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# Abundance, perceptions and utilizations of termite mounds in Cambodia

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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’ because termite bioturbation is considered to be at their origin. Termite mounds 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 abundance of mounds and their use by population were quantified in a catchment in Cambodia. We found that mounds density reached  $\sim 2$  mounds  $\text{ha}^{-1}$ . Interviews carried out within the catchments showed that most of the interviewees used 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 to their potential to increase plant productivity, the survey revealed that animals (rats and snakes), mushrooms and 13 plant species found on or in mounds were consumed by the population. In addition to potentially contributing to an increase in food diversity, mounds 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 termite mounds in Cambodia. This increase in the knowledge of the diversity of environmental and socioeconomic services provided by termite mounds 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 region.

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

## 1. Introduction

The “One Health” concept and framework was created as a need for holistic and transdisciplinary approaches in dealing with the health of humankind, animals, and ecosystems (Destoumieux-Garzón et al., 2018). This concept has 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 (hereafter the ‘Basin’), notably because this region is undergoing dramatic climatic, environmental and societal changes (Trisurat et al., 2018; Mainuddin et al., 2011; Thilakarathne and Sridhar, 2017; 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; Firbank et al., 2008; Dale and Polasky, 2007; 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 and their contribution to human health by local actors remain poorly evaluated.

Rice is the most cultivated plant in the Basin (Cramb, 2020). In this environment, understanding the services derived from paddy fields 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 Basin, 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’ (hereafter ‘mounds’) 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<sup>3</sup> of soil), mounds 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 soil properties and the resistance of plants to environmental hazards (e.g., drought) (Bonachela et al., 2015; Padonou et al., 2020). Regarding their improvement of soil properties, mounds have been reported to be used as soil nutrient amendments in Africa (Dossou-Yovo et al., 2014; Tilahun et al., 2012, 2021; Enagbonma and Babalola, 2019). They can also improve human health because mound 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).

Less is known about the importance and utilization of mounds by farmers in Southeast Asia. Information regarding the services provided by mounds in the Basin 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 abundance of mounds and their traditional use by the population, in particular the farmers, remain unknown, although mounds are a remarkable characteristic of the landscape at first glance. Therefore, the objectives of this study were to measure the abundance of mounds in cultivated areas in Cambodia, and to describe and quantify the perceptions and use of mounds by farmers. Our main hypothesis was that farmers' preservation of mounds relies on the use of this natural resource due to its positive effect on rice yield and potentially on dietary diversity and health.

## 2. Materials and Methods

### 2.1. Study site

The study site was located in the Chrey Bak long term observatory, in northwestern Phnom Penh Capital, Cambodia (Figure 1). This observatory is a catchment of approximately 800 km<sup>2</sup>, situated in the watershed of Tonle Sap Lake, and it is covered by two districts, namely the Tuek Phos and Rolea Biér districts. This region is influenced by the tropical monsoon and has two distinct seasons: the dry

season from November to April and the rainy season from May to October, with annual rainfall varying between 1400 and 2000 mm (MOWRAM, 2014). Soils are mainly Gleysols (Bridges et al., 1998) with varying sand contents (Muon, 2022). The lower part of the catchment is located in the Tonle Sap River floodplain. Based on the Japan International Cooperation Agency (JICA, 2003) land use map produced in 2003, forests cover 34% of the catchment area. The remaining corresponds to agricultural land (32%), shrubland (27.4%) and grassland (5.4%). The study site has an altitude varying between 10 and 1400 metres, being high in the mountainous area in the southwest region while it is very gently sloped or almost flat in the cultivated area, which is dominated by paddy fields (Mekong River Commission, 2003). The majority of Cambodia's rice is rain-fed and is usually planted at the end of May or early June when the first monsoon rains begin to fall (Chann et al., 2011).

In this environment, termite mounds and nests are conspicuous features of the landscape (Figure 2) (see Josens et al. 2016, Jouquet et al., 2017a for a definition of lenticular mounds and nests). Mounds have a large lenticular shape ~1 m high and 2-3 m in diameter on average (~6 m<sup>3</sup> and 17 m<sup>2</sup> on average). They are complex soil structures hosting many other animals (e.g., invertebrates such as termites, earthworms and spiders, and vertebrates such as rats) and plants. Although their dynamics are unknown, their origin is attributed to the activity of termites (Harit and Jouquet, 2021; Muon et al., 2022). Conversely, nests are freshly built structures produced by single well-identified termite colonies.

## **2.2. Density of termite mounds and their utilization by farmers**

### **2.2.1 Termite activity and diversity**

Thirty sampling plots (300 m x 300 m) were randomly selected within paddy fields along the toposequence of the Chrey Bak observatory (Figure 1). For each plot, the position of the center of mounds and nests, 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. The densities of mounds and nests were calculated using Spatial Join tools in ArcMap 10.7. Well-identified termite

122 nests were often found on mounds. For each nest, termites (20-30 individuals nest<sup>-1</sup>) were sampled  
123 after gently breaking the nest in one or several parts to investigate termite biodiversity in the study  
124 area. Both worker and soldier termites were collected and preserved in 99% (v/v) ethanol for further  
125 identification in the laboratory using taxonomic keys and molecular techniques (see supplementary  
126 information 1).

