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Conservation management and termites: a case study from central Côte d'Ivoire (West Africa)

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Abstract

Termites are essential components of tropical ecosystems, in which they provide fundamental ecosystem services, such as decomposition of dead plant material, fostering of soil mineralization and provisioning of new microhabitats. We investigated the termite communities of four habitats in two protected areas in West Africa, which differ in management effectiveness: the strictly protected Lamto Reserve (LR) and the Marahoué National Park (MNP), which suffers from anthropogenic disturbance despite its protection status. We tested the effect of disturbance on species composition, richness and abundance as well as on functional (feeding type) composition. The effect of disturbance was clearly visible in the termite communities. Compared to the LR, the MNP had less termite species overall and in all habitats except the shrub savannah. Also the abundance of termites was generally reduced and a decrease of soil feeders recorded. The latter is well-known to be sensitive to anthropogenic disturbance in forests. Comparing our results with other studies, we were able to identify suitable bioindicators of ecosystem health for West-African savannahs. Furthermore, we discuss the potential consequences of anthropogenic disturbance on ecosystem services provided by termites.

Introduction

Termites are among the most abundant arthropods in tropical ecosystems that provide essential ecosystem services (e.g. Ashton *et al.* 2019, Pringle *et al.* 2010). In lowland tropical ecosystems, they are the most important animals decomposing dead plant material, which can make up 95% of the soil insect biomass (Eggleton *et al.* 1996). In dry tropical forests, they consume between 40% and 100% of the dead wood and in savannahs up to 20% of the grass and leaf litters (Collins 1981). Termites are also essential with regard to the structure, functioning and dynamics of tropical ecosystems (Whitford 1991). Their mounds and their foraging activities have strong effects on soil structure, nutrient cycles (Lavelle *et al.* 1997) and soil chemical composition (Holt & Lepage 2000). They contribute to improve the water retention of soils that strongly affects vegetation structure and local primary productivity (e.g., Evans *et al.* 2011, Nash & Whitford 1995). In addition, as litter decomposers, they provide material for microbial attack, which fosters mineralization processes (Chapin *et al.* 2002). Yet, termites are also sensitive to disturbance. Their species richness, abundance and composition changes with anthropogenic disturbance, as do feeding type composition and community structuring mechanisms (Alves *et al.* 2010, Attignon *et al.* 2005, Bandeira *et al.* 2003, Eggleton *et al.* 1995, Jones *et al.* 2003, Vasconcellos *et al.* 2009, for West-African savannahs: Hausberger & Korb 2015, 2016, Schyra & Korb 2019, Schyra *et al.* 2019a). Due to these important roles and their sensitivity to habitat disturbance, termites are considered to be good bioindicators of tropical ecosystem health (Pribadi et al. 2011).

Protected areas are important for biodiversity conservation, especially given the strong human pressure on nature. The Convention for Biological Diversity encourages countries to increase their terrestrial protected area to 17% of a country's surface and to manage them in order to ensure permanent ecosystem services. In Côte d'Ivoire, only about 6% of the national territory has been put under strict protection. These 6% are divided into 16 national parks and reserves. The Marahoué National Park (MNP) is one of the most important parks in Côte d'Ivoire because it is located in the transition zone between forest and savannah. Therefore, it comprises both savannah and forest ecosystems and their biodiversity, including endemic species restricted to this transitional zone. During the last decades, the MNP suffered from illegal settlements and activities such as farming, tree cutting, cattle grazing and poaching (see Supplementary Material Figure S1). It lost several hectares of forest cover and natural habitat to the benefit of plantations. While the MNP's natural habitats are being destroyed, its

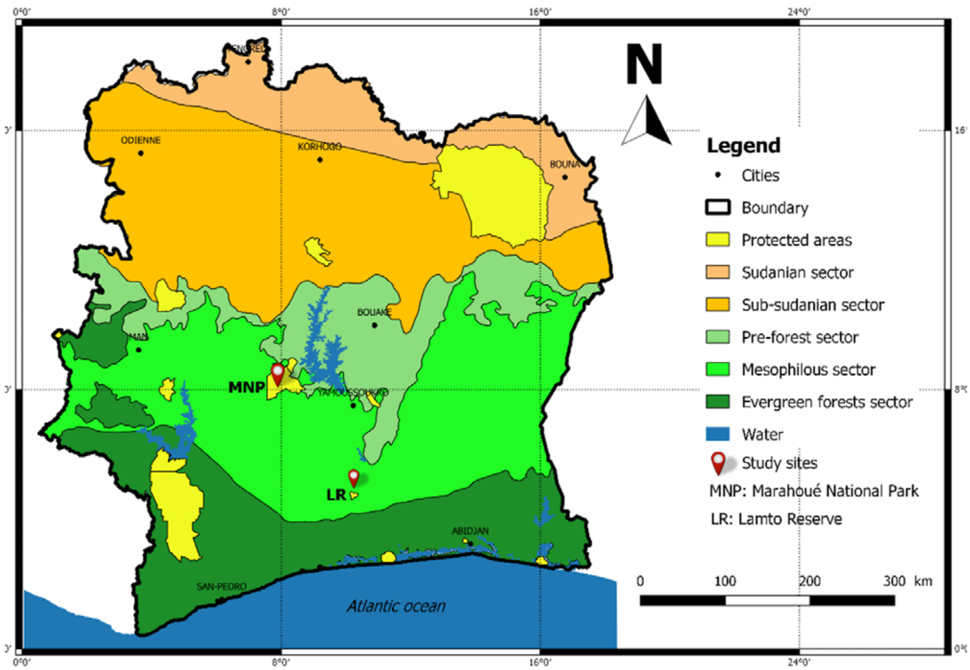

Figure 1. Map of Côte d'Ivoire showing the different phytogeographical zones and study sites. The red points LR (Lamto Reserve) and MNP (Marahoué National Park) indicate the study sites.

biodiversity is expected to disappear. To test this hypothesis, we studied termite communities and compared them with those of a better-protected area located in the same phytogeographical zone (i.e., the Guinean zone) in Côte d'Ivoire, the Lamto Reserve (LR). The LR is a relatively small, strictly protected area (Figure 1, Table 1).

