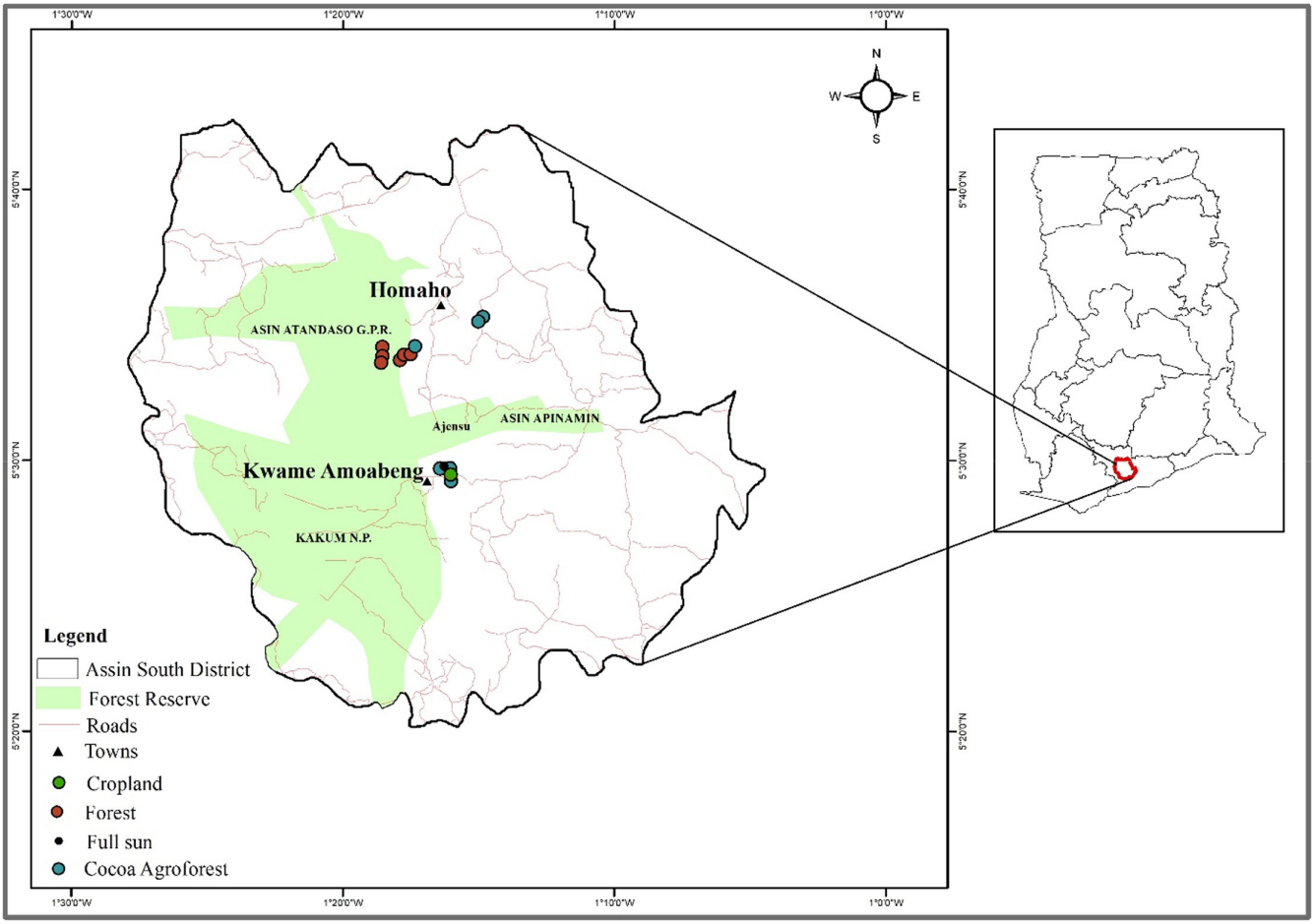


FIGURE 1 Map of the study location at Kakum National Park and the Assin-Attandanso Resource Reserve and surrounding cocoa farms in southern Ghana

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TABLE 1 Site location including percentage shade cover, distance from forest edge (DFE), coordinates, and elevations

Land use	Plot code	Shade (%)	DFE (m)	Latitude	Longitude	Elevation (m)
Forest	HMP14	80	−3000	5°34′20.6″	1°18′31.5″	154
	HMP13	80	−2500	5°34′0.59″	1°18′31.93″	156
	HMP12	80	−2000	5°33′45.68″	1°18′34.31″	151
	HMP5	80	−1000	5°33′51.52″	1°17′52.62″	170
	HMP3	80	−500	5°34′2.93″	1°17′44.23″	140
	HMP6	80	−100	5°34′4.37″	1°17′29.04″	149
Cocoa agroforest	HMP1	75	5000	5°35′26.99″	1°14′49.2″	155
	KAP7	59	500	5°29′51.43″	1°16′24.1″	143
	HMP4	43	100	5°34′22.15″	1°17′19.68″	154
	KAP9	40	1000	5°29′23.71″	1°15′59.62″	132
	KAP8	31	500	5°29′52.33″	1°16′2.1″	146
	HMP2	27	5000	5°35′17.05″	1°14′59.53″	141
Full sun	KAP10	0	100	5°29′57.37″	1°16′15.42″	142
Cropland	KAP11	0	500	5°29′38.26″	1°16′0.84″	128

Note: − sign indicates distance into the forest from the edge.

the cocoa farms correlates with the percentage shade cover on the cocoa agroforest plots. The tree density of cocoa agroforest plots was between 328 and 639 trees ha^{-1}. Leaf litter tended to be lower in forest sites than cocoa sites (Table S2, Figure S2a,b), but dead wood did not differ along the gradient. Full-sun cocoa farm had 2.002 and 5.943 Mg ha^{-1} leaf litter and deadwood biomass, respectively (Table S2), and the cultivated cropland (maize, cassava, and plantain crops) had previously harvested maize residues on the field. Coordinates and elevations for the forest, cocoa agroforests, full-sun cocoa, and cropland plots were taken using a GPS (Table 1).

