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# Abundance, perceptions and utilizations of termite mounds in Cambodia

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20 **Abstract**

21 In the Lower Mekong Basin, paddy fields often appear as mosaics, with soil mounds covered by trees  
22 or other plants in a spotty distribution. These soil mounds are commonly named termite ‘lenticular  
23 mounds’ because termite bioturbation is considered to be at their origin. **Termite mounds** host a large  
24 diversity of animals and plants, increasing landscape patchiness. Because the preservation of these  
25 islands of biodiversity is threatened by modern agricultural practices, the aim of this study was to  
26 quantify their abundance and the services they provide to the local population. The abundance of  
27 **mounds** and their use by population were quantified in a catchment in Cambodia. We found that  
28 **mounds** density reached  $\sim 2$  mounds  $\text{ha}^{-1}$ . Interviews carried out within the catchments showed that  
29 most of the interviewees used **mounds** for increasing the fertility of their field and for the cultivation  
30 of rice and other plants (e.g., sponge gourd and pumpkin). In addition to their potential to increase  
31 plant productivity, the survey revealed that animals (rats and snakes), mushrooms and 13 plant species  
32 found on or in **mounds** were consumed by the population. In addition to potentially contributing to an  
33 increase in food diversity, **mounds** also impacted farmers’ health by allowing access to 20 medicinal  
34 plant species and indirectly via a reduction in pesticide use. In conclusion, this study is a first attempt  
35 to quantify the large number of services provided by **termite mounds** in Cambodia. This increase in  
36 the knowledge of the diversity of environmental and socioeconomic services provided by **termite**  
37 **mounds** is likely to contribute to their preservation and provide a basis for the sustainable  
38 management of biodiversity in paddy fields in the Lower Mekong Basin region.

39

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

## 42 **1. Introduction**

43 The “One Health” concept and framework was created as a need for holistic and transdisciplinary  
44 approaches in dealing with the health of humankind, animals, and ecosystems (Destoumieux-Garzón  
45 et al., 2018). This concept has now expanded beyond emerging infectious diseases and zoonoses to  
46 incorporate a wider suite of health issues, such as the interdependence between the preservation of the  
47 environment, biodiversity and human wellbeing (i.e., the environmental, animal and human health  
48 concepts, respectively) (Lebov et al., 2017; Bongaarts, 2019). This approach has a special general  
49 resonance in Southeast Asia, especially in the Lower Mekong Basin (hereafter the ‘Basin’), notably  
50 because this region is undergoing dramatic climatic, environmental and societal changes (Trisurat et  
51 al., 2018; Mainuddin et al., 2011; Thilakarathne and Sridhar, 2017; Abhishek et al., 2021; Kang et al.,  
52 2021). The rapid economic growth and intensification of agricultural practices (Sebesvari et al., 2012;  
53 Bruun et al., 2017; Lam et al., 2017) have increased the homogenization, simplification and pollution  
54 of terrestrial, and thereafter aquatic ecosystems (Matson et al., 1997; Firbank et al., 2008; Dale and  
55 Polasky, 2007; Emmerson et al., 2016). In this context, however, the diversity of services delivered by  
56 agro-ecosystems as well as the mechanisms associated with the preservation of biodiversity and their  
57 contribution to human health by local actors remain poorly evaluated.

58 Rice is the most cultivated plant in the Basin (Cramb, 2020). In this environment,  
59 understanding the services derived from paddy fields requires a holistic perspective, taking into  
60 account not only the production and quality of rice but also the multifunctionality of agroecosystems  
61 and the diversity of regulating, provisioning, cultural and supporting ecosystem services they provide  
62 (Zabala et al., 2021). Traditionally, services have focused on the production of rice and the emission  
63 of greenhouse gases (Lantin et al., 2000), the quality of water and the cycling of nutrients (Berg et al.,  
64 2012). The relationship between biodiversity and human health remains, however, underestimated in  
65 paddy fields. In the Basin, paddy fields often appear as mosaics with soil mounds covered by trees or  
66 other plants spotted within large surfaces that are used for the cultivation of rice. These mounds are  
67 commonly named termite ‘lenticular mounds’ (hereafter ‘mounds’) because they are expected to be  
68 produced by termites, although their origin remains unknown and because they can host a large

69 diversity of other invertebrates (Choosai et al., 2009). Because of their size (~6 m<sup>3</sup> of soil), mounds  
70 increase heterogeneity at the landscape scale. Their abundance and physical and chemical properties  
71 are unknown, but research carried out in Africa suggests that they could be very old (Erens et al.,  
72 2015), constitute patches of nutrients (McCarthy et al., 1998; Sileshi et al., 2010; Jouquet et al., 2011,  
73 2016, 2017; Chen et al., 2021) and positively impact soil properties and the resistance of plants to  
74 environmental hazards (e.g., drought) (Bonachela et al., 2015; Padonou et al., 2020). Regarding their  
75 improvement of soil properties, mounds have been reported to be used as soil nutrient amendments in  
76 Africa (Dossou-Yovo et al., 2014; Tilahun et al., 2012, 2021; Enagbonma and Babalola, 2019). They  
77 can also improve human health because mound soil and some of the plants growing on them are  
78 consumed or used as traditional medicines (Sileshi et al., 2009; Dossou-Yovo et al., 2014).

