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Termite bioturbation in Cambodia – From characterization to application

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Par

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List of the publications and presentations

Publications

1. Jouquet, P., Harit, A., Hervé, V., Moger, H., Carrijo, T., Donoso, D.A., Eldridge, D., Ferreira da Cunha, H., Choosai, C., Janeau, J.-L., Maeght, J.-L., Thu, T.D., Briandon, A., Skali, M.D., van Thuyne, J., Mainga, A., Pinzon Florian, O.P., Issa, O.M., Podwojewski, P., Rajot, J.-L., Henri-des-Tureaux, T., Smaili, L., Labiadh, M., Boukbida, H.A., Shanbhag, **R., Muon**, R., Ann, V., Cheik, S., Fall, S., Traoré, S., Dupont, S., Chouvenc, T., Mullins, A.J., Syaukani, S., Zaiss, R., Tien, T.M., Šobotník, J., Auclerc, A., Qiu, R., Tang, Y.-T., Huot, H., Sillam-Dussès, D., Bottinelli, N. (2022). The impact of termites on soil sheeting properties is better explained by environmental factors than by their feeding and building strategies. Geoderma 412, 115706. https://doi.org/10.1016/j.geoderma.2022.115706
2. **Muon, R**., P. Ket, D. Sebag, H. Aroui, P. Podwojewski, V. Hervé, V. Ann, P. Jouquet. The importance of bioturbation by termites in Cambodian paddy fields varies with the amount of sand in soil. Applied Soil Ecology. Submitted to Geoderma regional
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Presentations

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Résumé

La biodiversité des sols joue un rôle clé dans la régulation des fonctions écologiques du sol et dans la fourniture de biens et services écosystémiques essentiels aux sociétés humaines. Parmi les organismes du sol, les termites jouent un rôle de premier plan dans les sols tropicaux, en tant qu'éléments des réseaux trophiques et en tant qu'ingénieur de l'écosystème avec des effets sur la dynamique des sols et la biodiversité à différentes échelles spatiales et temporelles. Bien que les termitières caractérisent les paysages des rizières dans le bassin inférieur du Mékong, leur abondance, leurs propriétés et leurs utilisations par les agriculteurs restent inconnues. L'objectif de cette étude était donc d'analyser les interactions entre les termitières et les agriculteurs dans les zones cultivées de cette région. A partir d'entretiens réalisés dans 13 villages au sein du bassin versant de Chrey Bak au Cambodge, nous avons montré que les termitières fournissent un grand nombre de services aux populations locales, faisant partie des pratiques culturales et contribuant à la diversité alimentaire et à la santé (par exemple, l'utilisation du sol des buttes termitiques comme amendement, l'accès aux plantes médicinales, et une moindre utilisation d'engrais chimiques et de pesticides). Nous avons ensuite évalué l'abondance et les propriétés de deux types de termitières (les monticules ou "buttes termitiques" et les "nids") dans les rizières du bassin versant de Chrey Bak. Nous avons montré que la densité des buttes termitiques atteint ~ 2 termitières ha^{-1}, et que ces constructions sont susceptibles de trouver leur origine dans l'activité de construction de *Macrotermes gilvus*. Nous avons mis en évidence que les buttes et les nids peuvent être considérés comme des îlots (ou 'hotspots') de fertilité dans les paysages avec des teneurs plus élevées en carbone et en nutriments, et des propriétés physiques du sol améliorées (e.g., teneur en argile plus élevée, ainsi qu'une meilleure capacité de rétention d'eau et une plus grande conductivité hydraulique en milieu saturé). Cependant, l'utilisation de photos aériennes acquises en 1953 par l'Institut Géographique National (IGN) questionne quant au temps probablement très long qui serait nécessaire pour obtenir des buttes termitiques, soulignant ainsi la possible fragilité de ces milieux au regard de leur exploitation par les agriculteurs. En conclusion, cette recherche interdisciplinaire a mis en évidence l'urgence d'une meilleure compréhension des impacts environnementaux et sociaux sur la biodiversité, et notamment sur l'activité des termites, et des facteurs déterminants leur préservation par les agriculteurs.

Summary

Soil biodiversity plays a key role in regulating key ecological functions and in providing essential ecosystem goods and services to human societies. Among soil organisms, termites play a prominent role in tropical soils, as elements of the food web and as ecosystem engineers with effects on soil dynamics and biodiversity at different spatial and temporal scales. Although termite mounds are conspicuous features of the landscapes in the lower Mekong basin, their abundance, properties and utilization by farmers remain unknown. Thus, the aim of this study was to analyze the interactions between termite constructions and farmers in cultivated areas in this region. Using interviews realized in 13 villages in Chrey Bak catchment in Cambodia, we showed that termite mounds provide a large number of services to local people, being part of the cultivation practices and contributing to food diversity and health (e.g., utilization of mound soil as amendment, access to medical plants, and lower use of chemical fertilizers and pesticides). We assessed the abundance and properties of two termite constructions (lenticular mounds and mound nests) in paddy fields in Chrey Bak. We showed that termite lenticular mound density reaches ~ 2 mounds ha^{-1}, and that these constructions are likely to find their origin in the building activity of *Macrotermes gilvus*. We evidenced that termite lenticular mounds and nests can be seen as fertility and biogeochemical islands or hotspots in the landscapes with higher carbon and nutrients contents, and improved soil physical properties (higher clay content, improved water holding capacity and saturated hydraulic conductivity). However, the utilization of historical aerial photographs taken in 1953 by the French Institute Geographique National (IGN) questions the time needed for the edification of termite mounds, thus raising the fragility of termite mounds regarding their exploitation by farmers. To conclude, this interdisciplinary research evidenced the urgent need for a better understanding of the environmental and social impacts on biodiversity, and especially on termite activity, and on the driving factors controlling their preservation by farmers.

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Chapter 1 . Introduction

Cambodia is one of the most vulnerable countries to climate change, especially because it is severely impacted by periods of drought that are expected to become more severe in the future (Nguyen and Shaw, 2011; Trisurat et al., 2018; Oeurng et al., 2019). Such periods of water shortage, as observed in 2019 with the prolonged and intense drought coupled with a coronavirus pandemic, have negative impacts on agriculture and ultimately on food security. For instance, while rice remains the principal crop in Cambodia, with 84% of the cultivated surface in rainfed areas (data from 1999, Sarom et al., 2001), rice production is almost every year negatively impacted by periods of drought in Cambodia, but also more generally in the Lower Mekong basin (LMB) (Trisurat et al., 2018), which can lead to up to 46% yield loss (Ouk et al., 2006). In addition, soil fertility management and the matching of nutrient supply to crop demand are very difficult in this region, because 35 to 42% of the paddy fields are cultivated in sandy soils (Sarom et al., 2001; White et al., 2006; Seng et al., 2007; Nguyen and Shaw, 2011; Thilakarathne and Sridhar, 2017; Trisurat et al., 2018), which are characterized by low soil organic matter and mineral nutrient contents (White et al., 1997; Seng et al., 2007), low cationic exchange and water holding capacities and high risk of leaching. Those two intertwined climatic and edaphic constraints constitute a major threat for food security and the livelihood of local population in the LMB (Jalota et al., 2012), and more specifically in Cambodia.

The LMB countries are also facing many changes in response to demographic and economic demands in the region. Agriculture tends to be more intensive with the use of agricultural machinery and the use of pesticides and chemical fertilizers (Bai et al., 2008; Ros et al., 2011; Panuwet et al., 2012; Pin and Mihara, 2013; Soni, 2016). Forest clearance for the expansion of agricultural land has been exacerbated and, together with the intensification of the agricultural practices, has been leading to land degradation (Hok et al., 2018). Between 1981 to 2003, 40 to 60% of the territory was estimated to be degraded due to the intensification of agricultural practices, depending on the countries, and soil degradation impacted between 25 to 57% of the population living in degraded areas in the region (Bai et al., 2008). As a consequence, soils have become more susceptible to erosion, soil organic carbon depletion, and nutrient imbalance (Montanarella et al., 2016). Soil compaction is also considered a serious form of soil degradation, mainly resulting from the use of modern and heavy machinery (Gürsoy, 2021) such as tractors for land preparation and transporting crop production, and overuse or incorrect use of chemical fertilizers (Ros et al., 2011; Chhun et al., 2015).

Our perception of agro-ecosystems has deeply changed over the last decades. While the conventional approach relies on provisioning services only (i.e., the production of food or biomass), the development of agro-ecology has complicated our perception of the importance of agro-ecosystems. Agro-ecosystems are now considered in a more holistic way in taking into account the large diversity of other provisioning, regulating, cultural and supporting services that can be provided to human societies (Costanza et al., 1997; Kibblewhite et al., 2008). In this context, ecological concepts and more specifically our perception of the role played by nature have become crucial (Altieri, 1999; Pauli et al., 2016). Together with this recognition of the services provided by biodiversity, the need to improve soil health and C sequestration (Hok et al., 2018) and the importance of local knowledge and traditional cultural practices have also been recognized important levers to highlight sustainable cultivation practices for the production of food, the preservation of biodiversity and environmental quality, and the livelihood of the local population (Jax et al., 2013; Cheik and Jouquet, 2020).

Paddy fields are very heterogeneous ecosystems in LMB. In addition to small dykes delimiting cultivated plots, large lenticular soil mounds are commonly observed in paddy fields (Figure 1). These mounds are usually covered by large trees and shrubs and host an abundant soil biodiversity (Choosai et al., 2009). Although their origin is unknown, local people consider that they result from the bioturbation activity of termites. Indeed, termites, as soil engineers, play a major role in the dynamics of tropical soils (Berke, 2010; Jouquet et al., 2014, 2018). Termites have profound effects on soil structure, aggregate formation, and soil organic matter dynamics at different spatial and temporal scales (Lavelle et al., 1992; Bottinelli et al., 2015; Jouquet et al., 2016). At the largest scale, they can build very old and large nest structures (see for instance the mounds built by *Syntermes dirus* in Brazil that can reach 9 m in diameter and 2 to 4 m in height (average volume ~24 m^3) with a density of 35 mound ha^{-1}; Funch, 2015). Therefore, regarding their large impact on soil dynamics, termite activity is considered to be important for the restoration of degraded soils and for maintaining the fertility of soil in agro-ecosystem (Tilahun et al., 2012; Jouquet et al., 2014; Amadou Issoufou et al., 2020; Apori et al., 2020a;). Indeed, several studies, mostly carried out in Africa, showed that lenticular mounds (LMs) can be considered patches of biodiversity and fertility, and that they can be used to reduce food insecurity and to provide a better access to health (Suzuki et al., 2007; Sileshi et al., 2009; Miyagawa et al., 2011; Chisanga et al., 2017; Farr, 2021). Traditional practices involving termite constructions have also been observed in the LMB, and especially in Laos where LM soils (mostly *Macrotermes* spp and *Odontotermes* spp) are used as amendments in paddy fields and vegetable gardens for increasing soil fertility and plant productivity (Miyagawa et al., 2011; Farr, 2021). In Thailand, farmers also traditionally recognized the value of clay material found in LMs for restoring the nutrient balance and the water holding capacity of soils, and therefore the productivity of degraded soils (Noble et al., 2004).

While LMs are conspicuous features of the landscapes in Cambodia, their abundance, properties and utilization by farmers remain unknown. Thus, the aims of this study were twofold:

(1) To quantify the services that LMs provide to the population. Do farmers consider that LMs provide ecosystem services? What types?

(2) To determine their abundance, soil physical and chemical properties, and dynamics. Are LMs patches or islands of fertility in paddy fields? Is their utilization by farmers sustainable?

Our main hypotheses were that LMs are enriched in clay, organic matter and nutrients in comparison with the surrounding paddy fields, with positive effects on soil physical and chemical fertility. However, since termite's impact on soil vary with the properties of the parent soil (e.g., Jouquet et al., 2022), we hypothesized that the impact of termites on soil fertility was more important in very poor soils (i.e., very sandy soils) than in more fertile soils (i.e., less sandy soils), and therefore that farmers preferred to keep LMs in very poor soils, thus reflecting a larger abundance of LMs in very sandy soils. We also expected that LMs offered more ecosystem services than only those associated with soil fertility, as observed in Laos (Miyagawa et al., 2011).

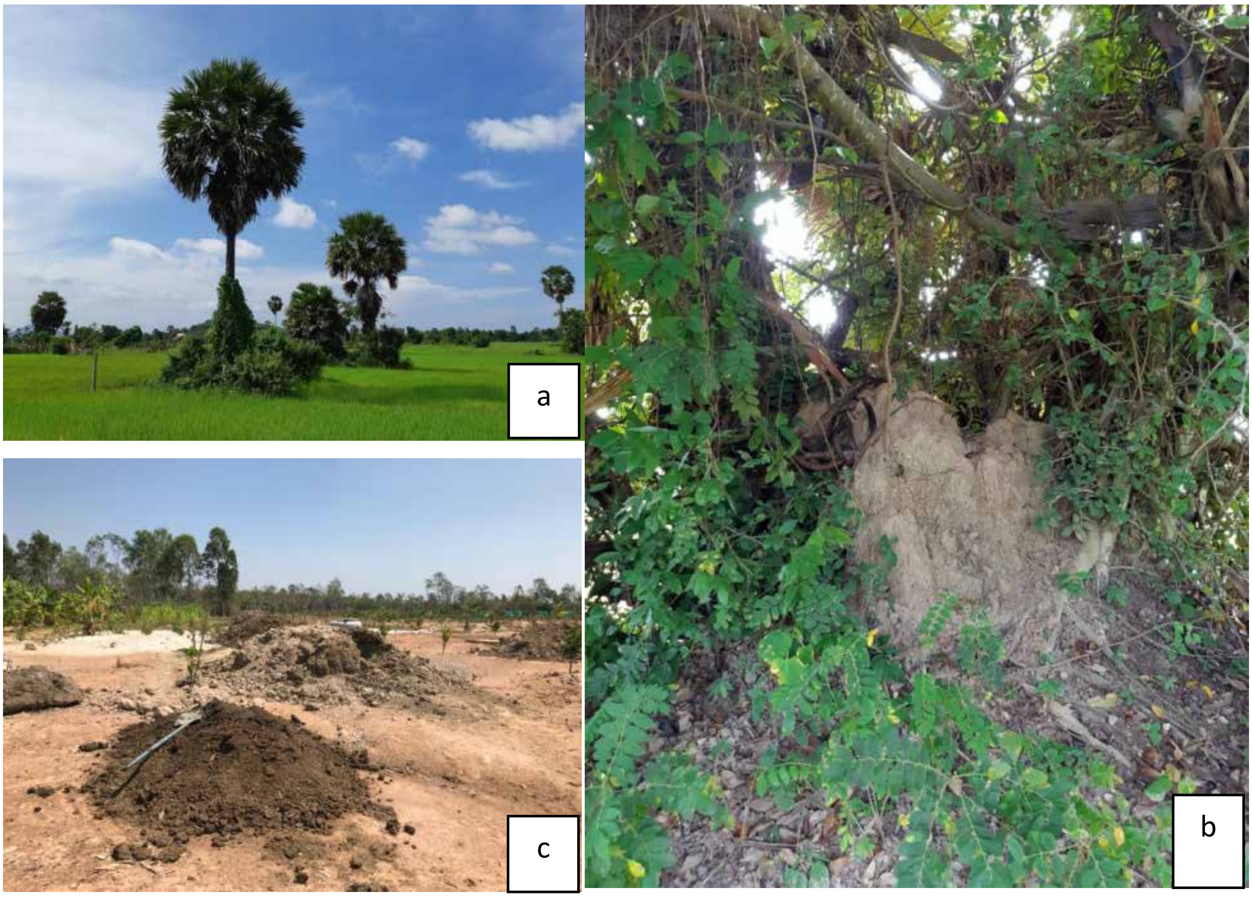

Figure 1. Termite construction in paddy fields in the Chrey Bak catchment, Cambodia: (a) Termite lenticular mounds (LMs) covered by vegetation, (b) Termite mound nests (TNs) built by *Macrotermes gilvus* on the top of a LM, and (c) soil from LM used by farmers to increase the fertility of soil (photos: R. Muon, 2021)

Chapter 2 . State of the art

2.1 The culture of rice in Cambodia

In Cambodia, agriculture is dominated by the cultivation of rice, mostly during the rainy season although its cultivation during the dry season tends to increase (Ros et al., 2011). Roughly, two types of rice varieties can be found: ‘heavy rice’, which takes almost 6 months to mature and is mostly planted during the rainy season, and ‘light rice’, which requires about 3 months of culture and is cultivated both during the rainy and the dry seasons. Four categories of agro-systems can be found for the rice production: irrigated, floating or deep in water during the dry season, and rainfed systems (Sarom et al., 2001). The irrigated system is based on traditional gravity-fed irrigation using open channels, tidal irrigation, and weirs to divert (river, Stung) water into streams or main canals. Paddy field can also be supplied via pumps, that are used to mechanically get water from streams or canals (Cramb, 2020). The use of irrigation systems has been increasing in recent years. These systems can be used to supplement rainfall water during the wet season, and for the cultivation of rice during the dry season. Because the soil is soft due to its high-water content, the land preparation remains often easy and usually starts from February to May (Cramb, 2020). Traditional ploughing and harrowing with animals are still popular until today but the utilization of hand-held walking tractors is also increasing almost everywhere in the country. Floating or deep-water rice systems have been practiced traditionally in areas that are deeply flooded during the wet season, such as around the Tonle Sap Lake (or Great Lake)(Pittock and Nguyen, 2016). These systems use medium to tall rice varieties that can reach up to 2 to 3 m in height for deep-water rice, and up to 5 to 6 m for floating rice.

Farmers prepare their fields by burning rice straw and ploughing using animals (cows or buffaloes). The soil is then harrowed twice, before and after sowing rice seeds. The first harrowing is done for leveling the soil and for having a good drainage. The second harrowing is done to protect the rice seeds from the birds, mice, and to maintain good soil moisture (Pittock and Nguyen, 2016). The cultivation of rice during the dry season is practiced in areas that are continuously flooded in the wet season (such as around the Tonle Sap River and the Great Lake, and in the Mekong and Bassac branches of the upper Delta). During the dry season, water is trapped by embankments, ponds, and dams that are used to irrigate dry season crops using canals and pumps. Farmers often apply farmyard manure to their field in April and May. At the beginning of the rainy season, farmers start to prepare the soil by ploughing twice and then harrowing once or twice to break up and to level the soil before sowing rice seeds in nurseries. The soil is ploughed once or twice depending on soil properties: after the first rain when the soil is soft and easy to work with, and one day before or on the day of transplanting. In sandy soils, soils are ploughed only once.

The International Rice Research Institute (IRRI) differentiated 11 types of soil for the cultivation of rice: Prey Khmer, Prateah Lang, Labansiek, Orung, Krakor, Bakan, Kbal Po, Kein Svay, Toul Samroung, Koktrap, and Kampong Siem (White et al., 1997) (Figure 2). Prey Khmer (deep sandy profile) and Prateah Lang (sand over clay) are the two most dominant soil types (42% of the surface). These soils are very sandy, extending deeper than 50 cm for Prey Khmer and being less than 40 cm for Prateah Lang. Prey Khmer soil accounts for 10-12% of the paddy fields, and they can be found in most provinces but more significantly in Pursat, Kampong Chhnang, Kampong Speu, and Siem Reap. The main cultural constraint of this soil type is its low water retention, as well as limited availability of nutrients to crops (Bell and Seng, 2003).

Since the 1990s, the utilization of fertilizers has gradually increased to compensate the low fertility of these soils. The use of agricultural machinery and pesticides has also become widespread with the modernization of agriculture and in response to the reduction in labor needs.

However, poor farmers continue to use traditional practices (e.g., ploughing with cows, buffalos, transporting with ox carts, and manual harvesting) because they cannot afford to buy or rent agricultural machinery. Before the early 1990s, rice farming was only based on traditional practices aiming to maintain soil quality without chemical fertilizers, pesticides and herbicides (Ros et al., 2011). Popular practices consisted in the amendment of raw materials available in the immediate environment to improve soil fertility, such as cow manure and dungs, that were spread out before soil preparation and rice sowing. An original practice also consisted in the amendment of soil from large lenticular mounds covered by trees, commonly named “termite mounds”.

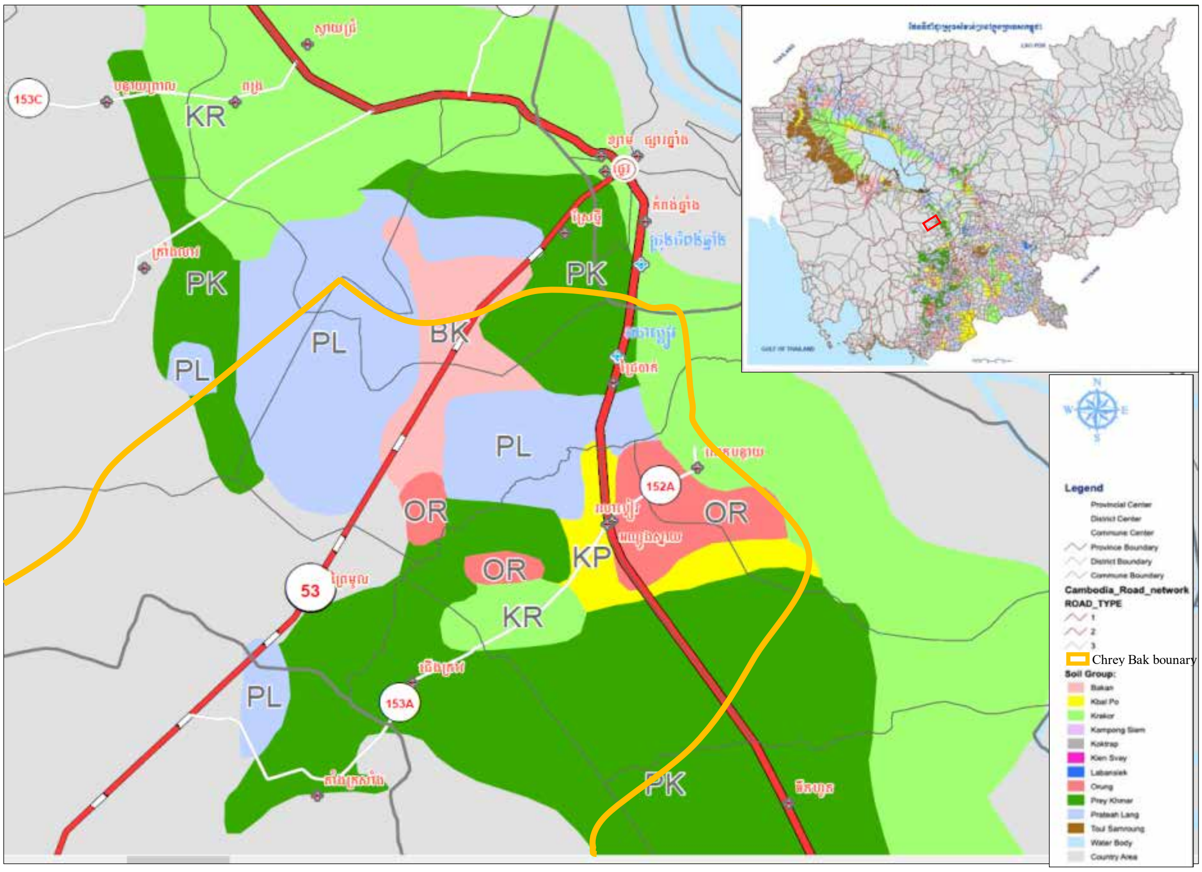

Figure 2. Soil maps of the main rice growing area in the lowland of Chrey Bak catchment classified by the International Rice Research Institute (IRRI). The lowland of the Chrey Bak, mainly locates along the road number 53 and 153A (inside orange rectangle), which is categorized by six soil types: Prey Khmer (PK), Prateah Lang (PL), Bakan (BK), Orung (OR), Kbal Po (KP), and Krakor (KR).

2.2 Soil biodiversity in agro-ecosystems

Soil health (*sensu* Kibblewhite et al., 2008) and biodiversity are strongly linked. Indeed, the soil system is the home of an extraordinary diversity of soil organisms, that are performing important ecological functions, such as those associated with the cycling of nutrients and the dynamics of water (Lavelle, 1997). For instance, it has been estimated that 1 g of soil contains up to 1 billion bacteria cells consisting of tens of thousands of taxa, up to 200 m fungal hyphae, and a wide range of mites, nematodes, earthworms, and arthropods (Wagg et al., 2014). Soil organisms contribute to the degradation of litter, the stabilization and destabilization of soil organic matter (SOM), the cycling of elements such as carbon, nitrogen and phosphorus (Fitter et al., 2005), by simultaneously regulating physical, chemical, and microbiological properties in soil (Lavelle, 1997; Wolters, 1998; Bottinelli et al., 2015). Due to their importance, it is commonly considered that ecosystem functions and sustainability are strongly influenced by changes in soil communities and the loss in soil biodiversity (Wagg et al., 2014).

In soil, microbes (i.e., bacteria, fungi, protozoa, algae and virus) form a vital component of agro-ecosystems. They drive a large list of ecological functions (Collins and Qualset, 1998), that contribute positively to the soil health status via their effects on soil formation and aggregation (Aislabie and Deslippe, 2018), nutrient cycling and soil fertility, and finally plant growth and yield (Kumar et al., 2010; Ahmad et al., 2012, 2013; Ashwani Kumar et al., 2013; Prashar and Shah, 2016; Hashem et al., 2017). The impact of microbes on the growth and productivity of plants includes the degradation and mineralization of organic matter, and therefore the release of nutrients to plants, as well as the protection of plants from harmful abiotic and biotic stresses (Neher and Barbercheck, 1998; Köhl et al., 2014; Kumar et al., 2015). Soil biodiversity also includes larger organisms that are usually differentiated according to their sizes into microfauna, mesofauna, macrofauna, and megafauna (> 20 mm length) (Lavelle, 1997; Neher and Barbercheck, 1998; Sofo et al., 2020). Microfauna includes organisms (e.g., protists, small nematodes, rotifers, and tardigrades) that have a body width lower than 0.1 mm. Mesofauna includes organisms with a body size between 0.2 to 2 mm (e.g., nematodes, enchytraeids, mites, and collembolan). Their role mostly consists in the comminution of the litter, the regulation of the soil food-web, and the stimulation of plant-microbial interactions (e.g., Bonkowski, 2004). The macrofauna consists in soil invertebrates larger than 2 mm in size (e.g., ants, earthworms, termites, spiders and some insect larvae). In addition to be part of the soil food-web, some species from the soil macrofauna group can also reshape the soil structure (Neher and Barbercheck, 1998). These species are called ecosystem engineers (*sensu* Jones et al.,1994, 1997) because they maintain and modify the habitats of many 'subordinate' organisms, therefore influencing nutrient and energy flows (Lavelle et al., 1994; Jouquet et al., 2006). If soil bioturbation is mostly performed by earthworms in temperate soils, this role is mostly devoted to both termites and earthworms in tropical soils. Finally, the megafauna consists of organisms larger than 20 mm in length (Neher and Barbercheck, 1998). This category includes mammals that can locally have an important role on soil dynamics, although their impact as pests is often considered to be more important (e.g., rats).

2.3 The importance of termites in paddy fields

Termites, are among the most important decomposers in most tropical ecosystems and they have been named "neglected soil engineers" in tropical soils, because of their large impact on soil dynamics and the low number of studies that have focused on their ecological impacts in comparison with earthworms (Jouquet et al., 2016a). Termites ingest large amounts of soil and/or litter and they are therefore a major regulator of SOM dynamics in tropical ecosystems (Holt and Lepage, 2000; Jouquet et al., 2011). Reviews on the impact of termites on soil functioning showed that termites can impact the soil system at different spatial and temporal scales, from clay minerals to the landscapes (Jouquet et al., 2016a). At these different scales, termites influence key ecological functions associated with the regulation of SOM dynamics and soil fertility, and water dynamics (Jouquet et al., 2018). Termites play a prominent role in maintaining biodiversity through the creation of biostructures with different soil physical and chemical properties (Holt and Lepage, 2000; Choosai et al., 2009; Jouquet et al., 2011; Bottinelli et al., 2015). They generally select small size particles (i.e., clay) from within the soil profile and bring them to the soil surface for building their constructions (i.e., nests and sheeting) (Holt & Lepage, 2000). They dig extensive networks of galleries, which consist in tunnels ranging from 1 to 20 mm and reaching up to 7.5 km ha^{-1} (Lavelle et al., 1992). They also build complex nests that might be very compact (e.g., nests of Macrotermitinae sp.) made of mineral, saliva and fecal materials (Holt and Lepage, 2000). At the death of a colony, if not colonized by other inquiline species, nests are usually eroded by the rain or mammals. However, the incomplete degradation of nests can be used for the settlement of other termite colonies and the activity of other soil invertebrates, including earthworms, then giving birth to termite lenticular mounds (e.g., Josens et al., 2016; Harit and Jouquet, 2021). These mounds can then be the refuge of many animals (Choosai et al., 2009) and host many plants that could find appropriate environmental conditions (e.g., Traoré et al., 2008a). In Africa, these mounds are considered as patches or islands of nutrients (McCarthy et al., 1998; Sileshi et al., 2010; Jouquet et al., 2011, 2016, 2017; Chen et al., 2021) with positive impacts on plant growth and resistance against environmental hazards such as drought (Bonachela et al., 2015; Padonou et al., 2020). Termite mounds are also observed in paddy fields in the LMB (Choosai, 2010; Miyagawa et al., 2011). Although their origin is unknown, it is commonly considered that they come from the degradation and colonization of abandoned termite nests (Josens et al., 2016; Harit and Jouquet, 2021). The research carried out in other environments suggest that they could be very old since termite mounds have been estimated to reach up to 2,000 years in Africa (Moore and Picker, 1991; Erens et al., 2015) and more than 4,000 years old in Brazil (Martin et al., 2018). Because paddy fields are temporarily flooded, the presence of soil fauna is limited to this environment, with the exception of earthworms that can remain active in flooded areas (Choosai, 2010). Therefore, termite mounds can constitute a refuge for soil fauna during the rainy season (Choosai et al., 2009).

