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RESEARCH ARTICLE

Structure and function of subterranean gallery systems of soil-feeding termites *Pericapritermes nitobei* and *Sinocapritermes mushae*

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Abstract Soil-feeding termites are a critical trophic guild comprising more than a quarter of all termite species. Most soil-feeding termites build subterranean and diffuse gallery systems that are difficult to observe. In this study, we excavated the gallery systems of two soil-feeding termite species, *Pericapritermes nitobei* (Shiraki) and *Sinocapritermes mushae* (Oshima & Maki). Termite-harboring spaces were clusters of small cells connected with tunnels, with the cells usually adjacent to underground pieces of wood, stone, thick roots, and fibrous roots. Clusters of cells in a gallery system are referred to as nodes. In total, 90 nodes of five *P. nitobei* colonies and 64 nodes of seven *S. mushae* colonies were examined. The forager proportion of *P. nitobei* was the highest in nodes adjacent to fibrous roots, and that of *S. mushae* was the highest in nodes adjacent to pieces of wood, indicating that organic matter accumulated between the fibrous roots and underneath wood acted as a carbon source for the termites to feed upon. Nursed castes of *P. nitobei*, including larvae and eggs, were most frequently observed under thick roots and stones, but those of *S. mushae* were not located under any specific object. The nesting and feeding sites of *P. nitobei* were separate, but those of *S. mushae* overlapped. We speculate that the various food sources and their distributions are likely the main selection force for the gallery structures of soil-feeding termites.

Keywords Nest structure · Functional group · Trophic niche · Life type classification

Introduction

Termites are abundant and crucial cellulose decomposers in numerous tropical and subtropical ecosystems (Haverty and Nutting 1975; Collins 1981; Takamura 2001; Schuurman 2005). Depending on their food sources, termites are classified as wood-feeding, grass-harvesting, fungus-growing, or soil-feeding termites. Soil-feeding termites constitute 38.3 % (794/2072) of Termitidae species, which dominate several subfamilies, including Apicotermitinae, Cubitermitinae, Foramitermitinae, and Termitinae (Jones and Eggleton 2011; Chiu 2014). The high diversity of soil-feeding termites indicates soil feeders as being a successful feeding guild of termites (Brauman et al. 2000). Because soil feeders belonging to Apicotermitinae, Nasutitermitinae, and Syntermitinae subfamilies have not been thoroughly studied, their overall diversity remains unclear.

Soil-feeding termites were found in the surface horizon of soil (Inoue et al. 2001), in the intermediate organic matter between wood and topsoil (Souza and Brown 1994), and in the mounds of other termite species (Eggleton and Bignell 1997). These termites increase the polysaccharide content of soil (Garnier-Sillam and Harry 1995) and facilitate the soil humification process (Brauman 2000). Their activity affects the physical and chemical properties of the soil, such as pH and kaolinite, quartz, and water content, and stabilizes organic matter by preventing it from being quickly mineralized (Brauman 2000).

Gut content analysis and stable isotope methods have been used to study the food sources of soil-feeding termites. Plant roots, arthropod parts, fungal hyphae, and plant tissues

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have been found in the hindguts of soil-feeding termites (Sleaford et al. 1996; Donovan et al. 2001). Plant tissue content in the hindguts of soil feeders is lower than that in the hindguts of wood-feeding termites. However, the amounts of plant roots, arthropod parts, and fungal hyphae were higher in the hindguts of soil feeders than in those of wood feeders (Sleaford et al. 1996; Donovan et al. 2001). Stable isotope ratios of carbon and nitrogen have shown that the trophic niche is partitioned between wood-feeding and soil-feeding termites (Tayasu et al. 1997; Bourguignon et al. 2011) and among sympatric soil-feeding species (Bourguignon et al. 2009). According to the most recent hypothesis regarding niche partitioning by soil-feeding termites, different species occupy niches with various humification degrees of soil organic matter (Bourguignon et al. 2009). This hypothesis is also supported by observations of several soil invertebrates, such as oribatid mites (Schneider et al. 2004) and collembolans (Chahartaghi et al. 2005; Hishi et al. 2007).

