

RESEARCH ARTICLE

Utilization of IGN historical aerial photographs and Google earth for measuring changes in land use and evolution of termite lenticular mound abundance in paddy fields in Cambodia

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Abstract

This study was conducted to investigate termite mounds' dynamics in paddy fields in Cambodia. Historical aerial images collected in the 50s by the French Institut Géographique National (IGN) and recent Google Earth (GE) were analysed to study land use changes and mound distribution in 30 plots. A significant decrease in the surface covered by scrublands and forests was measured (from 37% in 1953 to less than 2% in 2021). We observed that most mounds seen in the field in 2021 could also be seen in IGN and GE images (88.6%), indicating that mounds have a long lifespan but also that they can be built in less than 70 years. Mound density was neither influenced by the topography nor by the restructuring of the paddy field boundaries during the Khmer Rouge regime. However, areas that were more recently converted into paddy fields had more mounds compared to areas that were already paddy fields in 1953 (2.92 vs. 1.53 mounds ha⁻¹, respectively). Therefore, deforestation and other environmental changes have turned mounds into remnants of the forests that had almost completely disappeared. This highlights the importance of protecting these specific environments in a changing world facing a major crisis of biodiversity loss.

KEYWORDS

Cambodia, Chrey Bak observatory, deforestation, *Macrotermes gilvus*, paddy fields, spatial distribution

1 | INTRODUCTION

Termite mounds are among the most impressive soil constructions produced by living organisms. These biogenic structures can have different shapes and sizes. If

most of the species only build small epigeous nests or subterranean chambers, some constitute conspicuous topographical features of the landscapes, such as the termitaria produced by *Macrotermes* spp. in Africa and those of *Amitermes laurensis* in Australia (e.g. Wood

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et al., 1982; Coventry et al., 1988; Spain & McIvor, 1988). Termite mounds also include lenticular mounds or hills (also called hummocks) that can be covered by vegetation and even host-specific plant communities (e.g. Cramer & Midgley, 2015; Traoré et al., 2008), which in turn create specific environmental conditions for a variety of herbivores (Dangerfield et al., 1998; Davies et al., 2016; Muvengwi et al., 2014; Noble et al., 1989) but also soil biodiversity (Choosai et al., 2009). The origin and dynamics of these mounds are challenging to estimate regarding their potential long-life spans (i.e. until several centuries to millennia for some mounds found in Africa and Brazil, Erens et al., 2015; Cramer et al., 2017; De Souza et al., 2020). The recolonization of termite nests by other species, resulting in the formation of lenticular mounds, has been documented in various environments. For example, the recolonization of unoccupied *Macrotermes* nests by *Odontotermes aff. pauperans* was observed in West Africa (Josens et al., 2016). Similarly, in India, the recolonization of unoccupied *Odontotermes obesus* nests by other *Odontotermes* spp. was reported (Jouquet et al., 2017). Information on termite mound abundance and distribution also reveals very variable spatial patterns. The abundance of epigeal mounds or termite nests can be random (e.g. the termite nests of *Macrotermes viator* in South Africa or the termite nests of *Macrotermes bellicosus* in Nigeria, Collins (1981), or *Amitermes laurensis* in Australia, Holt & Greenslade, 1979), regular (e.g. “murundus” mounds in Brazil, De Souza & Delabie, 2018; mounds of harvester termites in Australia, Lee & Wood, 1971; or the fairy-circles in South Africa and Namibia, Getzin et al., 2015; Juergens, 2015) or tend to aggregate in specific areas such as with the nests of *Trinervitermes trinervoides* in South Africa (Nel & Malan, 1974) or the nests of *Armitermes euamignathus* and *Orthognathotermes gibberorum* in Cerrado, Brazil (Redford, 1984). These spatial patterns are usually driven by competitive interactions between termite colonies, soil properties, topography and hydrology (Davies et al., 2014; Freymann et al., 2010; Levick et al., 2010; Sarcinelli et al., 2009), and the distribution and type of vegetation (Bargués Tobella et al., 2014; Benzie, 1986), as well as the scale of observation (specific site vs. watershed or landscape) (Davies et al., 2014). However, knowledge on termite mound abundance, distribution and dynamics almost exclusively came from ‘natural’ or weakly anthropised ecosystems, and there is currently no information on termite mounds in cultivated rice areas.

In the Lower Mekong Basin, paddy fields can be seen as mosaics with the presence of mounds located in cultivated plots or on embankments that separate plots (Choosai et al., 2009; Miyagawa et al., 2011). The species *Macrotermes gilvus* is considered by farmers to be at the

origin of these mounds (Muon, Lai, et al., 2023), which are, after that, colonized by other invertebrates, including other termite species, reptiles, mammals, and plants. In Cambodia, most farmers consider that the dynamic of termite mounds is rapid and that less than 40 years is needed to produce these mounds (Muon, Lai, et al., 2023). In addition to contributing to preserving biodiversity in cultivated rice areas (Choosai et al., 2009), these mounds provide several ecosystem services to the population. For instance, farmers used the specific soil properties of termite mounds to improve the fertility of their land, and biodiversity associated with termite mounds can provide access to edible plants and animals and medicinal plants (Miyagawa et al., 2011; Muon, Lai, et al., 2023).