2.2.1 | Shade measurement

Leaf area index (LAI) photographs were taken to assess canopy cover on all the experimental plots. Each plot consisted of nine sub-plots of 20 m × 20 m. LAI photos were taken in the middle of each subplot of one plot (under forest, cocoa, and above cocoa canopy). At each sampling point, three images were taken in auto bracketing mode (the camera automatically takes all three at each go). The three images were from left: 0 standard exposure, −1 underexposure, and +1 overexposure. Two series of hemispherical images were acquired, one below the cocoa to characterize understory and a second set of images above the cocoa canopy to estimate shade tree LAI. Under the forest and cocoa, the camera was placed at 1 m above the ground using a tripod, directed upward. For above cocoa canopy, the camera was placed above the cocoa canopy using a standalone step-ladder (i.e., 4.5 m above the ground). We ensured that the top of the image was pointing north and using a remote camera control, and a series of three auto-bracketed images were taken. The ground and above cocoa canopy images were processed as two separate series. Images were taken under overcast conditions to minimize anisotropy of the sky radiance (Jonckheere et al., 2004). This was to avoid sun glares or sun flecks when taking upward hemispherical images and reduce occurrence of very over-exposed parts in the image that may make the class allocation more difficult in the image processing. Hemispherical photographs were taken in both the wet and dry season. Average canopy gap was calculated by averaging leaf area index (LAI) photos for all the nine sub-plots (Beckschäfer et al., 2013; Welles & Norman, 1991). Termites were sampled along a single belt transect at each site using the standardized transect method, as described by Jones and Eggleton (2000). Transects were 100 m long and 2 m wide, divided into 20 sections of 5 × 2 m each. Transects were geo-referenced, with GPS coordinates taken at the beginning and the end of each transect (Table 1). One person-hour of sampling effort per section was used to search for and collect termites from the soil (12 pits of approximately 12 cm × 12 cm × 10 cm [depth] were dug per section), accumulations of litter and humus at the base of trees, the inside of dead wood, tree stumps, soil within and beneath very rotten logs, subterranean nests, mounds, runways on vegetation, and arboreal nests up to a height of 2 m above ground level. Termites were searched for within each transect section, and samples were collected for each encounter and placed in separate vials. Where possible, termite samples for each encounter consisted of two to three soldiers and five to seven workers: in total, 7–10 individuals. The termites were placed in vials filled with 70% ethanol and labeled according to the section of transect they were collected within (e.g., 0–5 m, 5–10 m, in order to make the samples manageable when identifying them, by reducing the number of mixed species samples). The number of termite encounters is defined as the number of times termites were recorded and was used as a surrogate for abundance (Davies, 2002). Each transect was treated as a single large quadrat in statistical analyses. Termite species richness and abundance were determined along the shade gradient, as well as using distances from the forest edge separately for both forest interior and exterior.

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2.3 | Identification of termites

With samples containing soldiers, a soldier was first identified to genus using keys by Bouillon and Mathot (1965), and then sequenced to obtain an unambiguous species identity using deoxyribonucleic acid (DNA) barcoding. Also, samples with workers only, a worker was sampled and analyzed using molecular methods (Cytochrome C oxidase subunit II [COII] barcoding) at the Natural History Museum, London, UK. The morphological identification of workers was not possible with the time and expertise available to the project and the poor state of species-level termite taxonomy (especially within the soldierless Apicotermitinae). We extracted DNA from individual representative specimens of termites from each morphospecies (soldiers and workers). Specimens were dry-ground with a few grains of sand using a micro pestle in 1.5-ml Eppendorf tubes, with 180 µl ATL lysis buffer (Qiagen Ltd) and 20 µl Proteinase K [40 U ml^{-1}] (sigma) and left to digest overnight at 55°C with agitation. Standard Qiagen blood and tissue kits were used to perform extractions on the lysates, following manufacturer's instructions (Qiagen Ltd). The concentration of DNA in each extract was recorded using a Nanodrop 8000 DNA spectrophotometer (Thermo Fisher) to measure the amount of template being added to the PCR. A PCR was done on the resulting DNA using termite-specific COII primers (Sequences, 5′ to 3′: Modified A-tLeu: CAGATAAGTGCATTGGATTT, B-tLys: GTTTAAGAGACCAGTACTTG; [Inward et al., 2007]). CO II was used rather than the more commonly used cytochrome C oxidase I (CO I) because the number of available termite sequences is greater with a comprehensive taxon sampling for the former (~3665) than the latter (~2172). Individual PCR reactions were carried out in a 25 µl reaction volume comprising: 16.5 µl PCR grade water, 2.5 µl 10× reaction buffer (supplied with TAQ), 1.5 µl magnesium chloride [50 mM], 1 µl dNTP mix [100 mM], 1 µl of each primer [10 µM], 0.5 µl Hi fidelity BIOTAQ (Bioline), and 1 µl of DNA template [2–8 ng $µl^{-1}$]. PCR conditions for reactions utilizing primers Modified A-tLeu/B-tLys were as follows: 94.0°C for 5 min; 35 cycles at 94.0°C for 30 s, 53°C for 30 s and 72.0°C for 1 min; and 72.0°C for 10 min. All reactions were conducted using a Techne TC-512 thermo cycler (Bibby Scientific). The resulting ca. 900 base pair PCR products were purified using a purification plate method (Merck, Millipore). DNA strands in the forward and reverse direction were sequenced on an ABI 3730XL capillary DNA analyzer (Applied Biosystems), using Big Dye Terminator kit version 1.3 (Applied Biosystems) following manufacturer's instructions, and conducted at the Natural History Museum London sequencing facility. The text of sequences resulting from the AB1 chromatogram traces was edited by hand using BioEdit and poor-quality sequences were excluded (Hall, 1999); for example, there were few sequences where the chromatograms were hard to interpret, due to their faintness or overlap, and those that clearly represented DNA from a non-termite sequence. Only three of such sequences were excluded. NCBI BLAST (Altschul et al., 1990) was used to find the closest match for each sequence to existing DNA data bases, accepting genus matches at the 95% level, and species at the 97% level. Where there were no close matches, morphological criteria were used to assess genus and morphospecies identity (labeled "sp 1", "sp 2," etc.). Whether the species was already described morphologically was not investigated in these cases. This was particularly true of the soldier-less Apicotermitinae, where even genus level identifications were problematic, particularly of the paraphyletic catch-all genus, Astalotermes. Termites collected were categorized into one of four feeding groups following the classification by Donovan et al. (2001). The classification was based on the worker gut and mandible characteristics, which correlate with feeding preferences along a humification gradient of the feeding substrate (Group II is further divided into non-fungus and fungus-growing wood feeders [IIf]). The feeding groups were as follows: Group I (generally wood feeders). Termites feeding on wood predominantly, with some species feeding on grass; with flagellate symbionts in their guts. Group II: termites feeding on wood predominantly, but with some species feeding on grass, leaf litter, and micro-epiphytes, without flagellates in their gut (non-fungus-growing wood feeders). Group IIf: termites feeding on wood predominantly, but with some species feeding on grass, leaf litter, and micro-epiphytes, without flagellates in their gut but with a mutualistic relationship with Termitomyces fungus (fungus-growing wood feeders). Group III: termites (without flagellates) feeding on organic matter-rich soil or highly decayed soil-like wood, and poorly decayed soil (humus-feeders). Group IV: termites (without flagellates) feeding on soil with low organic matter content or mineral soil (true soil feeders). Termites were also grouped as pest or non-pest and, deep forest or non-deep forest species. Termite pest species in this context are species that cause severe damage to living plants; non pests are beneficial to plants; deep forest species are species that live predominantly in forested habitats and were defined by the top 25% of the species listed in Table 3 of Eggleton et al. (2002), which sampled termites along a disturbance gradient.