Termites and termite mounds can provide numerous ecosystem services in Africa (Enagbonma and Babalola, 2019; Tilahun et al., 2012, 2021) and in Asia (Miyagawa et al., 2011). For instance, some people use plants growing on termite mounds for traditional medicinal purposes (Sileshi et al., 2009; Dossou-Yovo et al., 2014), while others consume mushrooms, edible plants and insects (including termites) available in and on termite mounds (Sileshi et al., 2009; Miyagawa et al., 2011). In Benin, people perceive the termite mound soil as a fertilizer material. This utilization of termite mound soil has also been reported in Laos (Miyagawa et al., 2011). In Cambodia, the understanding of the ecological roles played by termite mounds and their ecosystem services are still largely ignored despite the fact that they are abundant in paddy fields and although some farmers practically use termite construction materials as soil amendment for increasing soil fertility.

Chapter 3 . Materials and Methods

3.1 Study site

The study was carried out in the Chrey Bak catchment, Cambodia, a long-term observatory and research infrastructure of the Institute of Technology of Cambodia. This catchment is located in the watershed of Tonle Sap Lake and in northwest of Phnom Penh, capital of Cambodia (Figure 3). Chrey Bak is covered by two districts, namely Tuek Phos and Rolea Biér, for a total of ~800 km^2. 34% of the catchment is covered by forests, and the remaining is used for agriculture (32%) or consists in shrublands (27.4%) and grasslands (5.4%) (JICA, 2003). The catchment is influenced by the tropical monsoon and 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). The slope of the catchment is variable and high (~37% on average) in the mountainous area in the southwest region, while it is very gentle (slope < 12%) or almost flat in the cultivated area (Mekong River Commission, 2003), which is dominated by rain-fed paddy fields (Figure 4a, b).

Small paddy field plots are separated by small dykes (Figure 4c,d). In this environment, soil bioturbation is mainly carried out by termites, especially *Macrotermes gilvus* (Bathellier, 1927) which builds termite mound nests (TN) usually found on large lenticular mounds (LMs, ~6 m^3 and 16.88 m^2 on average). The origin of LMs is attributed to the bioturbation activity of termites by local villagers, especially *M. gilvus*, but LMs represent complex soil structures hosting many plants and other animals, such as other termite species (e.g., *Odontotermes* spp.), as seen in Thailand by Choosai et al. (2009) (Figure 1).

Agricultural machinery for rice harvesting contributes to the compaction of soil, as observed in the lower part of the catchment (Muon R., pers. obs., 2020) (Figure 5a). Soil decompaction mostly occurs via the ploughing of soil and bioturbation by soil fauna. Indeed, earthworm casts and soil aggregates excavated by ants can be seen on the ground, while buffalo dung can rapidly be consumed by dung beetles which produce tunnels in soil (Figure 5b, c, d, e). Previous studies carried out by JICA (2003) described two main soil types in Chrey Bak: Arenosol (38%) and Acrisol (28.1%), although other soil types, such as Leptosols and Fulvisols can also be found (Figure 6).

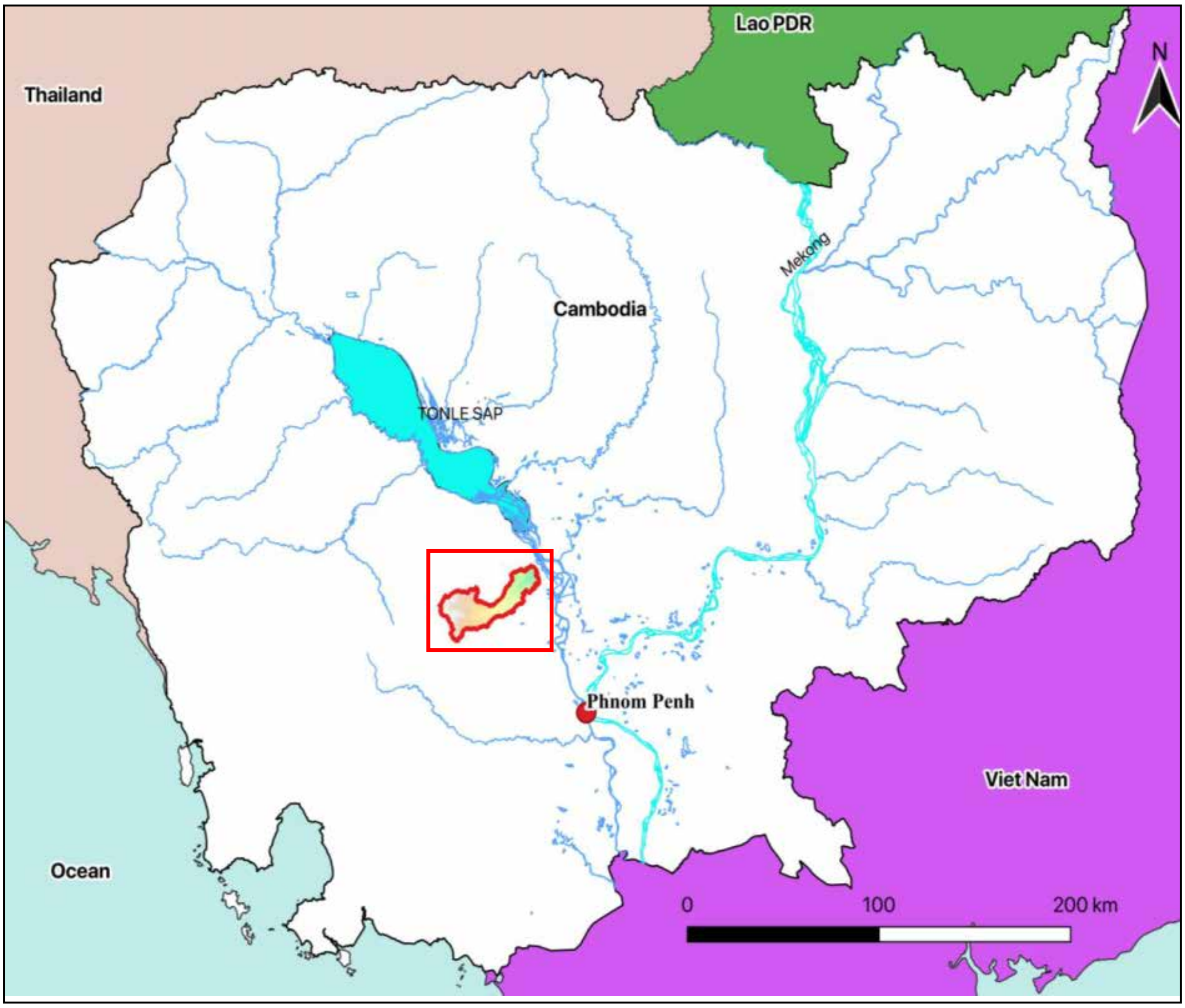

Figure 3. Location of Chrey Bak catchment in Cambodia

Landscape images

a. Chrey Bak catchment, NW upstream
b. Chrey Bak catchment, NE downstream
c. Rice field after harvesting
d. Rice field in Chrey Bak catchment. Little dykes (indicated by red arrows) separate small paddy field plots (Google Earth, 2021)
e. Rice fields and dykes separation

Figure 4. Landscape images in the Chrey Bak catchment, Nov 2020.

Soil surface features

a. Soil surface compaction after harvesting
b. Soil excavated by ants
c. Earthworm casts
d. Cow dung and on the right soil excavated by termites
e. Dung and rounded holes made by dung beetles.

Figure 5. Soil surface features in the Chrey Bak catchment, Nov 2020

3.2 Farmers' perception and utilization of termite mounds

A survey was carried out during the dry season in 2021 by randomly selecting a subset of 13 villages in the studied catchment, with a total of 61 respondents. Interviewed villages are shown in Figure 6. Village chiefs and villagers owning land with LMs were randomly selected for the interview. The questionnaire was designed with three main sections focusing on health, agronomy, and economics (see Table 1 for the list of questions). For each section, villagers were asked to explain if and how LMs are used and to list all the services they provide, such as their impact on soil fertility and the presence of plants used for their medicinal properties. Mean values and standard errors were calculated from the proportions of positive answers for each village (n = 13). Names of animals and plants that were used as medicine and food were obtained during the interview. Their occurrence was considered as a percentage of the total number of interviewees (n = 61). Khmer names were converted to English and/or Latin names using the list of Cambodia's Medicinal Plants (National Centre for Traditional Medicine, NCTM, 2013a, b). Differences in means density between LM and TN were assessed using one-way ANOVA and least significant difference (LSD) tests, after first verifying that residuals were normally distributed using Shapiro-Wilk test.

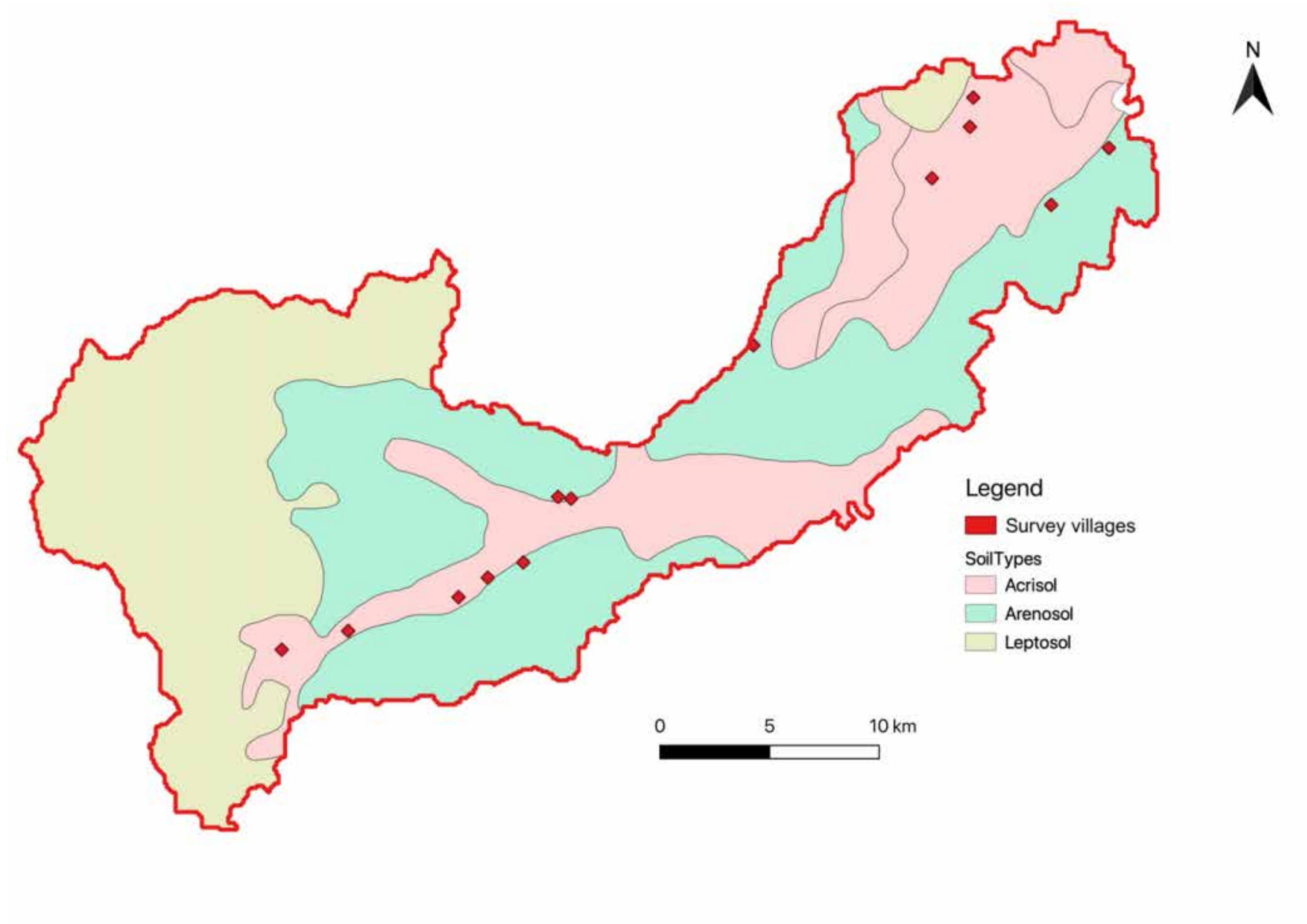

Figure 6. The location of 13 villages where the interviews were carried out in 2021

Table 1. List of the questions submitted to villages during the survey. Responses were either positive or negative (Yes vs. No) or open to the discussion. The total number of interviewees was n = 61 from 13 different villages.

Sections	Questions	Type of answers
Usefulness	Do you own land with a mound?	YES vs. NO
	Do you know the age of the mounds?	YES vs. NO
	Do you know how these mounds were produced/created?	YES vs. NO
	If yes, please specify the approximate age.	OPEN
	Are mounds useful?	YES vs. NO
	If yes, how?	OPEN
	Are they common (available to anyone) or private goods (only available to family members)?	COMMON vs. PRIVATE
	If not, why do you keep mounds on your land?	OPEN
	Do you think that mounds were more useful in the past?	YES vs. NO
	If yes, why?	OPEN
	Can you mention reasons why they were more useful in the past than currently?	OPEN
Agronomy	Do you use soil from mounds as an amendment for increasing soil fertility?	YES vs. NO
	If yes, how often?	OPEN
	Do you use specific sections (e.g., termite nests, external vs. top of the mounds)?	YES vs. NO
	Does this soil increase rice yield?	YES vs. NO
	Do you use less chemical fertilizer when you use this soil?	YES vs. NO
	Do you stop using chemical fertilizer when you use this soil?	YES vs. NO
	Does it increase rice resistance to drought or pests?	YES vs. NO
	Do you use less pesticides when you use this soil?	YES vs. NO
	Do you stop using chemical pesticides when you use this soil?	YES vs. NO
	Do you cultivate plants on mounds?	YES vs. NO
	What?	OPEN

Health	Do you use plants or animals from mounds in traditional medicine?	YES vs. NO
	What?	OPEN
	Why?	OPEN
	Do you consume wild plants or animals found on termite mounds?	YES vs. NO
	What?	OPEN
	How often?	OPEN
Economy	Do you sell plants, animals, mushrooms collected on mounds in the market?	YES vs. NO
	What?	OPEN
	How often?	OPEN
	How much do you earn each time?	OPEN

3.3 Abundance, distribution and lifespan of termite mounds

Thirty sampling plots (300 m x 300 m) were selected within paddy fields along the toposequence at the Chrey Bak observatory (Figure 7). For each plot, the position of the centre of LMs and TNs, as well as the plot boundaries, were recorded with a GPS tracker (Garmin GPSMAP 64s) during the dry season from December 2019 to February 2021. We also inventoried in the field for each LM their dimension (height and circumference), the presence of woody vegetation around and we collected species samples for later determination in the laboratory.

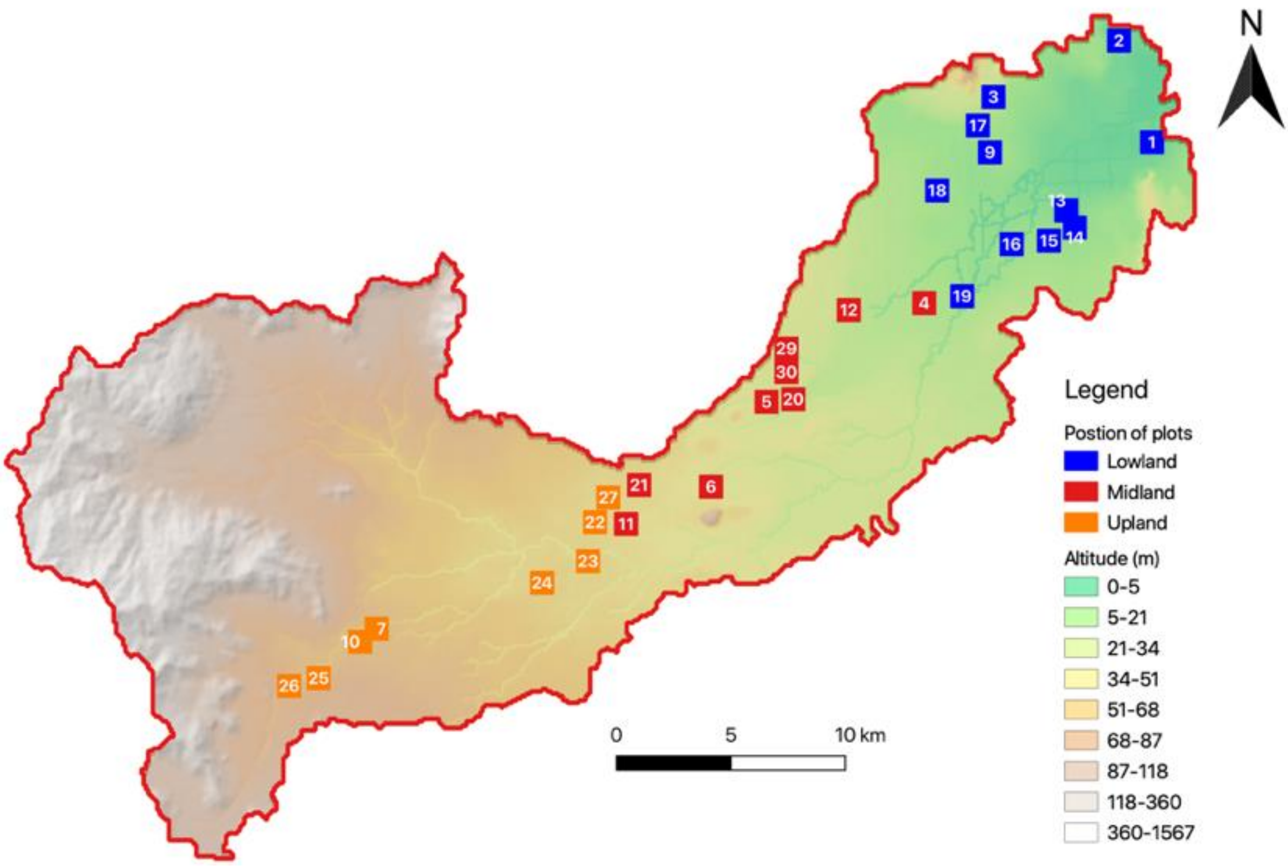

Figure 7. Locations of 30 plots used to the measure of lenticular mound and termite nest densities and distributions. The catchment is arbitrarily divided into a lowland (in blue), a midland (in red), and an upland (in orange).

Based on our field measures, we estimated the error associated to the identification of LMs from Google Earth (GE) images. Since LMs could not directly be seen using google earth images, we used the vegetation associated to LMs as target objects. This error was negligible (results of the model accuracy are shown in appendix 6 (A5).

In order to determine if LMs observed in the field were already associated with woody vegetation in the 50s, we used historical aerial images. We flagged all LMs surveyed in the field that had some woody vegetation nearby on the historical images. For this purpose, we processed 69 digitized historical aerial photographs from the French Institute Geographique National (IGN), acquired from the 10th to the 28th of February 1953. The metadata from IGN only indicated the focal length of the camera (125 mm), the flying height above mean sea level (5100-5700m), and the frame size of the camera (120 × 170 mm). According to this information the black-and-white panchromatic photos presented a scale of ca. 1:40 000. 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 and Zisserman, 2004) for image orientation, followed by dense image matching operated in a multi-view stereo fashion (Forlani et al., 2015). In general, the software is used for non-metric digital cameras, which do not feature a specific frame on borders. Without neither a calibration certificate nor any information about the used camera, the software computes the unknown camera calibration parameters based on the points extracted during SfM (Barazzetti et al., 2011). When dealing with digitized photos from airborne metric cameras, some considerations on how to deal with the interior orientation had to be applied as a preprocessing step. After the scan the coordinates of the principal point from one digitally scanned aerial image was not guaranteed to be identical to the next due to asymmetrical scanning and possible physical distortion of the film. In our case the image dimensions in pixels of the scanned historical aerial photographs varied from 5043 to 5162 in X and from 3763 to 3862 in Y. Unequally cropped images could not be readily mapped to a unique camera reference system. 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 in order 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 a nearest neighbor resampling. Another point was the fact that the image borders, where fiducial marks and other metadata appear, could interfere with the automated feature detection algorithm used in SfM workflows and could need to be masked. Therefore, a shapefile was produced to crop the images and to mask the information of the camera frame and the fiducial marks on the images. Correcting these misalignments assured that all of the images contained the same pixel size (4902 × 3416) and grid alignment, without which automatic tie point identification would be impossible. Some ground control points (GCP's) were necessary for establishing the ground coordinate system and to mitigate the instability in successive bundle block adjustment (BBA) (Verhoeven et al., 2015). The real problem in the case of old archive photos from IGN was how to derive the reference ground coordinates of GCP's. The objects in the photo could have dramatically changed from the time when the photo was captured and the present time. A solution to derive GCP's was to obtain their horizontal positions from recent orthoimages and the elevation from a Digital Terrain Model (DTM). For our region recent orthophotos and a precise DTM did not exist. Thus, GE was used to obtain the horizontal position of GCP's, with approximate georeferencing of 168 landmarks and the global DTM TanDEM-X was used for the altitude of the GCP's. 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. In order to assess the horizontal accuracy of the orthomosaic, a qualitative analysis was done by overlaying GE images. The agreement was very good throughout the image, and we estimated the horizontal precision of the orthomosaic at around ± 5 m.

To concentrate our study only on the area covered by paddy fields in 1953 (IGN) or 2021 (GE), we manually delineated the area occupied by paddy fields inside each sample plot at the fix scale between 1:600 to 1:800 on both GE and IGN (Figure 8) images using digitizing tools in QGIS. For further processing we kept only the LMs inside these two study areas. Finally, this processing excluded not only some areas of the plots but also some plots totally. First, the historical aerial photographs from IGN cover only the lower and middle part of the catchment. Seven plots in the upper part of the catchment not covered by the IGN image were excluded. Second, four sample plots were totally covered by scrubland in 1953. These plots were also excluded from the diachronic analysis (See Table 2 for a description of the selected plots).

Inside the two clearly defined study areas of paddy field we further digitized the area covered by the crown of trees or scrubs. We used this information for two analyses. First, to identify any relation between the number of LMs in each plot and the area covered by woody vegetation. Second, to calculate the evolution of the woody vegetation in and around paddy field between 1950 and 2021. The defined study area was also the backbone for other statistical analysis.

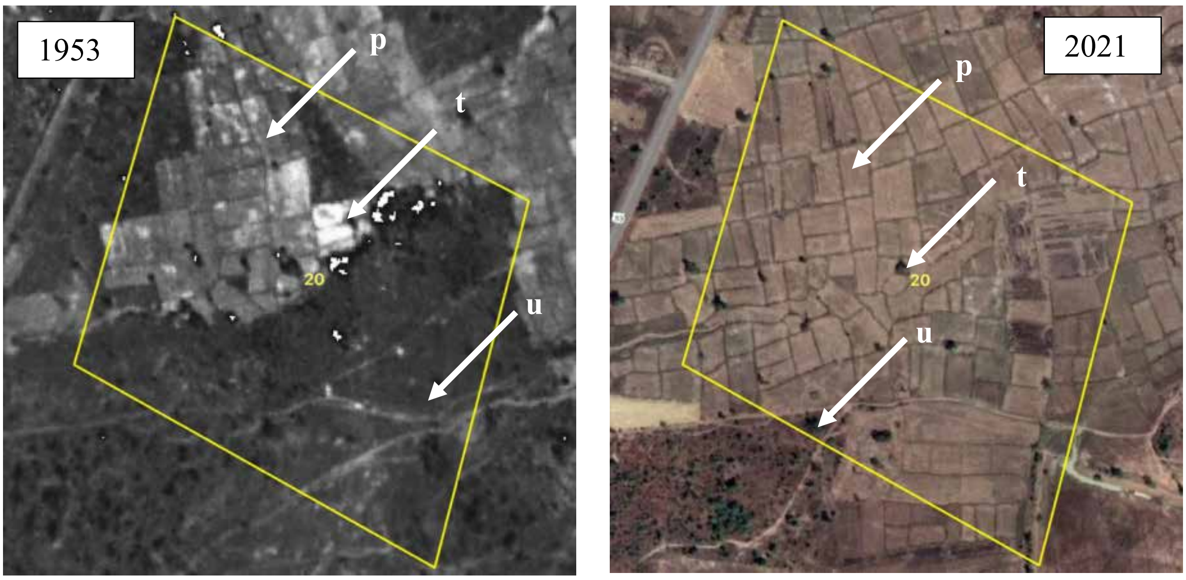

Figure 8. Example of images from IGN taken in 1953 and from Google Earth (2021) from the plot n°20 in the Chrey Bak catchment. Landscapes were differentiated into paddy fields (p) and uncultivated areas (tree covers (t) and unknown areas (u))

Table 2. Date, size (ha) and elevation (a.m.s.l.) of images obtained from Google Earth and the French Institute Geographique National (IGN) and the elevation data obtained from Mekong River Commission (2003)

IDplot	Area of plot (ha)	Mean Altitude of plot (m)	Date	
			Google Earth	IGN
1	8.98	5.89	2021-05-30	1953
2	11.18	9.36	2021-05-30	1953
3	5.97	27.40	2021-05-30	1953
4	10.45	23.50	2021-01-04	1953
5	8.87	38.33	2021-01-04	1953
6	14.58	48.69	2021-01-04	1953
7	12.00	78.67	2019-07-14	not covered
8	10.54	78.90	2019-07-14	not covered
9	10.74	19.22	2021-05-30	1953
10	9.99	79.00	2019-07-14	not covered
11	12.60	55.00	2019-10-26	1953
12	10.61	29.00	2021-01-04	1953
13	10.04	14.11	2021-05-30	1953
14	9.34	15.11	2021-05-30	1953
15	9.85	18.70	2021-05-30	1953
16	9.62	18.00	2021-05-30	1953
17	13.25	22.17	2021-05-30	1953
18	10.27	20.56	2021-01-04	1953
19	8.97	18.11	2021-05-30	1953
20	9.11	36.89	2021-01-04	1953
21	8.99	58.11	2019-10-26	1953
22	9.15	57.00	2019-10-26	1953
23	5.57	60.75	2019-10-26	1953
24	8.06	62.00	2019-10-26	not covered
25	6.68	73.00	2019-07-14	not covered
26	8.80	74.33	2019-07-14	not covered
27	11.02	57.50	2019-07-14	1953
28	6.89	70.14	2019-07-14	not covered
29	6.45	33.00	2019-10-26	1953
30	2.53	41.00	2019-10-26	1953

Densities of LMs were then calculated for each plot using tools in ArcMap 10.7. Liner regressions were used to assess relationships between the density of LMs and TNs and the elevation along the toposequence, and to compare the density of LMs in the field to the copses observed on GE and IGN images. In addition, ANOVA and least significant difference (LSD) tests were used to compare differences between means, after first verifying that residuals were normally distributed using Shapiro-Wilk test. Differences among treatments were declared significant at the $P < 0.05$ probability level. All statistical calculations were carried out using R version 4.1.1 (https://www.r-project.org/).

The distribution of LMs was estimated using Spatial Statistic Tools in ArcMap 10.7, and using the Average Nearest Neighbour function (Pimpler, 2017) and the Multi-Distance Spatial Cluster Analysis (Ripley's K Function) with 99% confidence levels (computed confidence envelope). Example of Average Nearest Neighbor results show in A6. For this analysis, only 28 plots were used since the other two plots were excluded from the analysis due to their too low abundance of LMs ($n < 10$). Results are given in Chapter 7: Abundance and distribution of termite lenticular mounds in paddy fields in Cambodia. Comparison between the current situation and that observed in the 1950s.