This study aimed to describe termite mound distribution in paddy fields in Cambodia and to discuss their age and dynamics using historical aerial images collected in the 50s by the French Institut Geographique National (IGN), recent very high-resolution images from Google Earth (GE), and ground truthing. Based on local knowledge, we assumed (1) that most of the termite mounds found in paddy fields were recent and could not be found in the photographs taken in the 50s by IGN and (2) that the abundance and distribution of termite lenticular mounds in paddy fields could be explained by land use changes that occurred between the 50s and nowadays, such as the conversion of scrublands into paddy fields and the restructuring of the paddy field boundaries during the Khmer Rouge regime.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site was in the Chrey Bak long-term observatory, northwest of Phnom Penh capital, Cambodia. This observatory catchment is one of the watersheds of the Tonle Sap Lake. It is covered by two districts, namely Tuek Phos and Rolea Biér districts, with a surface area of approximately 700 km². The tropical monsoon influences this region. It has two distinct seasons: the dry season from November to April and the rainy season from May to October, with annual rainfall varying between 1400 and 2000 mm (MOWRAM, 2014). Soils are mainly Gleysols with varying sand contents (Muon, Ket, et al., 2023). The lower part of the catchment is in the Tonle Sap floodplain, where agriculture has existed for a long time. Forests cover 34% of the catchment area, while scrublands and grasslands represent 27% and 5% of the surface area, respectively. The remaining corresponds to agricultural areas mostly used to grow rice (32%). Most of Cambodia's rice is rain-fed and is usually planted at the end of May or early June when the first monsoon rains begin to fall (Chann et al., 2011). The

topography of the catchment is variable and high in the mountainous area in the southwest region. Conversely, it is very gentle or almost flat in the cultivated areas, dominated by rain-fed paddy fields (Chann et al., 2011).

2.2 | Lenticular mounds in paddy fields

Agroecosystems often have mosaic aspects in the Lower Mekong Basin due to groves often elevated on lenticular termite mounds (LM). Although their dynamics are unknown, their origin is attributed to the activity of *Macrotermes gilvus* (Muon, Lai, et al., 2023). They are occupied by many other soil invertebrates (Choosai et al., 2009), reptiles and mammals (e.g. lizards, snakes, rats), and they are covered by grasses, shrubs, and trees.

2.3 | Field measurements and remote sensing analyses using GE

Thirty sampling plots (paddy fields, 300 m × 300 m) were selected along the toposequence from the lower to the upper limits of the catchment dedicated to current rice cultivation (Figure 1) (See Muon, Lai, et al., 2023 for a description of the sampling procedure). The catchment was divided into four areas based on their height and distance to the Tonle Sap River, namely the lowland (LL, average altitude ~17.0 m above sea level, $n=10$ plots), midlands (ML₁, 31.4 m a.s.l., $n=7$; and ML₂, 57.0 m a.s.l., $n=7$), and upland (UL, 75.7 m a.s.l., $n=4$) (see Figure 1). For each plot, we mapped the center of LM with a GPS tracker (Garmin GPSMAP 64s) during the dry season from December 2020 to February 2021. The volume of soil used by termites to produce LM was assessed by measuring the height and diameter of each LM in the field and comparing them as domes and using the following formula: $V (m^3) = (\pi \times h \times (3R^2 + h^2)) / 6$, where R is the average radius of LM at its base and h its height (Jouquet et al., 2017). Densities of LM on the plot level were calculated using Spatial Join tools in ArcMap 10.7. LM were always covered by either woody vegetation or shrubs. The ability to recognize LM from GE images via the presence of this specific vegetation was tested by comparing the relationship between the position of LM measured in the field by ground validation with those measured from GE images.

2.4 | Image analyses from the IGN library

Sixty-nine digitized historical aerial photographs from the French IGN were used to determine if the surveyed locations of LM were already observed in the 50s (i.e. they

were older than 40 years). Despite the numerous aerial archaeology campaigns undertaken over Cambodia between the 1930s and 1990s, only some resulting images have survived (Evans & Moylan, 2013). The French IGN photo library in Villefranche-sur-Cher still holds around 11,000 original glass plate negatives acquired by the French IGN around Cambodia's independence from France in 1953–1954. The lower and middle parts of the Chrey Bak catchment were partly covered by two missions in 1953. The first mission, “Indochine 074”, was flown by IGN from the 12th to the 25th of February 1953. The second mission, “Indochine 094”, acquired the images from the 10th to the 28th of February 1953. The metadata from IGN indicates only the focal length of the camera (125 mm), the flying height above sea level (5100–5700 m), and the frame size of the camera (120 mm × 170 mm). According to this information, the black-and-white panchromatic photos present a scale of ca. 1:40000. There was neither a calibration certificate nor any information about the used camera.