2.4 | Statistical analyses

The effect of shade and distance on abundance and richness of termites was tested using separate generalized linear mixed-effects models (Zuur et al., 2009). Site was included in the models as a random effect since plots within a given site may be expected to be similar and should not be considered independent. In each model, shade and distance were considered as the fixed effect. Generalized linear mixed-effects models were performed using the glmer function of the lme4 package in R statistical software 4.0.0 (R Core Team, 2020). To assess the influence of sites located inside and outside the forest on the abundance and richness of termites, a generalized linear model (GLM) with Poisson distribution was carried out. We used GLM since both abundance and richness are count data and GLM is suitable for the analysis of such data (Zuur et al., 2007). The generalized linear modeling was carried out in R programming using the package glm. To examine the influence of shade on the richness and abundance of different categories of termite pests (i.e., pest, non-pest, non-deep forest, and deep forest species) at the different sites. A generalized linear mixed model (GLMM) was used for this analysis with shade as the fixed factor and site as the random factor.

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TABLE 2 List of the 34 termite species collected from natural forest, six cocoa agroforest farms, a full-sun cocoa farm and an arable cropland; species are classified according to their feeding groups (FG), microhabitats (MH), pest status (PS), and their associated with deep forest (DF). FG: Group I, II, IIf, III, and IV; MH: w = wood; w/l = wood/litter; h = humus; s = soil; PS: N = non-pest; P = pest; DF: S = non-deep forest; D = forest specialists (shown in bold); U = uncertain; FS = full sun; CL = cropland. Figures under PS and DF (number of encounters and species) represent pest and deep forest species respectively

Land use					Forest (80%)						Cocoa (75%–27%)						FS	CL
Percentage shade cover					80	80	80	80	80	80	75	59	43	40	31	27	0	0
Dist. from forest edge (m)					−3000	−2500	−2000	−1000	−500	−100	5000	500	100	1000	500	5000	100	500
Species	FG	MH	PS	DF														
Kalotermitidae																		
Neotermes spA (13)	I	w	P	S	0	0	0	0	0	0	0	0	9	0	0	4	0	0
Rhinotermitidae																		
Rhinotermitinae																		
Schedorhinotermes putorius (3)	I	w	P	S	0	0	0	1	2	0	0	0	0	0	0	0	0	0
Termitidae																		
Macrotermitinae																		
Macrotermes subhyalinus (1)	IIf	w/l	P	S	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Microtermes spA (8)	IIf	w/l	P	S	0	4	0	0	0	0	0	0	0	0	4	0	0	0
Microtermes spB (211)	IIf	w/l	P	S	19	24	14	15	5	4	2	0	24	10	23	5	22	44
***Protermes prorepens* (14)**	IIf	w/l	N	D	5	3	0	1	5	0	0	0	0	0	0	0	0	0
Pseudacanthotermes spA (163)	IIf	w/l	P	S	0	0	0	4	28	88	11	5	22	0	0	1	4	0
Ancistrotermes crucifer (771)	IIf	w/l	P	S	37	32	42	64	35	80	37	94	49	64	51	6	114	66
Odontotermes spA (76)	IIf	w/l	P	S	1	5	4	1	0	0	43	0	0	7	0	4	2	9
Odontotermes spB (41)	IIf	w/l	P	S	0	0	0	0	5	0	0	0	1	11	4	20	0	0
Nasutitermitinae																		
***Leptomyxotermes doriae* (2)**	II	w	N	D	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Nasutitermes latifrons (102)	II	w	P	S	0	3	0	0	5	2	2	0	81	1	1	4	0	3
Termitinae																		
***Cephalotermes rectangularis* (13)**	II	w	N	D	1	0	11	1	0	0	0	0	0	0	0	0	0	0