## 128 2.2.2 Utilization of termite mounds by villagers

129 A survey was carried out during the dry season in 2021 by randomly selecting a subset of 13 villages  
130 in the studied catchment (Figure 1), with a total of 61 respondents. Village chiefs and villagers  
131 owning land with mounds were randomly selected for the interview. The questionnaire was designed  
132 with three main sections focusing on health, agronomy, and economics. For each section, villagers  
133 were asked to explain how mounds were used and to list all the services provided by mounds, such as  
134 their impact on soil fertility and the presence of plants with medicinal properties (see Table 1 for the  
135 list of questions). The names of animals and plants that were used as medicine and food were obtained  
136 during the interview. Their occurrence was considered as a percentage of the total number of  
137 interviewees (n = 61). Khmer names were converted to English and/or Latin names using the list of  
138 Cambodia's Medicinal Plants (National Centre for Traditional Medicine, 2013a, 2013b).

## 140 2.3. Statistical analyses

141 Differences in means between mound and nest densities were assessed using one-way ANOVA and  
142 least significant difference (LSD) tests, after first verifying that residuals were normally distributed  
143 using Shapiro-Wilk test. Data from the survey were analyzed using comparison of means and standard  
144 errors from the proportions of positive answers for each village (n = 13).

## 146 3. Results and discussion

### 147 3.1. Mound density and dynamics

On average, mound density reached 2.1 mounds ha<sup>-1</sup> in the Chrey Bak catchment (Figure 3) (i.e., less than 1% of the surface). This value was equivalent to the value measured in paddy fields in northeast Thailand (~2 mounds ha<sup>-1</sup>, Choosai, 2010), but it was lower than the value measured in Asian tropical forests (> 10 mounds ha<sup>-1</sup>, Matsumoto, 1976; Inoue et al., 2001; Jouquet et al., 2017a). This difference in density confirmed the lower abundance of mounds in agricultural land than in protected areas (Ekundayo and Aghatise, 1997; Davies et al., 2020; Ogoudedji et al., 2020). If mounds were observed in more natural environments, such as forests, in the catchment (Muon, pers. com.), the fact that mounds were observed in paddy fields also reflects their possible traditional utilization by farmers, as shown in Africa and Laos (Miyagawa et al., 2011; Yêyinou et al., 2017; Chisanga et al., 2020; Ogoudedji et al., 2020).

In total, 11 termite species belonging to nine 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 nests were produced by only two species, namely *M. gilvus* and *G. sulphureus*. These two types of nests 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., 2017b, 2011). Therefore, their nests have a light color and are extremely compact. Conversely, *G. sulphureus* produces rounded nests from a mixture of soil and faeces, giving its nests a characteristic dark color (Noirot 1959a). Therefore, *G. sulphureus* nests are more fragile than those of *M. gilvus*. Nests of *M. gilvus* and *G. sulphureus* were mostly observed on mounds with densities of 1.45 and 1.31 mounds ha<sup>-1</sup>, 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<sup>-1</sup>, except *Pericapritermes* sp. and *Microcerotermes* sp. with 0.64 and 0.68 mound ha<sup>-1</sup>, respectively), and their sizes were limited in comparison with those produced by *G. sulphureus* and *M. gilvus*.

Studies carried out in Africa and India have suggested that mounds might result from the degradation and colonization of abandoned nests (Josens et al., 2016; Harit and Jouquet, 2021). In line



with this hypothesis, farmers from Chrey Bak mostly attributed the origin of **mounds** to nests of *M. gilvus*, although they were aware that other termite species, as well as other organisms, might also impact **mound** properties and growth. Indeed, the **nests** of *M. gilvus* in Cambodian paddy fields were described as abundant in the 1950s and it was also reported that abandoned **nests** were often occupied by *Odontotermes* sp. (Noirot, 1959b). While 32.8% of the interviewees had no opinion on the age of **mounds** (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 **mounds** is needed to confirm these observations, these results suggest that **mounds** 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 **mounds** by farmers. A rapid **growth** of **mound** is likely to be associated with a sustainable utilization of this material as a soil amendment. Conversely, if **mounds** need more than **several years** to be produced, their exploitation is likely to be associated with an irreversible degradation of this natural resource.

### **3.2. Ecosystem services provided by termite mounds**

In Chrey Bak, most of the interviewees used **mounds** for either agronomic purposes or for improving their health and living standards. The utilization of termite construction for increasing soil fertility is a worldwide traditional practice (Suzuki et al., 2007; Miyagawa et al., 2011; Tilahun et al., 2012; Chisanga et al., 2019, 2020a,b; Apori et al., 2020a,b; Subi and Sheela, 2020). In our study, 95% of the respondents reported the utilization of **mounds** as an amendment for improving soil fertility (Figure 4) and 92.3% of the interviewees thought that **mound soil** application increased rice yield (Figure 5). The survey also provided evidence for utilization of **mounds** for growing cultivated plants, mostly for the farmers’ own consumption (57.6% of the interviewees, see Table 2 for a list of the plants that are cultivated directly on **mounds** and those that were fertilized by **mound** soil amendment). Therefore,

this result confirms the positive impact of **mounds** on food and probably dietary diversity, as observed in Laos by Miyagawa et al. (2011).