The method for deriving orthoimages was based on the workflow implemented in the photogrammetric software package Agisoft Metashape Professional® ver. 1.8.3 (www.agisoft.com). This software uses a Structure-from-Motion (SfM) approach (Hartley & Zisserman, 2003) for image orientation, followed by dense image matching operated in a multi-view stereo fashion (Forlani et al., 2015). The software is generally used for non-metric digital cameras, which do not feature a specific frame on borders. Without a calibration certificate or any information about the camera, the software computes the unknown calibration parameters based on tie points extracted during SfM (Barazzetti et al., 2011). The image dimensions in pixels of the scanned historical aerial photographs varied from 5043 to 5162 in X and 3763 to 3862 in Y. To correct the inner orientation of the digitally scanned aerial images, we placed ground control points (GCPs) on the four fiducial marks of the photos to resample and rotate the image coordinates to a common XY coordinate system centered on the principal point of the image using a Helmert transformation and the nearest neighbour resampling. Moreover, a shapefile was produced to crop the images and mask the camera frame's information and the fiducial marks on the images. Correcting these misalignments ensured that all the images contained the same pixel size (4902 × 3416) and grid alignment, without which automatic tie point identification would be difficult.

Some GCPs were also measured to establish the ground coordinate system and mitigate the instability in successive bundle block adjustment (BBA) (Verhoeven et al., 2015). The real problem in the case of old archive photos is how to derive the reference ground coordinates of GCPs since the objects in the image may have dramatically changed from when the photo was captured to the present time. A typical solution to derive GCPs is to obtain their horizontal

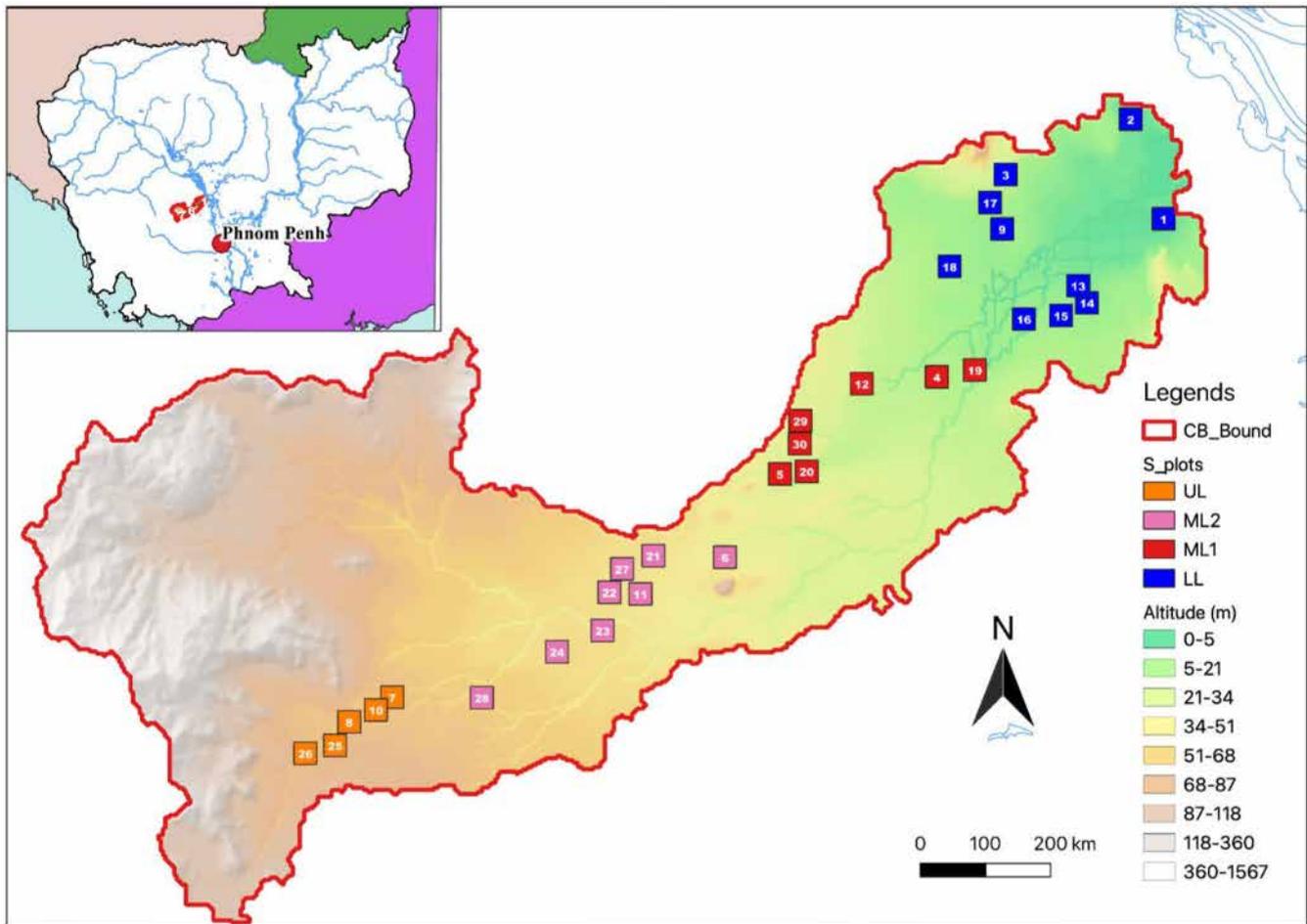


FIGURE 1 Locations of 30 plots were used to measure lenticular mound distribution. The catchment is divided into a lowland (LL, in blue), a midland 1 (ML₁, in red), midland 2 (ML₂, in light purple), and an upland (UL, in orange).

position from recent orthoimages and the elevation from a Digital Terrain Model (DTM). For our region, GE was used to obtain the horizontal position of GCPs, with approximate georeferencing of around 168 landmarks.