3.4 Termite species identification

Termites were sampled in the 30 abovementioned plots after gently breaking all the TN that were found. Both worker and soldier termites were collected and preserved in 99% (v/v) ethanol for further identification in the laboratory. Termites were first identified morphologically in collaboration with Dr. Syaukani from the Biology Department, Faculty of Mathematics and Natural Sciences, Universitas Syiah Kuala, Indonesia. In addition, molecular identification was performed for some species for which there remained a doubt using single worker individuals, in collaboration with Dr. Vincent Hervé from the University of Tours. DNA of each sample was extracted using the NucleoSpin Tissue kit (Macherey-Nagel), following the manufacturer's instructions. These DNA extracts were used to amplify the mitochondrial gene encoding the cytochrome oxidase subunit 2 (COII) using the primer pair A-tLeu_modified 5'-CAGATAAGTGCATTGGATTT-3' and TK-N-3785 5'-GTTTAAGAGACCATTACTTA-3' (Dedeine et al., 2016), with the following PCR scheme: one cycle of 95 °C for 2 min, then 35 cycles of 95 °C for 45 s, 52°C for 60 s, and 72°C for 90 s, ending with one cycle of 72°C for 10 min. PCR reactions were performed in a total volume of 40 µL with the DreamTaq PCR Master Mix (Thermo Scientific). Amplicons were sent for bidirectional Sanger sequencing at Eurofins (Cologne, Germany). After quality trimming, forward and reverse sequences were assembled into contigs with SeqTrace version 0.9.0 (Stucky, 2012). Lastly, taxonomic assignment of the sequences was performed by sequence similarity searching using the BLASTN algorithm (Zhang et al., 2000) and the nt database (updated on 2022/01/20 and restricting the search to Blattodea sequences). To further refine these taxonomic assignments, we also performed phylogenetic analyses (see Appendix, A1-A4). Our sequences were aligned with top BLASTN hits sequences using DECIPHER v2.22 (Wright, 2016). The resulting alignments were trimmed and Smart Model Selection (Lefort et al., 2017) was applied to determine the best model of nucleic acid evolution of each alignment based on the Akaike Information Criterion. Subsequently, maximum-likelihood phylogenetic trees were built with PhyML 3.0 (Guindon et al., 2010) and branch supports were calculated using a Chi2-based parametric approximate likelihood-ratio test (aLRT) (Anisimova and Gascuel, 2006). Sequences have been deposited in GenBank under the accession numbers OM472585-OM472595.

3.5 Soil profile description

Four soil profiles were randomly described in paddy fields in November 2020, namely CB1 to CB4 (Figure 9), results of this section are given in Chapter 5: Identification of soil types in Chrey Bak catchment. The elevation of the profile study varied from -5m to 64m relative to sea level (a.m.s.l.). The elevation was determined using a GPS tracker (Garmin GPSMAP 64s). For each soil horizon, the soils were sampled, air-dried during several days and sieved at 2 mm before to be analyzed. The soil texture was measured using ASTM 152H hydrometer and the soil bulk density, and soil field water content were determined using 100 cm^3 sample rings and dried at 105 °C for 48 h. The soil horizons were delimited from their soil colour, which was measured using the Munsell colour chart-IUSS working group WRB (2022) master symbols and suffixes were used to describe soil profiles(see Table 3).

Table 3. Master symbols and suffixes that were used for descripting soil profile in Chrey Bak (IUSS Working Group WRB, 2022)

Symbol	Criteria
Master symbols	
A	Mineral horizon at the mineral soil surface or buried; contains organic matter that has at least partly been modified *in-situ*; soil structure and/or structural elements created by cultivation in ≥ 50% (by volume, related to the fine earth), i.e. rock structure, if present, in < 50% (by volume); cultivated mineral layers are designated A, even if they belonged to another layer before cultivation.
B	Mineral horizon that has (at least originally) formed below an A or E horizon; rock structure, if present, in < 50% (by volume, related to the fine earth); one or more of the following processes of soil formation: - formation of soil aggregate structure - formation of clay minerals and/or oxides - accumulation by illuviation processes of one or more of the following: Fe, Al, and/or Mn species; clay minerals; organic matter; silica; carbonates; gypsum - removal of carbonates or gypsum. *Nota bene*: B horizons may show other accumulations as well.
Suffixes	
c	Concretions or nodules (only used if following another suffix (k, q, v, y) that indicates the accumulated substance) [c like concretion].
g	Accumulation of Fe and/or Mn oxides (related to the fine earth plus accumulations of Fe and/or Mn oxides of any size and any cementation class) predominantly inside soil aggregates, if present, and loss of these oxides on aggregate surfaces (A, B, and C horizons), or loss of Fe and/or Mn by lateral subsurface flow (pale colours in ≥ 50% of the exposed area; E horizons); transport in reduced form [g like stagnic].
p	Modification by cultivation (e.g. ploughing); mineral layers are designated A, even if they belonged to another layer before cultivation [p like plough].
r	Strong reduction [r like reduction]
t	Accumulation of clay minerals by illuviation processes [t like German Ton, clay].
v	Plinthite (related to the fine earth plus accumulations of Fe and/or Mn oxides of any size and any cementation class) [the suffix v has no connotation].

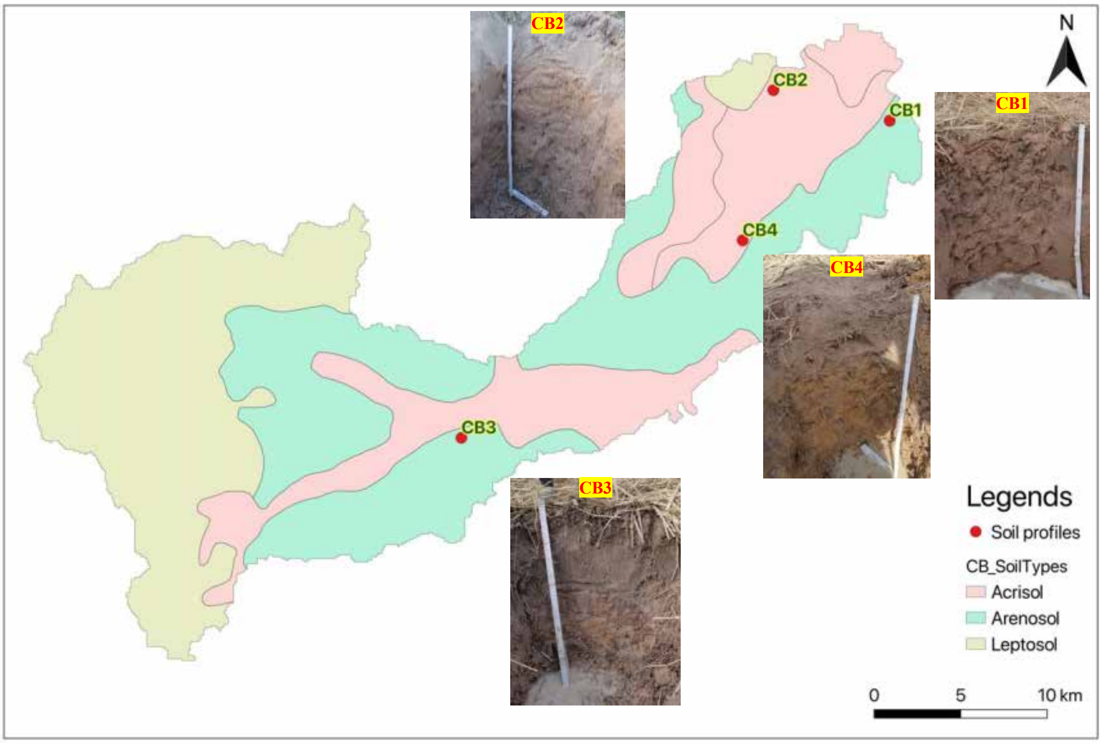

Figure 9. The locations of soil profiles in the Chrey Bak catchment (CB) conducted on Nov 2020 and map of soil types produced by JICA (2003)

3.6 Soil analyses

Soil sampling occurred during the dry season in February 2020 because sampling sites were unavailable during the rainy season when paddy fields were flooded. Soils were sampled in two positions in the catchment (see Figure 10). Three soil categories were identified based on their sand contents: Group I (GI, very sandy soils with > 80% sand), Group II (GII, moderately sandy, ~60% sand), and Group III (GIII, low sandy soils, ~40% sand). Five LMs were selected per soil group based on the presence of TN (n = 5 per soil group, locations of LMs can be found in the map shown in Figure 10). The influence of termite bioturbation on soil properties was measured via the sampling of soil in three locations: (i) in the topsoil (0–10 cm depth) of LMs, (ii) from the outer wall of TNs located on LMs, and (iii) in the surrounding soil environment in the paddy field (CTRL) at a distance of ~5 m ahead of each LM at 0–10 cm depth. The same procedure was repeated in the three soil groups (GI, II and III), giving a total of 3 soil groups × 3 locations (LMs, TNs and CTRL) × 5 replicates = 45 soil samples. Soil samples were air-dried at air temperature for several days and then were sieved to 2 mm.

The soil pH and electrical conductivity (EC) were determined in a 1:5 soil:water suspension (Pansu and Gautheyrou, 2006) with portable pH and EC devices. The soil particle size distribution was measured after the destruction of organic matter by 30% hydrogen peroxide (H_2O_2) and dispersion with sodium hexametaphosphate ($Na_6O_{18}P_6$). The proportion of sand (50–2000 µm) was obtained by sieving, while the proportions of silt (2–50 µm) and clay (< 2 µm) were obtained by using ASTM 152H hydrometers. The bulk densities of LMs and CTRL were measured using 100 cm^3 sample rings and dried at 105 °C for 48 h. Because of the hardness of TN soil, this method could not be used for measuring the soil bulk density of TNs, the paraffin-clod method (Blake, 1965) was used for TNs. Concentrations of C and N were analysed using a Thermo Scientific Flash 2000 organic elemental analyser. Total P was analysed by a spectrophotometer using a blank and standards prepared in the Olsen P extracting solution (Estefan et al., 2008) with a Thermo Scientific GENESYS 30 Visible Spectrophotometer. Exchangeable K was measured by the flame photometer method (Black et al., 1965) using S20 Superspec Series flame photometers. The saturated hydraulic conductivity (*Ksat*) was analysed in the laboratory using the falling head method (Reynolds and Elrick, 2002) with a *Ksat* device. Finally, the soil water holding capacity was determined at pF 0 by the sand box (Eijkelkamp) and pF 2.5, 3, 3.2, and 4.2 by the pressure plate method (Dane and Hopmans, 2002) using "Richards" pressure plate extractors.

Soil samples were analysed at IFPEN laboratory (Institut Français du Pétrole Énergies Nouvelles) with a Rock-Eval 6 device. This technique has been recommended for characterizing soil organic matter (Derenne and Quéné, 2015; Disnar et al., 2003) and has proven relevance in various contexts (Malou et al., 2020; Romanens et al., 2019; Sebag et al., 2016; Thoumazeau et al., 2020) and for studying the impact of soil engineering organisms (Schomburg et al., 2019, 2018; Le Mer et al., 2020). The method uses ramped pyrolysis of organic matter under an artificial air supply (N_2) between 200 and 650 °C and then the combustion of residual carbon under oxidative conditions between 200 and 850 °C. The released gases are quantified using a flame ionization detector (FID) for hydrocarbon compounds (HC) and infrared detectors (IR) for CO and CO_2. Qualitative and quantitative parameters are calculated by integrating the amounts of HC, CO, and CO_2 produced during thermal cracking of organic matter between defined temperature limits (Behar et al., 2001; Lafargue et al., 1998). Carbon contents were calculated by integrating the C moieties produced during thermal cracking and combustion-defined temperature limits, with TOC (%) calculated as the sum of all released carbon released at low temperatures from organic compounds and OrgC and MinC (%) consisting of organic and mineral carbon pools released at high temperatures. Soil organic matter quality was assessed with the hydrogen index (HI in mg HC/g TOC), calculated as the total amount of HC normalized to the TOC content. Soil organic matter thermal stability was assessed by combining two indices (denoted R- and I-index) calculated from five subdivided areas of the S2 thermograms related to HC (Sebag et al., 2016). By construction, the R-index relates to the thermally resistant and refractory pools of organic matter, while the I-index is related to the ratio between the thermally labile and resistant pools. As derived from a mathematical construct, these two indices may be inversely correlated when OM stabilization results from progressive decomposition of labile organic compounds and relative enrichment in refractory compounds. Then, in the I/R diagram, the same "decomposition line model" describes the decreasing labile pools and concomitant increase in more thermally stable pools, as observed in compost (Albrecht et al., 2015) and in soils (Sebag et al., 2016; Matteodo et al., 2018; Thoumazeau et al., 2020). I/R diagrams were used to calculate the deviation of I index values from LMs and TNs to those predicted from the regression line of the control soil.

Finally, since soils were sampled in different locations in the catchment, linear mixed models with elevation as random factor and Tukey tests were performed to assess differences between means for the different soil structures (LMs, TNs and CTRL) and soil groups (Group I to

III). Differences among treatments were declared significant at the P <0.05 probability level. All statistical analyses and visualizations were carried out with R version 4.1.1 (https://www.r-project.org/) using mainly "ggplot2" and "emmeans" packages. Results concerning this section can be found in Chapter 6.

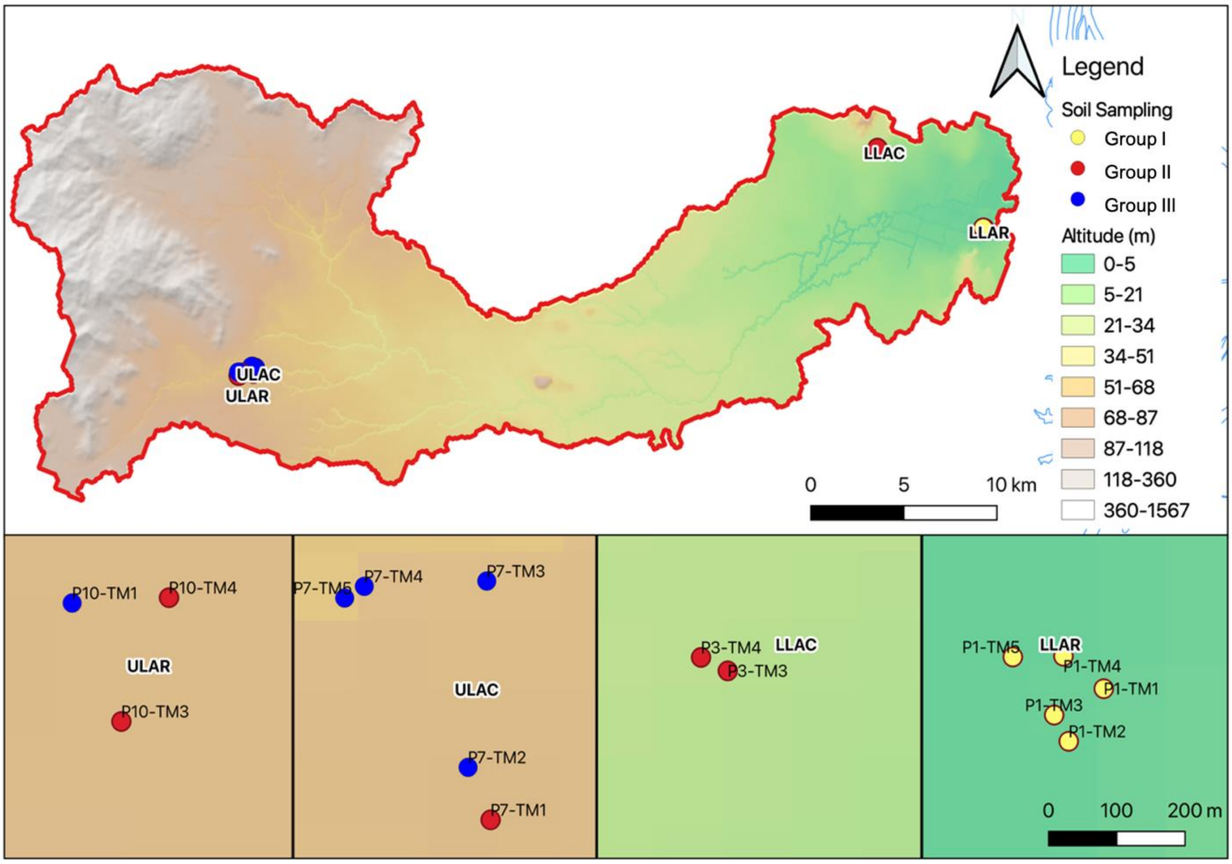

Figure 10. Locations of the soil samples used to describe lenticular mounds and termite mound nest properties. ULAR: Upland Arenosols, ULAC: Upland Acrisols, LLAR: Lowland Arenosols, LLAC: Lowland Acrisols

Chapter 4 . Perceptions and utilizations of termite mounds in Cambodia

Results from this chapter have been submitted to *Agronomy for Sustainable Development* on March 7th 2022 in the present form. It aims at describing termite diversity and questioning the perception and utilization of termite lenticular mounds in Cambodia using a survey carried out in the long term observatory of Chrey Bak.

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Abstract

In the Lower Mekong Basin, paddy fields often appear as mosaics, with soil mounds covered by trees or other plants in a spotty distribution. These soil mounds are commonly named 'termite lenticular mounds' (LMs) because termite bioturbation is considered to be at their origin. LMs host a large diversity of animals and plants, increasing landscape patchiness. Because the preservation of these islands of biodiversity is threatened by modern agricultural practices, the aim of this study was to quantify their abundance and the services they provide to the local population. The diversity of termites, the abundance of LMs and their use by the population were quantified in a catchment in Cambodia. The LM density reached ~2 mounds ha^{-1}, and the termite diversity was dominated by two species, *Macrotermes gilvus* and *Globitermes sulphureus*. Most of the interviewees used LMs for increasing the fertility of their field and for the cultivation of rice and other plants (e.g., sponge gourd and pumpkin). In addition to their potential to increase plant productivity, the survey revealed that animals (rats and snakes), mushrooms and 13 plant species found on or in LMs were consumed by the population. In addition to potentially contributing to an increase in food diversity, LMs also impacted farmers' health by allowing access to 20 medicinal plant species and indirectly via a reduction in pesticide use. In conclusion, this study is a first attempt to quantify the large number of services provided by LMs in the Lower Mekong Basin. This increase in the knowledge of the diversity of environmental and socioeconomic services provided by LMs is likely to contribute to their preservation and provide a basis for the sustainable management of biodiversity in paddy fields in the Lower Mekong Basin.

Keywords: Paddy field, termite mounds, soil fertility, utilization, ecosystem services, food diversity, medicinal plants

4.1 Introduction

The “One Health” concept and framework (Destoumieux-Garzón et al., 2018) have now expanded beyond emerging infectious diseases and zoonoses to incorporate a wider suite of health issues, such as the interdependence between the preservation of the environment, biodiversity and human wellbeing (i.e., the environmental, animal and human health concepts, respectively) (Lebov et al., 2017; Bongaarts, 2019). This approach has a special general resonance in Southeast Asia, especially in the Lower Mekong Basin (LMB), notably because of the current pandemic situation but also because this region is undergoing dramatic climatic, environmental and societal changes (Mainuddin et al., 2011; Thilakarathne and Sridhar, 2017; Trisurat et al., 2018; Abhishek et al., 2021; Kang et al., 2021). The rapid economic growth and intensification of agricultural practices (Sebesvari et al., 2012; Bruun et al., 2017; Lam et al., 2017) have increased the homogenization, simplification and pollution of terrestrial, and thereafter aquatic ecosystems (Matson et al., 1997; Dale and Polasky, 2007; Firbank et al., 2008; Emmerson et al., 2016). In this context, however, the diversity of services delivered by agro-ecosystems as well as the mechanisms associated with the preservation of biodiversity by local actors remain poorly evaluated.

Rice is the most cultivated plant in the LMB (Cramb, 2020). Understanding the services derived from paddy fields in LMB requires a holistic perspective, taking into account not only the production and quality of rice but also the multifunctionality of agroecosystems and the diversity of regulating, provisioning, cultural and supporting ecosystem services they provide (Zabala et al., 2021). Traditionally, services have focused on the production of rice and the emission of greenhouse gases (Lantin et al., 2000), the quality of water and the cycling of nutrients (Berg et al., 2012). The relationship between biodiversity and human health remains, however, underestimated in paddy fields. In the LMB, paddy fields often appear as mosaics with soil mounds covered by trees or other plants spotted within large surfaces that are used for the cultivation of rice. These mounds are commonly named ‘termite lenticular mounds’ (LMs) because they are expected to be produced by termites, although their origin remains unknown and because they can host a large diversity of other invertebrates (Choosai et al., 2009). Because of their size (~6 m^3 of soil), LMs increase heterogeneity at the landscape scale. Their abundance and physical and chemical properties are unknown, but research carried out in Africa suggests that they could be very old (Erens et al., 2015), constitute patches of nutrients (McCarthy et al., 1998; Sileshi et al., 2010; Jouquet et al., 2011, 2016, 2017; Chen et al., 2021) and positively impact the resistance of plants to environmental hazards (e.g., drought) (Bonachela et al., 2015; Padonou et al., 2020). Regarding their improvement of soil properties, LMs have been reported to be used as soil nutrient amendments in Africa (Dossou-Yovo et al., 2014; Enagbonma and Babalola, 2019; Tilahun et al., 2012, 2021). They can also improve human health because LM soil and some of the plants growing on them are consumed or used as traditional medicines (Sileshi et al., 2009; Dossou-Yovo et al., 2014).

Therefore, since information regarding the services provided by LMs in the LMB are limited to a descriptive report of Miyagawa et al. (2011) in Laos and to an ecological study of Choosai et al. (2009) in Northeast Thailand, the aim of this study was to determine the diversity of termites associated to LMs, the abundance of LMs and their use by population in Cambodian paddy fields. Our main hypothesis was that farmers' preservation of LMs relies on the use of these natural resources due to their positive effect on rice yield and potentially on dietary diversity and health.

4.2 Results and discussion

4.2.1 Mound density and termite diversity

On average, LM density reached 2.1 mounds ha^{-1} in the Chrey Bak catchment (Figure 11). This value was equivalent to the value measured in paddy fields in northeast Thailand (~2 mounds ha^{-1}, Choosai, 2010), but it was lower than the value measured in Asian tropical forests (> 10 mounds ha^{-1}) (Matsumoto, 1976; Inoue et al., 2001; Jouquet et al., 2017a). This difference in density confirmed the lower abundance of LMs in agricultural land than in protected areas (Ekundayo and Aghatise, 1997; Codjovi et al., 2020; Davies et al., 2020). If LMs were observed in more natural environments, such as forests, in the catchment (Muon, pers. com.), the fact that LMs were observed in paddy fields also reflects their possible utilization by farmers, as shown in Africa and Laos (e.g., Miyagawa et al., 2011; Yêyinou et al., 2017; Chisanga et al., 2020; Codjovi et al., 2020).

In total, 11 termite species belonging to 9 genera were found in the Chrey Bak catchment: *Macrotermes gilvus, Globitermes sulphureus, Odontotermes* spp. (2 species among DNA sequences), *Hypotermes* sp., *Pericapritermes* sp., *Nasutitermes* sp., *Coptotermes gestroi, Microcerotermes* spp. (2 species among DNA sequences), and *Termes* sp. Most of TN were produced by only two species, namely *M. gilvus* and *G. sulphureus.* These two types of TN were very different and could easily be recognized from their following characteristics. The species *M. gilvus* belongs to the Macrotermitinae subfamily, and its mound nests are mostly made of soil sampled at several cm depths (Inoue et al., 1997; Jouquet et al., 2011, 2017b). Therefore, their nests have a light color and are extremely compact. Conversely, *G. sulphureus* produces rounded mound nests from a mixture of soil and faeces, giving its nests a characteristic dark color (Noirot, 1959). Therefore, *G. sulphureus* nests are more fragile than those of *M. gilvus*. Nests of *M. gilvus* and *G. sulphureus* were mostly observed on LMs with densities of 1.45 and 1.31 mounds ha^{-1}, respectively. Nests of the other termite species were also observed in Chrey Bak but they were less obvious to identify in the field and their occurrence (< 0.05 mounds ha^{-1}, except *Pericapritermes* sp. and *Microcerotermes* sp. with 0.64 and 0.68 mound ha^{-1}, respectively), and their sizes were limited in comparison with those produced by *G. sulphureus* and *M. gilvus.*

Although the origin and dynamics of LMs are unknown, studies carried out in Africa and India have suggested that they might result from the degradation and colonization of abandoned TN (Josens et al., 2016; Harit and Jouquet, 2021). In line with this hypothesis, farmers from Chrey Bak mostly attributed the origin of LMs to nests of *M. gilvus*, although they were aware that other termite species, as well as other organisms, might also impact LM properties and growth. Indeed, the LMs of *M. gilvus* in Cambodian paddy fields were described as abundant in the 1950s and it was also reported that abandoned TNs were often occupied by *Odontotermes* sp. (Noirot, 1956). While 32.8% of the interviewees had no opinion on the age of LMs (i.e., reply to the survey = "I don't know"), a similar proportion believed that mounds were between 10 and 39 years old (32.8%), while others believed that they were younger (< 10 years old, 19.7%) or older (8.2% between 40 and 60 years old, 6.6% between 60 and 100 years old). Therefore, although dating of LMs is needed to confirm these observations, these results suggest that LMs were likely to be much younger than those found in Africa (up to 2,000 years in Africa, Moore and Picker, 1991; Erens et al., 2015) and in Brazil (> 4,000 years, Martin et al., 2018). Moreover, these results must also be considered in regard to the utilization of LMs by farmers. The rapid production of these LMs (< 2 human generations) is likely to be associated with the sustainable utilization of this material as a soil amendment. Conversely, if LMs need more than several human generations to be produced, their exploitation is likely to be associated with an irreversible degradation of these natural resources.

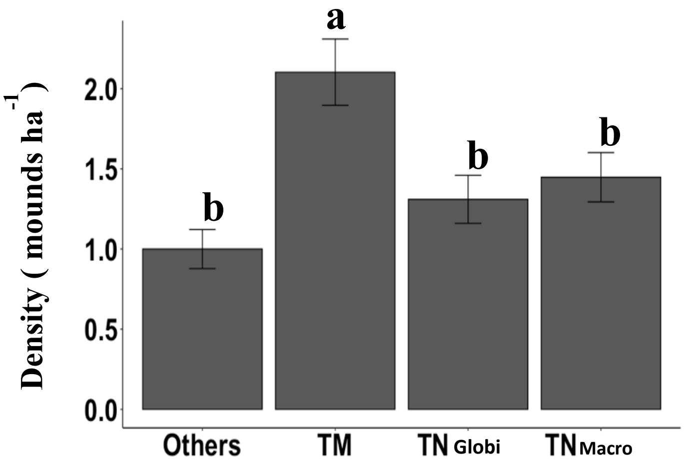

Figure 11. Average density (in mounds or nests ha^{-1}) of termite lenticular mounds (LMs) and termite nests (TNs) produced by *Macrotermes gilvus* (TN_{Macro}) and *Globitermes sulphureus* (TN_{Globi}) in the Chrey Bak catchment, Cambodia. 'Others' represents the sum of the density of TNs produced by species other than *Macrotermes gilvus* and *Globitermes sulphureus* (i.e., *Odontotermes spp.*, *Hypotermes sp.*, *Pericapritermes sp., Nasutitermes sp., Coptotermes gestroi, Microcerotermes spp., and Termes sp.*). Bar plots with the same letters are not significantly different at $P = 0.05$ (n = 30 plots).

4.2.2 Ecosystem services provided by termite mounds

In Chrey Bak, most of the interviewees used LMs for either agronomic purposes or for improving their health and living standards. The utilization of termite construction for increasing soil fertility is a worldwide practice (Suzuki et al., 2007; Miyagawa et al., 2011; Tilahun et al., 2012; Chisanga et al., 2019, 2020a, 2020b; Apori et al., 2020a, 2020b; Subi and Sheela, 2020). In our study, 95% of the respondents reported the utilization of LMs as an amendment for improving soil fertility (Figure 12) and 92.3% of the interviewees thought that LM application increased rice yield (Figure 13). The survey also provided evidence for utilization of LMs for growing cultivated plants, mostly for the farmers' own consumption (57.6% of the interviewees, see Table 4 for a list of the plants that are cultivated directly on LMs and those that were fertilized by LM soil amendment). Therefore, this result confirms the positive impact of LMs on food and probably dietary diversity, as observed in Laos by Miyagawa et al., (2011).

A large majority of farmers responded that LMs are used as a whole without preselection of the material (73% of the interviewees). The remaining (22%) reported preselection of the oldest section of LMs (14%), a selection of TNs (7%) or a combination of both (2%). These results are particularly interesting because they suggest a deep knowledge of some farmers on LM and TN properties. Indeed, although both LMs and TNs have better soil physical and chemical properties than paddy field soil (Muon et al., submitted), the potential use of TN soil is likely to be higher than that of LM soil due to its higher amount of clay and higher soil pH, possibly due to the presence of carbonates (Muon et al., submitted, see Chapter 6: Termite mounds as patches of soil fertility in Cambodian paddy fields). Moreover, the interview also showed that LM soil is applied more frequently if farmers grow vegetables (2-3 times a year for 11.5% of the interviewees and until 10-18 times a year for 1.6% of interviewees) than rice (frequency = once every year to once every 4 years for 75.4% of interviewees), probably because of the higher demand of vegetables for nutrients but also because the application of LM soil is likely to increase the water holding capacity of soil (Muon et al., submitted). However, since LMs were mostly reported by farmers as private goods (65.6% of the replies against 34.4% that described LMs as common goods), some farmers also mentioned that the frequency of application depends on the availability of mounds in their land. In addition to soil fertility, farmers also reported that LM application allowed for a reduction (19.9% of the interviewees) or absence of chemical fertilization (68.4%). Farmers also mentioned that LM application improved the resistance of rice to drought and/or pests (51.5%). A significant proportion of the interviewees also mentioned that LM application allowed a reduction (41%) in the use of pesticides, and the cessation of chemical pesticide use in paddy fields (38.4%). These responses are in line with studies carried out in Africa which showed that LM soil properties positively influence water dynamics and soil quality as well as plant resistance to drought and pests (Bonachela et al., 2015; Enagbonma and Babalola, 2019). These findings are also likely to be explained by the higher soil organic matter and clay contents and therefore higher water holding capacity at high potential (pF 4.2) of LM soil than the surrounding soil (Muon et al., submitted). Moreover, additional analyses also showed that LMs contain more available Si (43.18 *vs.* 5.1 mg kg^{-1}, Meunier and Muon pers. com.), which is likely to increase rice resistance to water, insect pest and disease stresses (Datnoff et al., 2001; Sacała, 2009; Alhousari and Greger, 2018).