79 Less is known about the importance and utilization of mounds by farmers in Southeast Asia.  
80 Information regarding the services provided by mounds in the Basin are limited to a descriptive report  
81 of Miyagawa et al. (2011) in Laos and to an ecological study of Choosai et al. (2009) in Northeast  
82 Thailand. The abundance of mounds and their traditional use by the population, in particular the  
83 farmers, remain unknown, although mounds are a remarkable characteristic of the landscape at first  
84 glance. Therefore, the objectives of this study were to measure the abundance of mounds in cultivated  
85 areas in Cambodia, and to describe and quantify the perceptions and use of mounds by farmers. Our  
86 main hypothesis was that farmers' preservation of mounds relies on the use of this natural resource  
87 due to its positive effect on rice yield and potentially on dietary diversity and health.

88

## 89 **2. Materials and Methods**

### 90 **2.1. Study site**

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

95 season from November to April and the rainy season from May to October, with annual rainfall  
96 varying between 1400 and 2000 mm (MOWRAM, 2014). Soils are mainly Gleysols (Bridges et al.,  
97 1998) with varying sand contents (Muon, 2022). The lower part of the catchment is located in the  
98 Tonle Sap River floodplain. Based on the Japan International Cooperation Agency (JICA, 2003) land  
99 use map produced in 2003, forests cover 34% of the catchment area. The remaining corresponds to  
100 agricultural land (32%), shrubland (27.4%) and grassland (5.4%). The study site has an altitude  
101 varying between 10 and 1400 metres, being high in the mountainous area in the southwest region  
102 while it is very gently sloped or almost flat in the cultivated area, which is dominated by paddy fields  
103 (Mekong River Commission, 2003). The majority of Cambodia's rice is rain-fed and is usually  
104 planted at the end of May or early June when the first monsoon rains begin to fall (Chann et al.,  
105 2011).

106 In this environment, termite mounds and nests are conspicuous features of the landscape  
107 (Figure 2) (see Josens et al. 2016, Jouquet et al., 2017a for a definition of lenticular mounds and  
108 nests). Mounds have a large lenticular shape ~1 m high and 2-3 m in diameter on average (~6 m<sup>3</sup> and  
109 17 m<sup>2</sup> on average). They are complex soil structures hosting many other animals (e.g., invertebrates  
110 such as termites, earthworms and spiders, and vertebrates such as rats) and plants. Although their  
111 dynamics are unknown, their origin is attributed to the activity of termites (Harit and Jouquet, 2021;  
112 Muon et al., 2022). Conversely, nests are freshly built structures produced by single well-identified  
113 termite colonies.

114

## 115 **2.2. Density of termite mounds and their utilization by farmers**

### 116 **2.2.1 Termite activity and diversity**

117 Thirty sampling plots (300 m x 300 m) were randomly selected within paddy fields along the  
118 toposequence of the Chrey Bak observatory (Figure 1). For each plot, the position of the center of  
119 mounds and nests, as well as the plot boundaries, were recorded with a GPS tracker (Garmin  
120 GPSMAP 64s) during the dry season from December 2019 to February 2021. The densities of  
121 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).

127

### 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).

139

### 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).

145

## 146 **3. Results and discussion**

### 147 **3.1. Mound density and dynamics**

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

158 In total, 11 termite species belonging to nine genera were found in the Chrey Bak catchment:  
159 *Macrotermes gilvus*, *Globitermes sulphureus*, *Odontotermes* spp. (2 species among DNA sequences),  
160 *Hypotermes* sp., *Pericapritermes* sp., *Nasutitermes* sp., *Coptotermes gestroi*, *Microcerotermes* spp. (2  
161 species among DNA sequences), and *Termes* sp. Most of nests were produced by only two species,  
162 namely *M. gilvus* and *G. sulphureus*. These two types of nests were very different and could easily be  
163 recognized from their following characteristics. The species *M. gilvus* belongs to the Macrotermitinae  
164 subfamily, and its mound nests are mostly made of soil sampled at several cm depths (Inoue et al.,  
165 1997; Jouquet et al., 2017b, 2011). Therefore, their nests have a light color and are extremely  
166 compact. Conversely, *G. sulphureus* produces rounded nests from a mixture of soil and faeces, giving  
167 its nests a characteristic dark color (Noirot 1959a). Therefore, *G. sulphureus* nests are more fragile  
168 than those of *M. gilvus*. Nests of *M. gilvus* and *G. sulphureus* were mostly observed on mounds with  
169 densities of 1.45 and 1.31 mounds ha<sup>-1</sup>, respectively. Nests of the other termite species were also  
170 observed in Chrey Bak but they were less obvious to identify in the field and their occurrence (< 0.05  
171 mounds ha<sup>-1</sup>, except *Pericapritermes* sp. and *Microcerotermes* sp. with 0.64 and 0.68 mound ha<sup>-1</sup>,  
172 respectively), and their sizes were limited in comparison with those produced by *G. sulphureus* and  
173 *M. gilvus*.