Abe (1987) classified termite nesting and feeding behaviors into three life types on the basis of the distance between their feeding and nesting sites: one-piece type, intermediate type, and separated type. The life type variation among termite groups exhibits a remarkable evolutionary pattern (Inward et al. 2007; Legendre et al. 2008). All genera belonging to the Kalotermitidae family (Krishna 1961; Krishna and Weesner 1970) are representative of the one-piece type because an entire colony is restricted within one piece of wood and no clear separation between nesting and feeding sites is observed (Abe 1987). Termites that connect separated food sources, usually wood, were classified as an intermediate life type; they nest in wood or soil near a food source (Shellman-Reeve 1997). Termites with centralized and well-defined nests at a certain distance from a food source were classified as a separated life type (Shellman-Reeve 1997). A centralized nest usually comprises a group of chambers and has enhanced structures, such as a mound (Noirot 1970). These termites gather food from outside their nest (Shellman-Reeve 1997). In the case of soil-feeding termites, only 22 of 116 (19 %) genera belonging to Apicotermitinae, Cubitermitinae, and Termitinae build epigeous nests (Chiu 2014) and most of them build complete subterranean gallery systems. Because of the small colony size and diffuse gallery systems (Brauman 2000), and difficulty in excavating soil for observing their behaviors, their gallery structure and function remain unknown. Because no field data were available to support the separation between the feeding and nesting sites in an individual colony, soil-feeding termites were thought to have a one-piece life type (Noirot and Darlington 2000).

Two soil-feeding termite species, *Pericapritermes nitobei* (Shiraki) and *Sinocapritermes mushae* (Oshima & Maki), have been recorded in Taiwan as exhibiting a sympatric distribution (Hsueh 1998). These species build complete subterranean gallery systems (Hsueh 1998) and were observed feeding on the roots of upland rice; hence, they were considered potential crop pests (Maki 1920; Tu 1954). In this study, we excavated the gallery systems of these two soil-feeding termite species to locate foraging workers and nursed castes as indicators of foraging and nesting sites. By analyzing the correlations among the occurrence of termite castes and underground objects to which the gallery systems are connected, such as fibrous roots, stones, thick roots, and wood, we determined colony food sources and nesting environments. Further analysis of the association between foraging and nesting sites allowed us to determine the life types of the species.

Materials and methods

Study sites and sample collection

Studies were conducted at five locations in Taiwan, namely Dakeng (Taichung City), Ermei (Hsinchu County), Huisun (Nantou County), Fushan (New Taipei City), and Tungmaoshan (Taichung City), between July 2011 and November 2012 (Tables S1, S2). The types of plant debris covering each study site and soil color surrounding each gallery system were recorded. *P. nitobei* and *S. mushae* could be differentiated morphologically (Tsai 2003). The soldiers of both the species have asymmetric snapping mandibles; however, *S. mushae* soldiers exhibit less drastic asymmetry (Hsueh 1998). To ensure that each gallery system belonged to a different termite colony, we selected the gallery systems of either species at least 100 m apart from each other. Subterranean gallery systems were excavated and traced from where the termites were first located. We used a shovel to clear ground litter and soil from near the galleries. Gallery systems were excavated manually. In the gallery systems, termites were most often located in flat, narrow, and irregular spaces beneath or around underground objects, such as wood pieces, stones, and thick or fibrous roots (Fig. 1). These termite-harboring spaces were clusters of small cells connected by complex tunnel systems (Fig. 1a) or a few cells connected by a straight tunnel (Fig. 1b). We defined a group of small cells in a gallery system as a *node*. Nodes were typically more than 10 cm away from each other. The depth of the nodes was measured as the vertical distance between the ground surface and top of the node. Underground objects adjacent to nodes were recorded and then removed for further gallery excavation. The gallery excavation ended when no more galleries were traceable. All termites encountered in each node were collected using an aspirator and then preserved in 80–85 % alcohol. Termites of each caste in each node were counted.