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TABLE 2 (Continued)

Land use					Forest (80%)						Cocoa (75%–27%)						FS	CL
Percentage shade cover					80	80	80	80	80	80	75	59	43	40	31	27	0	0
Dist. from forest edge (m)					−3000	−2500	−2000	−1000	−500	−100	5000	500	100	1000	500	5000	100	500
Species	FG	MH	PS	DF														
Microcerotermes parvus (105)	II	w	P	S	8	0	5	15	4	16	6	8	6	3	15	10	0	9
Amitermes evuncifer (5)	II	w	P	S	3	0	0	0	0	0	0	0	0	0	0	0	2	0
Promirotermes sp. (8)	III	h	N	S	0	0	0	2	0	0	3	0	0	0	0	3	0	0
***Pericapritermes nigerianus* (2)**	III	h	N	S	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Apicotermitinae																		
Adaiphrotermes sp. (23)	III		h	N	S	7	1	4	4	0	0	4	0	0	0	2	0	1	0
Astalotermes spB (3)	III		h	N	U	0	1	0	0	0	0	0	0	0	0	0	2	0	0
Astalotermes spC (4)	III		h	N	U	1	1	0	0	1	0	1	0	0	0	0	0	0	0
Astalotermes spD (20)	III		h	N	U	0	1	0	0	0	0	9	0	0	0	10	0	0	0
Astalotermes spF (1)	III		h	N	U	0	0	0	1	0	0	0	0	0	0	0	0	0	0
***Allognathotermes* sp. (5)**	IV		s	N	D	0	0	0	0	0	3	0	0	0	2	0	0	0	0
***Anenteotermes polyscolus* (5)**	IV		s	N	D	1	1	0	0	0	0	3	0	0	0	0	0	0	0
***Ateuchotermes* spA (2)**	IV		s	N	D	0	0	0	0	0	0	0	0	0	1	1	0	0	0
***Eburnitermes grassei* (2)**	IV		s	N	D	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Cubitermitinae																		
***Proboscitermes* sp. (16)**	IV		s	N	D	0	1	1	2	0	0	0	0	11	0	1	0	0	0
Macrotermes sp. (1)	IV		s	N	U	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Unguitermes sp. (4)	IV		s	N	U	0	0	0	4	0	0	0	0	0	0	0	0	0	0
Basidentitermes sp. (6)	IV		s	N	U	0	0	0	1	0	0	1	4	0	0	0	0	0	0
***Cubitermes fulvus* (4)**	IV		s	N	D	0	0	1	0	0	0	2	0	0	0	0	1	0	0
***Procubitermes undulans* (2)**	IV		s	N	D	1	1	0	0	0	0	0	0	0	0	0	0	0	0
***Noditermes* sp. (1)**	IV		s	N	D	0	1	0	0	0	0	0	0	0	0	0	0	0	0

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TABLE 2 (Continued)

Land use					Forest (80%)						Cocoa (75%–27%)						FS	CL
Percentage shade cover					80	80	80	80	80	80	75	59	43	40		31	27	0	0
Dist. from forest edge (m)					−3000	−2500	−2000	−1000	−500	−100	5000	500	100	1000		500	5000	100	500
Species	FG	MH	PS	DF															
			s	N	D				1	0	0	1	0	0	0	0	1	0	0
Pilotermes sp. (3)	IV				0	0	0	0											
No. of Encounters	1640			1499	69	84	80	85	120	90	193	125	111	203	99	112	61	146	131
No. of species	34			12	12	11	15	10	17	9	6	14	4	8	8	10	12	7	5

Note: Figure in parenthesis after species name is the number of encounters of species.

3 | RESULTS

3.1 | Richness and abundance

There were a total of 1640 termite encounters representing 34 species from 29 genera. Of this, 1528 encounters and 15 species were wood feeders while 112 encounters and 19 species were soil feeders, representing 93.2% and 6.8% encounters and 44.1% and 55.9% species for wood and soil feeders, respectively (Table 2). Three families (Kalotermitidae, Rhinotermitidae, and Termitidae) were represented, of which the Termitidae was by far the most frequently encountered, with 32 species representing some 99% of the total number of encounters. The subfamily Macrotermitinae (fungus growers) had 1285 encounters with eight species. The most common species were *Ancistrotermes crucifer*, *Microtermes* sp. B, *Pseudacanthotermes* sp. A, and *Microcerotermes parvus* with 771, 211, 163, and 108 encounters, representing 47%, 12.9%, 9.9%, and 6.6% of the total number of encounters respectively (Table 2). Most species were either fungus-growing wood/litter feeders (13 species), or soil feeders (12 species).

Forest plots did not consistently have higher numbers of encounters, however, there was weak evidence that shade affected the number of encounters across the shade gradient (p = .048) (Figure 2a and Table S3a).

There was also a similar trend in species richness across the shade gradient (p = .044) (Figure 2b and Table S3a). The highest number of species was observed on forest plots (80% shade at 1000 and 2500 m from forest edge), followed by cocoa agroforest plot of 75% shade cover with 17, 15, and 14 species, respectively. The lowest number of species (4 species) was observed on a cocoa agroforest plot of 59% shade cover.

The number of encounters peaked at the forest edge (Figure 2c) with *Ancistrotermes crucifer* contributing substantially (44.8%) to the number of encounters at the forest edge (Figure Supplementary information). There was significant difference in the number of encounters with distance from the forest edge (p = .0112) (Figure 2c and Table S3b). By contrast, species richness was lowest at the forest edge. The number of species showed no significant difference with distance (p = .0935) (Figure 2d and Table S3b).