Application of the methodology successfully processed all images, producing an orthomosaic of 69 orthorectified historical aerial photographs with a ground resolution of 1.45 meters. The horizontal accuracy was tested using GCPs from GE images. The horizontal precision of the orthomosaic was approximately 5 m. As with GE images, the ability to recognize LM from IGN images was tested by comparing the relationship between the position of LM measured in the field by ground truthing with those measured from IGN images.

2.5 | Land use changes and dynamics of lenticular mounds

The areas occupied by paddy fields inside each plot were manually delineated at the fixed scale between 1:600 to

1:800 on both IGN and GE images using digitizing tools in QGIS (Figure 2; Appendix S1). Since the historical aerial photographs from IGN cover only the lower and middle parts of the catchment, seven plots in the upper part of the catchment not covered by IGN were excluded from this comparison, giving a total of 23 plots (see Table 1 for a description of the selected plots). Three types of land uses were identified from the IGN images: paddy fields (RIC), scrubland (SCR), and a mix between paddy fields and scrubland (RIC/SCR). Because the Khmer Rouge regime led to an important restructuring of the paddy fields boundaries between 1975 and 1979 in some plots, the 23 plots were also classified into two groups according to whether it was possible to see differences in the limits of the paddy fields from the comparison between the IGN images and those from GE. The areas covered by the crown of trees and by cultivated areas (paddy fields and other arable lands) were digitized from IGN and GE images (i) to calculate the evolution of the surface covered by woody vegetation in and around paddy fields between 1953 and 2021, and (ii) to determine if locations of LM observed in 2021 were already covered

FIGURE 2 Example of images obtained from the French Institut Geographique National (IGN) taken in 1953 and from Google Earth (GE) in 2021 from the plot n°20 in Chrey Bak catchment. Landscapes were differentiated into paddy fields (p), tree covers (t), and other uncultivated areas (u).

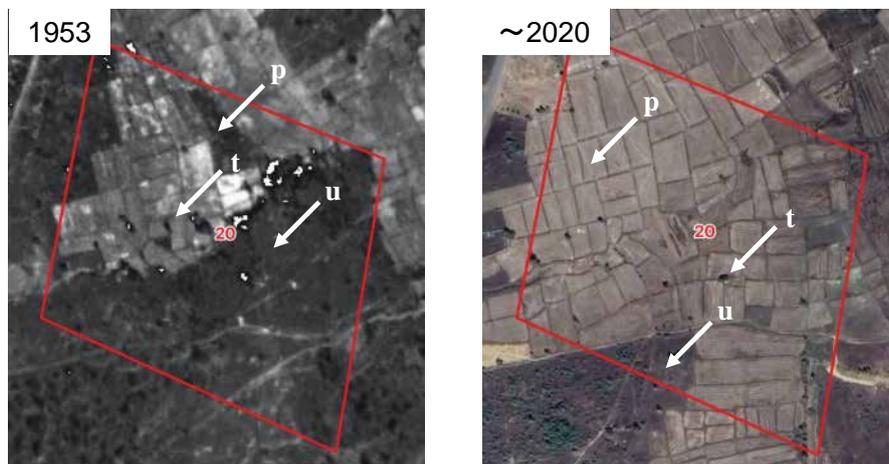


TABLE 1 Size of sample plots, mean altitude and image acquisition dates either from Google Earth (GE) or the French Institut Geographique National (IGN) in the lowland (LL), midland 1 (ML₁), midland 2 (ML₂) and upland (UL).

ID plots	Area (ha)	Locations	Mean altitude (m)	IGN	GE
1	8.98	LL	5.89	1953	2021
2	11.18	LL	9.36	1953	2021
3	5.97	LL	27.40	1953	2021
4	10.45	ML ₁	23.50	1953	2021
5	8.87	ML ₁	38.33	1953	2021
6	14.58	ML ₂	48.69	1953	2021
7	12.00	UL	78.67	Not covered	2019
8	10.54	UL	78.90	Not covered	2019
9	10.74	LL	19.22	1953	2021
10	9.99	UL	79.00	Not covered	2019
11	12.60	ML ₂	55.00	1953	2019
12	10.61	ML ₁	29.00	1953	2021
13	10.04	LL	14.11	1953	2021
14	9.34	LL	15.11	1953	2021
15	9.85	LL	18.70	1953	2021
16	9.62	LL	18.00	1953	2021
17	13.25	LL	22.17	1953	2021
18	10.27	LL	20.56	1953	2021
19	8.97	ML ₁	18.11	1953	2021
20	9.11	ML ₁	36.89	1953	2021
21	8.99	ML ₂	58.11	1953	2019
22	9.15	ML ₂	57.00	1953	2019
23	5.57	ML ₂	60.75	1953	2019
24	8.06	ML ₂	62.00	Not covered	2019
25	6.68	UL	73.00	Not covered	2019
26	8.80	UL	74.33	Not covered	2019
27	11.02	ML ₂	57.50	1953	2019
28	6.89	ML ₂	70.14	Not covered	2019
29	6.45	ML ₁	33.00	1953	2019
30	2.53	ML ₁	41.00	1953	2019

by woody vegetation in the 50s. This last information was used to differentiate mounds older than 70 years (because they were already associated with trees on the IGN images) and mounds younger than 70 years (because they were not observed on the IGN images).