In addition to their potential to increase plant productivity, the survey revealed that 78% of the respondents feed on animals (mainly rats and snakes) and at least 10 different plants (fruits and vegetables) found on or in LMs (Table 5). LMs have been considered hotspots of biodiversity in paddy fields because they constitute a refuge for animals and plants (Choosai et al., 2009) as well as a specific habitat for soil microorganisms (Baker et al., 2020). Indeed, the specific soil properties (Muon et al., submitted) and shade from the presence of trees on LMs offer a favorable environment for animals and plants during the dry season while it is the only exposed areas of paddy fields that are not flooded during the rainy season. If all the plants and animals found on LMs were used by most of the interviewees, when eaten, these food items would help increase the dietary diversity and could contribute to improving the consumption of nutrients such as vitamins and minerals. Quantitative nutrition surveys are now needed to assess the contribution of LM foods to the nutrient requirements of farm families.

As evidenced in other environments, plants growing on LMs can also be used in traditional medicine (Choosai, 2010; Dossou-Yovo et al., 2014; Sileshi et al., 2009). In Chrey Bak, 47% of the interviewees mentioned that they use plants growing on LMs for their medicinal properties during postpartum care (16.4%), for diseases such as malaria and fever (14.8%), as well as for bodily pain (3.3%) and digestion problems (1.6%) (Table 5).

Finally, approximately 10% of interviewees mentioned that they can earn small income by selling plants and mushrooms growing on LMs in the market (i.e., mushrooms (4.8%), tamarinds (3.2%), bamboo (3.2%), bamboo shoots (1.6%), and tomatoes (1.6%)). However, farmers generally reported that economic benefits are low, especially because plants are collected only once to twice a year, with the exception of tomatoes which can be sold up to 4 times a year (e.g., 1.25 to 2.25$ each time they sell mushrooms, 1.25$ for bamboo shoots, 8.75 to 10$ for bamboo, and approximately 125$ for tomatoes).

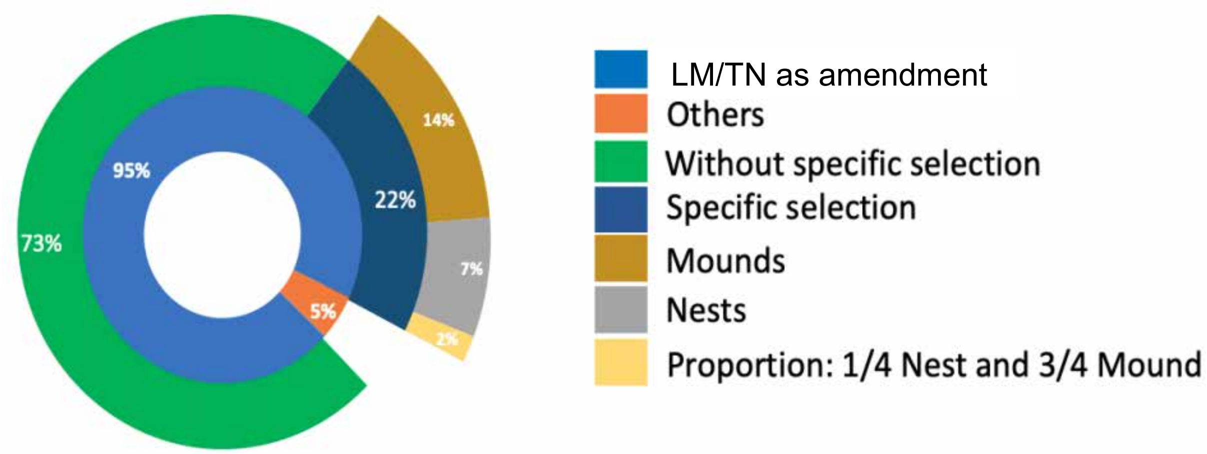

Figure 12. Doughnut chart representing the proportion of positive answers to the question "Do you use termite mounds as soil amendment" (in blue, first chart). The section in green represents the proportion of farmers using lenticular mounds (LMs) without selecting a specific type of termite material (opposite = selection of the material, in dark blue) (second chart). The section in brown represents the proportion of farmers selectively using the oldest part of LMs against the sections in grey and yellow, which display the proportion of farmers selectively using termite nests growing on mounds or a combination of both (1/4 nest vs. ¾ mound), respectively (third chart).

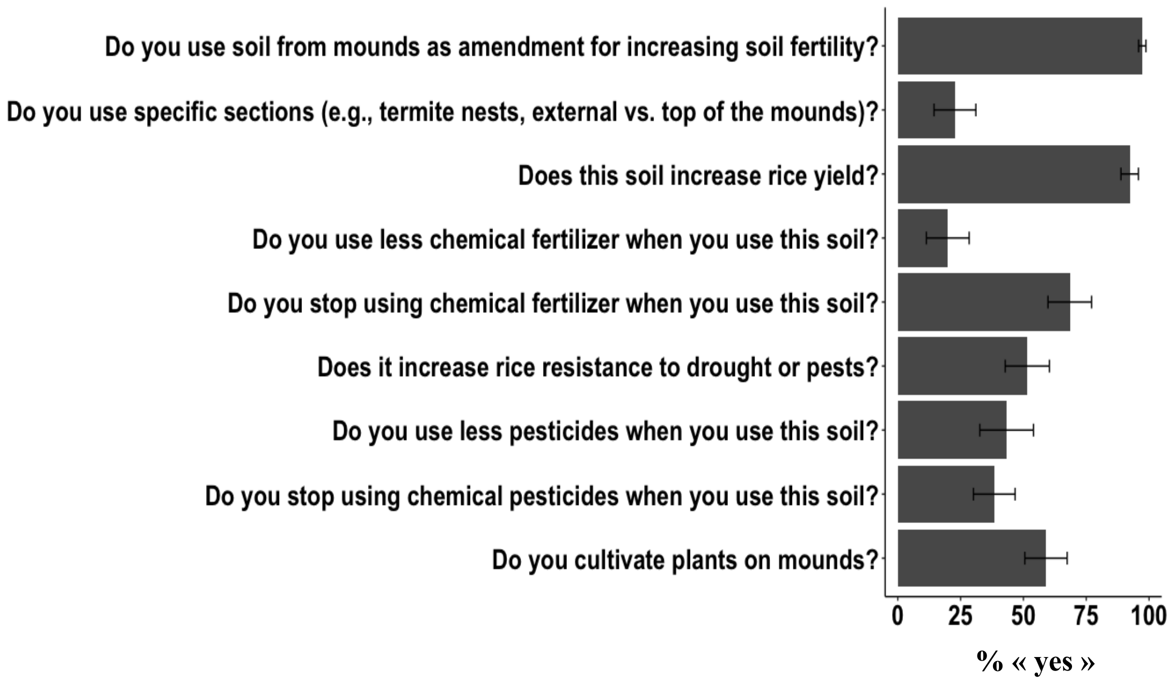

Figure 13. Proportions of positive answers related to the use of termite mounds for increasing soil fertility.

4.3 Conclusion and perspectives

Our study confirmed the traditional utilization of termite constructions by farmers, as reported previously in Africa and Laos (Miyagawa et al., 2011; Enagbonma and Babalola, 2019; Tilahun et al., 2012, 2021). In addition to potentially contributing to increasing food diversity, LMs can also impact farmers' health by allowing access to medicinal plants and indirectly well-being, via a reduction in pesticide use. However, land use changes in the LMB are resulting in the rapid disappearance of LMs, and with them in a loss of numerous ecosystem services. For instance, in northeast Thailand, their density dropped from more than 10 ha^{-1} in the 1970s, a density equivalent to that found in protected forests in Asia, to less than 1 ha^{-1} nowadays (Choosai, 2010). At our study site, 54.1% of the interviewees mentioned that mounds were more abundant in the past. This reduction in density could be explained by (i) an overexploitation of these natural resources, most likely because of the belief that LMs can rapidly be regenerated (in less than 2 generations), (ii) a lower utilization of the services provided by LMs, and/or (iii) a reduction in the ecological niche of termites (i.e., a reduction in tree density and food availability). Indeed, 65.6% of the interviewees reported that LMs were more useful in the past than currently, in particular because it is now more convenient to use chemical fertilizer than in the past (11.5%).

This study is a first attempt to quantify the services provided by LMs in the LMB. If LMs are threatened by intensive agricultural practices, it is possible that their preservation could be improved by a holistic understanding of the environmental and sociocultural services they provide to the local population. This knowledge could be useful for bringing about new sustainable agricultural practices that are less dependent on chemical fertilizers and pesticides. In particular, an economic assessment of LMs with quantitative economic surveys is needed in considering both the positive (e.g., resistance to drought and pests, use of medicinal plants, lower use of pesticides, diversity of crops, positive impact on rice yields, income, human nutrition and health) and negative (e.g., less area for rice, presence of pests including termites such as *Coptotermes gestroi,* and rats hosting pathogens) impact of termites and LMs on human wellbeing (e.g., rice yield, income, access to better health, food security, etc.)

Table 4. List of the plants fertilized by lenticular mound soil (LM) (LMs as amendments), and fertilized by LM soil and/or cultivated on LMs (LMs as amendments and media). The number of answers is given as the frequency from the total number of replies (n = 61 interviewees).

	Plant list
LMs as amendments	rice (95.08%) sponge gourd (11.48%) jackfruit tree (6.56%) mango tree (4.92%) cabbage (3.28%) cucumber (3.28%) lemon tree (3.28%) papaya tree (3.28%) aloe vera (1.64%) catjang (1.64%) pineapple (1.64%) tomatoes (1.64%)
LMs as amendments and media	banana (13.11%) pumpkin (11.48%) lemon grass (6.56%) water spinach (6.56%) garlic (4.92%) watermelon (4.92%) betel (1.64%) custard apple (1.64%) eggplant (1.64%) tamarind tree (1.64%)

Table 5. List of mushrooms, plants and animals found on termite mounds (LMs) and either consumed or used for medicinal purposes. The number of answers is given as a percentage of the total number of replies (n = 61 interviewees), and names of the items in Khmer are given in parentheses.

	Names	Section consumed/used	Type of disorder treated
Items used as food	Mushroom (Phsaet), 67.57%	All	
	Bamboo shoot (Tom pang), 8.20%	Stem	
	Erioglossum rubiginosum (Roxb.) Blume (Daun kay or Chonlous), 6.56%	Fruits	
	Flacourtia indica (Burm.f.) Merr (Kro kob prei), 4.92%	Fruits	
	Azadirachta indica A.Juss. (Sdao), 3.28%	Leaves, flowers	
	Aganonerion polymorphum Pierre (Thnoeng), 3.28%	Leaves, flowers, fruits	
	Snake (Pos), 3.28%	Meat	
	Rat (Kandor), 3/28%	Meat	
	Tamarindus indica L.(Ampil), 1.64%	Fruits, leaves	
	Alocasia macrorrhizos (L.) G.Don (Kdat), 1.64%	Stem	
	Moringa oleifera Lam (Mrom), 1.64%	Leaves	
	Crateva magna (Lour.) DC. (Tonlea), 1.64%	Fruits	
	Borassus flabellifer L. (Thnaot), 1.64%	Fruits	
	Syzygium cumini (L.) Skeels (Pring), 1.64%	Fruits	
	Coccinia grandis (L.) Voigt (Bas), 1.64%	Leaves, fruits	
Items used as medicine	*Aganonerion polymorphum* Pierre ex Spire (Thnoeng), 8.20%	Leaves	Malaria and fever
	Chromolaena odorata (L.) R.M.King & H.Rob (Tontrean khet), 8.20%	Part of plant	Malaria and fever
	Casearia grewiifolia Vent (Chruoy), 6.56%	Stem	Postpartum care
	Azadirachta indica A. Juss. (Sdao), 4.92%	Leaves	Malaria and fever, postpartum care

Diospyros helferi C.B. Clarke (Trayung), 3.28%	Part of plant	Malaria and fever, and postpartum care
Erioglossum rubiginosum (Roxb.) Blume (Daun kay or Chonlous), 1.64%	Fruit	Malaria and fever
Syzygium cumini (L.) Skeels (Pring), 1.64%	Stem	ND
Streblus asper Lour. (Snay), 1.64%	Stem	ND
Ficus hispida L.f. (Lvea), 1.64%	Stem	Malaria and fever
Drynaria quercifolia (L.) J.Sm (Borbrak), 1.64%	ND	Malaria and fever, and postpartum care
*Xylia xylocarpa (*Roxb.*)* W.Theob. (Sokrom), 1.64%	ND	Postpartum care
Dillenia hookeri Pierre (Phlou bat), 1.64%	ND	Postpartum care
Morinda citrifolia L. (Nhor), 1.64%	ND	ND
Atalantia citroides Pierre ex Guill (Krauch prei), 1.64%	Roots, leaves	Postpartum care
*Alocasia macrorrhizos (*L.*)* G.Don (Kdat), 1.64%	Part of plant	Digestion
Moringa oleifera Lam.(Mrom), 1.64%	Leaves, seeds, bark	Digestion
Capparis micracantha A.Rich. (Khancher Bay Dach), 1.64%	Stem, root, seed	Pain
Strychnos nux-vomica L. (Sleng), 1.64%	Part of plant	Malaria and fever
*Crateva magna (*Lour.*) DC.* (Tonlea), 1.64%	Roots, flowers, stem	Pain
Passiflora foetida L. (Sav mao prei), 1.64%	Fruit, stem	Malaria and fever

Chapter 5 . Identification of soil types in Chrey Bak catchment

Since Chapter 4 highlighted the use of termite mound soil to improve soil fertility, the next step taken in this thesis was to measure the soil properties of termite mounds. For this, a spatial approach was necessary in order to take into account the diversity of soils observed in the Chrey Bak catchment. Based on JICA's proposal to classify soils into Arenosol and Acrisol, termite mound soil samples were first analyzed in these different environments (Chapter 6). However, we quickly realized that the classification of soils into Arenosol and Acrisol was not appropriate for describing soil properties. The following chapter describes the soil properties along the catchment and confirms that the classification proposed by JICA was not relevant. This chapter proposes to differentiate the soils into three groups based on their sand content.

5.1 Introduction. An historical classification of soils in Cambodia

In Cambodia, soils were classified based on the parent rock or material into three main groups: soils formed on alluvial material, basalt, or sandstone (Saeki et al., 1959). The landscape of soils formed on basalt present gentle hilly lands and are most often modernly cultivated with rubber plantations. The unit of soils formed on sandstone soils are usually covered with either dense or open forests and comprise a large area in the regions of plateau, mountains, and surrounding the inland basin. Soils formed on alluvial deposits are found in a large area of the inland basin where they are mainly used for growing rice. They are widely distributed along the watershed areas of the Mekong River and around the Tonle Sap Lake and river, and they extend far towards the southern boundary. Soils formed on alluvial deposits have the lowest degree of acidity compared with the other two soil groups (i.e., soils formed on basaltic or sandstone parent rock), but their nutritional levels and cation exchange capacity have intermediate values (e.g., Saeki et al., 1959). Cambodian soils have also been classified by Crocker (1962) into 16 soil types: red-yellow podzols, latosols, planosols, plinthite podzols, cultural hydromorphics, grey hydromorphics, plinthitic hydromorphics, brown hydromorphics, alumisols, regurs, acid lithosols, basic lithosols, alluvial lithosols, brown alluvial soils, lacustrine alluvial soils, coastal complex. But since these previous works, no modern soil mapping with either Soil Taxonomy (Soil Survey Staff, 1999) or WRB (IUSS Working Group WRB., 2022) has been done.

Cultivated for the production of rice, alluvial deposits are important in Cambodia. Four groups have also been differentiated: Group A in the eastern region of the Mekong River (Steng Treng - Kratie), Group B in the eastern region of the Tonle Sap lake (Kampong Cham - Siem Reap), Goup C in the western region of the TonIe Sap lake (Sisophon - Phnom Penh), and Group D in the southern region of Phnom Penh (Phnom Penh- Svay Riem, Takeo). The four soil groups were ranged based on their basic soil fertility: Group A (highest nutrient contents) > Group C (highest exchange capacity, second highest nutrient contents, relative strong acidity) > Group D > Group B (lowest nutrient content and exchange capacity).

In 1997, the International Rice Research Institute (IRRI) conducted further studies focusing this time only on paddy fields in Cambodia. Eleven soil types were differentiated: Prey Khmer, Prateah Lang, Labansiek, Orung, Krakor, Bakan, Kbal Po, Kein Svay, Toul Samroung, Koktrap, and Kampong Siem (White et al., 1997). Prey Khmer and Prateah Lang are the two most dominant soil types (42% of the surface). These soils are very sandy, extending deeper than 50cm for Prey Khmer and less than 40 cm deep for Prateah soil. Prey Khmer soil accounts for 10-12% of the paddy fields. They can be found in most provinces but more significantly in Pursat, Kampong Chhnang, Kampong Speu, and Siem Reap. Prey Khmer, Prateach Lang, and Krakor.

This thesis was carried out in the observatory of Chrey Bak. According to the abovementioned definitions and classifications, soils in Chrey Bak belong to the Group C (because located in western region of the Tonle Sap lake) (Saeki et al., 1959). According to IRRI classification (White et al., 1997), six soil groups: Prey Khmer, Prateah Lang, Bakan, Orung, Kbal Po, and Krakor, were found in the lowland of the Chrey Bak catchment (Figure 2). Among them, Prey Khmer and Prateach Lang are the most dominant. According to Crocker (1962) , soils in the Chrey Bak catchment are also mostly red-yellow podzols (51%), Acid lithosols (32%), and in a lower extent planosols (3%) and lacustrine alluvial soils (3%). Red-yellow podzols extend almost in all the paddy fields of the catchment, while acid lithosols are mainly located in the mountain area and in small areas in the lowland. Finally, lacustrine alluvial soils are only dominant in the lowland. Finally, another study carried out by JICA (2003) described two main soil types in Chrey Bak: Arenosols (38%) and Acrisols (28.1%), although other soil types, such as Leptosols and Fluvisols, were also described in Figure 14.

These different classifications show the complexity to describe the soils in the Chrey Bak, and thus the need to better describe the soils observed in this observatory using an international reference system. Therefore, in order to better understand the soil diversity in Chrey Bak and their organization along the catchment, 4 profiles were made along the toposequence (see Chapter 5) and compared to 15 others described by Ann V. and Ket P. in 2012.

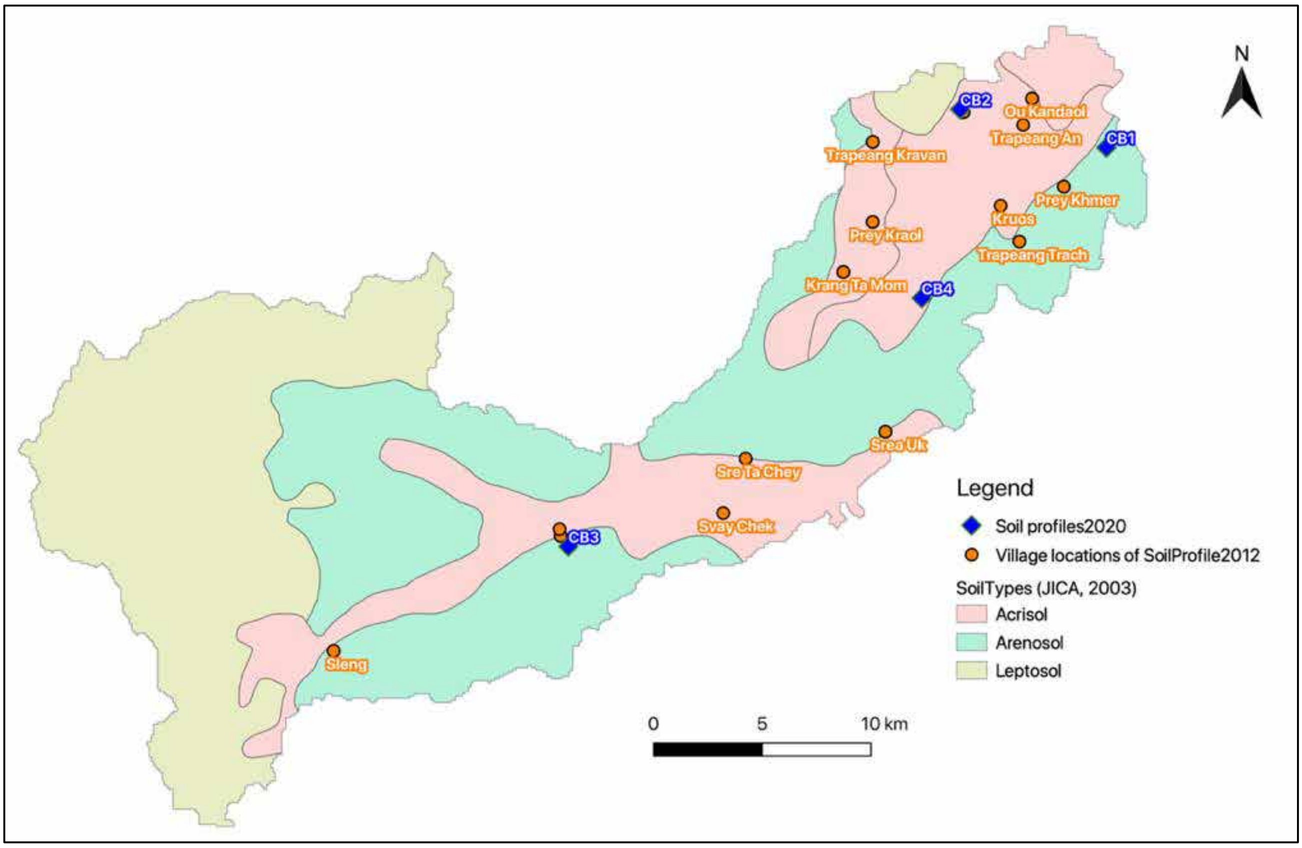

Figure 14. Map of soil types described by JICA (Acrisols are in pink, Arenosols are in green, and Leptosols are in grey) and locations of the soil profiles described in 2020 (in blue) and 2012 (in orange).

5.2 Results

The first soil profile (CB1) was located in the flood plain in the lower part (-5 m a.m.s.l.) of the catchment (see the location in Figure 14 and a photo of the soil profile in Figure 15, in a harvested area characterized by strong biological activities (presence of earthworm casts on the ground). The environment was relatively flat. The upper soil layer was compacted due to ploughing and the utilization of harvesting machine.

The soil was described as sandy Gleysols[1] with a first horizon (0-25 cm, Apr, see Table 3 given in section 5: Materials and Methods) described as an anthraquic[2] organo-mineral A horizon, reduced and ploughed. This soil horizon was sandy, its colour was mainly pinkish grey (5YR 7/2), with the presence of organic wet-spots that were dark greyish brown (10YR 4/2). This light colour corresponded to a claric[3] horizon with reductimorphic[4] features and a higher bulk density in the horizon below. The soil structure was massive and granular around rice roots with a few coarse porosities due to earthworms activity and plenty of fine roots in all directions (Figure 16). Results of soil physical properties analysis show that the first horizon had soil bulk density of 1.7 g cm^{-3}, soil porosity of 36.6%, soil moisture content of 12.5%, a clay content of 0.7%, a silt content of 8.8%, and a sand content of 87.9% (Table 6).

The second horizon (25-60 cm, Bg) was described as sandy, gleyic, with very coarse sand particles. This horizon was wet and loose. The soil colour was light reddish-brown (5YR 6/3) and the structure was particular and massive with inter-granular porosity, and contained few very fine roots in vertical direction. The water table was found at 60 cm depth. Results of soil physical

[1] **Gleysols** : soil with gleyic properties within 50cm of the surface, having no diagnostic horizons other than a histic, mollic, orchric, takyric, yermic, calcic, cambic, duric, gypic or vertic horizon (Bridges et al., 1998)

[2] **Anthraquic**: a surface horizon that results from wet-field cultivation and comprises a puddled layer and a plough pan (IUSS Working Group WRB, 2022).

[3] **Claric** (bright): having between 25 and 100cm of the mineral soil surface a layer, ≥ 30 cm thick that consists of claric material (IUSS Working Group WRB, 2022).

[4] **Reductimorphic** features: are the results of redox processes. Features reflect permanently wet condition (IUSS Working Group WRB, 2022).

properties show that second horizon had a soil bulk density of 1.79 g cm^{-3}, a soil porosity of 32.4%, a soil moisture content of 13.9%, a clay content of 0.8%, a silt content of 12.2%, and a sand content of 81.4%. The third layer (60-70 cm+, Bvc) was described as a Pisoplinthic[5] horizon (Bvc) with round Fe and Mn nodules 2 to 3 cm in diameter (Figure 17).

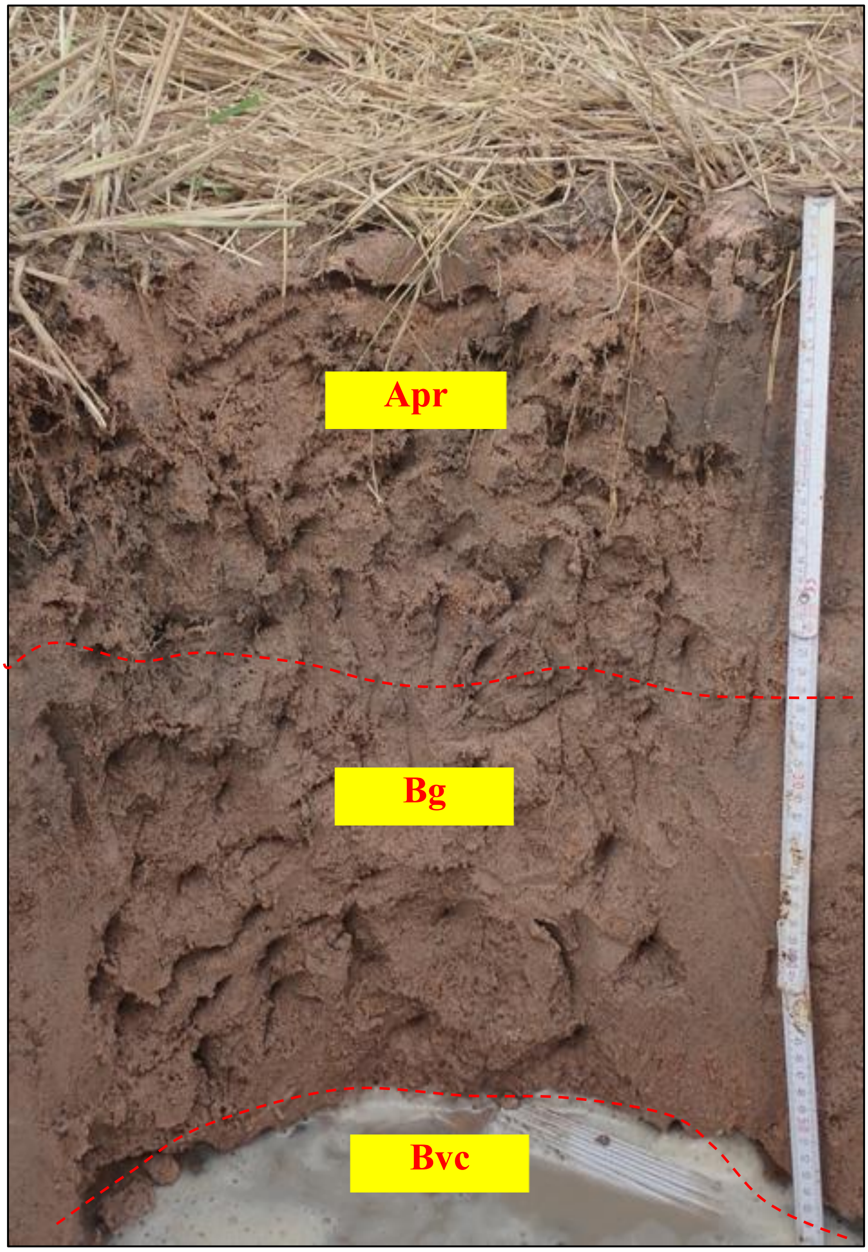

Figure 15. First soil profile (CB1). Red dashed lines are the transition line between each horizon. Photo (P. Podwojewski, 2020).

[5] **Pisoplinthic** horizon: a layer with high iron (associated with Mn) concentration is organized in round concretion (IUSS Working Group WRB, 2022).

Figure 16. Detail of earthworm galleries (red arrows).
Photo (Podwojewski, 2020)

Figure 17. Illustration of a Pisoplinthic horizon with round Fe and Mn nodules (a). See in (b) the utilization of Petroplinthite for construction purposes – Kompong Chhnang, (c) Detail of petroplinthite below profile CB1, (d) Petroplinthite. Evidences of root macroporosity. Photo (P. Podwojewski, 2020)

The second soil profile (CB2) was located in the lower part (see location in Figure 14 and soil profile in Figure 18) of the catchment (+ 19 m a.m.s.l.) in a grazing field, which was not cultivated with rice during several years. The environment was relatively flat and surrounded by harvested paddy fields.