A large majority of farmers responded that **mounds** are used without preselection of the material (i.e., no specific selection of mound or nest soil, 73% of the interviewees). The remaining (22%) reported preselection of the oldest section of **mounds** (14%), a selection of **nest soil** (7%) or a combination of both (2%). These results are particularly interesting because they suggest a deep knowledge of some farmers on **termite mound and nest** properties. Indeed, although both **mounds** and **nests** have better soil physical and chemical properties than paddy field soil (Muon, 2022), the potential use of **nest** soil is likely to be higher than that of **mound** soil due to its higher amount of clay and higher soil pH, possibly due to the presence of carbonates (Muon, 2022). Moreover, the interview also showed that **mound** 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 **mound** soil is likely to increase the water holding capacity of soil (Muon, 2022). However, since **mounds** were mostly reported by farmers as **private goods held by individuals or families** (65.6% of the replies against 34.4% that described **mounds** as **common goods belonging to the community**), 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 **mound soil** application allowed for a reduction (19.9% of the interviewees) or absence of chemical fertilization (68.4%). Farmers also mentioned that **mound** application improved the resistance of rice to drought and/or pests (51.5%). A significant proportion of the interviewees also mentioned that **mound soil** 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 **mound** 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 **mound** soil than the surrounding soil (Muon, 2022). Moreover,

additional analyses also showed that **mound soils** contain more available Si (43.18 vs. 5.1 mg kg<sup>-1</sup>, Meunier and Muon pers. com.), which is likely to increase rice resistance to water, insect pest and disease stresses (Datnoff et al., 2001; Sacala, 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 **mounds** (Table 3). **Mounds** 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, 2022) and shade from the presence of trees on **mounds** 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 **mounds** 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 **mound** food to the nutrient requirements of farm families.

As evidenced in other environments, plants growing on **mounds** can also be used in traditional medicine (Sileshi et al., 2009; Choosai, 2010; Dossou-Yovo et al., 2014). In Chrey Bak, 47% of the interviewees mentioned that they use plants growing on **mounds** 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 3).

Finally, approximately 10% of interviewees mentioned that they can earn **little** income by selling plants and mushrooms growing on **mounds** 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).

## 4. Conclusion and perspectives

Our study confirmed the traditional utilization of **termite mound material** by farmers, as reported previously in Africa and Laos (Miyagawa et al., 2011; Tilahun et al., 2021, 2012; Enagbonma and Babalola, 2019). In addition to potentially contributing to increasing food diversity, **termite mounds** 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 **Basin** are resulting in the rapid disappearance of **mounds**, and with them in a loss of numerous ecosystem services. For instance, in northeast Thailand, their density dropped from more than 10 ha<sup>-1</sup> in the 1970s, a density equivalent to that found in protected forests in Asia, to less than 1 ha<sup>-1</sup> 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 this natural resource, most likely because of the belief that **mounds** can rapidly be regenerated (in less **than 40 years**), (ii) a lower utilization of the services provided by **mounds**, 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 **mounds** 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 **termite mounds** in the **Basin**. If **mounds** 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 **mounds** 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 **mounds** on human wellbeing (e.g., rice yield, income, access to better health, food security, etc.).

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## Authors' contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Ratha Muon, Vannak Ann, Vincent Hervé, and Pascal Jouquet. The first draft of the manuscript was written by Ratha Muon and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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## Data availability

The datasets generated during the current study are available in the Dataverse repository (<https://dataverse.ird.fr/dataset.xhtml?persistentId=doi:10.23708/HUR10F>)

## Code availability

Not applicable

## Declarations

**Conflict of interests** Authors declare no conflict of interest that is relevant to the content of this article.

**Ethics approval** Not applicable

313 [Consent to participate](#) Informed consent was obtained from all individual participants included in the  
314 study

315 [Consent for publication](#) Authors affirm that human research participants provided informed consent  
316 for publication.

317

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

320

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

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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
Economy	How often?	OPEN
	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?	YES vs. NO