2.6 | Statistical analyses

One-way analysis of variance (ANOVA) and least significant difference (LSD) tests were performed to assess differences in land use changes between 1953 and 2021 and LM density between the catchment's upper, middle, and lower parts. Before the ANOVA, data were log-transformed (when required) to achieve homogeneity of variance and normality, which were confirmed using Levene and Shapiro–Wilk tests. Kruskal–Wallis Chi² and Wilcoxon–Mann–Witney U test post-hoc planned pairwise comparisons were performed with a false discovery rate correction when parametric analysis of variance was impossible to use. A T-test was used to compare the volume of LM (>70 years old vs. <70 years old). Linear regressions were also used to assess relationships between the density of LM and the elevation of the plots along the toposequence. The spatial distribution of LM was estimated using Spatial Statistic Tools in ArcMap 10.7 and the Average Nearest Neighbour function (Pimpler, 2017) with 99% confidence levels. Only 28 plots were used for this analysis since the other two plots were excluded from the analysis due to their too-low abundance of LM ($n < 10$). Differences among treatments were declared significant at the $p < .05$ probability level. All statistical calculations were done using R version 4.1.1 (<https://www.r-project.org/>) and Spatial Statistic Tools in ArcMap.

3 | RESULTS

3.1 | Utilization of aerial photographs for measuring changes in land uses and LM identification

The comparison between aerial photographs taken in 1953 and GE images showed an important conversion of uncultivated tree areas to paddy fields (Figure 3). Land use changes were more pronounced in the upper part (ML₂) of the catchment compared to the other locations (ML₁ and LL). In ML₂, the surface covered by trees decreased from 37.4% to 1.6% from 1953 to 2021, respectively. It also

decreased from 19.2% to 3.4% for ML₁ and 7.6% to 2.6% for LL. The percentage of surface covered by other arable lands also decreased from 1953 to the current period for the three locations.

The percentage of LM observed in the fields in 2021 passed from 96.5 to 88.6% on both GE and IGN aerial photographs, respectively. As a result significant linear models were measured between the number of LM in each plot measured by ground validation and their observations on IGN and GE images ($R^2 = .96$ and $.80$, respectively, $p < .001$ in both cases) (Figure 4).

3.2 | Effect of land use changes and topography on LM properties

The density of LM reached 1.39, 1.92, 2.14, and 1.64 mounds ha⁻¹ in 2021 in UL, ML₁, ML₂, and LL, respectively. Differences between locations were non-significant ($p = .157$). Moreover, no significant relationship between LM density and elevation could be measured (linear model, $p > .05$, data not shown). Differences in mound density between locations (UL, ML₁, ML₂, LL) and between plots that were influenced or not by the Khmer Rouge regime were not significant ($p > .05$ in all cases). Conversely, the abundance of LM in 2021 was significantly higher in SCR plots than in RIC and RIC/SCR plots (Figure 5) ($p < .001$).

The volume of LM older than 70 years (i.e. found on the IGN images) reached 31.9 m³ on average against only 5.9 m³ for recent LM (i.e. not found on the IGN images but observed in the field in 2020–2021). However, this difference was non-significant (T-test, $p = .707$).

3.3 | Spatial distribution of LM

The spatial distribution of LM was measured in 28 plots located along the transect from LL to UL areas. The result of Average Nearest Neighbour functions showed that LM were clustered, random, or dispersed depending on the plots (See Table 2 and Figure 6). From the 28 plots, half ($n = 14$) evidenced a random distribution, and half were either clustered ($n = 7$) or dispersed ($n = 7$). The tendency toward a random distribution did not follow a specific trend, but it was slightly more important in the lower part of the catchment than in the other locations, with 70.0, 42.9, 28.6 and 50.0% of the plots showing a random distribution, in LL, ML₁, ML₂, and UL areas, respectively.

FIGURE 3 Land cover types (paddy fields vs. trees, and uncultivated areas, in %) in the lower and middle parts of Chrey Bak catchment (LL, ML₁, and ML₂, respectively) assessed from historical aerial photographs from the Institut Geographique National (IGN) and Google Earth (GE) images.