The soil was described as a Gleysol with a first horizon (0-25 cm, Apr) described as anthraquic organo-mineral reductimorphic ploughed horizon with claric material. The soil was sandy, its colour was mainly light brown (7.5YR 6/3). The soil structure, was massive and granular around roots with many fine pores due to earthworm activity and grass roots in all directions. Results of soil physical properties analysis show that the first horizon had a soil bulk density of 1.55 g cm^{-3}, a soil porosity of 41.6%, a soil moisture content of 16.6%, a clay content of 2.8%, a silt content of 33.3%, and a sand content of 60.2%. The second horizon (25-50 cm, Bg) was described as oxygleyic[6] with a clay sandy loam texture. This horizon was wet and slightly sticky. The soil colour was red (2.5YR 5/8) following the roots and light brown (7.5YR 6/3). Its structure was massive with high fine pores due to earthworm activity and grass roots in all directions. Results of soil physical properties analysis show that the second horizon had a soil bulk density of 1.61 g cm^{-3}, a soil porosity of 39.2%, a soil moisture content of 17.6%, a clay content of 27.9%, a silt content of 19.3%, and a sand content of 52.2%. The third horizon (50-85 cm, Bg) was described as gleyic with a clay loam texture. This horizon was wet and sticky. The soil colour was red (2.5YR 5/8) and light brown around the pores (7.5YR 6/3). The soil structure was massive with high pores due to earthworm activity and grass roots in vertical directions. The water table was found at 110 cm depth. Results of soil physical properties analysis show that the third horizon had a soil bulk density of 1.63 g cm^{-3}, a soil porosity of 38.4%, a soil moisture content of 19.7%, a clay content of 35.6%, a silt content of 23.6%, and a sand content of 39.5%. The fourth horizon (85-110 cm, Bgvc) was characterized by gleyic and pisoplinthic features with round Fe and Mn oxide concretions and nodules between 1-2 cm in diameter. This horizon was wet and sticky. The soil colour was red

[6] **Oxygleyic** (wet bluish clay): not having, within 100cm of the mineral soil surface, a layer that has gleyic properties with ≥ 95% (by exposed area) reductimorphic features which have the following Munsell colours, moist: a hue of N, 10Y, GY, G, BG, B or PB; or a hue of 2.5Y or 5Y and a chroma of ≤ 2 (IUSS Working Group WRB, 2022).

(2.5YR 5/8) and light brown (7.5YR 6/3). The soil structure had no visible porosity and roots. Results of soil physical properties analysis show that the fourth horizon had a clay content of 11.3%, a silt content of 36.9%, and a sand content of 50.5%.

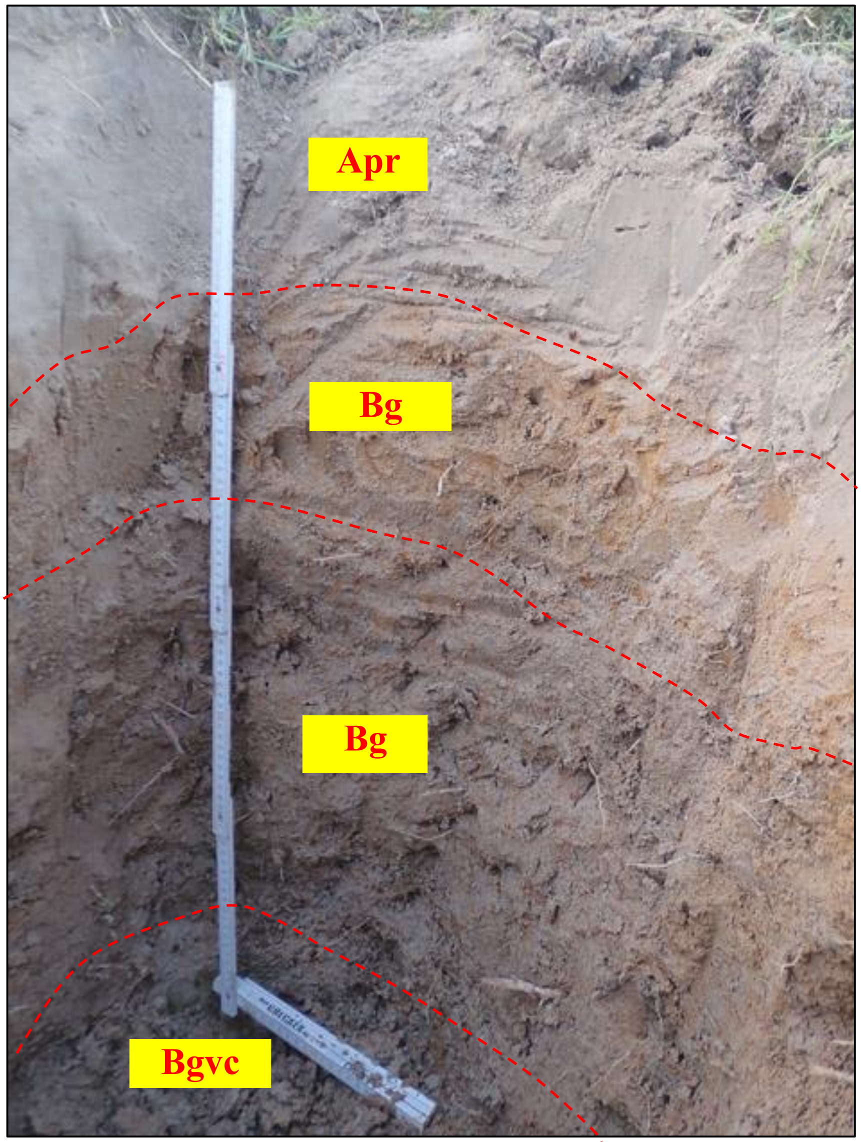

Figure 18. Second soil profile (CB2). Red dashed lines are the transition line between each horizon.Photos (P. Podwojewski, 2020)

The third profile (CB3) was located upstream (+ 64 m a.m.s.l.) of the catchment, in a harvested area (see location in Figure 14 and a picture of the soil profile in Figure 19). The environment was relatively flat and very humid. The soil was described as a Gleysol with a first horizon (0-25 cm, Apr) described as anthraquic organo-mineral ploughed reductimorphic horizon with claric material. The soil of the first horizon was sandy, its colour was mainly greyish brown (10YR 5/2). This horizon was wet and very loose. The soil structure was massive and granular around roots with many fine pores due to earthworm activity and plenty of fine roots in all directions.

Results of the soil physical properties analysis show that the first horizon had a soil bulk density of 1.89 g cm^{-3}, a soil porosity of 28.6%, a soil moisture content of 14.9%, a clay content of 3.2%, a silt content of 26.4%, and a sand content of 68.5%. The second horizon (25-33 cm, ABg) was described by gleyic features and had a sandy clay loam texture. This horizon was wet, loose, and slightly sticky. The soil colour was reddish grey (5YR 5/2) and yellowish red (5YR 5/6). The reddish grey corresponded to the accumulation of coarse sand on the vertical surface and the yellowish red suggested leaching of sand quartz from the top soil in possible cracks during the dry season. The soil structure was massive with many pores due to earthworm activity and fine roots in all directions. Results of soil physical properties analysis show that the second horizon had a soil bulk density of 1.94 g cm^{-3}, a soil porosity of 26.9%, a soil moisture content of 10.8%, a clay content of 3.1%, a silt content of 22.1%, and a sand content of 73.2%. The third horizon (33-50 cm, Bg) was described as gleyic with a sandy texture. This horizon was wet and sticky. The soil colour was pinkish grey (7.5YR 6/2) and reddish yellow (7.5YR 6/6) around the roots. The soil structure was massive and was highly porous due to earthworm activity and the presence of fine roots in all directions. The water table was found at 50 cm. Results of the soil physical properties analysis show that the third horizon had a soil bulk density of 1.77g cm^{-3}, a soil porosity of 33.1%, a soil moisture content of 16.1%, a clay content of 8.7%, a silt content of 35.7%, and a sand content of 54.9%. The fourth horizon (50-60 cm+, Bvc) was described as Pisoplinthite with round Fe and Mn concretions and nodules between 1 to 5 cm in diameter.

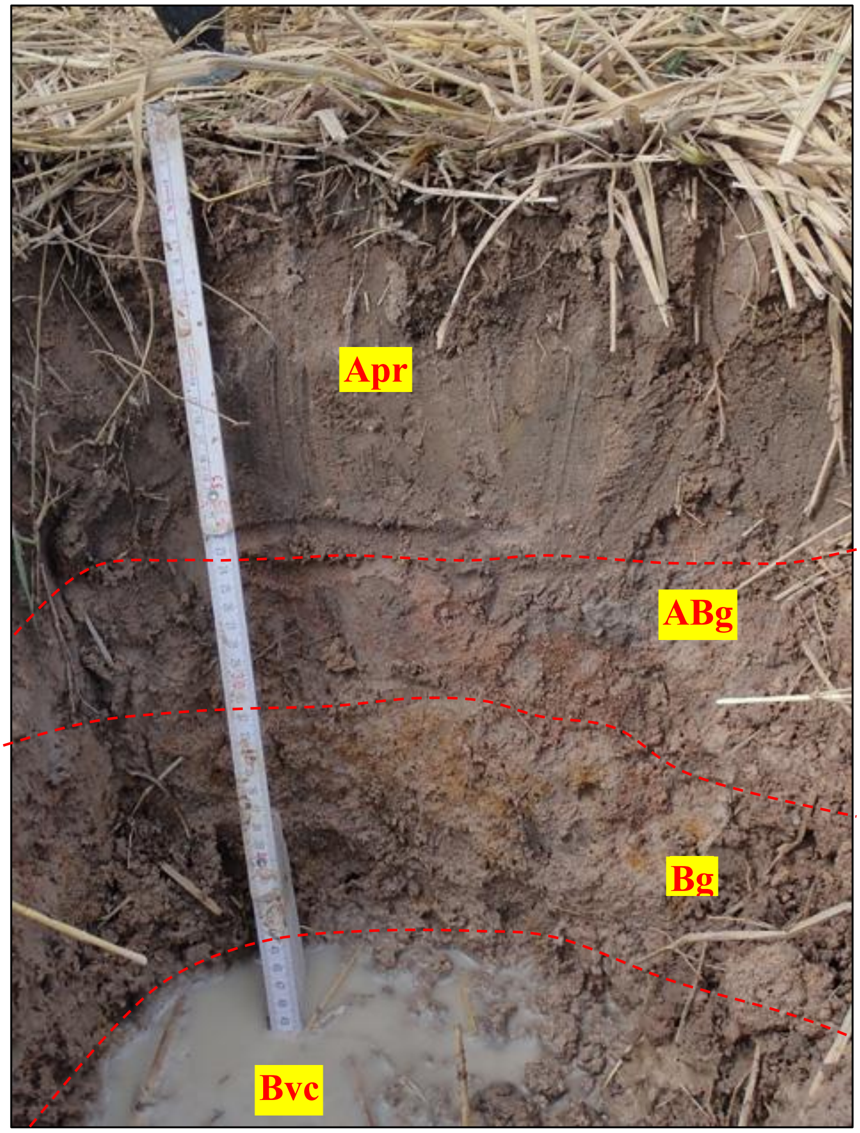

Figure 19. Third soil profile (CB3) Red dashed lines are the transition line between each horizon. Photo (P. Podwojewski, 2020)

The fourth profile (CB4) was located in the middle part (+25m a.m.s.l.) of the catchment, located in a harvested area (see location in Figure 14 and a picture of the soil profile in Figure 20). The environment was relatively flat and the soil was less compact compared with the three previous soil profiles, mainly because ploughing was done manually in this plot. The soil was described as a Luvic Gleysol with a first horizon (0-20 cm, Apr) described as anthraquic reductimorphic organo-mineral ploughed horizon with claric material. The soil of the first horizon had a gleyic feature and a sandy texture. The soil colour was reddish grey (5YR 5/2) and its structure was massive and granular with a high porosity due to earthworm activity and plenty of fine to medium rice roots in all directions. Results of soil physical properties analyses show that the first horizon had a soil bulk density of 1.70 g cm^{-3}, a soil porosity of 36.0%, a soil moisture content of 18.1%, a clay content of 2.2%, a silt content of 17.1%, and a sand content of 78.6%. The second horizon (20-35 cm, Btg) was described as gleyic feature with a sandy clay loam texture. The soil particle size distribution was dominated by very coarse sand particles. The soil was wet and slightly sticky. The soil colour was reddish yellow (7.5YR 6/8) and with a pinkish grey colour (7.5YR 6/2) and its structure was massive with a medium porosity due to earthworm activity and a few fine to medium rice roots in all directions. Results of the soil physical properties show that the second horizon had a soil bulk density of 1.89 g cm^{-3}, a soil porosity of 28.6%, a soil moisture content of 14.2%. The profile showed a clay enrichment from 2.2% to 28.9%, and 19.7 % below it. It also had a silt content of 7.5% and a sand content of 63.1%, but the cause of the enrichment for an argic[7] horizon should be natural clay leaching and not ploughing pan effect. The luvic properties are conditioned by an argic horizon, a CEC higher than 8 cmol kg^{-1} (higher than 24 cmol kg^{-1} for 100% clay content) and a base saturation < 50%. The third horizon (35-85 cm, Bg) was described as gleyic features with a sandy clay loam texture. The soil particle size distribution was dominated by very coarse sand particles. The soil was wet and very sticky. The soil colour was reddish yellow (7.5YR 6/8) and its structure was massive with a medium porosity due to earthworm activity and a few fine to medium rice roots in all directions. The water table was found at 85 cm. Results of the soil physical properties analyses show that the third horizon had a soil bulk density of 1.72 g cm^{-3}, a soil porosity of 35.1%, a soil moisture content of 18.6%, a clay content of 19.7%, a silt content of 14.3%, and a sand content of 64.2%, The fourth horizon (85-90 cm+, Bvc) corresponded to the Pisoplinthite shown in Figure 17.

[7] **Argic** horizon (white clay): a subsurface horizon with a distinctly higher clay content than the overlying horizon (IUSS Working Group WRB, 2022).

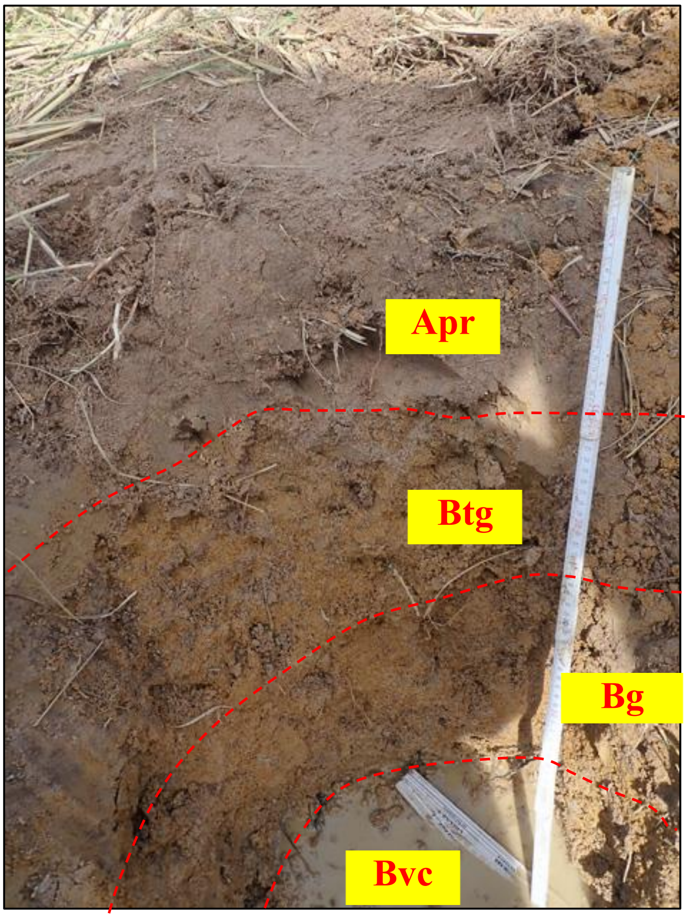

Figure 20. Fourth soil profile (CB4). Red dashed lines are the transition line between each horizon. Photo (P. Podwojewski, 2020)

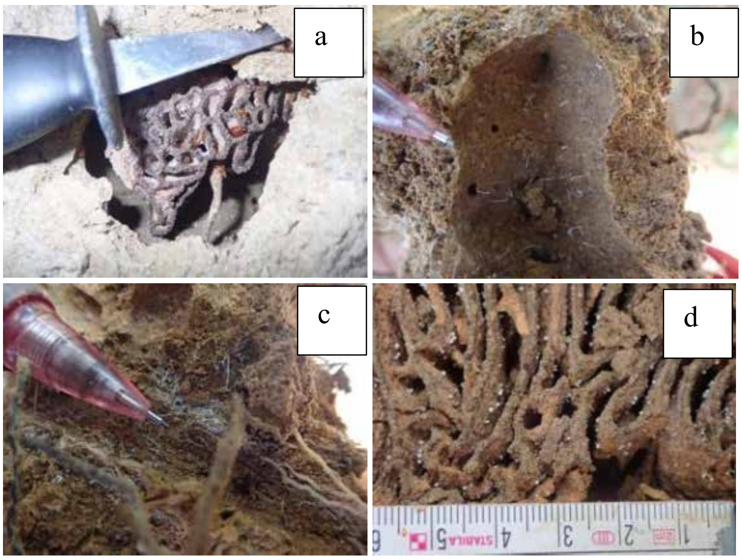

Figure 21. Soil features next to the fourth soil profile (CB4) with (a) comb chamber in a termite nest, (b) evidences of fungi mycelium in a comb chamber, (c) mycelium in the soil material of the termite mound, and (d) detail of exosymbiotic fungus Termitomyces.

Table 6. Data of bulk density (BD), soil porosity, soil moisture, particle size (sand, clay, and silt) by horizons at each soil profiles.

Horizon	Horizon Type	Horizon depth (cm)	Sampling depth (cm)	BD (g cm^{-3})	SD	Porosity (%)	SD	Moisture (%)	SD	Clay (%)	Silt (%)	Sand (%)	Coarse sand (%)	Fine sand (%)
CB1.1 (0.1)	Apr	0-25	0-10	1.68	0.02	36.59	0.92	12.53	0.59	0.72	8.84	87.88	43.95	43.61
CB1.1 (0.18)	Apr	0-25	15-18	NA	NA	NA	NA	NA	NA	0.63	10.27	85.78	46.15	38.42
CB1.2	Bg	25-60	35-42	1.79	0.03	32.37	1.17	13.92	0.45	0.84	12.22	81.37	39.38	41.65
CB1.3	Bvc	60-70+	70-75	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
CB2.1	Apr	0-25	0-10	1.55	0.06	41.56	2.27	16.63	1.01	2.78	33.25	60.20	11.95	48.05
CB2.2	Bg	25-50	35-42	1.61	0.01	39.19	0.37	17.65	0.40	27.95	19.34	52.23	13.50	38.72
CB2.3	Bg	50-85	50-85	1.63	0.03	38.39	1.24	19.66	1.13	35.56	23.63	39.46	11.03	28.15
CB2.4	Bgvc	85-110	90-100	NA	NA	NA	NA	NA	NA	11.25	36.88	50.49	23.06	27.29
CB3.1 (0.1)	Apr	0-25	0-10	1.89	0.02	28.64	0.79	14.90	0.39	3.15	26.35	68.49	41.01	27.01
CB3.1(0.25)	Apr	0-25	10-25	1.88	0.07	28.87	2.70	12.22	0.37	2.87	23.86	71.31	45.41	25.50
CB3.2	ABg	25-33	25-33	1.94	0.06	26.93	2.11	10.76	0.32	3.13	22.11	73.23	52.91	19.88
CB3.3	Bg	33-50	30-40	1.77	0.10	33.14	3.77	16.11	2.44	8.66	35.68	54.86	35.14	19.03
CB3.4	Bvc	50-60+	50-60	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
CB4.1	Apr	0-20	0-15	1.70	0.06	36.03	2.31	18.14	1.11	2.21	17.08	78.62	36.74	41.58
CB4.2	Btg	20-35	23-30	1.89	0.04	28.65	1.44	14.20	0.64	28.91	7.52	63.12	32.27	32.47
CB4.3	Bg	35-85	40-55	1.72	0.03	35.14	1.11	18.63	0.43	19.71	14.32	64.23	34.77	28.69
CB4.4	Bvc	85-90+	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

According to IUSS working group WRB (2022), the definition of the horizon types are given below:

- ***Apr****:* A cultivated organo-mineral horizon which was modified by ploughing and had strong reduction
- ***ABg:*** A transitional horizon between A and B horizons with a presence of stagnic feature of accumulation of Fe and/or Mn oxide.
- ***Bg****:* A mineral horizon that had formed below an A horizon with stagnic features and accumulation of Fe and/or Mn oxides. Or mottles with gley features of structurally altered associated with periodic reduction
- ***Btg****:* An illuvial horizon characterized by greyish colours of stagnic features and/or prominent mottles 50 cm below the soil surface indicating permanent or periodic intense reduction. It had formed below A horizon.
- ***Bgvc****:* A mineral horizon with stagnic features and accumulation of Fe and/or Mn oxide as concretions of plinthite, and, had formed close to the water table.
- ***Bvc****:* A mineral horizon with plinthite, and concretion, had formed below an A horizon close to the water table

5.3 Discussion

The first conclusion of this study is that we did not confirm previous observations made by Crocker (1962) and JICA (2003), who described Podzols, and both Acrisol and Arenosols in the study field, respectively. The main finding of this study is that soils in Chrey Bak can be described as Gleysols due to the water table and very clear mottles and redoximorphic features.

Podzols are characterized by the movement of iron due to acidic organic matter and complexed iron with organic acids (Bridges et al., 1998; IUSS Working Group WRB, 2022). In Chrey Bak, the accumulation of iron was not due to the lixiviation of fulvic acids and the chelation of iron. Soils had no E bleached top soil horizon, and iron accumulation in B was due to water logging and has a redoxymorphic origin.

Acrisol was defined by JICA (2003) and SoilGrids (https://soilgrids.org), however despite the possible lixiviation and accumulation of clay in an Argic horizon in CB4.2 horizon, the oxymorphic features of a Gleysol prevailed to those of an Acrisol in the WRB.

Arenosols. Similarly, the presence of Arenosols in Chrey Bak was not confirmed because the oxymorphic features characteristic of a Gleysol prevailed to those of an Arenosol. The arenic qualifier was mentioned in the description of soils. The gleyic and stagnic properties were dominant in the classification. Some soil profiles had arenic features but they were Gleysols – arenic is a supplementary qualifyer - due to the permanent water table and spots in soils. The soil could be a Fluvisol if there was evidences of stratification and no evident Gleyic or stagnic features. Arenosols are defined as deep sandy soils with sand particles that are coarser than sandy loams to a depth of at least 100 cm from the surface with no redoxymorphic, plinthitic, leaching, or stratification features. On the other hand, Gleysols comprise soils saturated with groundwater during long periods, then developing reducing condition resulting in gleyic properties, including underwater and tidal soils (FAO, 2006).

Soils in Chrey Bak develop all Gleysols characteristics because of:

(i) A visible water table often < 1.0 m deep;

(ii) An Anthraquic diagnostic surface horizon. It is a « surface horizon that results from wet-field cultivation and comprises a *puddled layer* (irrigated rice fields) and a *plough pan* (def. WRB 2022). This A horizon had reductic[8] and stagnic[9] properties. The topsoil developed also claric material with pale colours and the plough pan was evidenced by a strong increase of the bulk density of the horizon below that could reach values > 1.8 g cm^{-3}; The sole limit of the Anthraquic diagnostic horizon was a colour slightly more pale than the colour requested for the WRB Anthraquic characters.

(iii) A Bg horizon with clear mottles of pale pink, gray and strong brown reddish or orange brown mottles around the roots. These reductimorphic features were due to the *upward moving agent* (water table and capillary rising) (WRB, 2022) but also combined with stagnic properties dues to the irrigation process from above the profile. This increases the complexity of the pedogenesis redoximorphic process. All have plinthic features with clear Fe concretions at the base of the profile at the level of the fluctuation of the watertable and completely cemented below it. They

[8] **Reductic** (drawn back): having reducing condition caused by gaseous emissions, e.g. methane or carbon dioxide, or caused by liquid intrusion other than water (IUSS Working Group WRB, 2022).

[9] **Stagnic** (to flood): the area of reductimorphic feature plus the area of oximorphic features is ≥ 25cm (weight average) of the layer's total area.

were oxygleyic, pisoplinthic, stagnic, eutric[10] (depending on the cation saturation) Gleysols. They were all ochric[11] due to the pale colour of the top soil.

In conclusions, soils could be differentiated by the soil texture as sandy, silty or loamy.

The sandy profile 1 was panto[12]-arenic[13], if the sandy texture began from the top to deeper 1.0 m, but ano[14]-anenic if the sandy level stopped at less than 1.0 m depth. The profiles 2 and 3 were panto or ano-loamic[15] according to the presence of a petroplinthic[16] horizon deeper or shallower than at 1.0 m depth, respectively. The profile 4 was amphi[17]-loamic due to the sandy topsoil horizon and the presence of petroplinthic at less than 1.0 m depth. The last soil profile was characterized by a

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[10] **Eutric**: having one or more layers consisting of mineral material, between 20 and 100 cm of the mineral soil surface, or between 20cm of the mineral soil surface and a limiting layer starting > 25cm from the mineral soil surface, whichever is shallower, that have exchangeable (Ca+Mg+K+Na) ≥ exchangeable Al in the major part of their combined thickness ? (IUSS Working Group WRB, 2022)

[11] **Ochric**: the horizon is not dark and does not have dark organic matter content, having ≥ 0.2% soil organic carbon (weighted average) in the upper 10cm of the mineral soil.

[12] **Panto-** (all): the layer starts at the (mineral) soil surface and has its lower limit ≥ 100cm of the (mineral) soil surface or at a limiting layer starting > 50cm from the (mineral) soil surface.

[13] **Arenic** (sand): consisting of mineral material and having, single or in combination, a texture class of sand or loamy sand in one or more layers with a combined thickness of ≥ 30cm, occurring within 100cm of the mineral soil surface, or in the major part between the mineral soil surface and a limiting layer starting > 10 and < 60 cm from the mineral soil surface.

[14] **Ano-** (upwards) : the layer starts at the (mineral) soil surface and has its lower limit > 50 and < 100cm of the (mineral) soil surface; and no such layer occurs between 99 to 100cm of the (mineral) soil surface or directly above a limiting layer.

[15] **Loamic** (loam): consisting of mineral material and having, single or in combination, a texture class of loam, sandy loam, clay loam, sandy clay loam, sandy clay loam or silty clay loam in one or more layers with a combined thickness of ≥ 30cm, occurring within 100cm of the mineral soil surface, or in the major part between the mineral soil surface and a limiting layer starting > 10 and < 60cm from the mineral soil surface.

[16] **Petroplinthic** horizon (petros, rock, and plinthos, brick): a continuous and inundated layer with high iron (associated with Mn) concentration is organized in round concretion (IUSS Working Group WRB, 2022)

[17] **Amphi-** (around): the layer starts >0 and < 50 cm for the (mineral) soil surface and has its lower limit >50 and <100 cm of the (mineral) soil surface; and no such layer occurs <1cm of the (mineral) soil surface; and no such layer occurs between 99 and 100 cm of the (mineral) soil surface or directly above a limiting layer.

leaching of clay and could be considered as luvic (it could be also acric[18], alic[19], lixic[20] depending on the CEC and the base saturation). However, the textural discontinuity corresponded to a plough pan and the clay leaching process could have been observed with more precision.

Gleysols. The specific environment in paddy fields matches with the definition of a Gleysol since soils in Chrey Bak are often saturated with water during the rainy season or almost during the whole period of the cultivation of rice, while they become dry during the dry season. Water regime changes in paddy soils are responsible for the reddish, brownish or yellowish colors observed in soil. The redox process could also be caused by rising gases, such as CO_2 or CH_4 and evidenced of reduction processes with segregation of Fe compounds starting within 40 cm of the ground surface, which was exactly what we found on the ground in 2020.

Catchments are usually **heterogeneous environments.** Assuming differences in soil properties with the elevation, in particular due to the flooding of soil and the transportation of sediments from the Tonle Sap River to the cultivated fields during the rainy season, we expected a gradient in sand content along the topography. This relationship was tested using unpublished data (Ann V. and Ket P., pers. obs., 2012) describing 15 soil profiles along the catchment (see Figure 22) and our own dataset. The ground elevation varied from -5 to 86 m a.m.s.l. and the sand content in the

[18] **Acric** (sharp): having an *argic horizon* starting ≤ 100 cm from the mineral soil surface with a CEC (by 1 M NH4OAc, pH 7) of < 24 $cmol_c\ Kg^{-1}$ clay in some subhorizon within 150cm of the mineral soil surface; and having exchangeable Al> exchangeable (Ca+Mg+K+Na) in half or more of the depth range between 50 and 100cm of the mineral soil surface or the lower half of the mineral soil above a limiting layer starting ≤ 100cm from the mineral soil surface, whichever is shallower.

[19] **Alic** (alum): having an *argic horizon* starting ≤ 100 cm from the mineral soil surface with a CEC (by 1 M NH_4OAc, pH 7) of ≥ 24 $cmol_c\ Kg^{-1}$ clay throughout within 150cm of the mineral soil surface; and having exchangeable Al>exchangeable (Ca+Mg+K+Na) in half or more of the depth range between 50 and 100cm of the mineral soil surface or the lower half of the mineral soil above a limiting layer starting ≤ 100 cm from the mineral soil surface, whichever is shallower.