**Table 2.**

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

	Plant list
Mounds as soil 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%)
Mounds 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 3** List of mushrooms, plants and animals found on **termite mounds** 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	
	<i>Erioglossum rubiginosum</i> (Roxb.) Blume (Daun kay or Chonlous), 6.56%	Fruits	
	<i>Flacourtia indica</i> (Burm.f.) Merr (Kro kob prei), 4.92%	Fruits	
	<i>Azadirachta indica</i> A.Juss. (Sdao), 3.28%	Leaves, flowers	
	<i>Aganonerion polymorphum</i> Pierre (Thnoeng), 3.28%	Leaves, flowers, fruits	
	Snake (Pos), 3.28%	Meat	
	Rat (Kandor), 3/28%	Meat	
	<i>Tamarindus indica</i> L.(Ampil), 1.64%	Fruits, leaves	
	<i>Alocasia macrorrhizos</i> (L.) G.Don (Kdat), 1.64%	Stem	
	<i>Moringa oleifera</i> Lam (Mrom), 1.64%	Leaves	
	<i>Crateva magna</i> (Lour.) DC. (Tonlea), 1.64%	Fruits	
	<i>Borassus flabellifer</i> L. (Thnaot), 1.64%	Fruits	
	<i>Syzygium cumini</i> (L.) Skeels (Pring), 1.64%	Fruits	
	<i>Coccinia grandis</i> (L.) Voigt (Bas), 1.64%	Leaves, fruits	
Items used as medicine	<i>Aganonerion polymorphum</i> Pierre ex Spire (Thnoeng), 8.20%	Leaves	Malaria and fever
	<i>Chromolaena odorata</i> (L.) R.M.King & H.Rob (Tontrean khet), 8.20%	Part of plant	Malaria and fever
	<i>Casearia grewiaefolia</i> Vent (Chruoy), 6.56%	Stem	Postpartum care
	<i>Azadirachta indica</i> A. Juss. (Sdao), 4.92%	Leaves	Malaria and fever, postpartum care
	<i>Diospyros helferi</i> C.B. Clarke (Trayung), 3.28%	Part of plant	Malaria and fever, and postpartum care
	<i>Erioglossum rubiginosum</i> (Roxb.) Blume (Daun kay or Chonlous), 1.64%	Fruit	Malaria and fever
	<i>Syzygium cumini</i> (L.) Skeels (Pring), 1.64%	Stem	ND
	<i>Streblus asper</i> Lour. (Snay), 1.64%	Stem	ND
	<i>Ficus hispida</i> L.f. (Lvea), 1.64%	Stem	Malaria and fever
	<i>Drynaria quercifolia</i> (L.) J.Sm (Borbrak), 1.64%	ND	Malaria and fever, and postpartum care

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<i>Xylia xylocarpa</i> (Roxb.) W.Theob. (Sokrom), 1.64%	ND	Postpartum care
<i>Dillenia hookeri</i> Pierre (Phlou bat), 1.64%	ND	Postpartum care
<i>Morinda citrifolia</i> L. (Nhor), 1.64%	ND	ND
<i>Atalantia citroides</i> Pierre ex Guill (Krauch prei), 1.64%	Roots, leaves	Postpartum care
<i>Alocasia macrorrhizos</i> (L.) G.Don (Kdat), 1.64%	Part of plant	Digestion
<i>Moringa oleifera</i> Lam.(Mrom), 1.64%	Leaves, seeds, bark	Digestion
<i>Capparis micracantha</i> A.Rich. (Khancher Bay Dach), 1.64%	Stem, root, seed	Pain
<i>Strychnos nux-vomica</i> L. (Sleng), 1.64%	Part of plant	Malaria and fever
<i>Crateva magna</i> (Lour.) DC. (Tonlea), 1.64%	Roots, flowers, stem	Pain
<i>Passiflora foetida</i> L. (Sav mao prei), 1.64%	Fruit, stem	Malaria and fever

### Figure captions

**Figure 1.** Chrey Bak catchment location in Cambodia (ArcMap 10.7). Dots represent the villages where interviews were carried out and squares represent the location of plots where termite mound and nest densities were measured.

**Figure 2.** Example of a termite mound and a termite nest in a paddy field of the Chrey Bak catchment, Cambodia: (a) Mounds in a paddy field covered by trees and other plants, (b) Nest produced by *M. gilvus* built on the top of a LM (photo: P. Jouquet, 2020).

**Figure 3.** Average density (in  $\text{ha}^{-1}$ ) of termite mounds and nests (TN) produced by *Macrotermes gilvus* ( $\text{TN}_{\text{Macro}}$ ) and *Globitermes sulphureus* ( $\text{TN}_{\text{Globi}}$ ) in the Chrey Bak catchment, Cambodia. ‘Others’ represents the sum of the density of TN 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).

**Figure 4.** 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 termite lenticular mounds 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 mounds 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. 3/4 mound), respectively (third chart).

**Figure 5.** Proportion of positive answers related to the use of termite mounds for increasing soil fertility.

## Supplementary files

### Supplementary file 1. DNA extraction and termite identification

Molecular identification was performed using single worker individuals. 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 Supplementary Figures 6-9). 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.