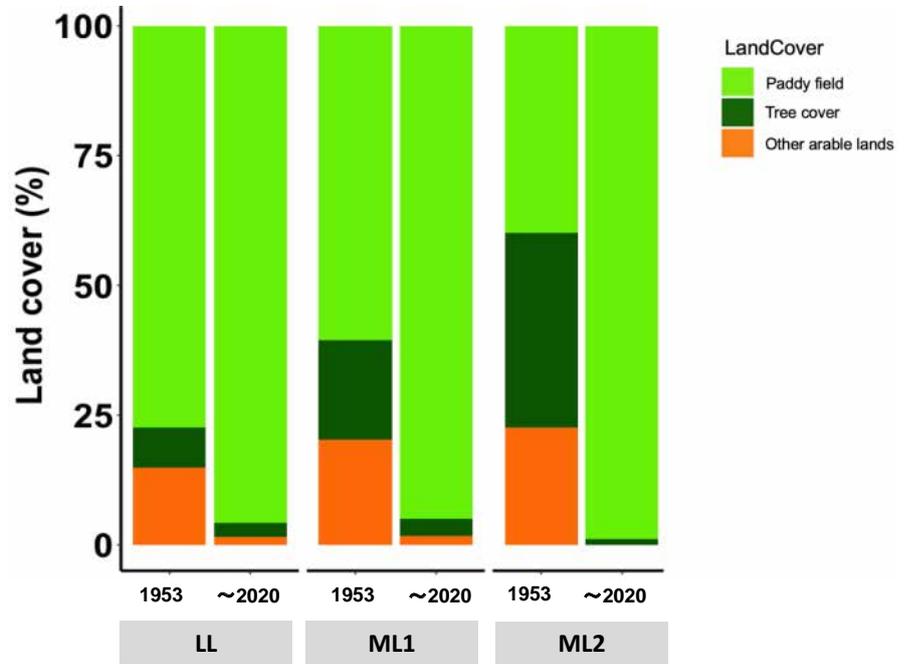
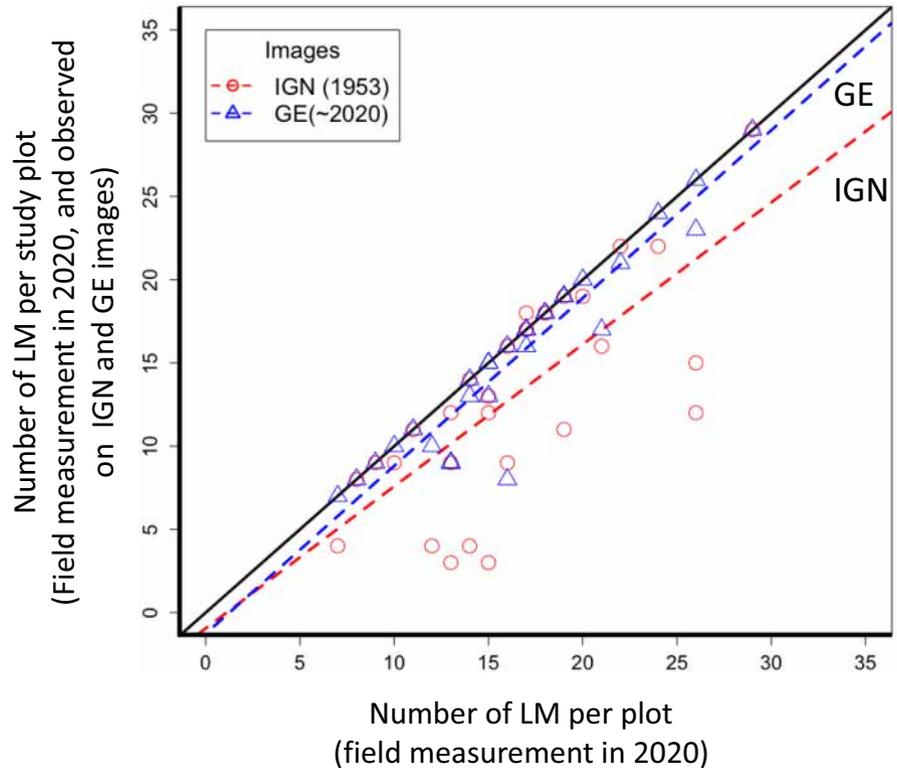


FIGURE 4 Relationship between the number of lenticular mounds (LM) found in each plot by ground truthing (X axis) and the number of mounds that could be observed in the photographs from the Institut Geographique National (IGN), and from Google Earth (GE) images (Y axis) ($n=23$). The bisecting line ($y=x$) is displayed in black. Linear regressions are also given in dashed lines for IGN and GE.



4 | DISCUSSION

4.1 | Utilization of IGN images for assessing changes in land uses and LM density

Remote sensing technologies have been used to capture land use changes in Cambodia that occurred these last decades and to estimate deforestation rates (Kong et al., 2019; Shimizu et al., 2022). Deforestation in the

tropics and the conversion from natural to arable land removes plant biomass and disturbs the soil habitat, with large consequences in biodiversity loss and termite abundance (Turner & Foster, 2009). Remote-sensing technologies have also been used to measure termite mound abundance, although most studies have been carried out in Africa (e.g. Davies et al., 2014; Isabelle et al., 2014; Ozsahin et al., 2022) and to a lesser extent in South America (e.g. Sim & Lee, 2014). Moreover, these studies could be seen as ‘snapshots’ without the possibility of