[20] **Lixic** (washed-out substances): having an *argic horizon* starting ≤ 100 cm from the mineral soil surface with a CEC (by 1 M NH_4OAc, pH 7) of < 24 $cmol_c\ kg^{-1}$ clay in some subhorizon within 150 cm of the mineral soil surface; and having exchangeable Al ≤ exchangeable (Ca+Mg+K+Na) in half or more of the depth range between 50 and 100 cm of the mineral soil surface or the lower half of the mineral soil above a limiting layer starting ≤ 100 cm from the mineral soil surface, whichever is shallower.

topsoil varied from 60 to 90%, Figure 22 shows that no clear relationship could be evidenced between these two variables ($P > 0.05$). The same relationship was tested between the sand content in the topsoil and the distance to the Tap river, and the relationship was here again non-significant ($R^2 = 0.001$, $P = 0.97$). Therefore, we could not confirm our hypothesis and the elevation or the distance to the river could not be considered as a discriminant factor for characterizing differences in soil texture.

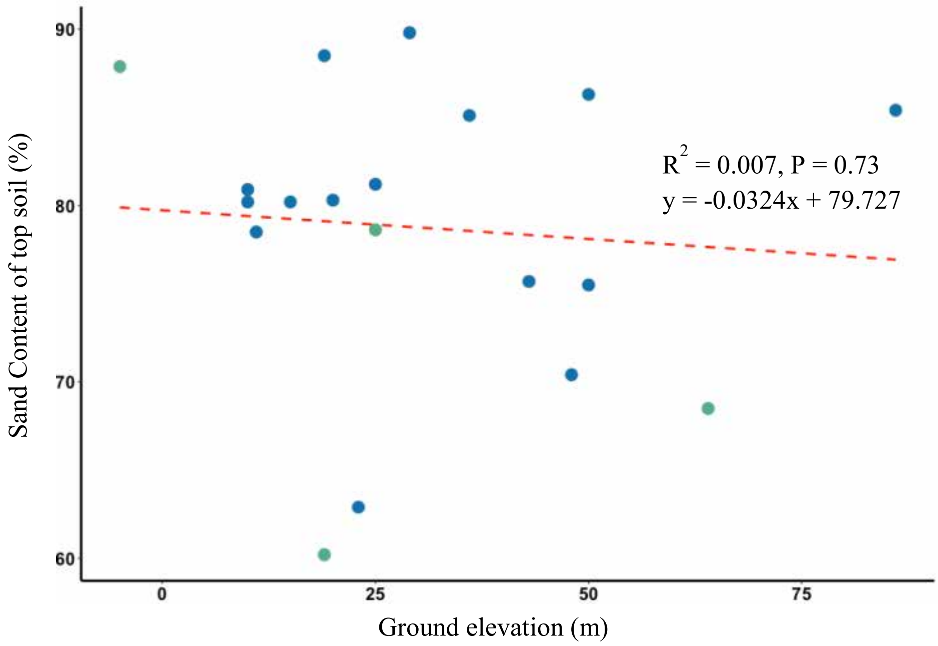

Figure 22. Relationship between the sand content in the topsoil and the ground elevation (compared with mean sea level) using 15 soil profiles described in 2012 by Ann V. and Ket P. (in blue) and 4 others described in 2020 by Podwojewski P. and Muon R. (in green).

Chapter 6 . Termite mounds as patches of soil fertility in Cambodian paddy fields

Results from this chapter have been submitted to *Geoderma Regional* on September 19th in the present form. It aims at measuring the impact of termite bioturbation on soil properties. Locations of the soil samples were selected based on the soil map proposed by JICA (2003). However, data were afterwards analyzed from the results obtained and described in Chapter 5, i.e., in comparison three soil groups from their sand contents.

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Abstract

In Cambodia, termite mounds are commonly used by farmers as amendments to increase the fertility of their paddy fields. However, despite their utilization, their chemical and physical properties have not been described yet. Therefore, the aim of this study was to analyze the chemical and physical properties of two termite constructs commonly found in paddy fields: (a) termite nests built and occupied by the fungus-growing termite *Macrotermes gilvus* and (b) lenticular mounds that are initially built by termites but host a large diversity of other invertebrates and plants. This study shows that these biogenic structures have very specific properties. Termite mound nests were characterized by higher clay, phosphorus and electrical conductivity than the surrounding soil. However, their effect on carbon dynamics was limited to a modification of the interactions between soil organic matter and minerals and to the presence of carbonates. At the same time, lenticular mounds appeared as patches of nutrients in paddy fields because they were always enriched in carbon, nitrogen, and phosphorus in comparison with the surrounding cultivated soil. Lenticular mounds were also enriched in clay, although this effect was only measured when the sand content in the surrounding environment was > 60%. Together with these changes, lenticular mounds were characterized by a lower bulk density, higher saturated hydraulic conductivity (*Ksat*), and higher water holding capacity. In conclusion, this study shows that termite constructions can be considered fertility and biogeochemical hotspots in paddy fields, thus explaining their use by farmers for improving the fertility of their land.

Keywords: Bioturbation, ecosystem services, water holding capacity, C sequestration, gley soil

6.1 Introduction

Termites are among the most important soil invertebrates across the tropics (Wood and Sands 1978) due to their high abundance and impact on the decomposition of litter and other plant-derived materials (Collins 1981; Schuurman 2005; Griffiths et al. 2019). However, what makes termites almost unique among soil invertebrates is their capacity to regulate soil biological, chemical, and physical properties through the construction of soil biogenic structures, such as galleries, sheeting, and mounds (Jouquet et al. 2016b). For this reason, termites are commonly considered key soil bioturbators and soil engineers (Dangerfield et al. 1998; Black and Okwakol 1997; Jouquet et al. 2006).

Through their bioturbation activity, termites impact the dynamics of soil and water at different spatial and temporal scales (Bottinelli et al. 2015; Jouquet et al. 2016a). At a small scale, termites have been compared to weathering agents because they influence the mineralogy of clay and the properties of soil aggregates, which in turn influence soil organic matter and nutrient dynamics (Abbadie and Lepage 1989; Jouquet et al. 2002) as well as soil water-holding capacity (Konaté et al. 1999; Suzuki et al. 2007; Traoré et al. 2019). At the soil profile scale, termites use soils from various soil depths or specifically select soil particles of small sizes for the construction of their nest structures (Abe et al. 2009; Jouquet et al. 2017, 2002). If the capacity of termites to enrich the soil in clay particles seems to be the rule (Holt and Lepage 2000), their impact on soil organic matter is highly variable. For instance, several studies showed higher C content in termite mounds than in the surrounding soil (Jouquet et al. 2005; De Souza et al. 2020; Chen et al. 2021; Wakbulcho and Kenea 2021), while Cheik et al. (2018) found a negative or neutral effect of termite bioturbation activity. Finally, termites act as heterogeneity drivers and shape the distribution of natural resources such as water and nutrients at the landscape scale through the edification of mounds that are comparable to nutrient patches or fertility islands (Dangerfield et al. 1998; Jouquet et al. 2011. 2016a; Muvengwi and Witkowski 2020; Chen et al. 2021).

The specific soil biological, chemical, and physical properties of termite mounds have largely been described, especially in Africa, where they play a key role in the dynamics of vegetation (e.g., Traoré et al. 2008a) and increase the robustness and resilience of African dryland ecosystems against water shortages and desertification (Bonachela et al. 2015). In Brazil, termite activity is considered to be at the origin of the "*murundus*" structures, which represent a quantity of soil equivalent to approximately 4,000 great pyramids of Giza (De Souza and Delabie 2018; Martin et al. 2018; De Souza et al. 2020). In Asia, studies considering the properties of termite mounds have mainly been restricted to India (Jouquet et al. 2017, 2015, 2020) and China (Chen et al. 2021). However, termite mounds are also conspicuous features of the landscapes in the Lower Mekong Basin (Choosai et al. 2009; Miyagawa et al. 2011). In Laos, lenticular mounds provide numerous ecosystem services, and their soil is also used for growing vegetables or as an amendment for increasing the soil fertility of paddy fields (Miyagawa et al. 2011). In northeastern Thailand, their higher concentrations of C and nutrients and higher clay content in comparison with the surrounding topsoil explain why farmers spread termite mound soil in their lands to increase their soil fertility (Choosai, 2010; Noble et al., 2004; Suzuki et al., 2007). Despite the fact that termite mounds are also commonly observed in paddy fields in Cambodia and that their soil is also used as an amendment for increasing the soil fertility of paddy fields or for growing vegetables (Muon pers. com.), there is a dearth of information on their chemical and physical properties. The question of the impact of termites on soil properties is, however, very important in paddy fields in Cambodia, where soils are mainly sandy and are characterized by low soil fertility and poor soil physical properties (i.e., soils are highly compact with a low water-holding capacity) (White et al. 2006; Seng et al. 2007). In this environment, any enrichment in clay particles is likely to have a positive impact on soil chemical and physical properties, especially the retention of organic matter and water (Noble et al. 2004).

Therefore, the aim of this study was to analyse the impact of termite bioturbation on soil properties in Cambodian paddy fields. Our main hypothesis was that termite mounds can be considered biogeochemical hotspots in paddy fields with higher clay, organic matter, and nutrient contents, as well as higher water hydraulic conductivity and a higher water-holding capacity.

6.2 Results

6.2.1 Soil physical and chemical properties

The three soil groups were mostly differentiated from their soil particle size distribution (i.e., no significant differences in C, N, or P contents, C:N ratio, pH or EC) (Figure 23 and Table 7). The K content was higher in GIII than in GI, with intermediate value for GII. Conversely, the amount of sand was the highest in GI and the lowest in GIII, while intermediate sand contents were measured in GII. The opposite was found for the clay and silt contents, which were the highest in GIII and the lowest in GI.

Bioturbation by termites significantly influenced soil properties apart from the C:N ratio, which was influenced neither by termite bioturbation nor by the soil groups (Table 7). The C, N and P contents and EC were only influenced by termite bioturbation (i.e., not influenced by soil groups). Higher C, N and P contents were measured in LM than in CTRL (Figure 23). LM was also characterized by intermediate EC value between those measured in CTRL and TN ($P > 0.05$ for both CTRL and TN). TN had similar C content to CTRL but intermediate N content to those measured in CTRL and LM ($P > 0.05$ for both). TN was also characterized by a higher P content and a higher EC than that of CTRL ($P < 0.05$ for both).

Termite bioturbation did not influence the soil pH, except in the sandiest soil group (GI) where a higher soil pH was measured in TN than in CTRL (Figure 23). In GI, LM had intermediate soil pH values between those of CTRL and TN ($P > 0.05$ in both cases). Clay and sand contents were also influenced by termite bioturbation. The clay content was always higher in TN than in CTRL, while the enrichment in clay was only measured in GI and GII for LM. Conversely, the sand content was reduced in TN in comparison with CTRL, although this impact was only measured in the first soil group (i.e., $P > 0.05$ for GII and GIII).

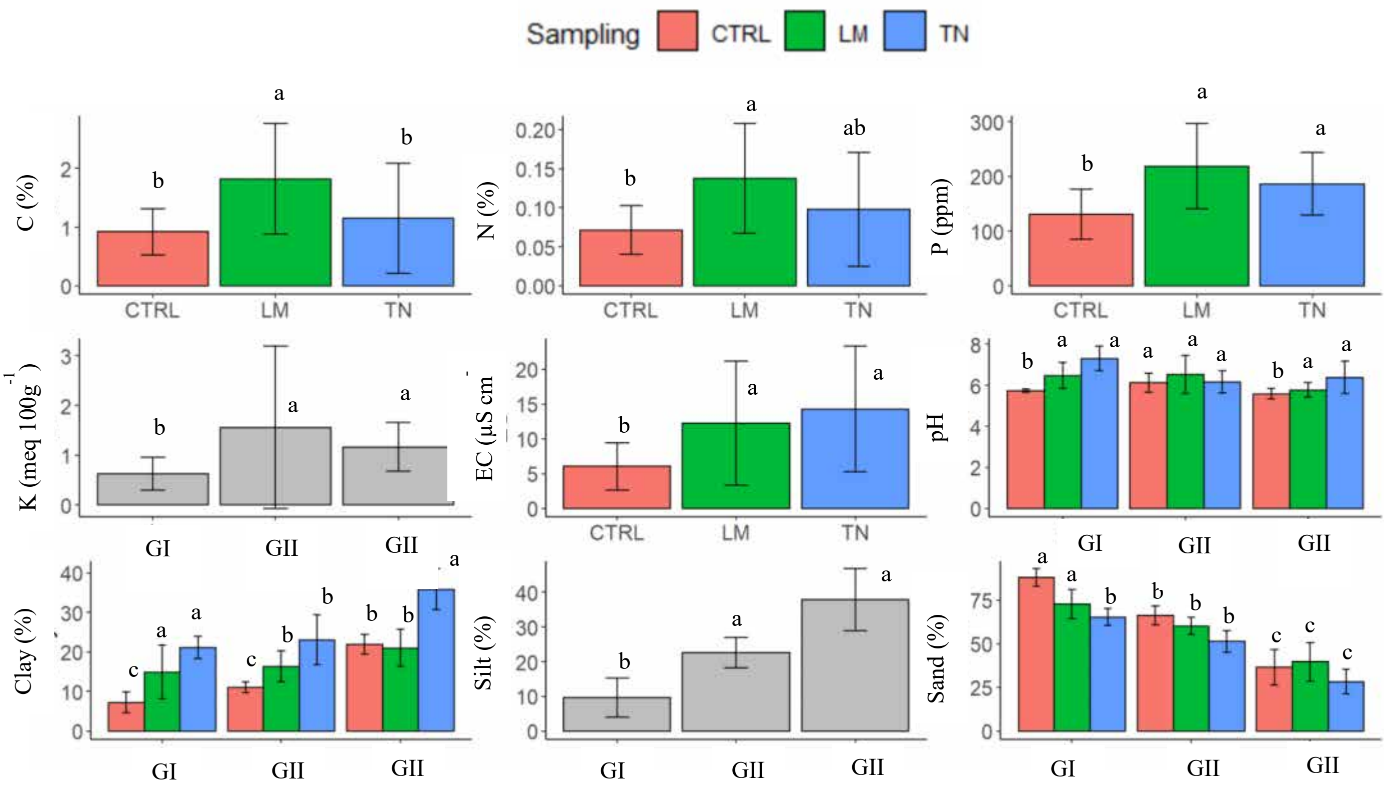


Figure 23. Histograms showing the impact of termite bioturbation (control soil "CTRL" in orange, lenticular mounds "LM" in green, and termite mound nests "TN" in blue) in the three soil groups (GI, GII and GIII) on the C, N, and P contents, pH and electrical conductivity (EC), and soil particle sizes (clay, silt and sand contents). Histograms with different letters are significantly different at $P < 0.05$ (mixed linear model with elevation as random factor).

Table 7. Results of the linear mixed models testing the influence of termite bioturbation (i.e., termite mound nests, lenticular mounds, and reference soil) and soil groups (i.e., GI, GII and GIII) on soil properties with elevation as random factor. *** < 0.001, ** < 0.01, * < 0.05

	Bioturbation (a)		Soil Groups (b)		(a) × (b)	
	F-values	*P*-values	*F*-values	*P*-values	*F*-values	*P*-values
C (%)	5.53	0.008 **	2.30	0.302	32.87	0.829
N (%)	5.20	0.011 *	5.42	0.156	0.46	0.760
C:N	1.68	0.201	4.64	0.177	0.10	0.980
P (ppm)	9.028	< 0.001 ***	0.15	0.899	1.09	0.377
K (meq $100g^{-1}$)	3.67	0.036 *	2.05	0.328	4.09	0.008 **
EC (µS cm^{-1})	6.32	0.005 **	1.18	0.458	1.60	0.197
pH	8.92	< 0.001 ***	4.47	0.182	3.21	0.024 *
Clay (%)	35.02	< 0.001 ***	11.75	0.078	3.15	0.026 *
Silt (%)	0.45	0.637	32.18	0.030 *	1.61	0.193
Sand (%)	16.48	< 0.001 ***	115.74	< 0.001 ***	2.14	0.096

6.2.2 Carbon pools measured by Rock-Eval® analysis

Soil groups had no influence on the soil properties measured by Rock-Eval (Table 8). Higher Corg content was measured in LM than in TN and CTRL (*P* > 0.05 between TN and CTRL). In general, MinC content was very low. However, their concentrations were the highest in TN in comparison with the other treatments for all soil groups (*P* > 0.05 in all cases). While HI was lower in TN than in LM and CTRL, the differences were nonsignificant. Finally, no significant differences in R-index values were measured (*P* > 0.05).

Comparatively, I/R values from LM and CTRL were lower than those of the general regression model (Figure 24). The distribution of the data was more variable for TN, with values both higher and lower than those of the general model. This difference in variability shows a higher deviation of the I-index from control soils for TN than for LM (Figure 25).

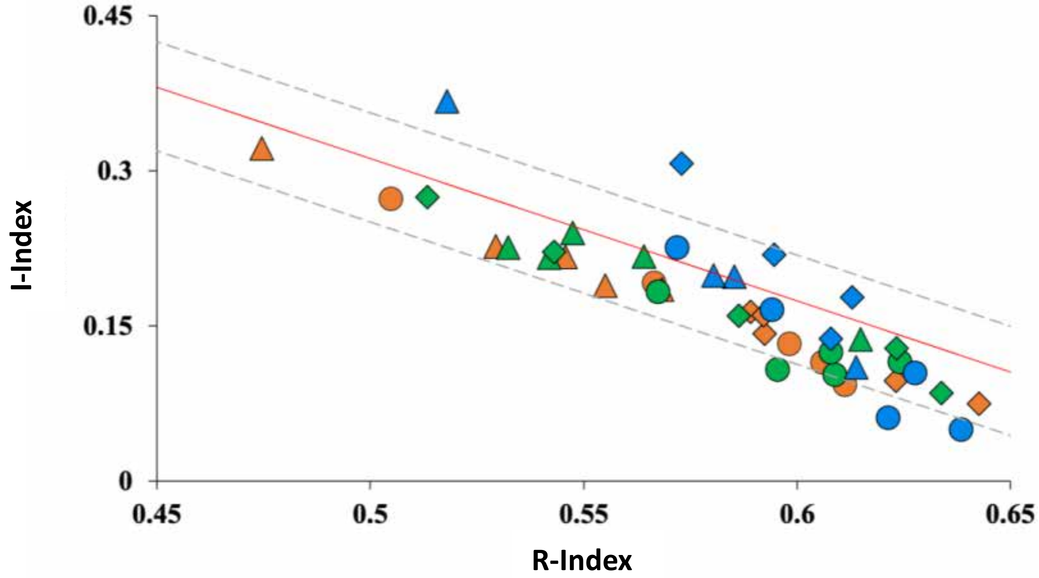


Figure 24. I- *vs.* R-index diagram for termite mound nests and lenticular mounds, and control soils. The dashed line represents the 'humic trend' measured by Sebag et al. (2016). The I-index is shown on the vertical axis (control 'CTRL' in orange, lenticular mounds 'LM' in green, and termite mound nests 'TN' in blue). Soil groups are GI in circles, GII in triangles, and GIII in squares.

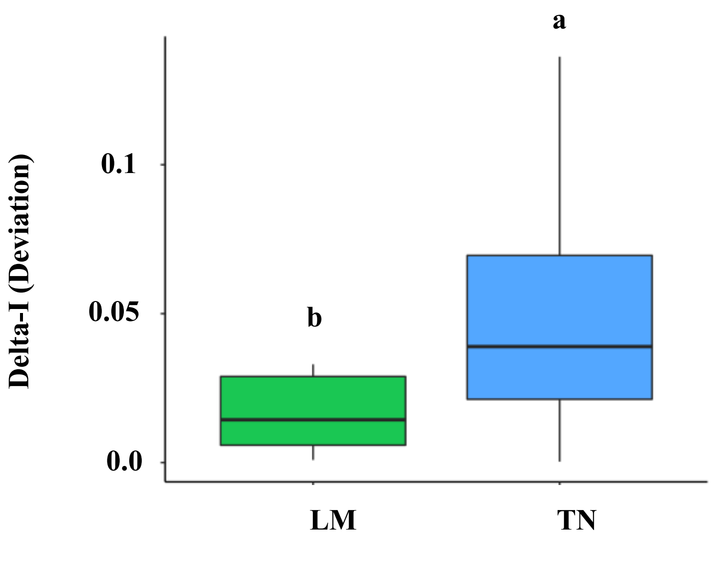


Figure 25. Histogram showing the deviation of I-index values of lenticular mounds (LMs) and termite mound nests (TNs) from those of the control soils (CTRL) (average values for the three soil groups). Vertical bars are standard errors (n = 15). Differences are significantly different at $P < 0.05$.

Table 8. Results from the Rock Eval analysis showing the percentages of organic (OrgC) and mineral C contents (MinC) and HI (in mg HC g^{-1} TOC) and the R index for termite mound nests (TNs), lenticular mounds (LMs), and the surrounding paddy field (control, CTRL) found in the three soil groups (GI, GII, and GIII) in the Chrey Bak catchment. Numbers in parentheses are standard errors of the means (n = 5).
P-values correspond to the results of the linear mixed models testing the influence of termite bioturbation (i.e., LM, TN, and CTRL) and soil groups (i.e., groups I, II and III) on soil properties with elevation as random factor. Values with similar letters are significantly similar at $P > 0.05$.
*** $P < 0.001$, * $P < 0.05$

	Soil types	OrgC (%)	MinC (%)	HI (mg HC g^{-1} TOC)	R index
	CTRL	0.49^{b} (0.12)	0.01^{b} (0.00)	238.6 (9.15)	0.58 (0.02)
GI	LM	1.06^{a} (0.16)	0.00^{b} (0.01)	215.8 (10.28)	0.60 (0.01)
	TN	0.62^{b} (0.06)	0.07^{a} (0.02)	191.0 (20.60)	0.61 (0.01)
	CTRL	0.85^{b} (0.09)	0.00^{b} (0.00)	253.4 (14.22)	0.53 (0.02)
GII	LM	1.63^{a} (0.40)	0.02^{b} (0.02)	215.4 (23.63)	0.56 0.01)
	TN	0.74^{b} (0.19)	0.03^{a} (0.00)	158.6 (10.43)	0.55 (0.03)
	CTRL	1.08^{b} (0.11)	0.00^{b} (0.00)	191.2 (7.96)	0.61 (0.01)
GIII	LM	1.94^{a} (0.45)	0.01^{b} (0.00)	197.4 (18.72)	0.58 (0.02)
	TN	1.60^{b} (0.59)	0.05^{a} (0.01)	136.6 (28.48)	0.61 (0.01)
Bioturbation (a)		$P = 0.011$ *	$P < 0.001$***	$P = 0.7531$	$P = 0.490$
Soil groups (b)		$P = 0.285$	$P = 0.117$	$P = 0.139$	$P = 0.092$
(a) × (b)		$P = 0.786$	$P = 0.320$	$P = 0.489$	$P = 0.435$

6.2.3 Soil porosity and water dynamics

The soil bulk density (BD) reached between 1.4 and almost 1.7 g cm^{-3} in CTRL. The BD value was influenced both by both the location (i.e., soil group effect, $P < 0.001$) and the termite bioturbation ($P < 0.001$) (Table 9). CTRL and TN had similar BD values, independent of the soil groups. Conversely, the soil BD was lower in LM than in CTRL and TN, except in GI, where BD in TN was similar to that in LM and CTRL. The lower BD in LM was also associated with a higher *Ksat* in LM soil than in CTRL ($P = 0.005$), independent of the soil groups ($P = 0.084$) (Figure 26). Water-holding capacity was also significantly higher in LM than in CTRL at pF 4.2, 3.2 and 2.5, independent of the location (soil group effect, $P > 0.05$) (Table 10 and Figure 27).

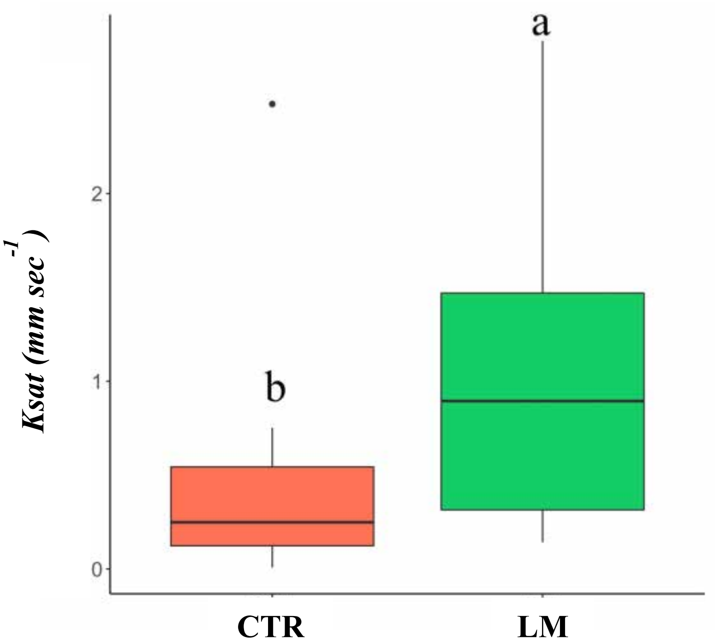


Figure 26. Saturated hydraulic conductivity (Ksat) in lenticular mounds (LMs) and control soil (CTRL) (average values for the three soil groups). Vertical bars are standard errors (n = 13). Histograms with different letters for the same location are significantly different at $P < 0.05$.

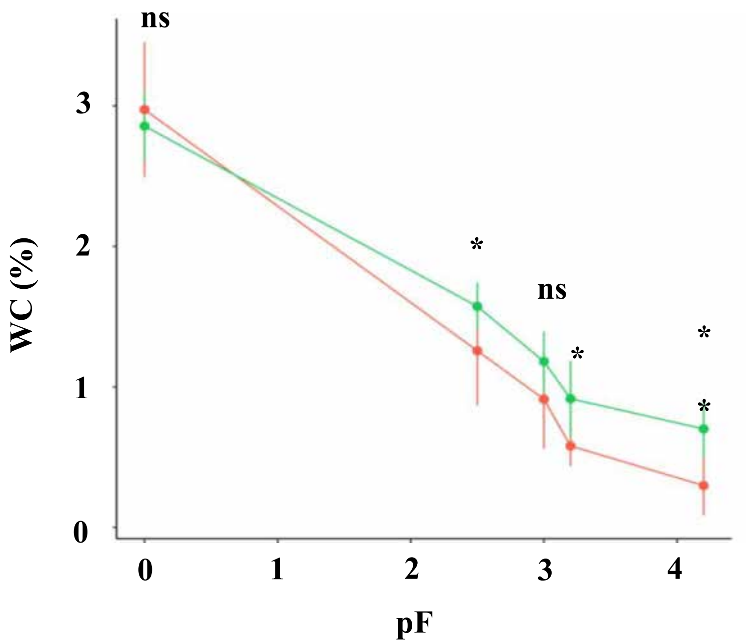


Figure 27. Soil water content at different pF for the lenticular mound (LM) in green and control soils (CTRL) in orange in the different soil groups. Vertical bars are the standard errors, and the stars are significantly different at $P < 0.05$.