- Anisimova, M., & Gascuel, O. (2006) Approximate Likelihood-Ratio Test for Branches: A Fast, Accurate, and Powerful Alternative. *Systematic Biology* 55, 539–552. <https://doi.org/10.1080/10635150600755453>
- Dedeine, F., Dupont, S., Guyot, S., Matsuura, K., Wang, C., Habibpour, B., Bagnères, A.-G., Mantovani, B. & Luchetti, A. (2016) Historical biogeography of *Reticulitermes* termites

- (Isoptera: Rhinotermitidae) inferred from analyses of mitochondrial and nuclear loci. *Molecular Phylogenetics and Evolution* 94, 778–790. <https://doi.org/10.1016/j.ympev.2015.10.020>
- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. *Systematic Biology* 59, 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Lefort, V., Longueville, J.-E., Gascuel, O. (2017) SMS: Smart Model Selection in PhyML. *Molecular Biology and Evolution* 34, 2422–2424. <https://doi.org/10.1093/molbev/msx149>
- Stucky, B.J. (2012) SeqTrace: A Graphical Tool for Rapidly Processing DNA Sequencing Chromatograms. *Journal of Biomolecular Techniques* 23, 90–93. <https://doi.org/10.7171/jbt.12-2303-004>
- Wright, E.S. (2016) Using DECIPHER v2.0 to Analyze Big Biological Sequence Data in R. *R J.* 8, 352. <https://doi.org/10.32614/RJ-2016-025>
- Zhang, Z., Schwartz, S., Wagner, L., & Miller, W. (2000) A greedy algorithm for aligning DNA sequences. *Journal of Computational biology* 7, 203–214

**Supplementary file 2.** Phylogenetic tree of the *Macrotermitinae* with *Reticulitermes* as an outgroup. Labels on the tree correspond to GenBank accession numbers.

**Supplementary file 3.** 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.

**Supplementary file 4.** Phylogenetic tree of the *Pericapritermes* and the *Nasutitermes* group. Labels on the tree correspond to GenBank accession numbers.

**Supplementary file 5.** 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.

## References

- Abhishek, A., Das, N.N., Ines, A.V.M., Andreadis, K.M., Jayasinghe, S., Granger, S., Ellenburg, W.L., Dutta, R., Hanh Quyen, N., Markert, A.M., Mishra, V. & Phanikumar, M.S. (2021) Evaluating the impacts of drought on rice productivity over Cambodia in the Lower Mekong Basin. *Journal of Hydrology* 599, 126291. <https://doi.org/10.1016/j.jhydrol.2021.126291>
- Alhousari, F. & Greger, M. (2018) Silicon and mechanisms of plant resistance to insect pests. *Plants* 7, 33. <https://doi.org/10.3390/plants7020033>
- Apori, S.O., Flarian, M.M., Hanyabui, E., Muli, G.K. & Wamuyu, B. (2020a). Role of Military Termites (*Pseudocanthotermes militaris*) in Improving Soil Productivity in Tropical Agroecosystems. *Annual Research & Review in Biology* 35, 14–19. <https://doi.org/10.9734/arrb/2020/v35i530221>
- Apori, S.O., Murongo, M., Hanyabui, E., Atiah, K. & Byalebeka, J. (2020b) Potential of termite mounds and its surrounding soils as soil amendments in smallholder farms in central Uganda. *BMC Reserch Notes* 13, 397. <https://doi.org/10.1186/s13104-020-05236-6>
- Baker, C.C.M., Castillo Vardaro, J.A., Doak, D.F., Pansu, J., Puissant, J., Pringle, R.M. & Tarnita, C.E. (2020) Spatial patterning of soil microbial communities created by fungus- farming termites. *Molecular Ecology* 29, 4487–4501. <https://doi.org/10.1111/mec.15585>
- Berg, H., Berg, C., & Nguyen, T.T. (2012) Integrated Rice-Fish Farming: Safeguarding Biodiversity and Ecosystem Services for Sustainable Food Production in the Mekong Delta. *Journal of Sustainable Agriculture* 36, 859–872. <https://doi.org/10.1080/10440046.2012.712090>
- Bonachela, J.A., Pringle, R.M., Sheffer, E., Coverdale, T.C., Guyton, J.A., Caylor, K.K., Levin, S.A. & Tarnita, C.E. (2015) Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science* 80, 347, 651–655. <https://doi.org/10.1126/science.1261487>
- Bongaarts, J. (2019) IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science- Policy Platform on Biodiversity and Ecosystem Services. *Population and Development Review* 45, 680–681. <https://doi.org/10.1111/padr.12283>
- Bridges, E.M., Batjes, N.H., & Nachtergaele F.O. (1998) World Reference Base for Soil Resources:



Atlas. ISSS Working Group RB, ISRIC-FAO-ISSS.