Our study aimed at evaluating the impact of anthropogenic pressure on ecosystems and their biodiversity by using the MNP and the LR as a case example and termites as target organisms. To this end, we (i) sampled termites and determined species identity of termite communities in both areas, (ii) compared estimated species richness and abundance across four habitats between study sites and (iii) identified termite feeding types to characterize their functional role. We analyzed our data set to reveal species, which could serve as bioindicators of ecosystem health and discuss expected long-term consequences of anthropogenic disturbance on ecosystem services provided by termites. This study is the first systematic assessment of termites from the MNP.

Materials and methods

Study sites

The study was done in the LR and the MNP (for details see Table 1). Within each study site (MNP and LR), four homologous plots of 2.5 hectares each were selected, in which the termite communities were studied: Forest Islands (FI), Woodland Savannahs (WS), Shrub Savannahs (SS) and Grass Savannahs (GS).

Sampling design

Sampling in both study sites was done following the standardized belt transect protocol, first developed for sampling termites in forests (Jones & Eggleton 2000) and then adapted to savannahs (Dosso *et al.* 2010, Hausberger *et al.* 2011). In each plot, five transects were established. Each transect was 100 m long and 2 m wide and divided into 20 sections of 5 m × 2 m. The sampling consisted of a thorough search of dead plant material on the ground, on and in trees and mounds as well as soil sampling to assess termite diversity (Jones & Eggleton 2000). Each transect section was systematically searched by four trained people for termites. The search time per transect section was in total 10 and 15 minutes for savannah and forest, respectively. Forests have higher termite abundances, which therefore require more effort than savannahs (Hausberger *et al.* 2011). Additionally, 12 soil scrapes of 12 cm × 12 cm × 10 cm were done and searched per transect section. Whenever we found/encountered termites during the search within a transect section, this was treated as a single sample as it consisted of conspecific foraging individuals, probably nestmates from the same colony. Then a few specimens (5–10 individuals) were collected in a vial; priority was given to soldiers as they were easier to identify. The sampled termites were stored in 97% alcohol for identification. Then, we continued searching within the same section and when we encountered termites again, they were placed in a separate vial. Within a single section, the presence of a species represents one encounter regardless of how often it was encountered within this section. This means that there could be a maximum of 20 encounters (corresponding to the 20 sections) of a species per transect. Total encounter of each termite species in each given transect or habitat was used as a surrogate for abundance (Davies *et al.* 2003).

Identification of termites

Termites were identified to morpho-species level using individuals of the soldier caste, a low-power stereo microscope with a reticle (Leica MZ6) and identification keys (Bouillon & Mathot 1965, Webb 1961), including region-specific illustrations and keys (Josens 1972, Konaté 1998).

For soldierless species, identification was mainly based on workers' gut structure, especially the armature of the enteric valves, which can provide species-specific information (Sands 1998). Enteric valves were dissected by excising the second proctodeal segment.

After identification, all termite species were classified into four feeding types according to Dosso *et al.* (2012, 2013) and Koné *et al.*

Table 1. Description of study sites located in the forest savannah mosaic of the Guinean biome in Côte d'Ivoire

	Lamto Reserve (LR)	Marahoué National Park (MNP)
Status	Well conserved Scientific Reserve	Endangered National Park
Location	Center of Côte d'Ivoire (6°13' and 6°15' N and 4°06' and 5°03' W)	West-center of Côte d'Ivoire (6°51' and 7°17' N and 5°45' and 6°13' W)
Size	2,617 ha	101,000 ha
Climate (https://power.larc.nasa.gov/data-access-viewer/)	• Mean annual precipitation: 1397 ± 163.3 • Mean annual temperature: 26.0 ± 0.3°C. • Mean relative humidity: 76 ± 2.4 % • Main dry season: December to February; large rainy season: March to July; short dry season: August; short rainy season: September to November.	• Mean annual precipitation: 1396 ± 17.1 • Mean annual temperature: 26.0 ± 0.3 °C. • Mean relative humidity: 79 ± 2.1% • Main dry season: December to February; large rainy season: March to July; short dry season: August; short rainy season: September to November.
Management effectiveness	• Well protected site; • Many scientific studies • Many termite studies	• Bad conservation status • Many fields and plantations inside • No studies on termites
Main anthropogenic impacts	• No infiltration by humans • Controlled bush fire in the savannah	• Illegal farming, generally in woody habitats • Poaching and uncontrolled bushfire
Biodiversity	• 60 species of large mammals (Boulière *et al.* 1974) • More than 400 species of birds, 150 species of amphibians (Konaté & Touao 2010) • 176 plant species (Gnahoré *et al.* 2018)	• 22 species of large mammals • 256 species of birds (Schulenberg *et al.* 1999) • Around 607 plant species (N'da *et al.* 2008)

(2018), namely (1) fungus growers, Macrotermitinae, species which live in an obligate exosymbiosis with fungi of the genus *Termitomyces* (Lyophillaceae family); (2) wood feeders, which consume dead wood; (3) grass feeders, which thrive on grass and (4) soil feeders, which feed on soil organic matter and very decayed wood.