Table 9. Differences in soil bulk density (BD, in g cm^{-3}) in termite mound nests (TNs), lenticular mounds (LMs), and control soils (CTRL) in the three groups of soil. Numbers in parentheses are standard errors of the mean. *P*-values correspond to the results of the linear mixed models testing the influence of termite bioturbation (i.e., LM, TN, and CTRL) and soil groups (i.e., GI, GII and GIII) on soil properties with elevation as random factor. Values with similar letters are significantly similar at $P > 0.05$. *** $P < 0.001$

	Soil types	BD (g cm^{-3})
	CTRL	1.66^{a} (0.08)
GI	LM	1.41^{ab} (0.06)
	TN	1.58^{a} (0.05)
	CTRL	1.51^{a} (0.03)
GII	LM	1.18^{b} (0.10)
	TN	1.54^{a} (0.04)
	CTRL	1.38^{ab} (0.04)
GIII	LM	1.21^{b} (0.06)
	TN	1.45^{ab} (0.06)
Bioturbation (a)		$P < 0.001$ ***
Soil groups (b)		$P < 0.001$***
(a) × (b)		$P = 0.436$

Table 10. Results of the linear mixed models testing the influence of termite bioturbation (i.e., termite mound nests, lenticular mounds, and reference soil) and soil groups (i.e., GI, GII and GIII) on water the content at pF 0, 2.5, 3, 3.5 and 4.2 with elevation as random factor. *** < 0.001, ** < 0.01, * < 0.05

	Bioturbation (a)		Soil Groups (b)		(a) × (b)	
	F-values	*P*-values	*F*-values	*P*-values	*F*-values	*P*-values
pF0	0.38	0.545	0.69	0.590	0.81	0.455
pF2.5	8.24	0.009 **	7.79	0.114	0.02	0.975
pF3	3.31	0.082	13.74	0.068	0.02	0.978
pF3.2	4.95	0.036 *	12.66	0.073	0.11	0.893
pF4.2	14.71	< 0.001 ***	5.96	0.144	0.46	0.638

6.3 Discussion

6.3.1 Termite constructions as nutrient patches

Abundant literature has described the specific properties of termite constructions in African savannahs and forests and showed how they regulate the distribution of nutrients at the landscape scale (e.g., Sileshi et al. 2010; Van der Plas et al. 2013; Cramer and Midgley 2015; Davies et al. 2016; Muvengwi et al. 2017; Muvengwi and Witkowski 2020). Comparatively, termites have been considered neglected soil engineers in Asia due to the comparatively low number of studies describing their properties (Jouquet et al. 2016a). In the Lower Mekong Basin, lenticular mounds are, however, conspicuous features of the landscape. If the dynamics of these structures are unknown, the local population explains their presence and properties from the degradation of *M. gilvus* mound nests, which are always found on lenticular mounds (data not shown), as well as the activity of other soil invertebrates (Choosai et al. 2009) and the presence of plants (Choosai, 2010; Miyagawa et al., 2011). At our study site, the density of LM was not influenced by the location within the catchment or by the soil types, reaching 2 mounds ha^{-1}, which corresponds to ~6 m^3 soil ha^{-1} on average. One striking conclusion of this study is that LM always constitutes patches of nutrients in paddy fields, with higher C and nutrient (N and P) contents than the surrounding topsoil. TN was also enriched in P in comparison with the reference soil, but no difference in C or N content was found. Enhancement in C content in LM was confirmed by Rock-Eval® analysis. However, termite bioturbation did not influence the R- index and HI value, suggesting similar soil organic matter quality (Barré et al. 2016; Sebag et al. 2016). Nevertheless, the I/R diagram showed specific SOM-mineral interactions in TN in comparison with both LM and CTRL. Indeed, while LM and CTRL samples were distributed along the 'decomposition line, red line in Figure 3', TN samples were characterized by high variability, suggesting the presence of variable proportions of labile but unstable organic matter fractions in TN, most likely of saliva origin and/or of organic fractions stabilized by adsorption onto mineral surfaces. Such changes could be attributed to the total reorganization of the interactions between SOM and minerals during the molding of individual soil pellets by termites, as well as the enrichment of clay particles in TN. Indeed, TN was always enriched in clay in comparison with the surrounding soil, although a reduction in sand was only measured when the sand content of the paddy field was > 80% (i.e., GI). LM was also enriched in clay, but this effect was only measured when the sand content of the paddy field was > 60% (i.e., GI and GII). Therefore, these findings confirm the general assumption that termites' impact on soil texture is preponderant in sandy and poor soils, while it is more limited in more clayey soil (e.g., Jouquet et al. 2015; Bera et al. 2020). In sandy soil, the construction of termite mound nests usually requires the selection of clay particles, which might come from the deeper soil layers (Abe et al., 2009; Jouquet et al., 2017a), and the incorporation of organic matter (C and N), *i.e.,* mostly saliva that fungus-growing termites use for ensuring cohesion between particles (Holt and Lepage 2000; Zachariah et al. 2017; Jouquet et al. 2022).

As observed by others (Jouquet et al. 2015; Cheik et al. 2018; Bera et al. 2020; Subi and Sheela 2020), a higher soil pH was found in termite constructions in comparison with the surrounding soil in GI. Interestingly, this higher soil pH was associated with the highest MinC values in TN. Although its concentration was very low (< 1%), the presence of mineral C was highly surprising in the Chrey Bak catchment, where the soil is acidic. Since a Pisoplinthic horizon was found at approximately 80 cm depth, we consider it unlikely that mineral C came from the deeper soil layers. Examination of the thermograms measuring the fluxes of CO_2 and CO during pyrolysis shows the presence of 2 synchronous peaks between 500 and 525 °C, observed in oxalate-rich samples. These peaks are not observed in CTRL and suggest that high MinC value in TN could correspond to biogenic carbonate, which may be related to the release of oxalate crystals by termites and their associated fungi and bacteria from decaying oxalogenic plant tissues (Cailleau et al. 2011; Mujinya et al. 2011; Suryavanshi et al. 2016; Francis and Poch 2019; Jouquet et al. 2022). Additionally, these oxalate crystals could also have a bacterial (Hervé et al. 2016) or fungal origin (Hervé et al. 2021). Since termite constructions harbour microbial communities distinct from those present in the surrounding soil (Baker et al. 2020), oxalogenic microorganisms could be more abundant in termite constructions than in soil. To form $CaCO_3$ from the oxidation of calcium oxalate, the soil pH needs to reach the stability of calcite, i.e., pH 8.4 under conventional surface conditions of temperature and pressure. This pH is likely to be reached during the digestion of organic residues by termites (pH = 9.5 in the paunch of *Macrotermes subhyalinus*, Anklin-Mühlemann et al. 1995). Even if the soil pH is lower than 8.4 in TN, it is also possible that such a value could be reached at a very small scale (e.g., Kim and Or 2019) within the soil pellets produced by termites by building their nests. Enhancement in soil pH increases the cationic exchange capacity of soil (Brady and Weil 2010) and therefore its ability to hold nutrients. Indeed, together with these enrichments in clay, C and N contents, termites also enhanced the concentrations of exchangeable cations and nutrients in their constructions (Jouquet et al. 2011; Abe et al. 2011; Bera et al. 2020; Chisanga et al. 2020). Our study confirmed this increase in soil fertility with higher amount of P in termite constructs. The impact of termite bioturbation activity on the amount of available P is usually related to the functional groups to which termite species belong (López-Hernández et al. 2006). Previous studies showed that fungus-growing termites increase the sorption of P in soil (i.e., reduce the amount of available P) in comparison with the surrounding soil (López-Hernández et al. 2006; Bera et al. 2020). Therefore, more research is needed to determine whether the higher amount of P in LM and TN is associated with a higher availability of P in soil.

6.3.2 Termite bioturbation improves soil water dynamics

As shown in other ecosystems, sandy soils can be highly susceptible to compaction (Huang and Hartemink, 2020). This is especially true in the Lower Mekong Basin when the ploughing of soil and the harvesting of rice are mechanized (Gürsoy 2021). At our study site, the high compaction of soil is unlikely to be a problem for the cultivation of rice when it is submerged by water, and it can even be looked at to avoid the leaching of nutrients (Patel and Singh 1981). However, a high bulk density can become a real issue in periods of water shortage (Hoque and Kobata 2000) because of the low water-holding capacity of soil and because of the hardness of soil, which can reduce the ability of rice roots to grow (Olubanjo and Yessoufou 2019). In Cambodia, agriculture is hampered by erratic rainfall at the beginning of the rainy season, with a temporary period of drought threatening the growth of rice seedlings and thus, rice productivity (Tsubo et al. 2009). Therefore, the lower bulk density measured in lenticular mounds is interesting because it shows that bioturbation (i.e., the production of subterranean tunnels by termites and other invertebrates and the production of macropores by roots) associated with a limited increase in clay particles and organic matter can significantly improve soil structure and both the infiltration of water and the water-holding capacity of soil. This was evidenced by the higher values of *Ksat* measured in lenticular mounds in comparison with the surrounding topsoil, as well as by the significantly higher water retention measured at pF 2.5, 3.2, and 4.2.

The high compaction (i.e., extremely low soil porosity) of *Macrotermes* spp. mound nests has been described in several ecosystems (Holt and Lepage 2000; Abe et al. 2009; Traoré et al. 2019; Bera et al. 2020) and explains the extremely high resistance of these soil structures to the attack of predators and to the weathering impact of rain (Jouquet et al. 2004). Our study confirmed the very high bulk density of *M. gilvus* mound nests. Moreover, although the water retention curves and *Ksat* could not be measured from TN samples, the similar soil bulk density between TN samples and CTRL, despite a higher clay content in TN, suggested a very specific organization of the soil porosity and a very low diffusion of water within termite mound nests.

6.4 Conclusion

Two key conclusions and perspectives came out from this study. First, we confirmed that termite constructions could be seen as nutrient patches in paddy fields, explaining why farmers use these soil types to improve the fertility of their lands (Noble et al. 2004; Suzuki et al. 2007; Sarcinelli et al. 2013; Subi and Sheela 2020; Chisanga et al. 2020). In addition to increasing the chemical fertility of soil, the amendment of LM and TN is also likely to improve the physical properties of soil. More research is now needed to determine if the amendment of LM soil can also enhance the water holding capacity of cultivated soils. This impact could be very important in Cambodian paddy fields, where the management of water is considered to be a key issue (Chem et al. 2011).

Second, we evidenced the presence of carbonates in TN, most likely due to the stimulation of specific bacteria and fungi associated with the production of carbonate nodules within microhabitats. This result is especially interesting because, although the concentration of carbonat e is very low, it can favourably impact both the soil fertility and the sequestration of C in paddy fields, which are known to be important emitters of methane (Li 2010). Therefore, more research is also needed to identify the ecological processes and biological actors associated with the production of carbonates in TN and to determine if they could be used to increase the soil fertility and the sequestration of C in cultivated soils.

Chapter 7 . Abundance and distribution of termite lenticular mounds in paddy fields in Cambodia. Comparison between the current situation and that observed in the 1950s.

7.1 Introduction

Termite mounds are among the most impressive soil-constructions produced by living organisms. These biogenic structures have different shapes and sizes and, if most of the species only build small epigeous nests or subterranean chambers, some constitute conspicuous topographical features in the landscapes, such as the termitaria produced by *Macrotermes* spp. in Africa and those of *Amitermes laurensis* in Australia (e.g., Wood et al., 1982; Coventry et al., 1988; Spain and McIvor, 1988). Termite mounds also include lenticular mounds or hills (also called hummocks) that can be covered by the vegetation and even host specific plant communities (e.g., Traoré et al., 2008b; Cramer and Midgley, 2015) which in turn create specific environmental conditions for a variety of herbivores (Noble et al., 1989; Dangerfield et al., 1998; Muvengwi et al., 2014; Davies et al., 2016b) but also soil biodiversity (Choosai et al., 2009).

The origin and dynamics of lenticular mounds are difficult to estimate, in particular 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). Information on termite mound abundance and distribution reveals very variable 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 and Greenslade, 1980), regular (e.g. “murundus” mounds in Brazil, De Souza and Delabie, 2016; De Souza and Delabie, 2018; mounds of harvester termites in Australia, Lee and Wood, 1971; or the fairy-circles in South Africa and Namiby, Getzin et al., 2015; Juergens, 2015) or tend to aggregate in certain areas such as in the case of the nests of *Trinervitermes trinervoides* in South Africa (Redford, 1974) or the nests of *Armitermes euamignathus* and *Orthognathotermes gibberorum* in Cerrado, Brazil (Redford, 1984). These patterns are usually driven by competitive interactions between termite colonies, soil properties, topography and hydrology (Sarcinelli et al., 2009; Freymann et al., 2010; Levick et al., 2010; Davies et al., 2014), the distribution and type of vegetation (Benzie, 1986; Bargués Tobella et al., 2014; De Souza et al., 2017), 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 comes from 'natural' or weakly anthropized ecosystems, and there is currently no information on termite mounds in cultivated areas.

In the lower Mekong basin, paddy fields can be seen as mosaics with the presence of lenticular mounds (LMs) located in cultivated plots or on the embankments that separate plots (Choosai et al., 2009; Miyagawa et al., 2011). In Cambodia, farmers consider that the dynamics of LM is rapid and that less than 40 years is needed for their production (Muon et al., submitted). In this region, the species *Macrotermes gilvus* is considered by farmers to be at the origin of LM. This termite species builds cone shape epigeous mound nests (TN, for 'termite nest'), which are thereafter colonized by other invertebrates, including other termite species, and plants, when colonies die (Muon et al., submitted). In addition to contribute to the preservation of biodiversity in cultivated areas (Choosai et al., 2009), LM and TN provide several ecosystem services to the population. For instance, LM and TN soils can be used by farmers to increase the fertility of their land, and biodiversity associated to LM can provide an access to edible plants and insects, and to medicinal plants (Miyagawa et al., 2011; Muon et al., submitted). However, there is dearth of information on the density and distribution of LM and TN in paddy fields in Cambodia. Is the density of LM and TN equivalent to the one found in natural environments? Is their distribution random or does it follow a specific pattern at local and at large scale depending on the properties of the environment?

Therefore, the aim of this study was to describe LM and TN distributions in paddy fields in Cambodia and to discuss their dynamics. The main hypothesis of this study was that the distribution and density of LM and TN in paddy fields vary according to the environment with differences according to the topography and the elevation. Based on local knowledge, we also assumed rapid land use changes and that most of LM found in paddy fields are recent (i.e., less than 40 years old).

7.2 Results and discussion

7.2.1 Abundance and distribution of lenticular mounds along the toposequence

Because termites are sensitive to land use changes, they have been considered bio-indicators of habitat changes in the tropics (Dosso et al., 2012) and as very suitable groups for illustrating the effects of ecosystem fragmentation (De Souza and Brown, 1994). In particular, termite nest distribution and abundance have been extensively studied, especially in Africa and with termite nests produced by *Macrotermes* spp. However, much less information is available in Asia and with lenticular mounds, which are complex soil features occupied by several termite species and other invertebrates (Jouquet et al., 2017a).

Termite mound abundance, distribution and properties are determined by various abiotic and biotic variables. At broader scales, abiotic factors such as the underlying geology and mean annual precipitation shape mound densities, while local hillslope morphology and the habitat type (i.e., vegetation cover and biological interactions) influence mound distribution at finer scales (e.g., Wood, 1988; Holt and Lepage, 2000; Awadzi et al., 2004; Donovan et al., 2007; Picker et al., 2007; Deblauwe et al., 2008; Davies et al., 2014). For instance, the density of living *Macrotermes bellicosus* mounds differs greatly between shrub savannas and gallery forest in the Comoé-National Park, Côte d'Ivoire (from 0 to 22.7 ha^{-1} *vs*. 2.1 to 6.5 ha^{-1}, in savanna and gallery forest, respectively) (Lepage, 1984; Korb and Linsenmair, 1998). Soil properties and the distance to the water table are also two key variables explaining termite mound densities (e.g., Bodot, 1967; Ahmed II and Pradhan, 2019; Jamilu Bala Ahmed et al., 2019). In our study, no relationships could be evidence between the density of LMs and TNs and the elevation (linear models, $P > 0.05$, data not shown). In average, the density of LMs reached 2.21, 1.59 and 1.78 mounds ha^{-1} in the upland, midland, and lowland of the Chrey Bak catchment, respectively (Figure 28). Despite a higher density in the upland, no significantly differences could be measured between positions ($P > 0.05$ in all cases). Similarly, no significant differences in TN density along the catchment could be measured ($P > 0.05$) with 1.71, 1.19 and 1.49 mounds ha^{-1} in the upland, midland and lowland, respectively. These densities are low in comparison with those observed in natural environments in Africa (Abbadie et al., 1992; Traoré et al., 2008a) and in Asia (Inoue et al., 2001; Jouquet et al., 2017a) 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). Therefore, we assume that the low abundance in LMs and TNs and the absence of a gradient between the upper to the lower part of the catchment are likely to be explained: First, by farmer's practices and decisions to maintain or limit the presence of these biostructures; and second by the fact that the slope was rather gentle in the catchment (i.e., 17.0 and 67.8 meters a.m.s.l. on average in the lowland and in upland, respectively), suggesting a lack of influence of the distance to the water table.

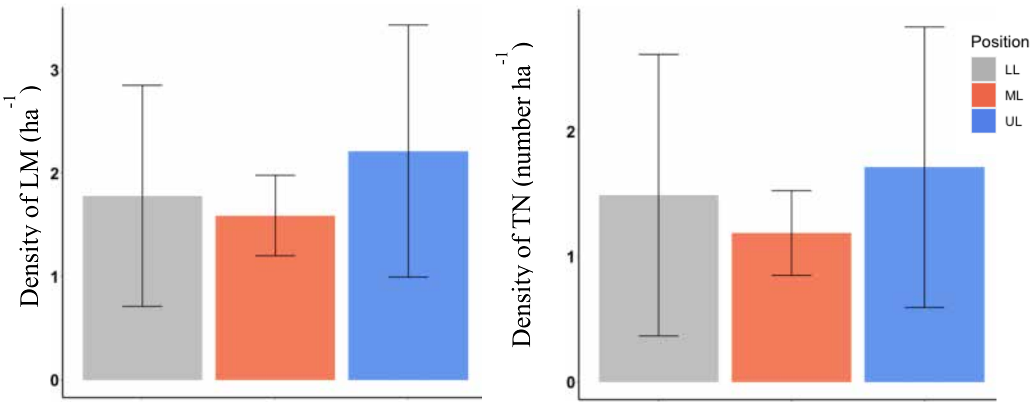


Figure 28. Average density of lenticular (LMs) and termite nests (TNs) mounds in paddy fields at Chrey Bak, in the lowland (LL, in grey), midland (ML, in orange), and upland (UL, in blue) of the catchment, n=30 plots.

The importance of farmers' strategies was also evidence with the measure of LM distribution. In our study, LM distribution was measured in twenty-eight plots located in the lower, middle, and upper part of the catchment (See Figure 29). The result of Average Nearest Neighbor functions show that LMs were clustered, random, or dispersed depending on the plots (See Table 11 and Figure 30). From the twenty-eight plots, half (n = 14) evidenced a random distribution, and half were either clustered (n = 7) or dispersed (n = 7). This trend was slightly more important in the upper part of the catchment than in the other locations since 63, 44 and 43% of the plots evidenced a random distribution, in the lowland, midland and upland, respectively (Figure 29). Although it is not possible to reject the hypothesis that termite's ability to settle and build LMs varied between sites, this study rather suggests that the distribution of LMs was mainly explained by farmers' practices. Indeed, with the assumption that random distribution reflects a lack of impact of the environment, including farmer's practices, these results suggest lower interactions between LMs and farmers in the lowland than in midland and upland. The main difference between the locations being the irrigation and access to water (less hazardous in the lowland due to the enlargement of the river bed), we consider that LMs patterns in the mid- and uplands could mostly be explained by farmers' strategies and on whether they used LMs or not, or on their access to water to irrigate the plots.

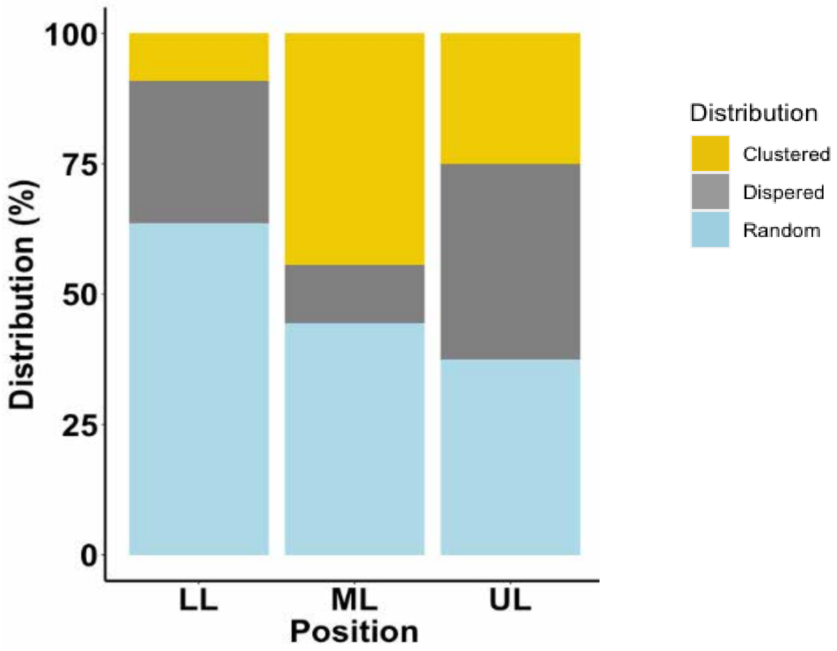


Figure 29. Bar plots showing the percentage of LMs show a clustered (in yellow), dispersed (in grey) and random (in blue) distribution in the lowland (LL), midland (ML), and upland (UL) in the Chrey Bak catchment.

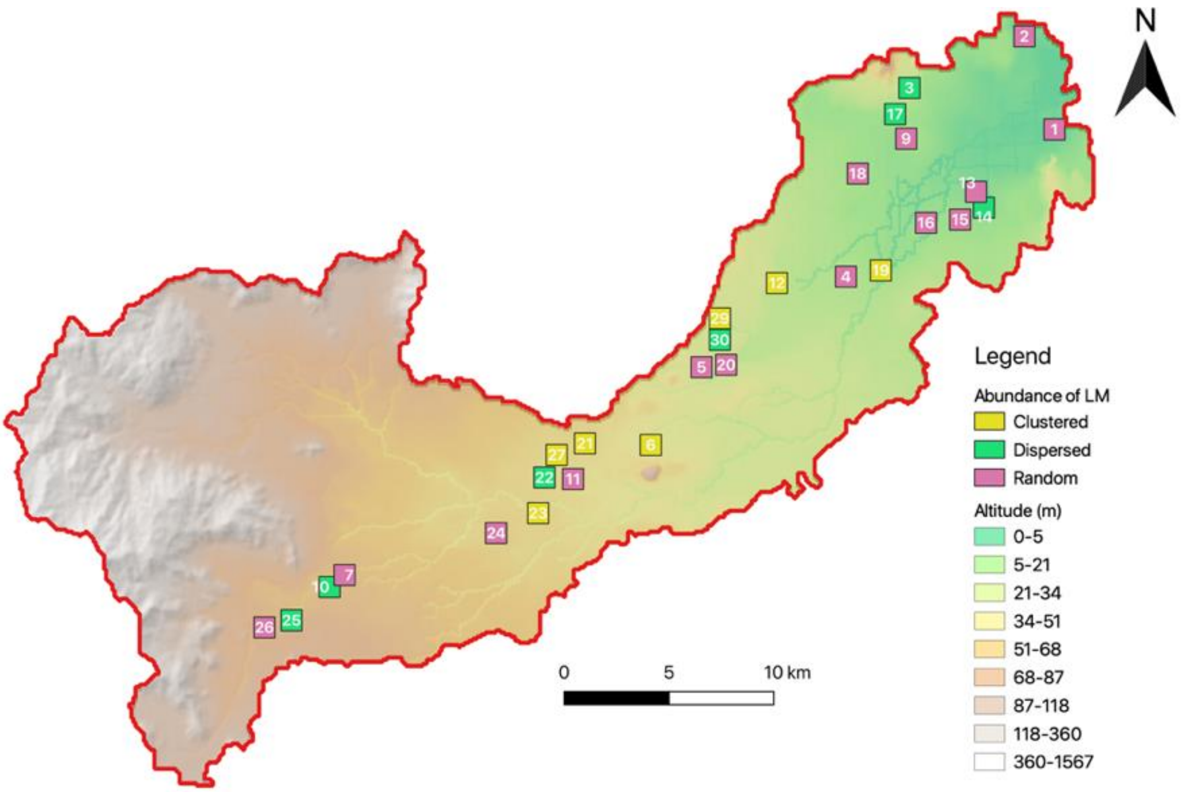


Figure 30. Distribution of lenticular mounds (LMs) over the Chrey Bak catchment using Average Nearest Neighbor analyze (clustered, dispersed or random). The numbers inside the square plots indicate the ID plots given in Table 11.

Table 11. Spatial distribution analysis of lenticular mounds obtained from the Average Nearest Neighbor (ANN) function (Euclidean) in the lowland (LL), midland (ML), and upland (UL). Both Z scores and P-values indicate significant level, associate with the standard normal distribution. Non-random distributions are evidence in bold characters.

Position	ID Plot	Z-score of ANN	p-Value of ANN	Distribution of ANN
LL	1	0.712671	0.4760	Random
	2	-0.77367	0.4391	Random
	14	2.434231	0.0149	**Dispersed**
	15	0.455205	0.6490	Random
	16	-0.385628	0.6998	Random
	18	1.612444	0.1069	Random
	3	2.116201	0.0343	**Dispersed**
	17	1.685215	0.0919	**Dispersed**
	13	-1.088562	0.2763	Random
	9	1.116516	0.2642	Random
	19	-2.781141	0.0054	**Clustered**
ML	4	1.39568	0.1628	Random
	5	0.009945	0.9921	Random
	6	-3.180216	0.0015	**Clustered**
	12	-1.790479	0.0734	**Clustered**
	20	0.346303	0.7291	Random
	21	-1.904572	0.0568	**Clustered**
	29	-2.145439	0.0319	**Clustered**
	30	2.19066	0.0285	**Dispersed**
	11	-0.600018	0.5485	Random
UL	10	3.371766	0.0007	**Dispersed**
	22	2.035942	0.0418	**Dispersed**
	7	0.448829	0.6536	Random
	23	-4.424913	0.0000	**Clustered**
	24	1.533229	0.1252	Random
	25	1.898735	0.0576	**Dispersed**
	26	-0.499475	0.6174	Random
	27	-1.884532	0.0595	**Clustered**

7.2.2 LM dynamics assessed from remote sensing and image analyses

There is a growing literature on the use of remote sensing to measure termite mound abundance, but most of these have been carried out in Africa (e.g., Davies et al., 2014; Isabelle et al., 2014; Ozsahin et al., 2022) and in a lesser extent in South America (e.g., Sim and Lee, 2014). Moreover, these studies could be seen as 'snapshots' without the possibility of comparing results from a chronological point of view, simply because the means associated with remote sensing are recent. Here, we used GE and IGN images to estimate the presence of LMs and to determine if those were likely to be already present in 1953.

The main limit of this approach is that LMs can only be measured in the field because they are hidden by the vegetation (100% of the LMs were covered by trees in Chrey Bak, pers. obs.), and because all the vegetation patches in the landscapes are not LMs. Reciprocally, the presence of copses in old photos may hide LMs that are no longer present, and recent LMs (i.e., made by young termite colonies) might not be associated with trees, and therefore not identified using GE and IGN images. However, a good match between the presence of LMs observed by ground truthing and GE images was found ($R^2 = 0.96$, $P < 0.001$, see appendix A5). Interestingly, most of the LMs observed in the field were also evidenced on IGN images ($R^2 = 0.80$, $P < 0.001$, Figure 31). In other words, while 96.5% of LMs observed in the field could be found in GE image, this value reached 88.6% using IGN images.

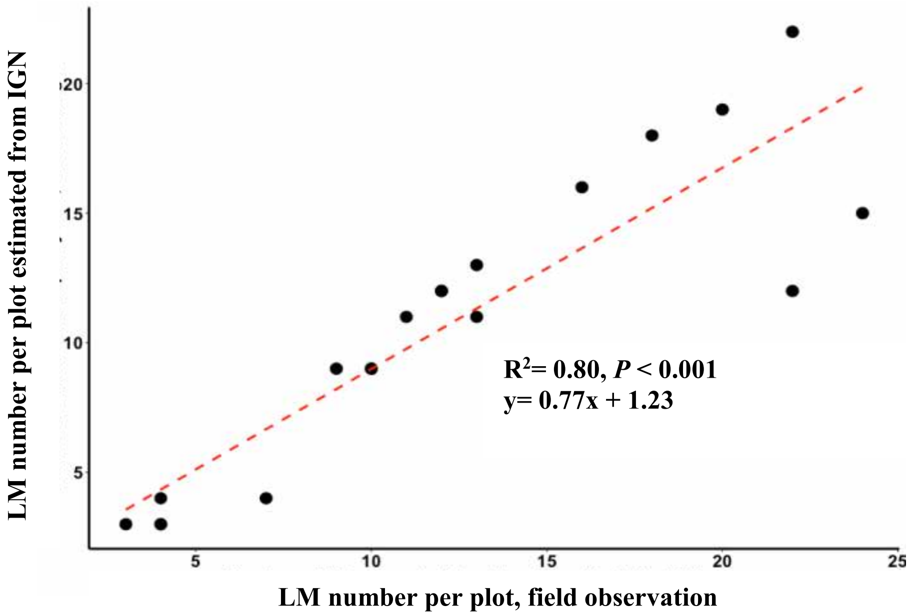


Figure 31. Relationship between lenticular mound (LMs) number associated with tree on IGN images and the number of LM measured by ground truthing in each plot.

Therefore, these results suggest that most of LMs in Chrey Bak were likely to be older than 70 years old, although some could be more recent (~ 11.4%). These results have 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 (Moore and Picker, 1991; Martin et al., 2018). In Chrey Bak, LMs are likely to be very old, although ^{14}C labelling should be done to confirm this statement. However, we also observed that a few LMs were recent, thus suggesting that only a few decades could be enough to get new LMs. Therefore, in a very intensively cultivated area such as paddy fields, LMs could be seen as relics of old forests and/or habitats for biodiversity. This consideration is likely to be very important in South-East 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). Indeed, using IGN and GE images, we found that paddy fields inside our sampling plots occupied less surface in the 50s than in the current time, although the difference was not significant (Kruskal Wallis test, $P > 0.05$) (Figure 32a), and that the percentage of tree cover was much more important in the past (~10% of the paddy fields against less than 5% nowadays) (Figure 32b, Kruskal Wallis test, $P < 0.001$). In these circumstances, LMs are likely to be a last refuge for the plants and animals that once populated the lost groves or wilderness areas.