- Bruun, T.B., Neergaard, A., Burup, M.L., Hepp, C.M., Larsen, M.N., Abel, C., Aumtong, S., Magid, J., & Mertz, O. (2017) Intensification of Upland Agriculture in Thailand: Development or Degradation? *Land Degradation Development* 28, 83–94. <https://doi.org/10.1002/ldr.2596>
- Chann, S., Wales, N., & Frewer, T. (2011) An Investigation of Land Cover and Land Use Change in Stung Chrey Bak Catchment, Cambodia. CDRI Work. Pap. Ser. No. 53 70.
- Chen, C., Zou, X., Wu, J., Zhu, X., Jiang, X., Zhang, W., Zeng, H. & Liu, W. (2021) Accumulation and spatial homogeneity of nutrients within termite (*Odontotermes yunnanensis*) mounds in the Xishuangbanna region, SW China. *Catena* 198, 105057. <https://doi.org/10.1016/j.catena.2020.105057>
- Chisanga, K., Mbega, E. & Ndakidemi, P.A. (2019) Socio-Economic factors for anthill soil utilization by smallholder farmers in Zambia. *Sustainability* 11, 4849. <https://doi.org/10.3390/su11184849>
- Chisanga, K., Mbega, E. & Ndakidemi, P.A. (2020a) Maize (*Zea mays*) response to anthill soil (Termitaria), manure and NPK fertilization rate under conventional and reduced tillage cropping systems. *Sustainability* 12, 928. <https://doi.org/10.3390/su12030928>
- Chisanga, K., Mbega, E.R. & Ndakidemi, P.A. (2020b) Prospects of using termite mound soil organic amendment for enhancing soil nutrition in Southern Africa. *Plants* 9, 649. <https://doi.org/10.3390/plants9050649>
- Choosai, C. (2010) Biological activity in paddy fields. The role of soil engineers in ecosystem functioning. Sorbonne University (ex-UPMC University Paris 06), 140 pp.
- Choosai, C., Mathieu, J., Hanboonsong, Y. & Jouquet, P. (2009) Termite mounds and dykes are biodiversity refuges in paddy fields in north-eastern Thailand. *Environmental Conservation* 36, 71. <https://doi.org/10.1017/S0376892909005475>
- Cramb, R. (2020) White Gold: The commercialisation of rice farming in the lower mekong basin. Springer Singapore, Singapore. <https://doi.org/10.1007/978-981-15-0998-8>
- Dale, V.H. & Polasky, S. (2007) Measures of the effects of agricultural practices on ecosystem services. *Ecological Economics* 64, 286–296. <https://doi.org/10.1016/j.ecolecon.2007.05.009>
- Datnoff, L.E., Snyder, G.H. & Korndörfer, G.H. (2001) Silicon in agriculture. Elsevier.

- Davies, A.B., Brodrick, P.G., Parr, C.L. & Asner, G.P. (2020) Resistance of mound-building termites to anthropogenic land-use change. *Environmental Research Letters* 15, 094038. <https://doi.org/10.1088/1748-9326/aba0ff>
- Destoumieux-Garzón, D., Mavingui, P., Boetsch, G., Boissier, J., Darriet, F., Duboz, P., Fritsch, C., Giraudoux, P., Le Roux, F., Morand, S., Paillard, C., Pontier, D., Sueur, C. & Voituron, Y. (2018) The One Health Concept: 10 Years Old and a Long Road Ahead. *Frontiers in Veterinary Science* 5, 1–13. <https://doi.org/10.3389/fvets.2018.00014>
- Dossou-Yovo, H.O., Vodouhe, F.G. & Sinsin, B. (2014) Assessment of the medicinal uses of plant species found on termitaria in the Pendjari biosphere reserve in Benin. *Journal of Medical Plants Research* 8, 368–377. <https://doi.org/10.5897/JMPR10.124>
- Ekundayo, E.O. & Aghatise, V.O. (1997) Soil properties of termite mounds under different land use types in a Typic Paleudult of Midwestern Nigeria. *Environmental Monitoring and Assessment* 45, 1–7. <https://doi.org/10.1023/A:1005794628150>
- Emmerson, M., Morales, M.B., Oñate, J.J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tschardtke, T., Weisser, W., Clement, L. & Bengtsson, J. (2016) How Agricultural Intensification Affects Biodiversity and Ecosystem Services. *Advances in Ecological Research* 55, 43–97. <https://doi.org/10.1016/bs.aecr.2016.08.005>
- Enagbonma, B.J. & Babalola, O.O. (2019) Potentials of termite mound soil bacteria in ecosystem engineering for sustainable agriculture. *Annals of Microbiology* 69, 211–219. <https://doi.org/10.1007/s13213-019-1439-2>
- Erens, H., Boudin, M., Mees, F., Mujinya, B.B., Baert, G., Van Strydonck, M., Boeckx, P. & Van Ranst, E. (2015) The age of large termite mounds-radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology* 435, 265–271. <https://doi.org/10.1016/j.palaeo.2015.06.017>
- Firbank, L.G., Petit, S., Smart, S., Blain, A. & Fuller, R.J. (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B, Biological Sciences* 363, 777–787. <https://doi.org/10.1098/rstb.2007.2183>
- Harit, A.K. & Jouquet, P. (2021) Origin and Dynamics of Termite Mound Soils in Southern India.

*Asian Soil Research Journal* 5, 19–23. <https://doi.org/10.9734/asrj/2021/v5i430115>

Inoue, T., Vijarnsorn, P. & Abe, T. (1997) Mound structure of the fungus-growing termite *Macrotermes gilvus* in Thailand. *Journal of Tropical Ecology* 13, 115–124.