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



176 with this hypothesis, farmers from Chrey Bak mostly attributed the origin of **mounds** to nests of *M.*  
177 *gilvus*, although they were aware that other termite species, as well as other organisms, might also  
178 impact **mound** properties and growth. Indeed, the **nests** of *M. gilvus* in Cambodian paddy fields were  
179 described as abundant in the 1950s and it was also reported that abandoned **nests** were often occupied  
180 by *Odontotermes* sp. (Noirot, 1959b). While 32.8% of the interviewees had no opinion on the age of  
181 **mounds** (i.e., reply to the survey = “I don’t know”), a similar proportion believed that mounds were  
182 between 10 and 39 years old (32.8%), while others believed that they were younger (< 10 years old,  
183 19.7%) or older (8.2% between 40 and 60 years old, 6.6% between 60 and 100 years old). Therefore,  
184 although dating of **mounds** is needed to confirm these observations, these results suggest that **mounds**  
185 were likely to be much younger than those found in Africa (up to 2,000 years in Africa, Moore and  
186 Picker, 1991; Erens et al., 2015) and in Brazil (> 4,000 years, Martin et al., 2018). Moreover, these  
187 results must also be considered in regard to the utilization of **mounds** by farmers. A rapid **growth** of  
188 **mound** is likely to be associated with a sustainable utilization of this material as a soil amendment.  
189 Conversely, if **mounds** need more than **several years** to be produced, their exploitation is likely to be  
190 associated with an irreversible degradation of this natural resource.

191

### 192 **3.2. Ecosystem services provided by termite mounds**

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

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

204 A large majority of farmers responded that **mounds** are used without preselection of the  
205 material (i.e., no specific selection of mound or nest soil, 73% of the interviewees). The remaining  
206 (22%) reported preselection of the oldest section of **mounds** (14%), a selection of **nest soil** (7%) or a  
207 combination of both (2%). These results are particularly interesting because they suggest a deep  
208 knowledge of some farmers on **termite mound and nest** properties. Indeed, although both **mounds** and  
209 **nests** have better soil physical and chemical properties than paddy field soil (Muon, 2022), the  
210 potential use of **nest** soil is likely to be higher than that of **mound** soil due to its higher amount of clay  
211 and higher soil pH, possibly due to the presence of carbonates (Muon, 2022). Moreover, the interview  
212 also showed that **mound** soil is applied more frequently if farmers grow vegetables (2-3 times a year  
213 for 11.5% of the interviewees and until 10-18 times a year for 1.6% of interviewees) than rice  
214 (frequency = once every year to once every 4 years for 75.4% of interviewees), probably because of  
215 the higher demand of vegetables for nutrients but also because the application of **mound** soil is likely  
216 to increase the water holding capacity of soil (Muon, 2022). However, since **mounds** were mostly  
217 reported by farmers as **private goods held by individuals or families** (65.6% of the replies against  
218 34.4% that described **mounds as common goods belonging to the community**), some farmers also  
219 mentioned that the frequency of application depends on the availability of mounds in their land. In  
220 addition to soil fertility, farmers also reported that **mound soil** application allowed for a reduction  
221 (19.9% of the interviewees) or absence of chemical fertilization (68.4%). Farmers also mentioned that  
222 **mound** application improved the resistance of rice to drought and/or pests (51.5%). A significant  
223 proportion of the interviewees also mentioned that **mound soil** application allowed a reduction (41%)  
224 in the use of pesticides, and the cessation of chemical pesticide use in paddy fields (38.4%). These  
225 responses are in line with studies carried out in Africa which showed that **mound** soil properties  
226 positively influence water dynamics and soil quality as well as plant resistance to drought and pests  
227 (Bonachela et al., 2015; Enagbonma and Babalola, 2019). These findings are also likely to be  
228 explained by the higher soil organic matter and clay contents and therefore higher water holding  
229 capacity at high potential (pF 4.2) of **mound** soil than the surrounding soil (Muon, 2022). Moreover,

230 additional analyses also showed that mound soils contain more available Si (43.18 vs. 5.1 mg kg<sup>-1</sup>,  
231 Meunier and Muon pers. com.), which is likely to increase rice resistance to water, insect pest and  
232 disease stresses (Datnoff et al., 2001; Sacala, 2009; Alhousari and Greger, 2018).