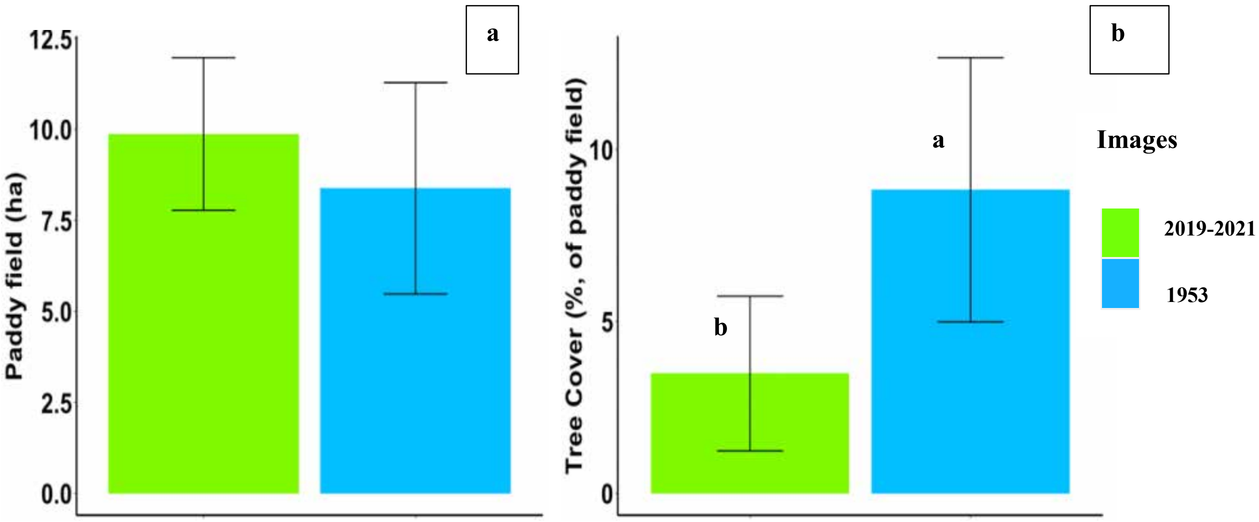


Figure 32. (a) Evolution of the landscapes in Chrey Back measured from the surface occupied by paddy fields in each plot (in ha), and (b) percentage of tree cover in each plot calculated from Google Earth and IGN images (n = 19 plots).

7.3 Conclusion

In conclusion, this chapter evidences that LMs are not epiphenomena but rather specific and conspicuous geomorphological structures (*sensu* Van Thuyne et al., 2021) of Cambodian paddy fields. Despite their low density, these structures increase the heterogeneity in the landscapes. They are also likely to be seen as relics of the previous ‘natural’ environments, whose importance has greatly diminished since the 50s. More research is now needed to confirm and understand the specific interactions between LMs and farmers. Why do farmers decide to maintain these structures on their lands and do they derive ecosystem services from them, thus justifying the decision not destroy them but rather to use them as natural (and sustainable) resources?

Chapter 8 . Discussion and conclusions

This chapter contains the main conclusions of the thesis and the remaining identified challenges regarding the study of the services provided by termite bioturbation in Cambodian agro-ecosystems.

8.1 Summary of the main findings and insights

In order to understand the importance of termite bioturbation in Cambodian paddy fields, and the ecosystem services delivered by these structures on the local population, we first carried out a survey in 13 villages (Chapter 4) in the observatory of Chrey Bak, which has been extensively studied in many national and international projects. Interestingly, a key result of this survey was that many farmers use termite mound soil as an amendment for improving the fertility of their land. Regarding the heterogeneity in soil properties and water dynamics at the catchment scale, we first characterized the soil types in our study site (Chapter 5). Soils were described as Gleysols with variable sand contents. We then studied the properties (Chapter 6) and dynamics (Chapter 7) of termite mounds (lenticular mounds and termite nests produced by *Macrotermes gilvus*), and arrive to the conclusion that termite mounds are fragile patches of fertility in paddy fields, that provide several key ecosystem services to the population. A perspective of this work would be to lay the foundations for a sustainable management of these natural resources.

8.2 Perception and utilization of termite mounds?

Termite mounds are conspicuous features of paddy fields in Cambodia. A key finding of this thesis is that farmers have precise ideas of the roles played by these islands of biodiversity within paddy fields, and on their dynamics (e.g., the fact that *M. gilvus* is likely to be at the origin of lenticular mounds) (Chapter 4). Several key ecosystem services were revealed by the survey. As expected, and observed in other environments (Sileshi et al., 2009; Miyagawa et al., 2011; Dossou-Yovo et al., 2014; Enagbonma and Babalola, 2019; Tilahun et al. , 2012, 2021), the most important service was associated to the management of soil fertility. Indeed, most of the interviewees used termite mounds for increasing the fertility of their field and for the cultivation of rice and other plants (e.g., sponge gourd and pumpkin). In addition, farmers identified termite mounds as refuges for edible animals and plants, and they declared to eat several animals, such as rats and snakes, but also mushrooms and thirteen plant species found on termite mounds. In addition to increase food diversity, termite mounds could also increase the livelihood of the population by providing an access to medicinal plants (20 medicinal plants were reported in our survey), or indirectly via a reduction in the use of pesticides. A limit of this study is, however, that we did not take into account the harvesting of edible animals and plants, and medicinal plants in other locations (i.e., in the wild or in non-cultivated areas). This information is crucial for understanding the importance of mounds and their influence on farmers' livelihoods. Are medicinal plants restricted to termite mounds or can they also be harvested in other proximal environments? Is the consumption of animals and plants found on termite mounds significant or is it an epi-phenomenon with respect to the quantities harvested in the wild or purchased? Despite the fact that these questions remain unresolved, we have some clues that the effect of mounds could be significant. Indeed, farmers mentioned during the survey that they prefer plants growing on mounds (i) because of their taste and quality, and (ii) because it is more convenient and easier to harvest them on termite mounds than forests that might be far and difficult to access. Therefore, a main perspective of this study would be to quantify the services provided by termite mounds in taking into account the resources that are also likely to be freely available in the wild or that can be purchased in markets.

8.3 A strategy to understand the impact of the environment on termite mound properties.

Termite diversity, abundance and impact are highly context-dependent and they are influenced by several key environmental variables such as the precipitation, the distance to the water table or the properties of soil (Bodot, 1967; Ahmed II and Pradhan, 2019; Jamilu Bala Ahmed et al., 2019). At the catchment scale, the most important variables explaining termite mound properties are the soil types and the distance to the river. Several soil types have been described in Chrey Bak. However, soil description is sometimes complicated and confusing in Cambodia since different sources suggest different soil types. Therefore, understanding the importance and properties of termite mounds in the Chrey Bak catchment necessitated a thorough description of the soil types, which was done in Chapter 5. Unlike the soil description proposed by Crocker (1962) and JICA (2003), Chapter 5 showed that paddy soils in Chrey Bak could be described as Gleysols with sand contents varying from 60 to 88%. Although our study only focused on paddy fields, and that it is possible that other soil types could be found in the catchment, perhaps where soils were not cultivated or used for other cultures than rice, a finding of this chapter was that the distinction between Acrisols and Arenosols was not relevant for studying the impact of termite mounds on agroecosystem functioning. On this basis, the study of the properties of termite mounds (Chapter 6) was carried out by distinguishing three soil groups from their sand contents: Group I (very sandy soils with > 80% sand), Group II (moderately sandy, ~60% sand), and Group III (low sandy soils, ~40% sand). Moreover, while the proportion of fine silt-sized particles usually vary with the elevation and the distance to the river (Badia et al., 2016; Pahlavan-Rad and Akbarimoghaddam, 2018), our study showed that the soil texture could not be explained by neither the elevation nor the distance to the Tonle Sap river. This lack of relationship could perhaps be explained by the gentle slope of the catchment (i.e., from –5 to +86 m a.m.s.l.). However, it mostly raised the need to better understand the hydro-sedimentary processes that occurred in Chrey Bak, which were likely to be related to the management of water in the catchment and the erosion of soil from the mountain.

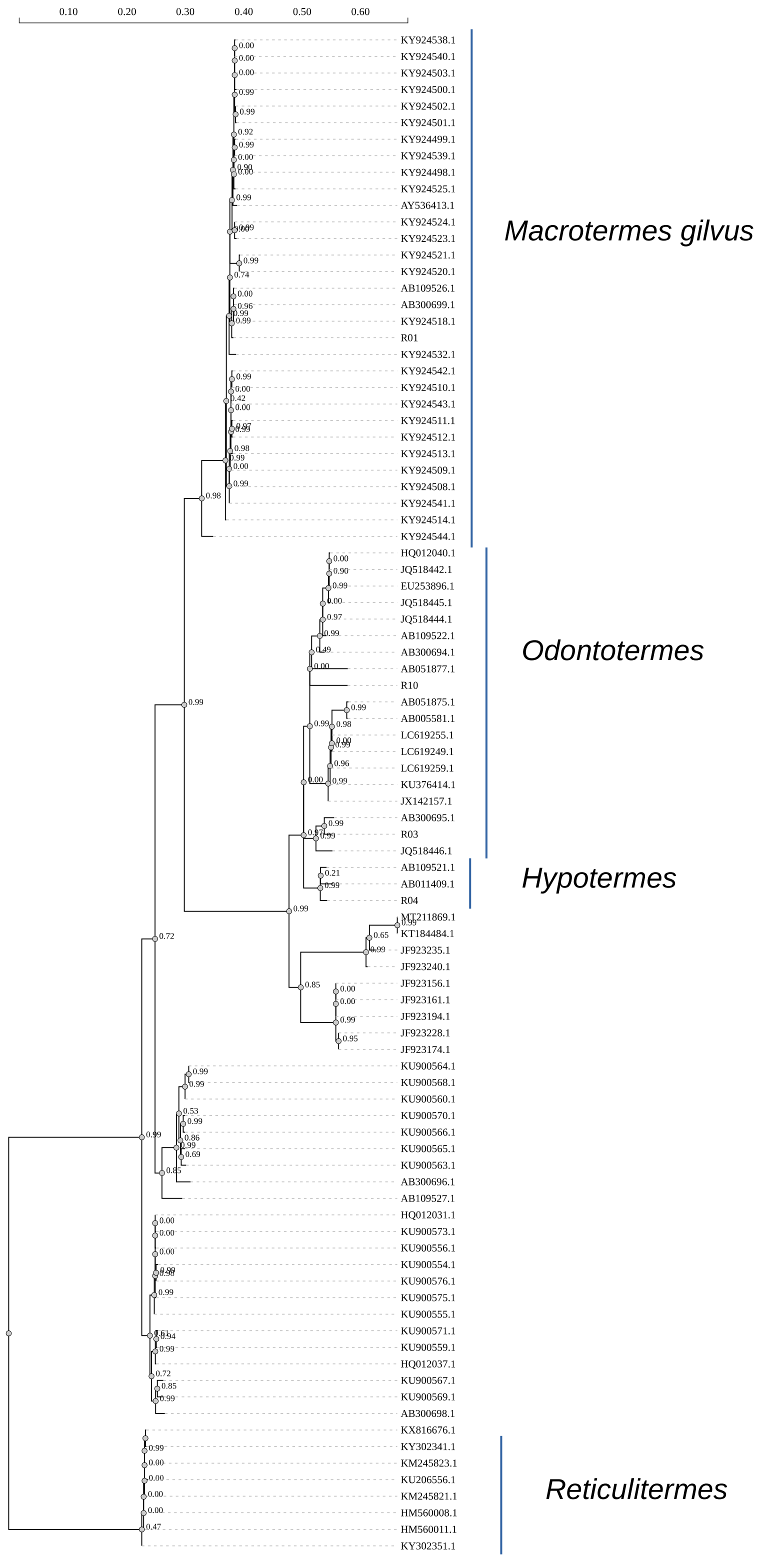
8.4 Are termite mounds patches of fertility in paddy fields?

In this chapter, we compared the properties of two termite constructions to their surrounding environment: mound nests produced by *Macrotermes gilus*, a fungus-growing termite species, and lenticular mounds, whose origin is also attributed to the activity of *M. gilvus*. Because a key finding of Chapter 5 is that soils are mostly differentiated from their sand content, the impact of termite bioturbation was measured in taking into account the three soil groups. As expected, we showed that termite mounds could be considered patches of chemical and physical properties owing to their higher organic matter and clay contents in comparison with the surrounding soil environment, and independently of the location (i.e., the impact was similar whatever the soil group for most of the parameters). We assume that this impact is likely to explain why farmers use termite mound soil as amendment for improving the fertility of their land. The utilization of termite mound soil could also favorably impact the resistance of rice to drought spells, especially at the beginning of the rainy season and on the upper and central parts of the catchment where the management of water is crucial, and can be a possible source of conflicts. Therefore, a key perspective of this thesis would be to determine if the amendment of termite mound soil enhances the water holding capacity of cultivated soils, and improves the growth, productivity and resistance of rice to environmental hazards. These questions were to be addressed in this thesis. Unfortunately, due to complications with the COVID-19, the experiments initially planned had to be cancelled. Other perspectives are related to the higher soil organic matter content found in termite mounds, and in the presence of carbonates evidenced in termite nests. Although the amount of carbonate was low in termite nests, its presence in soil was surprising and requires more research in order to understand the ecological processes associated to their production. Carbonates are likely to increase soil fertility because they enhance the soil pH and the cationic exchange capacity of soil (Watson, 1976; Brady and Weil, 2010; Jouquet et al., 2015; Cheik et al., 2018; Subi and Sheela, 2020; Bera et al., 2020). Moreover, while paddy fields are known for their important emission of methane (Li 2010), more research is therefore now needed to determine if the presence of termite mounds in paddy fields can contribute to reduce the negative impact of paddy fields on greenhouse gas emissions, via the protection of organic matter with termite constructions and/or the sequestration of C in the form of carbonates. Since termite mound soil is afterwards spread in paddy fields by farmers, further studies should be also carried out in order to determine the fate of this protected C (within termite-soil and in the form of carbonates).

8.5 Towards a sustainable use of termite mounds. Questions on the abundance and dynamics of termite mounds.

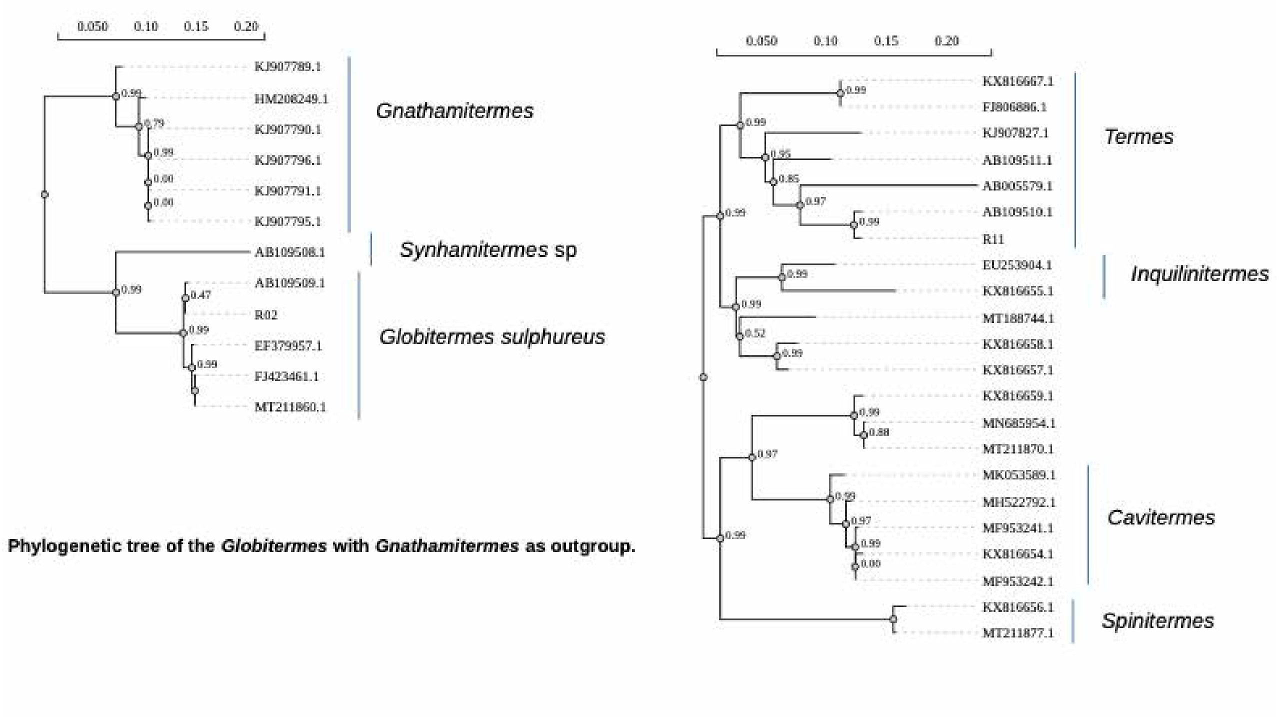
Another conclusion of Chapter 4 is that most of the farmers considered that termite mound dynamics is rapid, or in other words that less than 100 years are needed for the production of a termite mound. This information is very important for the sustainable management of termite mounds. Indeed, a rapid turnover or production of termite mounds can be associated to an intensive utilization of termite mound soil. Conversely, if centuries are needed for the production of termite mounds, as observed in Africa (up to 2,000 years, Erens et al., 2015; Moore and Picker, 1991) and in Brazil (> 4,000 years, Martin et al., 2018), an annual removal of soil from termite mounds is likely to be unsustainable and to lead to the irremediable destruction of these natural resources. Therefore, the hypothesis of a rapid termite mound dynamics was tested using historical aerial photographs taken by IGN in 1953. Our hypothesis was that termite mounds currently observed in the field would not be observed in 1953 if their dynamics was rapid. Although we could not observe with certainty the presence of mounds in the photographs from IGN, our study strongly suggested that mounds are long-lasting structures, much older than the estimation of farmers. More research is, however, needed to confirm this study. An extension of this thesis could be to determine the age of termite mound soil using ^{14}C (e.g., see Erens et al., 2015 in Africa) or simply to follow the growth of termite mounds over time, using photogrammetry technics and/or wood stakes installed on and in the border of termite mounds. Obviously, this finding raised concern concerning the sustainable use of termite mounds in paddy fields. With a density of ~2 mounds ha^{-1}, and rapid land use changes observed between 1953 and the current situation (i.e., mostly deforestation and the conversion of trees or forests to annual crops), key questions raised by our study are (i) if these structures were more abundant in the past and if this low density reveals their overexploitation by farmers, and (ii) if termite mounds can be seen as relics of "natural" ecosystems that existed in the past, but that vanished due to the homogenization and simplification of the (agro)ecosystems. If the specific properties of termite mounds, and the usefulness of termite bioturbation, in terms of nutrient cycling and preservation of biodiversity have been clearly evidenced, the preservation of these natural resources and the underlying ecosystem services associated to them, strongly depend on the perception and interest of farmers to maintain them in their land. Therefore, we assume that the preservation of termite mounds in Cambodian paddy fields can only be achieved using more integrative and transdisciplinary activities.

Appendix



Phylogenetic tree of the Macrotermitinae with *Reticulitermes* as outgroup.

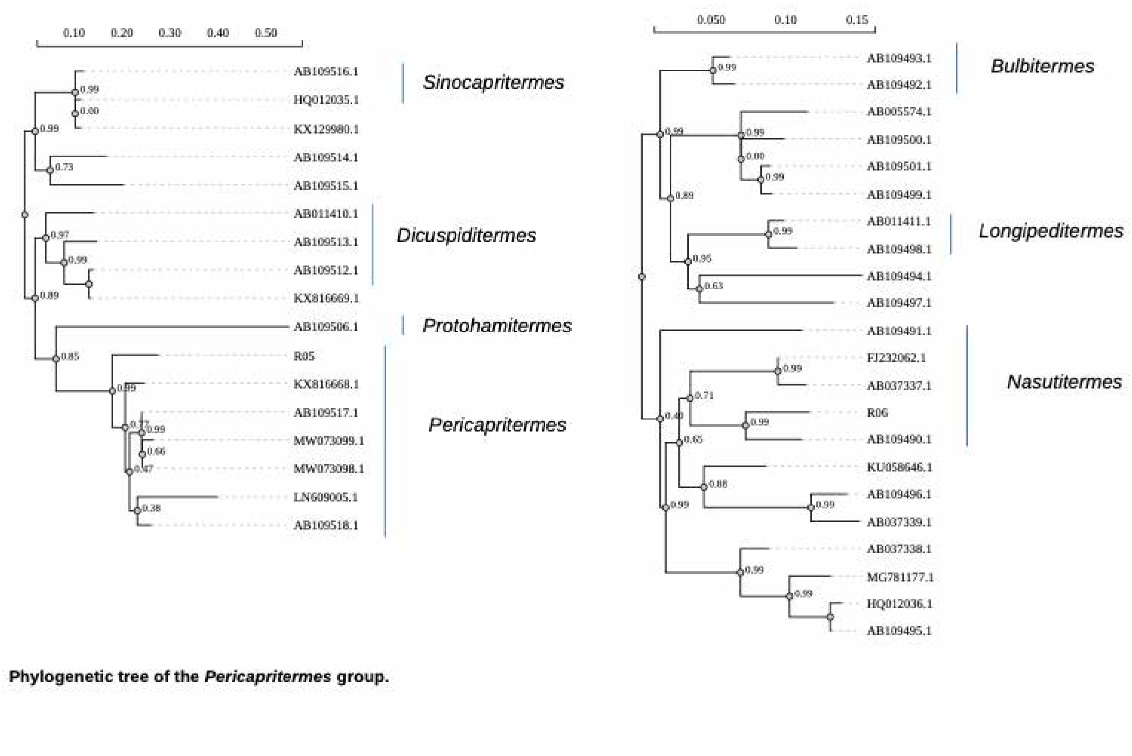
A1. Phylogenetic tree of the Macrotermitinae with Reticulitermes as an outgroup. Labels on the tree correspond to GenBank accession numbers.



Phylogenetic tree of the *Globitermes* with *Gnathamitermes* as outgroup.

Phylogenetic tree of the *Termes* group.

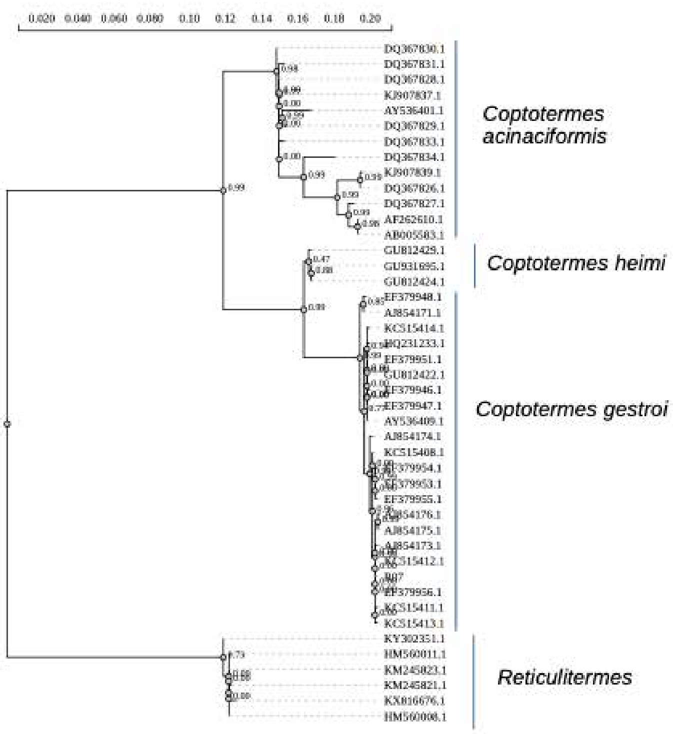
A2. Phylogenetic tree of the Globitermes with Gnathamitermes as the outgroup and phylogenetic tree of the Termes group. Labels on the trees correspond to GenBank accession numbers.



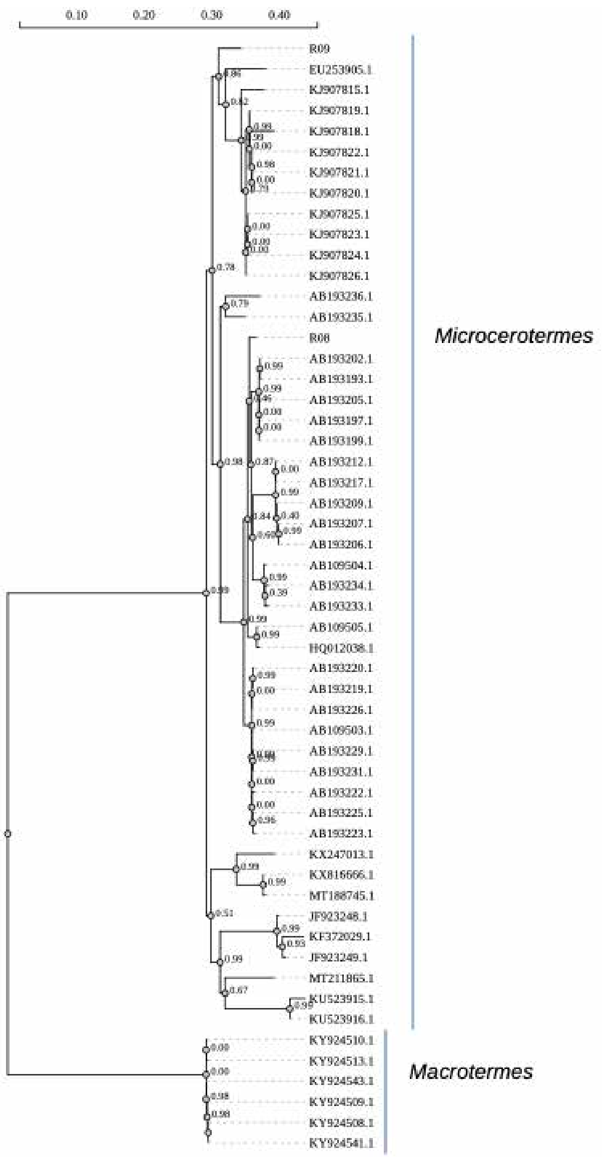
Phylogenetic tree of the *Pericapritermes* group.

Phylogenetic tree of the *Nasutitermes* group.

A3. Phylogenetic tree of the Pericapritermes and the Nasutitermes group. Labels on the tree correspond to GenBank accession numbers.

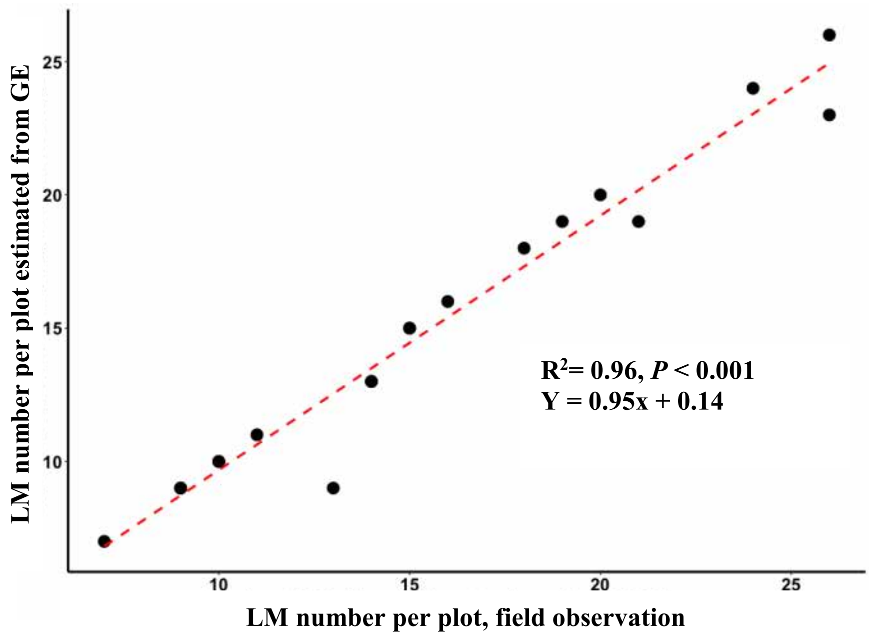


Phylogenetic tree of *Coptotermes* with *Reticulitermes* as outgroup.

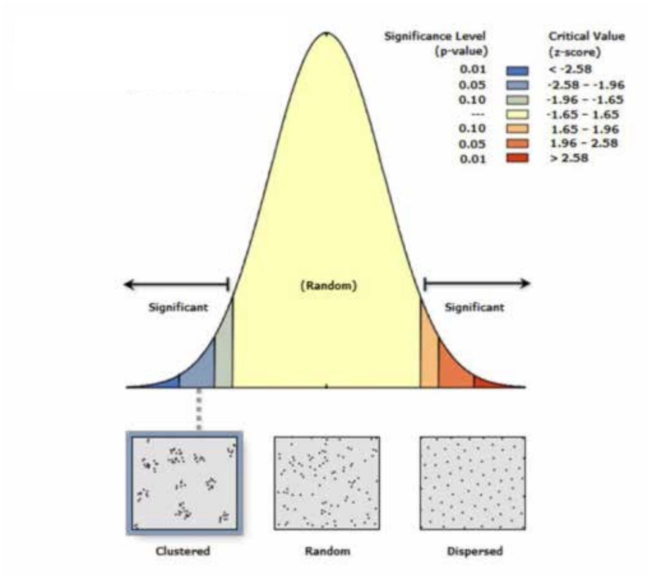


Phylogenetic tree of *Microcerotermes* with *Macrotermes* as outgroup

A4. Phylogenetic tree of Coptotermes with Reticulitermes as an outgroup and phylogenetic tree of Microcerotermes with Macrotermes as the outgroup. Labels on the trees correspond to GenBank accession numbers.



A5. Number of lenticular mounds (LMs) with trees nearby inventories in the field in 2019 and estimated using Google Earth images (n =19 plots)



A6. Example of theoretical Average Nearest Neighbor results calculated using ArcMap 10.7. Both z-scores and p-values are associated with the standard normal distribution. At P < 0.10, very low (negative) z-scores indicate significantly clustered distributions, while dispersed distributions correspond to very high z-scores. Random distributions are given for P > 0.10.

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