Data analyses

Termite sampling efficiency was evaluated by analyzing the sampling coverage for each habitat. Sampling coverage is the percentage of the cumulative number of observed species (Sob) in relation to the cumulative number of estimated species (Chao2 mean). It was calculated with EstimateS 8.0.0 (Robert K. Colwell, Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06869-3043, USA; Website: http://purl.oclc.org/estimates) using 500 randomizations (Cao *et al.* 2002). Chao2 mean is a non-parametric estimator used to estimate species richness for incidence data (present = 1/absent = 0). We used the calculated sampling coverage to compare the sampling effort for each plot. For each plot, each single transect was considered one sampling unit for the inference tests (N = 5 per plot; each plot characterizes one habitat type at a study site). Species richness was calculated as the total number of termite species in a community, which can be (i) a transect, (ii) a plot consisting of five transects that represent a habitat or (iii) a study site, which is either the MNP or the LR. Species abundance is the total number of termite encounters per species within a community. In the present study, we considered a species as common within a study site if it was encountered at least 20 times within a plot representing a habitat (maximum possible encounters: 5 transects × 20 sections = 100).

Inference statistics at the 5% significance level were used to test for significant differences between the study sites with R version 4.0.2 (R Core Team 2016). After testing for normality and homogeneity of variances, we used parametric or non-parametric tests, accordingly. As the same data set was analyzed repeatedly, we used the false discovery rate approach (Benjamini & Hochberg 1995) to correct for multiple testing.

Table 2. Termite species richness, abundance and sampling coverage for both study sites, separated by habitat

	Species richness		Species abundance		Sampling coverage (%)	
Habitats	LR	MNP	LR	MNP	LR	MNP
Forest Island	25	16	151	185	94	70
Woodland Savannah	18	11	160	110	85.5	100
Shrub Savannah	14	14	162	118	93.3	90
Grass Savannah	10	8	98	28	85	94
Total	30	22	571	441	89	89

Termite species richness: total number of termite species in each habitat; Species abundance: the total number of encounters in each habitat; Sampling coverage: proportion (in %) of the cumulative number of observed species in relation to the cumulative number of estimated species (Chao2 mean) for each habitat. LR (Lamto Reserve) and MNP (Marahoué National Park) were the study sites.

Results

Sampling efficiency

For the LR, we had a mean sampling coverage of 89% with the highest values in FI (94%) and SS (93%). Sampling coverage was lower for WS (86%) and the GS (85%). In the MNP, we also reached a mean sampling coverage overall plots of 89% with the highest value (100%) recorded for the WS and the smallest value (70%) for the FI (Table 2). In the GS and SS, sampling coverage accounted to 94% and 90%, respectively.

Taxonomic comparison across both study sites, covering all habitats

In the LR, 30 termite species belonging to two families (Termitidae and Rhinotermitidae) and 21 genera were recorded (see Supplementary Material Table S1). Species from five subfamilies of the Termitidae were collected: Macrotermitinae (12 species), Termitinae (six species), Nasutitermitinae (five species), Cubitermitinae (two species) and Apicotermitinae (three species).

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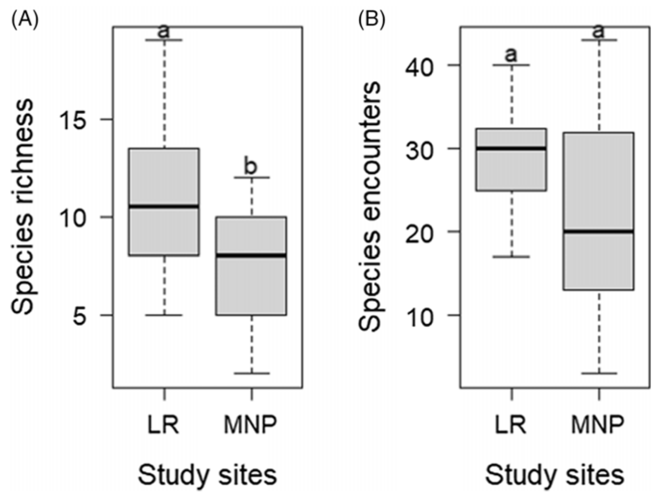

Figure 2. Comparison of (A) termite species richness and (B) termite encounters between both study sites, the LR (Lamto Reserve) and the MNP (Marahoué National Park). Shown are boxplots with the quartiles, median (bold line) and whiskers representing the minimum value and the maximum value. Different letters within graphs indicate significant differences at $P < 0.05$ level (Wilcoxon test, N = 40).

For the Rhinotermitidae, only one species was found for each of the two encountered subfamilies, Coptotermitinae and Rhinotermitinae.

In the MNP, 22 termite species from 14 genera were collected and all belonged to five subfamilies of the Termitidae: Macrotermitinae (11 species), Termitinae (three species), Nasutitermitinae (five species), Apicotermitinae (two species) and Cubitermitinae (one species) (Table S1).

Across both study sites, we collected 21 termite genera, all being present in the LR, but only 14 genera were found in the MNP. In total, we identified 37 termite species in our study. Fifteen out of the 37 termite species were common to both study sites, and also 15 species were found in the LR only and not in the MNP. The remaining seven species were discovered only in the MNP. Using transects as replicates, over all habitats, termite species richness was significantly higher in the LR than the MNP (Wilcoxon test: N = 40, W = 295, p = 0.010) (Figure 2A).

In total, there were 571 encounters of termites in the LR and 441 in the MNP. Using transects as replicates, across all habitats, the number of termite encounters did not differ significantly between both study sites, though there was a trend for more encounters in the LR than the MNP (Wilcoxon test: N = 40, W = 267, p = 0.071) (Figure 2B). Species of all four feeding groups (fungus growers, wood feeders, grass feeders and soil feeders) were recorded in both study sites.