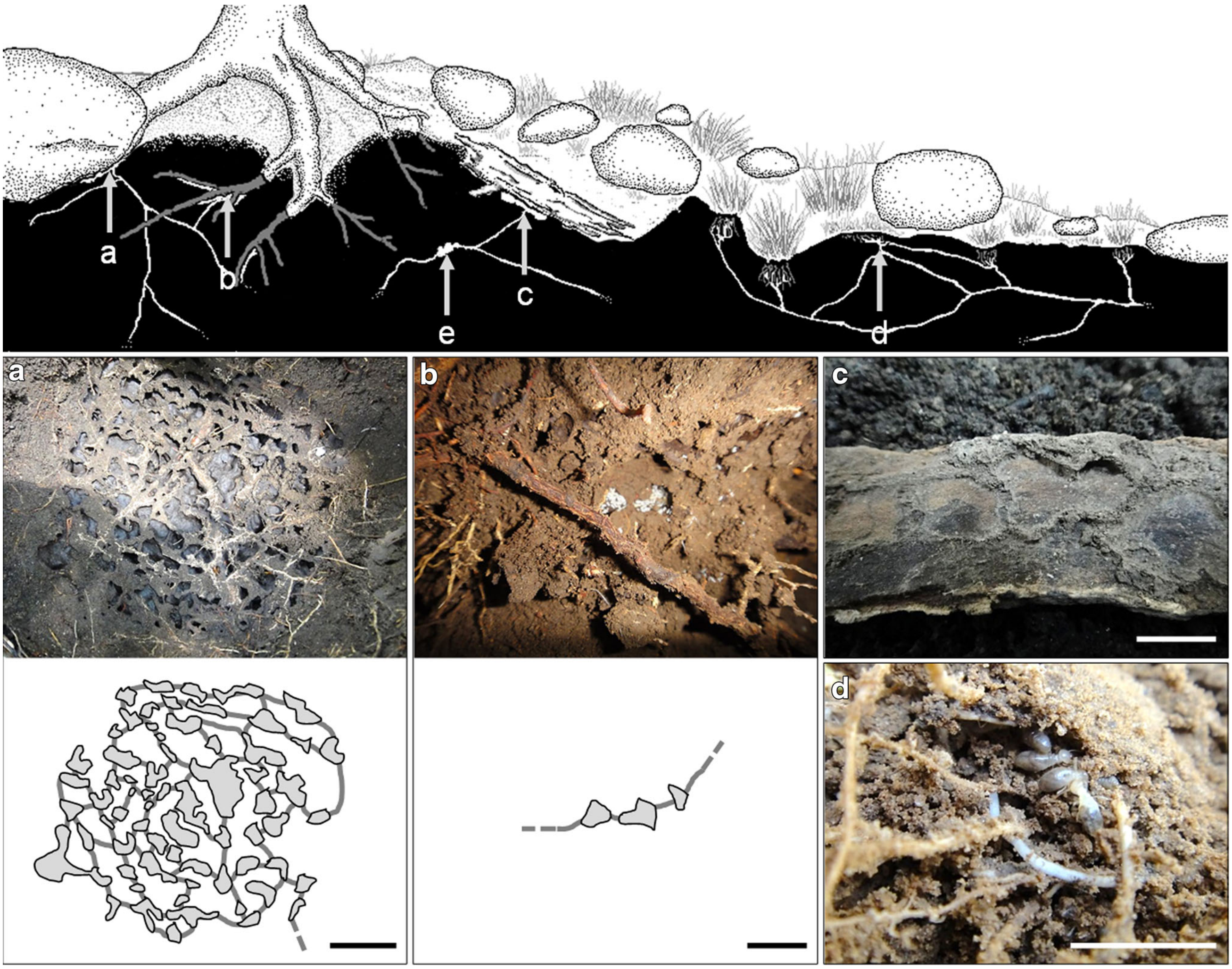

Fig. 1 Illustrations of five types of harboring spaces, nodes (*arrows*), in the subterranean gallery systems of soil-feeding termites. A node is a cluster of cells connected by tunnels. **a** Photograph (*top*) and line drawing (*bottom*) of a node under a stone with associated fibrous roots (tree root). This node was composed of multiple cells connected by numerous short tunnels. **b** Photograph (*top*) and line drawing (*bottom*) of a node adjacent to thick roots, which was composed of three cells connected by one tunnel. **c** Node under a piece of wood. **d** Node adjacent to fibrous roots (grass root). **e** Node without underground objects (no photograph). *Scale bars* represent 1 cm

Termite species were first identified according to a morphological key (Tsai 2003), and confirmation was based on the mitochondrial gene 16S sequences of several samples.