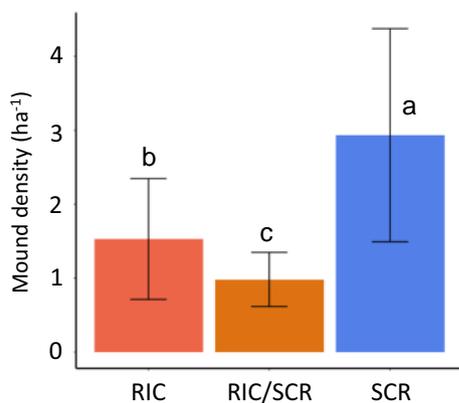


FIGURE 5 Average density of lenticular mounds (LM, in mounds ha^{-1}) in paddy fields at the Chrey Bak catchment in 2021, in lands that were described scrublands (SCR), paddy fields (RIC) or a combination of scrublands and paddy fields (RIC/SCR), $n = 23$ plots.

comparing results from a chronological point of view simply because the means associated with remote sensing are recent. Here, we used IGN and GE images to estimate the presence of LM and determine if those were likely already present in 1953. The main limitation of this approach was that LM could only be measured in the field because they were hidden by vegetation (trees covered 100% of the LM in the Chrey Bak catchment, pers. obs.), while on the contrary, all vegetation patches in the landscapes were not LM. Reciprocally, groves in old photos may have hidden LM that were no longer present, and recent LM (i.e. made by young termite colonies) could not be associated with trees and, therefore, were not identified using IGN and GE images. However, despite these limitations, a good match between the presence of LM observed in the field and using GE images was found, thus justifying the approach used in this study. The finding that most LM in 2021 were likely to be already associated with woody vegetation in 1953 suggests that most LM were older than 70 years. These results had to be considered in line with the studies carried out in Africa and South America, where termite nests could be several centuries to millennium old (Martin et al., 2018; Moore & Picker, 1991). Therefore, an interesting perspective would be to use ¹⁴C labeling to determine if LM in Cambodia are as old as in Africa and South America, thus raising the need to protect these particular environments and all the biodiversity they host. However, since 11.4% of LM were younger than 70 years (i.e. because not observed in the IGN images), this study also showed that only a few decades could be enough to recover and establish new LM. Although the difference in LM size between 'recent' and 'old' paddy fields was insignificant, it suggested a continuous growth of LM over time in paddy fields despite, and perhaps at the detriment of, the space used for rice culture.

TABLE 2 Spatial distribution analysis of lenticular mounds (LM) obtained from the Average Nearest Neighbour (ANN) function (Euclidian) in the lowland (LL), midland 1 (ML₁), midland 2 (ML₂) and upland (UL). Both Z scores and *p*-values indicate a significant level, associated with the standard normal distribution.

Locations	ID plots	Z-scores	<i>p</i> -value	Patterns
LL	1	0.713	.476	Random
	2	-0.774	.439	Random
	14	2.434	.015	Dispersed
	15	0.455	.649	Random
	16	-0.386	.700	Random
	18	1.612	.107	Random
	3	2.116	.034	Dispersed
	17	1.685	.092	Dispersed
	13	-1.088	.276	Random
ML ₁	9	1.116	.264	Random
	19	-2.781	.005	Clustered
	4	1.396	.163	Random
	5	0.010	.992	Random
	12	-1.790	.073	Clustered
	20	0.346	.729	Random
ML ₂	29	-2.145	.032	Clustered
	30	2.190	.028	Clustered
	6	-3.180	.001	Clustered
	21	-1.904	.057	Clustered
	11	-0.600	.548	Random
	22	2.036	.042	Dispersed
UL	23	-4.425	.001	Clustered
	24	1.533	.125	Random
	27	-1.884	.059	Clustered
	10	3.372	.001	Dispersed
	7	0.449	.654	Random
	25	1.899	.058	Dispersed
	26	-0.499	.617	Random

4.2 | Abundance and distribution of LM

Because termites are sensitive to land use changes, they have been considered bio-indicators of habitat changes in the tropics (Dosso et al., 2012). They are a very suitable group for illustrating the effects of ecosystem fragmentation (De Souza & Brown, 1994). In particular, soil properties and the distance to the water table are key variables explaining termite mound densities at the region scale (e.g. Bodot, 1967; Ahmed II & Pradhan, 2019). In a previous study, Muon, Lai, et al. (2023) found an average density of 2.1 mounds ha^{-1} in the Chrey Bak catchment. Therefore, termite mound density was low in this catchment in comparison with the one observed in natural environments in

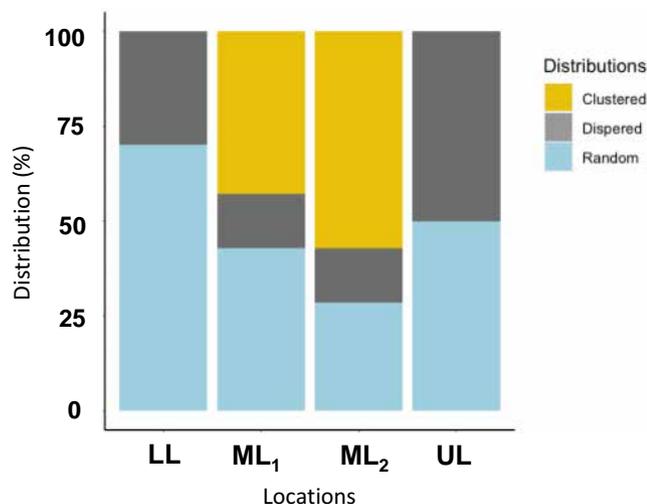


FIGURE 6 Bar plots showing the percentage of LM displaying a clustered (in yellow), dispersed (in grey), and random (in blue) distribution in the lowland (LL), midland 1–2 (ML1–2) and upland (UL) in the Chrey Bak catchment in 2021.