The majority of encounters were with potential pest species (1499, representing 88.4% of total encounters), although these pest species comprised only 12 species (35.3% of total richness). Deep forest specialists comprised only 69 encounters (4.2% of all encounters) but were represented by 12 species (35.3% of all species) (Figures 3c,d). Shade had no significant influence on the richness of pest species (p = 0.616) but had a significant effect on the abundance of termite pest species (p = .000117) (Table S3c). However, we observed positive relationships with the proportion of non-pest species across the shade gradient (p = .000414 and p = .0000423) for richness and abundance, respectively (Figure 3a,b, and Table S3d). Whereas shade had a significant influence (p = .00843) on the richness of deep forest species, the shade had no effect (p = .0721) on the abundance of deep forest species (Table S3f). By contrast, the reverse is true for non-deep forest species. That is, the shade had

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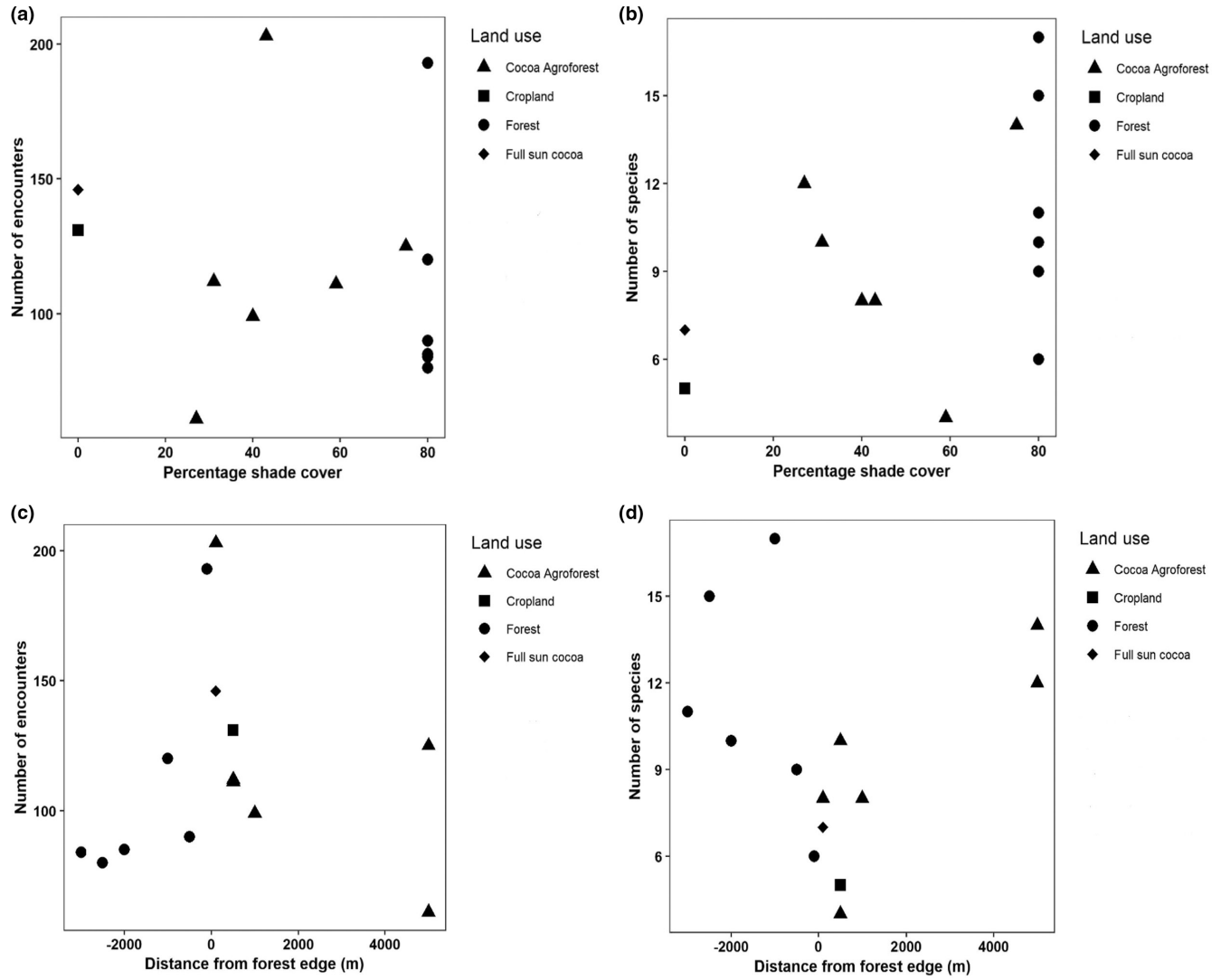


FIGURE 2 (a) Number of encounters and (b) number of species as a function of percentage shade cover; (c) number of encounters and (d) number of species as a function of distance from forest edge

no significant influence ($p = .973$) on the richness of non-deep forest species, but had a significant effect (.000713) on the abundance of non-deep forest species (Figure 3c,d, and Tables 3Se).

3.2 | Feeding group composition

There was no systematic change in composition of feeding groups along the shade gradient (Figure 4a,b), although the most disturbed sites (full-sun cocoa and arable cropland) had no true soil-feeding termites. Feeding group I termites (lower termite wood feeders) were represented by two species (*Neotermes* sp. A and *Schedorhinotermes putorius*). The most common feeding group collected was fungus-growing wood/litter-feeding termites (Group IIf), accounting for 78.4% of all encounters and 23.5% of all species, with *Ancistrotermes crucifer* dominating this group (Table 2). The combined humus-feeding (Group III) and true soil-feeding termites (Group IV) also accounted for 6.8% and 55.9% of all encounters and species respectively with *Adaiphrotermes* sp. dominating the humus-feeding group (Group III), while *Proboscitermes* sp. dominated the true soil-feeding group (Group IV) (Table 2). Wood feeders (i.e., wood ingesting, non-fungus, and fungus feeders) constituted over 90% of the total number of encounters across the forest, cocoa and arable crop land plots (Figure 4c) representing majority of the termite community. By comparison, the soil feeders (humus [FGIII] and true soil feeders [FGIV]) constituted more species despite fewer encounters; most occurred in the forest and were generally rare (Figure 4d). None of the pest termites were soil feeders (Table 2).