233 In addition to their potential to increase plant productivity, the survey revealed that 78% of  
234 the respondents feed on animals (mainly rats and snakes) and at least 10 different plants (fruits and  
235 vegetables) found on or in mounds (Table 3). Mounds have been considered hotspots of biodiversity  
236 in paddy fields because they constitute a refuge for animals and plants (Choosai et al., 2009) as well  
237 as a specific habitat for soil microorganisms (Baker et al., 2020). Indeed, the specific soil properties  
238 (Muon, 2022) and shade from the presence of trees on mounds offer a favorable environment for  
239 animals and plants during the dry season while it is the only exposed areas of paddy fields that are not  
240 flooded during the rainy season. If all the plants and animals found on mounds were used by most of  
241 the interviewees, when eaten, these food items would help increase the dietary diversity and could  
242 contribute to improving the consumption of nutrients such as vitamins and minerals. Quantitative  
243 nutrition surveys are now needed to assess the contribution of mound food to the nutrient  
244 requirements of farm families.

245 As evidenced in other environments, plants growing on mounds can also be used in traditional  
246 medicine (Sileshi et al., 2009; Choosai, 2010; Dossou-Yovo et al., 2014). In Chrey Bak, 47% of the  
247 interviewees mentioned that they use plants growing on mounds for their medicinal properties during  
248 postpartum care (16.4%), for diseases such as malaria and fever (14.8%), as well as for bodily pain  
249 (3.3%) and digestion problems (1.6%) (Table 3).

250 Finally, approximately 10% of interviewees mentioned that they can earn little income by  
251 selling plants and mushrooms growing on mounds in the market (i.e., mushrooms (4.8%), tamarinds  
252 (3.2%), bamboo (3.2%), bamboo shoots (1.6%), and tomatoes (1.6%)). However, farmers generally  
253 reported that economic benefits are low, especially because plants are collected only once to twice a  
254 year, with the exception of tomatoes which can be sold up to 4 times a year (e.g., 1.25 to 2.25\$ each  
255 time they sell mushrooms, 1.25\$ for bamboo shoots, 8.75 to 10\$ for bamboo, and approximately 125\$  
256 for tomatoes).

257

#### 258 4. Conclusion and perspectives

259 Our study confirmed the traditional utilization of **termite mound material** by farmers, as reported  
260 previously in Africa and Laos (Miyagawa et al., 2011; Tilahun et al., 2021, 2012; Enagbonma and  
261 Babalola, 2019). In addition to potentially contributing to increasing food diversity, **termite mounds**  
262 can also impact farmers' health by allowing access to medicinal plants and indirectly well-being, via a  
263 reduction in pesticide use. However, land use changes in the **Basin** are resulting in the rapid  
264 disappearance of **mounds**, and with them in a loss of numerous ecosystem services. For instance, in  
265 northeast Thailand, their density dropped from more than 10 ha<sup>-1</sup> in the 1970s, a density equivalent to  
266 that found in protected forests in Asia, to less than 1 ha<sup>-1</sup> nowadays (Choosai, 2010). At our study site,  
267 54.1% of the interviewees mentioned that mounds were more abundant in the past. This reduction in  
268 density could be explained by (i) an overexploitation of this natural resource, most likely because of  
269 the belief that **mounds** can rapidly be regenerated (in less **than 40 years**), (ii) a lower utilization of the  
270 services provided by **mounds**, and/or (iii) a reduction in the ecological niche of termites (i.e., a  
271 reduction in tree density and food availability). Indeed, 65.6% of the interviewees reported that  
272 **mounds** were more useful in the past than currently, in particular because it is now more convenient to  
273 use chemical fertilizer than in the past (11.5%).

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

285

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292

293 **Authors' contributions**

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

298

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301

302 **Data availability**

303 The datasets generated during the current study are available in the Dataverse repository

304 (<https://dataverse.ird.fr/dataset.xhtml?persistentId=doi:10.23708/HUR10F>)

305

306 **Code availability**

307 Not applicable

308

309 **Declarations**

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

312 **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
Health	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?	YES vs. NO



321 **Table 2.** List of the plants fertilized by termite mound soil (**mounds** as amendments), and  
 322 fertilized by **mound** soil and/or cultivated on **mounds** (**mounds** as amendments and  
 323 media). The number of answers is given as the frequency from the total number of  
 324 replies (n = 61 interviewees).

325

	Plant list
<b>Mounds as soil</b> 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%)
	<b>Mounds</b> as amendments and media
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%)	

326

327

**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 grewiifolia</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.

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**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.

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