<https://doi.org/10.1017/S0266467400010294>

Inoue, T., Kirtibutr, N. & Abe, T. (2001) Underground passage system of *Macrotermes carbonarius* (Isoptera, Termitidae) in a dry evergreen forest of northeast Thailand. *Insectes Sociaux* 48, 372–

377. <https://doi.org/10.1007/PL00001794>

JICA (2003) The study on the establishment of GIS Base Data for the Kingdom of Cambodia.

Josens, G., Dosso, K. & Konaté, S. (2016) Lenticular mounds in the African savannahs can originate from ancient *Macrotermes* mounds. *Insectes Sociaux* 63, 373–379.

<https://doi.org/10.1007/s00040-016-0476-0>

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C. & Bignell, D. (2011) Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology* 47, 215–222.

<https://doi.org/10.1016/j.ejsobi.2011.05.005>

Jouquet, P., Chintakunta, S., Bottinelli, N., Subramanian, S. & Caner, L. (2016) The influence of fungus-growing termites on soil macro and micro-aggregates stability varies with soil type.

*Applied Soil Ecology* 101, 117–123. <https://doi.org/10.1016/j.apsoil.2016.02.001>

Jouquet, P., Airola, E., Guilleux, N., Harit, A., Chaudhary, E., Grellier, S. & Riotte, J. (2017a) Abundance and impact on soil properties of cathedral and lenticular termite mounds in southern

Indian woodlands. *Ecosystems* 20, 769–780. <https://doi.org/10.1007/s10021-016-0060-5>

Jouquet, P., Caner, L., Bottinelli, N., Chaudhary, E., Cheik, S. & Riotte, J. (2017b) Where do south-Indian termite mound soils come from? *Applied Soil Ecology* 117–118, 190–195.

<https://doi.org/10.1016/j.apsoil.2017.05.010>

Kang, H., Sridhar, V., Mainuddin, M. & Trung, L.D. (2021) Future rice farming threatened by drought in the Lower Mekong Basin. *Scientific Reports* 11, 9383.

<https://doi.org/10.1038/s41598-021-88405-2>

Lam, S., Pham, G. & Nguyen-Viet, H. (2017) Emerging health risks from agricultural intensification in Southeast Asia: a systematic review. *International Journal of Occupational and*

*Environmental Health* 23, 250–260. <https://doi.org/10.1080/10773525.2018.1450923>

- Lantin, R.S., Wassmann, R., Neue, H.U. & Buendia, L.V. (2000) Mitigating methane emissions from rice fields in Asia, in: *Non-CO<sub>2</sub> greenhouse gases: scientific understanding, control and implementation*. Springer Netherlands, Dordrecht, pp. 283–290. [https://doi.org/10.1007/978-94-015-9343-4\\_46](https://doi.org/10.1007/978-94-015-9343-4_46)
- Lebov, J., Grieger, K., Womack, D., Zaccaro, D., Whitehead, N., Kowalczyk, B. & MacDonald, P.D.M. (2017) A framework for one health research. *One Health* 3, 44–50. <https://doi.org/10.1016/j.onehlt.2017.03.004>
- Mainuddin, M., Kirby, M. & Hoanh, C.T. (2011) Adaptation to climate change for food security in the lower Mekong Basin. *Food Security* 3, 433–450. <https://doi.org/10.1007/s12571-011-0154-z>
- Martin, S.J., Funch, R.R., Hanson, P.R. & Yoo, E.-H. (2018) A vast 4,000-year-old spatial pattern of termite mounds. *Current Biology* 28, R1292–R1293. <https://doi.org/10.1016/j.cub.2018.09.061>
- Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997) Agricultural intensification and ecosystem properties. *Science* 277, 504–509. <https://doi.org/10.1126/science.277.5325.504>
- Matsumoto, T. (1976) The role of termites in an equatorial rain forest ecosystem of West Malaysia. *Oecologia* 22, 153–178. <https://doi.org/10.1007/BF00344714>
- McCarthy, T.S., Ellery, W.N. & Dangerfield, J.M. (1998) The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes and Landforms* 23, 291–316. [https://doi.org/10.1002/\(SICI\)1096-9837\(199804\)23:4<291::AID-ESP844>3.0.CO;2-A](https://doi.org/10.1002/(SICI)1096-9837(199804)23:4<291::AID-ESP844>3.0.CO;2-A)
- Mekong River Commission (2003) Digital Terrain Model (DTM) for the Lower Mekong Basin. [http://archive.iwlearn.net/mrcmekong.org/spatial/meta\\_html/topo10.htm#](http://archive.iwlearn.net/mrcmekong.org/spatial/meta_html/topo10.htm#)
- Miyagawa, S., Koyama, Y., Kokubo, M., Matsushita, Y., Adachi, Y., Sivilay, S., Kawakubo, N. & Oba, S. (2011) Indigenous utilization of termite mounds and their sustainability in a rice growing village of the central plain of Laos. *Journal of Ethnobiology and Ethnomedicine* 7, 24. <https://doi.org/10.1186/1746-4269-7-24>
- Moore, J.M. & Picker, M.D. (1991) Heuweltjies (earth mounds) in the Clanwilliam district, Cape Province, South Africa: 4000-year-old termite nests. *Oecologia* 86, 424–432.