4 | DISCUSSION

Overall, our results showed a relatively low species richness across our sites, recording an average of 10 species per transect (maximum of 17 species) from 14 transects sampled. This may be because most of the sites were transformed, although the forest sites also had

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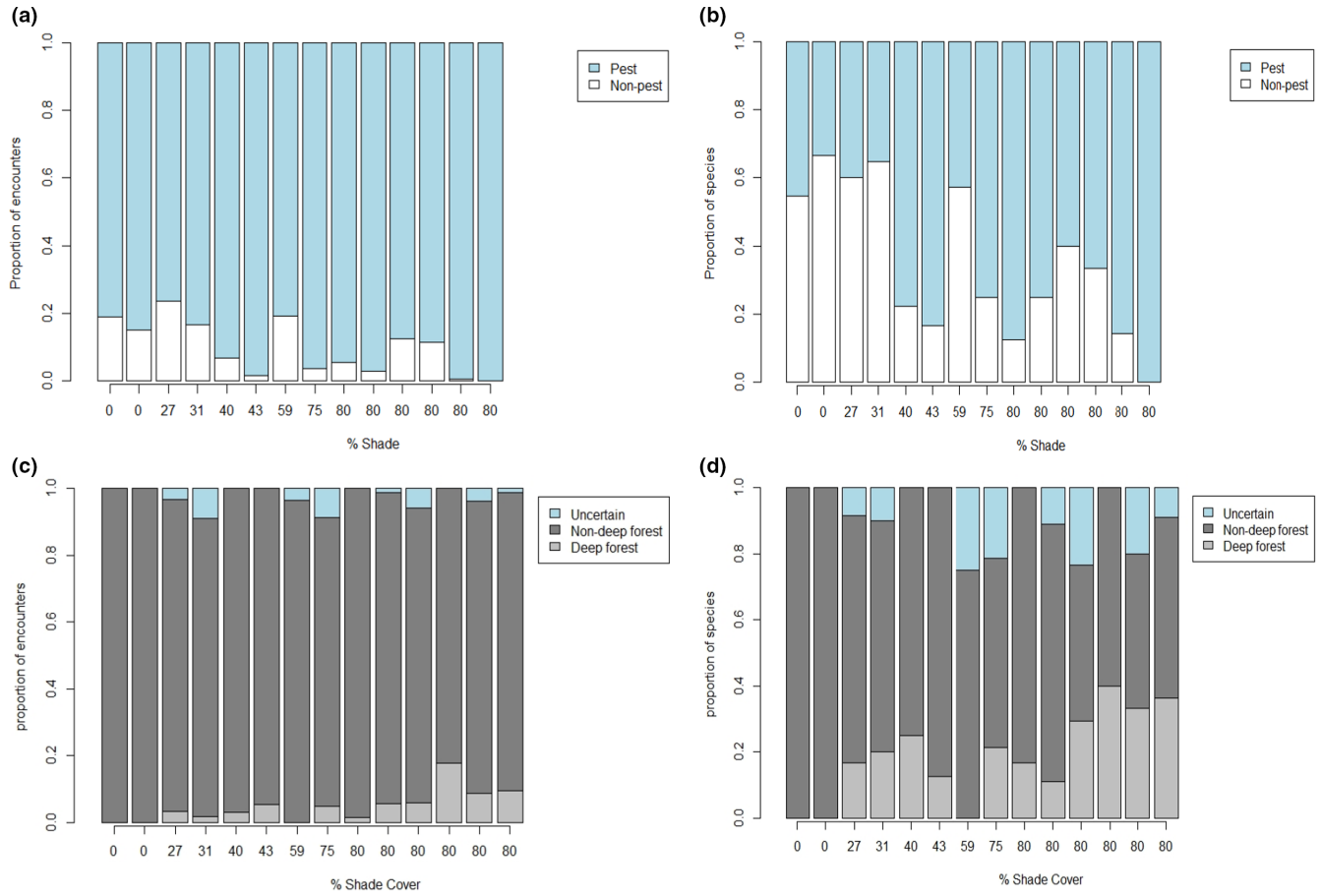


FIGURE 3 (a) Proportion of encounters of pest and non-Pest. (b) Proportion of species of Pest and non-pest along forest, cocoa, and cropland plots of the study site. (c) Proportion of encounters of deep and non-deep forest species. (d) Proportion of species of deep and non-deep forest species along forest, cocoa, and cropland plots of the study site

relatively low richness (mean 11.3 species). This contrasts with other studies in Central African forests (rather than in West Africa). For example, in a Cameroonian old-growth forest, Eggleton et al. (2002) recorded more than 50 species per transect from two transects sampled. A similar result was obtained in a Congolese forest, where ~55 species per transect from two transects sampled were recorded (Eggleton et al., 2001).

However, our 11 species per transect found in natural forest is in line with species richness reported for natural forests in West Africa (Table 3) where richness ranges from 9 species (Benin, Hausberger & Korb, 2016) to 16 species (The Gambia, Ndiaye et al., 2019). These studies suggest natural forests in West African have lower termite species compared with natural forests in Central Africa, and also South America and Asia where termite species richness tends to be higher. For example, in Ecuador Dahlsjö et al. (2020) reported 33 species per transect for Yasuni forest reserve, and Jones and Prasetyo (2002) report 31 and 29 species per transect for an old logged forest and a recently logged forest in Kalimantan and Indonesia, respectively.