Habitat-specific comparisons between study sites

In both study sites, we investigated four different habitats using 'homologous' plots with five transects each as replicates (e.g. termite species richness and abundance in the FIs of the LR compared to those of FIs in the MNP). In FIs, there were significantly more species in the LR than the MNP (Wilcoxon test: N = 10 W = 25, p = 0.010) (Figure 3A), while species encounters did not differ significantly (Wilcoxon test: N = 10, W = 6, p = 0.207) (Figure 3B). In total, the cumulative species richness in the FIs of the LR was 25 species compared to 16 species for the MNP, while total encounters were 151 *versus* 185 for the LR and the MNP, respectively (Table 2).

In the WSs, species richness and encounters were significantly higher in the LR than in the MNP (Wilcoxon test: richness: N = 10, W = 25, p = 0.011; encounters: N = 10, W = 24.5, p = 0.015) (Figure 3C, D). The cumulative species richness and encounters in the WS of the LR were 18 species in 160 encounters and for the MNP, 11 species in 110 encounters (Table 2).

For the SSs, both species richness and encounters did not differ significantly between the LR and the MNP (Wilcoxon test: richness: N = 10, W = 11, p = 0.832; encounters: N = 10, W = 11, p = 0.115) (Figure 3E, F). In the SS of the LR, we found in total 14 species in 162 encounters compared to 14 species also in 118 encounters in the MNP.

For the GSs, species richness and encounters were significantly higher in the LR than in the MNP (Wilcoxon test: richness: N = 10, W = 25, p = 0.010; encounters: N = 10, W = 25, p = 0.011) (Figure 3G, H). The cumulative species richness was 10 species and 98 encounters in the LR and 8 species and 28 encounters in the MNP.

Comparison of feeding type frequencies between both study sites

Comparing the frequencies of feeding types between both study sites across all habitats, the number of species with different feeding types did not differ significantly between sites (Fisher's Exact test: p = 0.704; Figure 4A), while encounters of different feeding types differed significantly ($chi^2 = 111.38$, N = 8, df = 3, $p < 0.001$). In the LR, there were relatively more encounters with soil feeders while the proportion of wood feeders, and partly fungus growers were reduced (Figure 4B).

The most common termite species in the LR belonged to the fungus growers (*Ancistrotermes cavithorax, Microtermes* sp.2, *Pseudacanthotermes militaris*) and the soil feeders (*Adaiphrotermes* sp., *Aderitotermes* sp., *Basidentitermes* sp.) (Table S1). In the MNP, the most common termite species were wood feeders (*Microcerotermes* sp.1), grass feeders (*Trinervitermes geminatus*) and several fungus growers (*Microtermes* sp.1, *Microtermes* sp.2, *Odontotermes* sp.3, *Pseudocanthotermes spiniger*, *Ancistrotermes guineensis* and *Ancistrotermes cavithorax*) (Table S1). *Microtermes* sp.2 and *Ancistrotermes cavithorax* were found across all plots in both sites. Soil feeders were not common in the MNP (Table S1).

Discussion

The objective of this study was to compare two protected areas with a diverse range of habitats that differ in management effectiveness so that one, the LR, is very well protected, while the other, the MNP, is strongly impacted by human disturbance (see also Supplementary Material Figure S1). We assessed effects on termite communities as they are fundamental components of these habitats that provide essential ecosystem services. Our results showed that overall the less-well protected MNP had significantly fewer termite species within a standardized study unit (i.e., a transect) than the well protected LR (Figure 2). This applied to all habitats, except the SS (Figure 3). Termite abundance, measured as termite encounters per study unit/transect, was also often significantly lower in the MNP than in the LR (Figure 3). Additionally, the abundance of soil feeders, indicators of ecosystem health in woody habitats, was significantly lower in the MNP than the LR. All these results support the notion that the MNP is a less-well protected area and that this lack of efficient protection has ecosystem consequences.

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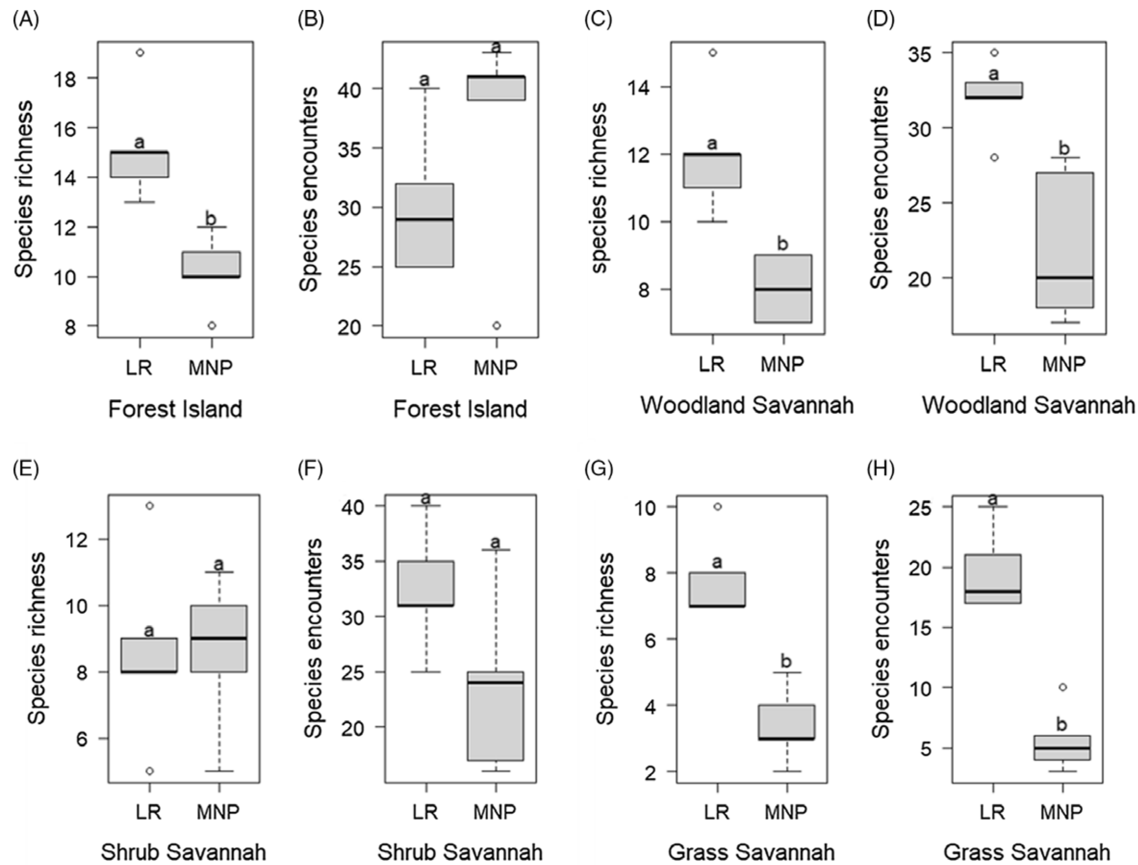