Africa (Abbadie et al., 1992; Traoré et al., 2008) and in Asia (Inoue et al., 2001; Jouquet et al., 2017) with ~ 10 mounds ha^{-1} in average, but similar to the one measured in paddy fields by Choosai (2010) (~ 2 mounds ha^{-1} in Northeast Thailand). In this study, we compared the density of LM along the toposequence and in considering the land use changes from 1953. The hypothesis of a gradient of LM density along the toposequence could not be confirmed in this study. The re-drawing of the limit of paddy field plots during the Khmer Rouge regime (1975–1979) had also no influence on the density of LM observed in 2020–2021. However, we found that plots converted into paddy fields after 1953 were characterized by a higher density of LM than plots that were already paddy fields in 1953. The size of LM can be very important in some locations ($>30 \text{ m}^3$). Therefore, the conversion of scrublands to rice fields could have been very costly in terms of land preparation and LM destruction (Lao, pers. com.). This constraint is likely to explain the higher abundance of LM in more recent paddy fields. Therefore, this study suggests that the abundance of LM in the Chrey Bak catchment is likely to be explained both by (1) the low environmental gradient between the lower and upper parts of the cultivated areas (i.e. the slope was relatively gentle in the catchment from 0.6% to 3% meters above sea level on average in the lowland and upland, respectively), suggesting a low or lack of influence of the distance to the water table; and (2) by farmer's practices and their decisions and means available to maintain or limit the presence of LM.

The measure of LM distribution also evidenced the importance of farmers' strategies. Although it is not possible to reject the hypothesis that termites' ability to settle and build LM varied between sites, this study instead

suggested that farmers' practices mainly explained the LM distribution. Indeed, with the assumption that random distribution reflects a lack of impact on the environment, including farmer's practices, these results suggest lower interactions between LM and farmers in the lowland and the upland than in the midland. However, the higher proportion of LM distributed randomly in the upper part of the catchment has to be considered with caution because of the limited number of plots ($n = 4$ against 10 in the lowland and 2×7 plots in the midland). The main differences between the locations are (i) the irrigation and access to water (less hazardous in the lowland and the upland due to the enlargement of the river bed in the lowland and the continuous flow from the mountain in the upland) and (ii) agricultural practices (i.e. the lower part of the catchment being more intensively and cultivated for a more extended period than the upper part, Muon, pers. com.), we consider that LM patterns in the midland could mainly be explained by farmers' strategies and on whether they used LM or not (Muon, Lai, et al., 2023), or on their access to water to irrigate the plots.

5 | CONCLUSION

Although this study did not allow measuring the impact of the land use changes on plant and animal diversity, it highlighted the consequences of the intensification of the agricultural practices with an essential loss in tree cover, a homogenization, and simplification of the landscapes, especially in the midland of the catchment. However, this study's results have to be considered with caution because only 30 plots ($\sim 9 \text{ ha}$ each) were considered in the catchment. While plots were sampled randomly along the toposequence, all of them were cultivated with rice in 2020. Therefore, more exhaustive research is needed to confirm our findings and quantify the changes occurring at the whole catchment scale. We consider that this upscaling is now necessary to determine if the impact of land use changes and the disappearance of LM have important consequences in terms of plant and animal loss and, therefore, a reduction of the ecosystem services provided by biodiversity (e.g. Miyagawa et al., 2011; Muon, Lai, et al., 2023).

This study also evidenced that LM are not epiphenomena but instead specific and conspicuous geomorphological structures (sensu Van Thuyne et al., 2021) of Cambodian paddy fields. Despite their low density, their mostly random distributions increase the heterogeneity in the landscapes. In a very intensively cultivated area such as paddy fields, LM could be seen as relics of old and 'natural' forests and/or habitats for biodiversity, whose importance has dramatically diminished since the 50s,

especially in more remote and less accessible ecosystems such as those close to the forest in the upper part of the catchment. This consideration is likely to be very important in Southeast Asia, and especially in Cambodia, where biodiversity is threatened by the modernization of agricultural practices (e.g. the use of pesticides, chemical fertilizers, and mechanization) (Bai et al., 2008; Hok et al., 2018). More research is now needed to confirm and understand the specific interactions between LM and farmers and the dynamics of LM. Why do farmers decide to maintain these structures on their lands, and do they derive ecosystem services from them, thus justifying their decision not to destroy them but rather to use them as natural (and sustainable) resources?

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DATA AVAILABILITY STATEMENT

The datasets generated during the current study are available in the dataverse repository.

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SUPPORTING INFORMATION

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