The reason for the low termite richness in West African forests may be attributed to the long history of logging and exploitation of the Upper Guinean Forest block (Conservation International, 2007). This is consistent with a decline in species numbers due to forest disturbance (Felicitas et al., 2018; Gathorne-Hardy et al., 2001). Twelve (12) genera of forest specialists identified in the Eggleton et al. (2002) study were missing in Kakum forest reserve based on our study. While we have no data from pristine old-growth forests in the region because all forests have been subject to some kind of anthropogenic disturbance, comparisons of forested and transformed habitats in this area may inflate the value of disturbed habitats and baselines should be interpreted with caution. An alternative, although non-mutually exclusive possibility is that the depauperate forest termite assemblages may be attributed to high soil pH; higher pH soils tend to have lower termite diversity (Jones et al., 2010). Soil pH in Kakum ranges from 6.00 to 6.66 (Table S2), which fits a soil pH range of A horizons in ultramafic soils (5.0–7.0), which is considered high for most tropical lowland forests (Proctor, 1992). It is, therefore, possible that heavy deposition of Saharan dust during Harmattans may make the soils more alkaline and, therefore, less favorable for termites.

Nevertheless, possibly because the forest community appears somewhat depauperate, termite species richness, abundance, and feeding group composition did not show strong change along the shade gradient as anticipated, although, at the extreme end of the

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TABLE 3 Summary of termite studies conducted in some selected West and Central African countries indicating habitats and species per transect obtained

Country of study	Land use/habitat	No. of transects	Species/transect	References
The Gambia	Forest reserve	3	16	Ndiaye et al. (2019)
	Secondary forest	3	13	
	Savannah reserve	3	10	
Togo	Forest reserve	30	12	Schyra et al. (2019)
	Teak plantation	21	8	
	Savannah reserve	42	10	
	Savannah fallow	39	10	
Benin	Forest reserve	4	10	Attignon et al. (2005)
	Teak plantation	4	7	
Benin	Forest reserve	9	9	Hausberger and Korb (2016)
	Buffer zone	3	8	
	Disturbed Area	3	4	
Côte d'Ivoire	Forest reserve	5	25	Dosso et al. (2012)
	Savannah woodland	5	18	
	Burned savannah	5	14	
	Disturbed forest	5	13	
	Savannah woodland	5	16	
	Burned savannah	5	13	
Côte d'Ivoire	Forest reserve	3	18	Akpesse et al. (2018)
	Cocoa plantation	3	10	
Congo Brazzaville	Forest reserve	2	55	Eggleton et al. (2001)
Cameroon	Complete clearance		10	Eggleton et al. (2002)
	Mixed crop fields		15	
	Short fallow		20	
	Cocoa plantation		28	
	Young plantation		52	
	Old secondary forest		50	
	New primary forest		45	

gradient with no shade, there were few species. Although studies have shown that termite abundance declines with disturbance (Dawes, 2010; Dosso et al., 2013; Felicitas et al., 2018; Vasconcellos et al., 2010), shade trees clearly add some buffering capacity as there was only weak evidence that richness and abundance declined. Deep forest and non-pest termite species were, by in large, maintained under shade trees which provide a relatively conducive environment for termites to survive, especially, the soil-feeding termites (Davies, Eggleton, et al., 2003a; Palin et al., 2011). In our study, sites with the highest shade (i.e., forest sites) tended to have less leaf litter, and there was no relationship between the amount of leaf litter and either, the number of encounters or number of species (Figure S2a,b). This suggests that differences in leaf litter along the shade gradient cannot explain our findings. Furthermore, deadwood also did not systematically change along the shade gradient and therefore is unlikely to have influenced species richness and abundance.

We also expected a decrease in termite richness with increasing distance from forest edge into agricultural fields, that is, cocoa agroforest plots away from forest edge; however, we found a positive effect of distance from forest edge on termite richness where the number of species increased with increasing distance from forest edge. This, however, may be spurious since only two sites at the 5000-m distance influenced the observed pattern.

Of the feeding groups encountered, the fungus growers were the most abundant group with Ancistrotermes crucifer being dominant in all of the plots sampled. Ancistrotermes crucifer is commonly found in savannas, forest edges, and savanna-forest mosaics (Harris, 1966), and these habitats are suitable for the generalist feeding habit nature of the Ancistrotermes crucifer, which also may have contributed to its widespread dominance (Muvengwi et al., 2017). They have been reported to tolerate semiarid and arid environmental conditions such as full-sun cocoa plantations (Felicitas et al., 2018). Thus, the mere presence and dominance of Ancistrotermes crucifer may be an indication of a disturbed forest. Kakum forest reserve has a long period of disturbance through logging and subsistence hunting (Wiafe, 2016), which may have led to the forest being depauperate before it was gazetted under wildlife reserve regulations (LI 1525) of 1992 coupled with the fact that Ancistrotermes is resilient to disturbance (Gathorne-Hardy et al., 2001) and largely contributed to the number of encounters of termites across the shade gradient.