Figure 3. Comparison of the termite species richness and termite encounters between both study sites, the LR (Lamto Reserve) and the MNP (Marahoué National Park) separated by habitat types. (A) Richness in forest islands, (B) encounters in forest islands, (C) richness in woodland savannah, (D) encounters in woodland savannah, (E) richness in SS, (F) encounters in shrub savannah, (G) richness between grass savannah, and (H) encounters in grass savannah. Shown are boxplots with the quartiles, median (bold line) and whiskers representing the minimum value and the maximum value. Different letters on or under the boxplots within graphs indicate significant differences at $P < 0.05$ level (Wilcoxon test, $N = 10$), are outliers, defined as data that fall not within the whiskers.

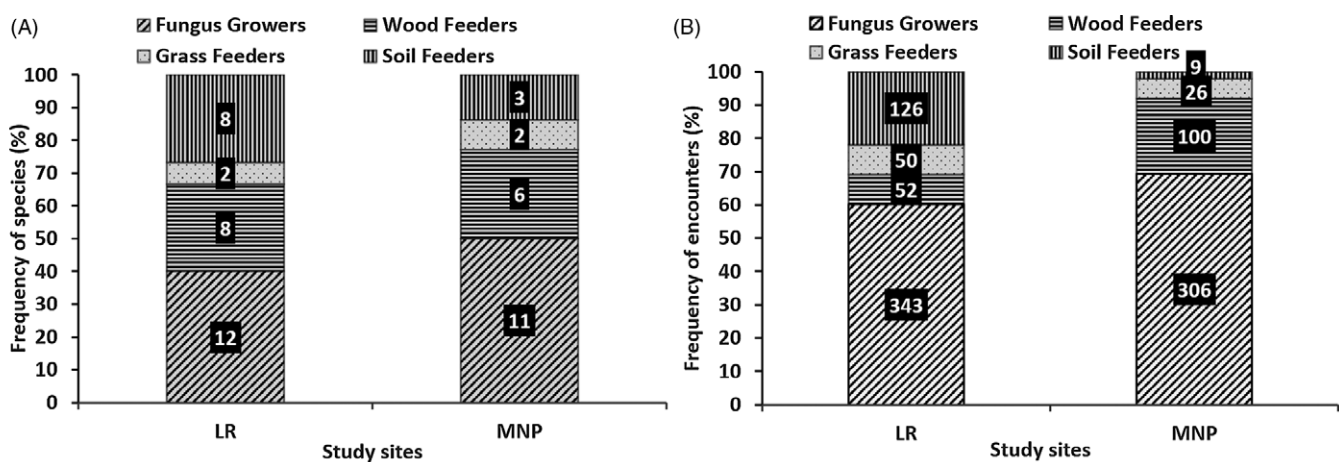

Figure 4. Comparison of feeding type frequencies at (A) species level and (B) encounter level between both study sites, the LR (Lamto Reserve) and the MNP (Marahoué National Park). Shown are the numbers of species/encounters of different feeding types (numbers inside bar) and their relative frequencies (y-axis). Fungus growers: black diagonal stripes in bold; wood feeders: black horizontal stripes in bold; grass feeders: black dotted, and soil feeders: black vertical stripes in bold.

We obtained high values of sampling coverage (70–100%). This can be explained by our increased sampling effort, as we investigated five transects per plot rather than one, suggested by Jones & Eggleton (2000). Similarly, Dosso *et al.* (2010) and Koné *et al.* (2018) achieved high sampling coverage with five transects. This extensive sampling effort ensured high data quality.

A potential weakness of our study concerns the lack of longitudinal data. Assessing the same area repeatedly can provide more

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direct estimates of changes of diversity over time and its causes, especially when combined with measures of the effectiveness of park management than a cross-sectional snapshot study that we did. Unfortunately, a longitudinal study was impossible as our study was the first assessment of termite diversity in the MNP and very generally, one of very few systematic diversity studies in the MNP. Thus, we had to rely on a cross-sectional design using a better-protected area from the same biome and with similar environmental conditions as a reference. The LR is the best available reference and if anything, we would expect as a null hypothesis lower diversity in the LR than the MNP because of the smaller size and the lower legal status in the former (Table 1). However, repeated monitoring over longer time periods is advisable to follow the development of the MNP.