<https://doi.org/10.1007/BF00317612>

- Muon, R. (2022) Termite bioturbation in Cambodia. From characterization to application. Thesis, Sorbonne University, 137 pp.
- MOWRAM (2014) The national water status report 2014, ADB TA 7610-CAM Supporting Policy and Institutional Reforms for Capacity Development in the Water Sector. Phnom Penh.
- National Centre for Traditional Medicine (2013a) Cambodia medicinal plants Vol 1.
- National Centre for Traditional Medicine (2013b) Cambodia medicinal plants Vol 2.
- Noirot, C. (1959a). Les nids de *Globitermes sulphureus* Haviland au Cambodge. *Insectes Sociaux*, 6(3), 259-268. <https://doi.org/10.1007/BF02224409>
- Noirot, C. (1959b). Sur le nid et la biologie de *Macrotermes gilvus* Holmgr. Dans les rizières du Cambodge. *Insectes sociaux* 6(2), 179-184. <https://doi.org/10.1007/BF02225949>
- Ogoudedji, G.P.C., Yabi, J.A., & Yegbemey, R. N. (2020). Effect of termite mounds and chemical fertilizer on the cotton and maize yield: An evidence from the pendjari region (north west Benin). *Agronomie Africaine*, 32(4), 389-402.
- Padonou, E.A., Djagoun, C.A.M.S., Akakpo, A.B., Ahlinvi, S., Lykke, A.M., Schmidt, M., Assogbadjo, A. & Sinsin, B. (2020) Role of termites in the restoration of soils and plant richness on bowé in West Africa. *African Journal of Ecology* 58, 828–835. <https://doi.org/10.1111/aje.12778>
- Pomeroy, D.E. (1978) The abundance of large termite mounds in Uganda in relation to their environment. *Journal of Applied Ecology* 15, 51. <https://doi.org/10.2307/2402920>
- Sacala, E. (2009) Role of silicon in plant resistance to water stress. *Journal of Elementology* 14, 619–630. <https://doi.org/10.5601/jelem.2009.14.3.20>
- Sebesvari, Z., Le, H.T.T., Van Toan, P., Arnold, U. & Renaud, F.G. (2012) Agriculture and water quality in the vietnamese mekong delta. pp. 331–361. [https://doi.org/10.1007/978-94-007-3962-8\\_13](https://doi.org/10.1007/978-94-007-3962-8_13)
- Sileshi, G.W., Arshad, M.A., Konaté, S. & Nkunika, P.O.Y. (2010) Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of Vegetation Science* 21, 923–937. <https://doi.org/10.1111/j.1654-1103.2010.01197.x>

- Sileshi, G.W., Nyeko, P., Nkunya, P.O.Y., Sekematte, B.M., Akinnifesi, F.K. & Ajayi, O.C. (2009) Integrating ethno-ecological and scientific knowledge of termites for sustainable termite management and human welfare in Africa. *Ecology & Society* 14, 48. <https://doi.org/10.5751/ES-02877-140148>
- Subi, S. & Sheela, A.M. (2020) Review on termite mound soil characteristics and agricultural importance. *Journal of Agriculture and Ecology Research International* 21, 1-12. <https://doi.org/10.9734/jaeri/2020/v21i730152>
- Suzuki, S., Noble, A.D., Ruaysoongnern, S. & Chinabut, N. (2007) Improvement in water-holding capacity and structural stability of a sandy soil in Northeast Thailand. *Arid Land Research and Management* 21, 37–49. <https://doi.org/10.1080/15324980601087430>
- Thilakarathne, M. & Sridhar, V. (2017) Characterization of future drought conditions in the Lower Mekong River Basin. *Weather and Climate Extremes* 17, 47–58. <https://doi.org/10.1016/j.wace.2017.07.004>
- Tilahun, A., Cornelis, W., Sleutel, S., Nigussie, A., Dume, B. & Van Ranst, E. (2021) The potential of termite mound spreading for soil fertility management under low input subsistence agriculture. *Agriculture* 11, 1002. <https://doi.org/10.3390/agriculture11101002>
- Tilahun, A., Kebede, F., Yamoah, C., Erens, H., Mujinya, B.B., Verdoodt, A. & Van Ranst, E. (2012) Quantifying the masses of *Macrotermes subhyalinus* mounds and evaluating their use as a soil amendment. *Agriculture Ecosystem Environment* 157, 54–59. <https://doi.org/10.1016/j.agee.2011.11.013>
- Trisurat, Y., Aekakkararungroj, A., Ma, H. & Johnston, J.M. (2018) Basin-wide impacts of climate change on ecosystem services in the Lower Mekong Basin. *Ecological Research* 33, 73–86. <https://doi.org/10.1007/s11284-017-1510-z>
- Zabala, J.A., Martínez-Paz, J.M. & Alcon, F. (2021) A comprehensive approach for agroecosystem services and disservices valuation. *Science of the Total Environment* 768, 144859. <https://doi.org/10.1016/j.scitotenv.2020.144859>