As was expected, there were no soil feeders at the most disturbed site (zero shade, arable cropland plot). This is in line with the findings of Felicitas et al. (2018) and Eggleton et al. (1998, 2002) that in cleared forests, soil feeders may prefer environment provided by shade trees or are more likely to be wholly subterranean. This may be because hotter and drier microclimates associated with disturbed

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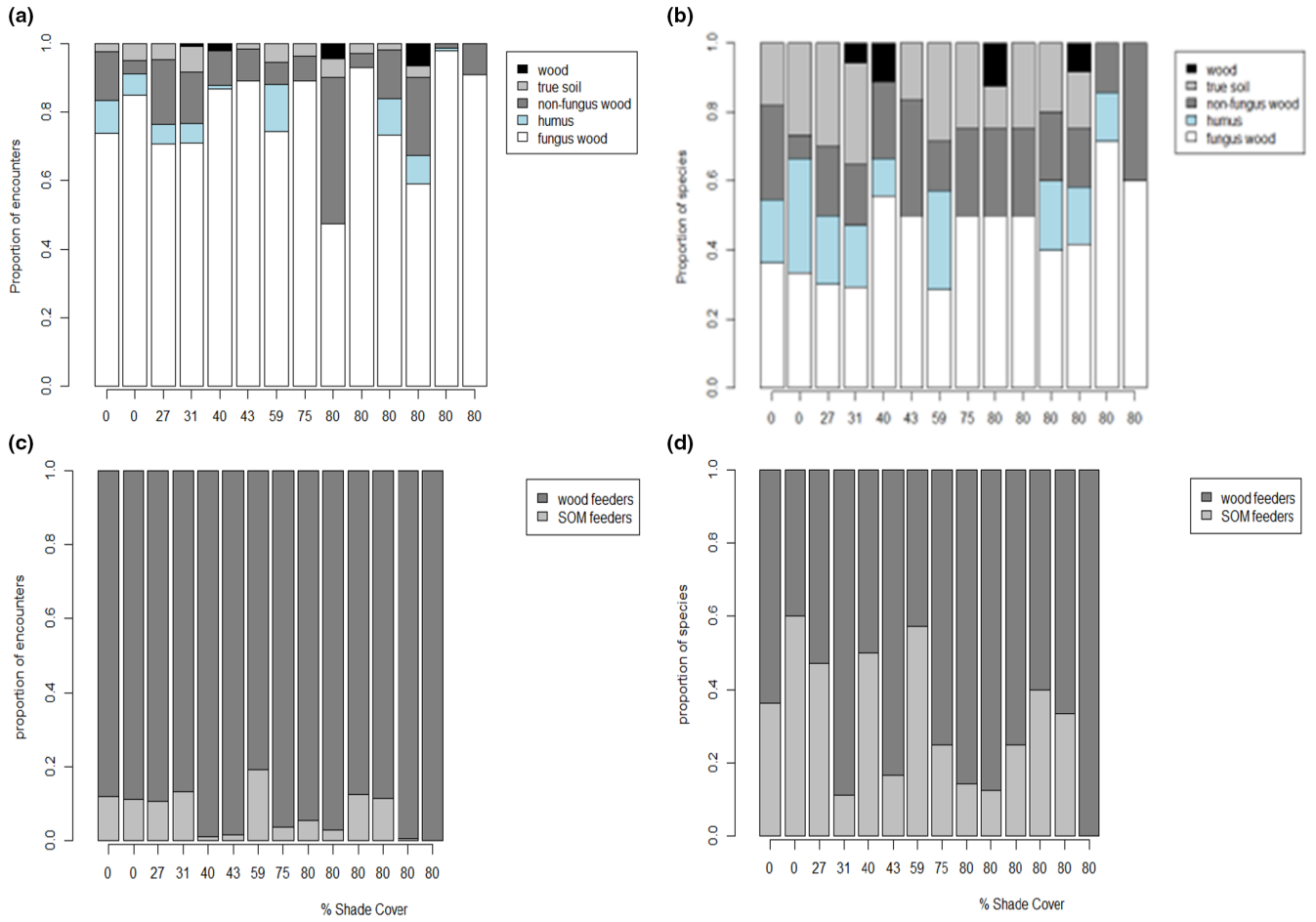


FIGURE 4 (a) Proportion of encounters of feeding groups and (b) proportion of species of feeding groups along forest, cocoa agroforest, and cropland plots; (c) proportion of encounters of wood and soil feeders and (d) proportion of species of wood and soil feeders along forest, cocoa agroforest, and cropland plots

forest (Eggleton et al., 2002; Felicitas et al., 2018; Muvengwi et al., 2017) are less suitable for the survival of many soil feeders; many of which are subterranean and soft-bodied, and therefore may be more sensitive to variation in microclimate (Davies et al., 2012; DeSouza & Brown, 1994).

Most species recorded (19 species) were found on both forest and cocoa agroforest plots (exceptions were *Noditermes* sp., *Procubitermes undulans*, *Unguitermes* sp., *Macrotermes* sp., *Eburnitermes grassei*, and *Pericapritermes nigerianus*: all soil-feeding termites, which occurred only in the forest plots). This may be attributed to the moist and buffered microhabitats provided by the trees in both the forest and cocoa agroforests habitats, thereby facilitating the survival of this group of termites (DeSouza & Brown, 1994; Eggleton et al., 1997, 1998, 2002; Jones et al., 2003).

In conclusion, our study revealed that the forest sites are relatively poor quality and may have over-estimated cocoa agroforests and the presentation of the system as comparable to natural forest habitat. This is a cause for concern, especially in situation where shifting baseline issues could affect strategies or programs for conservation, restoration, and management of degraded natural habitats.

Yet, it is also clear that shade trees confer a level of buffering to termite communities in these transformed habitats, providing a favorable habitat and microclimate, which is conducive for the survival of termites, thus maintaining biodiversity and environmental quality under such agricultural landscape. Because termite abundance was maintained across shade gradient, this suggests that their functions may also be maintained. Next steps should include examining how key processes that are mediated by termites, such as decomposition and soil bioturbation, alter along land-use gradients and whether the influence of termites can be maintained despite habitat transformation.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.lgljwsv00 (Quansah et al., 2022).

CONSENT TO PARTICIPATE AND PUBLISH

There was a full consent of all authors to participate; all authors accepted to the revised draft and gave consent to the corresponding author to submit it for publishing.

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