Termite communities, anthropogenic disturbance and bioindicators of ecosystem health

Termites have been proposed for use as bioindicators of habitat quality in monitoring programs of tropical ecosystems due to their sensibility to anthropogenic disturbance (Pribadi *et al.* 2011). In tropical forests, soil feeding termites have been identified as the most sensitive group to anthropogenic disturbance (e.g. Davies 2002, Eggleton *et al.* 2002). In African savannahs, strong anthropogenic disturbance is considered as an environmental filter that selects for a subset of termite species, which are generally well-known pests of crops (Schyra & Korb 2019; Schyra *et al.* 2019a). In addition, even slight disturbance seems to affect the processes of termite community assembly in African savannahs (Hausberger & Korb 2015, 2016).

Also in the current study, we found a decline in the encounters of soil feeders in the less-well protected MNP compared to the LR, while the species richness of different feeding types was not significantly affected. Fungus-growing termites seemed to be equally abundant in both sites, where they made up the highest proportion of all feeding types (≥40 % of the species, >60 % of all encounters) (Figure 4). This is similar to previous studies in savannahs (Hausberger *et al.* 2011, Hausberger & Korb 2015, 2016, Muvengwi *et al.* 2017, Schyra *et al.* 2019a, 2019b). A reason for the ecological success of fungus-growing termites seems to lie in their ectosymbiotic mutualistic relationship with fungi of the genus *Termitomyces* (Wood & Johnson 1978, Nobré *et al.* 2011, Korb 2022). This symbiosis seems to give fungus-growing termites an advantage especially in drier ecosystems, although the symbiotic interaction can also come with costs limiting the distribution of the termites (Korb *et al.* 2020, Korb 2022). At the species level, however, some fungus growers seemed to be strongly affected by disturbance (Table S1). *Macrotermes bellicosus* and *Macrotermes subhyalinus* as well as *Pseudacanthotermes militaris*, *Ancistrotermes crucifer* and *Odontotermes* sp.1 only occurred in the LR. Thus, these species (except for *Odontotermes* sp.1, which is ambiguous to identify) could serve as good bioindicators of ecosystem health, especially as they are among the few termite species, which can be easily and unambiguously identified (Korb *et al.* 2019). Comparisons with other regions are difficult because of problems in species identification, especially for fungus-growing termites that lack gut characteristics, which are useful to determine soil-feeding termites to species level (Korb *et al.* 2019). In line with our results for Côte d'Ivoire, *Macrotermes bellicosus* is also extremely rare in disturbed areas in northern Benin and northern Togo, though this is only partly apparent from the published studies, which specifically aimed to include plots with this important mound-building species (Hausberger & Korb 2015, 2016; Schyra & Korb 2019, Schyra *et al.* 2019a, 2019b). *Pseudacanthotermes militaris* and *Ancistrotermes crucifer* have not been recorded in the northern regions, while *Macrotermes subhyalinus* becomes more dominant there and is also found in disturbed areas (Hausberger & Korb 2015, 2016; Schyra & Korb 2019, Schyra *et al.* 2019a, 2019b). This implies a need for region-specific bioindicators, although *Macrotermes bellicosus* might be a suitable indicator species of ecosystem health across West-African savannah biomes. This is good news as this mound-building species is easy to identify. The rarity/absence of *Macrotermes bellicosus* in anthropogenically disturbed areas seems less related to a strong sensitivity of this species to disturbance as it can be commonly found in cities or villages when protected. Its absence seems to be rather due to the utilisation of *Macrotermes bellicosus* and its mounds by humans as chicken feed, for construction, for traditional medicine and/or for fetishes (Van Huis 2017).

Potential consequences of disturbance for ecosystem services provided by termites

The occurrence of different termite species in an area is partly dependent on vegetation and on the availability of the food they feed upon. Accordingly, grass-feeding specialists like *Trinervitermes* are most abundant in GSs but absent in forests (Schyra *et al.* 2019a). In line, wood-feeding termites were relatively more abundant in the MNP where more wood was available due to logging than in the LR. However, many savannah termites, like the fungus-growing species, are non-specialists that feed on a broad variety of dead plant material (da Costa *et al.* 2019 and references therein). They seem to replace each other depending on anthropogenic disturbance with some species being more resilient than others (Table S1). Thus, we do not expect a huge impact of anthropogenic disturbance on ecosystem services like decomposition of dead plant material or water retention capacity of soils (all these termites' tunnel within soils) if their abundance does not drop too drastically with strong disturbance. The latter is, however, often the case in modern agricultural fields (Schyra & Korb 2019) (and in some habitats also in the MNP; Figure 3) with negative consequences for soil quality and problems of erosion (Vanacker *et al.* 2014). Yet traditional methods can overcome these problems, like the Zai system, a tradional West-African technique, in which termites are purposefully lured into degraded soil by deposition of dead plant material to improve its quality (e.g., Fatondji *et al.* 2009). Severe negative consequences, even with lower levels of disturbance as in the MNP, might however occur with regard to other ecosystem services that termites provide. Soil mineralization processes might be retarded due to the decline of soil feeders. Furthermore, the lack of mound-building *Macrotermes bellicosus* colonies is expected to have severe consequences. Such mounds create habitat heterogeneity and provide special microhabitats, which are essential for the occurrence and the long-term stable co-existence of a broad range of species, ranging from plants and other arthropods to amphibian, reptiles and mammals (e.g. Pringle *et al.* 2010). Thus, strong emphasis should be placed in protecting the MNP to guarantee its long-term ecosystem services and biodiversity.

Conclusion

Our study illustrates the impact that less effective park management can have on a fundamental group of tropical organisms, the termites. It identifies suitable bioindicator species of ecosystem health for West-African savannahs and outlines the consequences of anthropogenic disturbance for ecosystem services provided by termites. It stresses the importance of effective management of protected areas to maintain their long-term biological diversity.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467422000207

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Conflict of interest. None.

Ethical standards. None.

References

Alves WF, Mota A, Lima DR, Bellezoni R and Vasconcellos A (2010) Termites as bioindicators of habitat quality in the Caatinga, Brazil: is there agreement between structural habitat variables and the sampled assemblages? *Neotropical Entomology* **40**, 39–46.

Ashton LA, Griffiths HM, Parr CL, Evans TA, Didham RK, Hasan F, Teh YA, Tin HS, Vairappan CS and Eggleton P (2019) Termites mitigate the effects of drought in tropical rainforest. *Science* **363**, 174–177.

Attignon SE, Lachat T, Sinsin B, Nagel P and Peveling R (2005) Termite assemblages in West-African semi-deciduous forest and teak plantation. *Agriculture Ecosystems & Environment* **110**, 318–326.

Bandeira AG, Vasconcellos A, Silva M and Constantino R (2003) Effects of habitat disturbance on the termite fauna in a highland humid forest in the Caatinga Domain, Brazil. *Sociobiology* **42**, 117–127.

Benjamini Y and Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B Methodology* **57**, 289–300.

Bouillon A and Mathot G (1965) Quel est ce termite Africain? [What is this African termite?] Leopoldville: Université de Leopoldville, pp. 115.

Bourlière F, Minner E and Vuattoux R (1974) Les grands mammifères de la région de Lamto, Cote d'Ivoire [The large mammals of the Lamto region, Cote d'Ivoire]. *Mammalia* **38**, 383–433.

Cao Y, Williams DD and Larsen PD (2002) Comparison of ecological communities: the problem of sample representativeness. Ecological Monographs 72, 313–318.

Chapin FS, Matson PA and Mooney H (2002) *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag.

Collins NM (1981) The role termites in the decomposition of wood and leaf litter in the southern Guinea Savannah of Nigeria. *Oecologia* **51**, 389–399.

da Costa RR, Hu H, Li H and Poulsen M (2019) Symbiotic plant biomass decomposition in fungus-growing termites. *Insects* **10**, 87.

Davies RG (2002) Feeding group responses of Neotropical termite assemblage to rain forest fragmentation. *Oecologia* **133**, 233–242.

Davies RG, Hernández LM, Eggleton P, Didham R, Fagan L and Winchester N (2003) Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. *Journal of Tropical Ecology* **19**, 509–524.

Dosso K, Deligne J, Yéo K, Konaté S and Linsenmair KE (2013) Changes in the termite assemblage across a sequence of land-use systems in the rural area around Lamto Reserve in central Cote d'Ivoire. *Journal of Insect Conservation* **17**, 1047–1057.

Dosso K, Konaté S, Aïdara D and Linsenmair KE (2010) Termite diversity and abundance across fire-induced habitat variability in a tropical moist savannah (Lamto, central Côte d'Ivoire). Journal of Tropical Ecology 26, 323–334.

Dosso K, Yéo K, Konaté S and Linsenmair KE (2012) Importance of protected areas for biodiversity conservation in central Côte d'Ivoire: comparison of termite assemblages between two neighbouring areas under differing levels of disturbance. Journal of Insect Science 12, 131.

Eggleton P, Bignell DE, Hauser S, Dibog L, Norgrove L and Madong B (2002) termite diversity is a cross ananthropogenic disturbance gradient in humid forest zone of West Africa. *Agriculture, Ecosystems & Environment* **90**, 189–202.

Eggleton P, Bignell DE, Sands WA, Mawdsley NS, Lawton JH, Wood TG and Bignell NC (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. *Philosophical Transactions of the Royal Society B* **351**, 51–68.

Eggleton P, Bignell DE, Sands WA, Waite B, Wood TG and Lawton JH (1995) The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Journal of Tropical Ecology* **11**, 85–98.

Evans TA, Dawes TZ, Ward PR and Lo N (2011) Ants and termites increase crop yield in a dry climate. *Nature Communications* **2**, 262.

Fatondji D, Martius C, Zougmore R, Vlek PLG, Bielders CL and Koala S (2009) Decomposition of organic amendment and nutrient release under the Zai technique in the Sahel. *Nutrient Cycling in Agroecosystems* **85**, 225–239.

Gnahoré E, Missa K, Koné M, Gueulou N and Bakayoko A (2018) Dynamique et structure de la flore de la Savane Protégée des Feux dans la Réserve Scientifique de Lamto (Centre de la Côte d'Ivoire) [Dynamic and structure of the flora in the protected savannah against bush fires in the Scientific Reserve of Lamto (Central Côte d'Ivoire)]. *European Scientific Journal* **14**, 1857–7881.

Hausberger B, Kimpel D, Van NA and Korb J (2011) Uncovering cryptic species diversity of a community in a West African Savannah. *Molecular Phylogenetics and Evolution* **61**, 964–969.

Hausberger B and Korb J (2015) A phylogenetic community approach for studying termite communities in a West African savannah. *Biology Letters* **11**, 20150625.

Hausberger B and Korb J (2016) The impact of anthropogenic disturbance on assembly patterns of termite communities. *Biotropica* **48**, 356–364.

Holt J A and Lepage M (2000) *Termites and soil properties*. In Abe T, Bignell DE and Higashi M (eds), *Termites: Evolution, Sociality, Symbiosis, Ecology*. Dordrecht: Kluwer Academic Publishers, pp. 389–407.

Jones DT and Eggleton P (2000) Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology* **37**, 191–203.

Jones DT, Susilo FX, Bignell DE, Hardiwinoto S, Gillison AN and Eggleton P (2003) termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal of Applied Ecology* **40**, 380–391.

Josens G (1972) Etudes biologiques et écologiques des termites (Isoptera) de la savane de Lamto [Biological and ecological studies of the termites (Isoptera) in Lamto savannah]. Thèse de doctorat de l'Université Libre de Bruxelles, pp. 262.

Konaté S (1998) Structure dynamique et rôle des buttes termitiques dans le fonctionnement d'une savane préforestière (Lamto, Côte d'Ivoire): le termite champignonniste Odontotermes comme ingénieur de l'écosystème [Dynamic structure and role of the termite mounds in the functioning of a pre-forest savannah (Lamto, Côte d'Ivoire): Odontotermes fungus-growing termite as an ecosystem engineer]. Thèse de doctorat de l'Université Paris 6, pp. 252.

Konaté S and Touao MT (2010) La réserve de Lamto [The Lamto reserve]. In Konaté S and Kampmann D (eds), Biodiversity Atlas of West Africa, Volume iii: Côte d'Ivoire. Pliezhausen, Germany: Abidjan & Frankfurt/main, Druckerei Grammlich, pp. 296–302.

Koné NA, Silué KS, Konaté S and Linsenmair KE (2018) Determinants of termite assemblages' characteristics within natural habitats of a Sudano-Guinean Savanna (Comoé National Park, Côte d'Ivoire). *Insects* **9**, 189.

Korb J (2022) Fungus-growing termites: an eco-evolutionary perspective. In Schultz TR, Peregrine P and Gawne R (eds), The Convergent Evolution of Agriculture in Humans and Insects. Harvard: MIT Press, pp. 89–104.

Korb J, Kasseney BD, Cakpo YT, Casalla Daza RH, Gbenyedji JN, Ilboudo ME, Josens G, Koné NA, Meusemann K, Ndiaye AB, Okweche SI, Poulsen M, Roisin Y and Sankara F (2019) Termite taxonomy, challenges and prospects: West Africa, a case example. *Insects* **10**, 32.

Korb J, Silué SK and Koné NA (2020) Can differences in symbiont transmission mode explain the abundance and distribution of fungus-growing termites in West Africa? *Frontiers in Ecology and Evolution* **8**, 600318.

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW and Dhillion S (1997) Soil function in changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology* **33**, 159–193.

Muvengwi J, Mbibal M, Ndagurwa GT, Nyamadzawo G and Nhokovedzo P (2017) Termite diversity along a land use intensification gradient in a semi-arid savanna. *Journal of Insect Conservation* **21**, 801–812.

N'da D H, Adou YCY, N'guéssan KE, Koné M and Sagné YC (2008) Analyse de la diversité floristique du parc national de la Marahoué, Centre-Ouest de la Côte d'Ivoire [Analysis of the floristic diversity in the Marahoué National Park, Central-Western Côte d'Ivoire]. *Afrique SCIENCE* **04**, 552–579.

Nash MH and Whitford WG (1995) Subterranean termites: regulators of soil organic matter in the Chihuahuan Desert. *Biology and Fertility of Soils* **19**, 15–18.

Nobré TC, Lefèvre R, and Aanen DK (2011) *Comparative biology of fungus cultivation in termites and ants*. In Bignell DE, Roisin Y and Lo N (eds), *Biology of Termites: A Modern Synthesis*. Dordrecht: Springer, pp. 193–210.

Pribadi T, Raffiudin R and Harahap S (2011) Termites community as environmental bioindicators in highlands: a case study in eastern slopes of Mount Slamet, Central Java. *Biodiversitas* **12**, 235–240.

Pringle RM, Doak DF, Brody AK, Jocque R, Palmer TM (2010) Spatial pattern enhances ecosystem functioning in an African Savanna. *PLoS Biol* **8**, e1000377.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. Vienna, Australia: R Foundation for Statistical Computing.

Sands WA (1998) The Identification of Worker Castes of Termite Genera from Soils of Africa and the Middle East. Wallingford, UK: CAB International UK, pp. 512.

Schulenberg TS, Short CA and Steohenson PJ (1999) A biological assessment of Parc National de la Marahoué, Cote d'Ivoire. RAP Working Papers 13. Washington: Conservation International, pp. 1–109.

Schyra J, Gbenyedji JN and Korb J (2019a) A comparison of termite assemblages from West African savannah and forest ecosystems using morphological and molecular markers. *PLoS ONE* **14**, e0216986.

Schyra J and Korb J (2019) Termite communities along a disturbance gradient in a West African savanna. *Insects* **14**, 10–17.

Schyra J, Scheu S and Korb J (2019b) Cryptic niche differentiation in West African savannah termites as indicated by stable isotopes. *Ecological Entomology* **44**, 190–196.

Van Huis A (2017) Cultural significance of termites in sub-Saharan Africa. *Journal of Ethnobiology Ethnomedicine* **13**, 8.

Vanacker V, Bellin N, Molina A and Kubik PW (2014) Erosion regulation as a function of human disturbances to vegetation cover: a conceptual model. *Landscape Ecology* **29**, 293–309.

Vasconcellos A, Adelmar GB, Flavia MS M, Virgınia FP, Maria Avany B, and Reginaldo C (2009) Termite assemblages in three habitats under different disturbance regimes in the semi-arid Caatinga of NE Brazil. *Journal of Arid Environments* **74**, 298–302.

Webb GC (1961) *Keys of the Genera of the African Termites*. Ibadan: University Press, Ibadan, pp. 35.

Whitford WG (1991) Subterranean termites and long-term productivity of desert rangelands. *Sociobiology* **19**, 235–243.

Wood TG and Sands WA (1978) *The role of termites in ecosystems*. In Brian MV (ed), *Production Ecology of Ants and Termites*. Cambridge: Cambridge University Press, pp. 245–292.