Locating feeding and nesting sites

To locate termite feeding sites, the worker–forager proportion in each node of a gallery system was estimated. Twenty workers in each node were randomly selected for examination. If a node contained fewer than 20 workers, all workers were examined. Foragers were identified as individuals containing soil in their esophagus or pharynx (Fig. 2). This method is based on the time taken by food to pass through the alimentary canal. Soil remains in the termite foregut for 1–2 h after ingestion, and the total duration for which food remains in the gut is approximately 24 h (Kovoor 1967). Workers with soil in their foregut were considered foragers, and the nodes in which numerous foragers were found were considered feeding sites. The nesting sites were defined as locations where nursed castes were found. The nursed castes included eggs, larvae and the king and queen. The occurrence of each nursed caste in each node was recorded.

Data analysis

To determine whether the two soil-feeding termite species feed at specific locations in the ground, the associations between termite forager proportions and underground objects were analyzed using linear mixed-effects (LME)

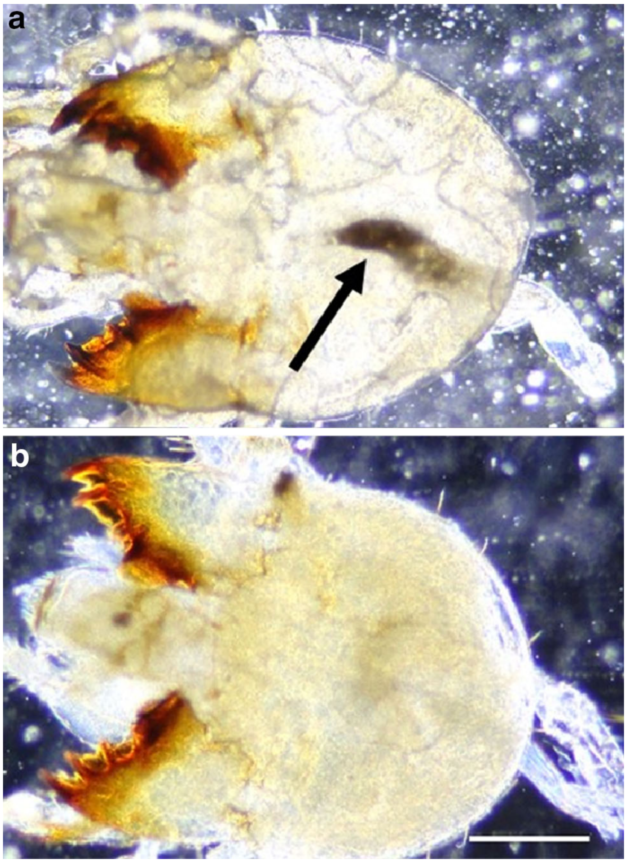

Fig. 2 Identification of foraging workers by checking the presence of soil in the esophagus. **a** Esophagus with ingested soil (*arrow*) of a *P. nitobei* worker. **b** Esophagus containing no soil. *Scale bar* represents 250 μm

models. The models with delta Akaike information criterion ≤ 2 were selected and averaged. The goodness of fit of the selected models was examined using the likelihood ratio test. The Wald test was used to evaluate the effect of each independent variable. To determine whether the termites nest at specific locations, the associations between each underground object and the occurrence of larvae or eggs were analyzed individually using generalized linear mixed models (GLMMs). The likelihood ratio test and Wald test were also performed for this analysis. Bonferroni correction was used to adjust *P* values for controlling Type I error. The correlation between the forager proportion and occurrence of nursed castes was analyzed using GLMMs to test whether the feeding and nesting sites were separated. Additional procedures were conducted as described previously. All statistical analyses were performed using R version 2.13.2 software (R Development Core Team 2013). Analyses involving the LME models and GLMMs were performed using the package *lme4* (Bates et al. 2014). To determine whether the feeding and nesting sites of *P. nitobei* were separated vertically, we used the Mann–Whitney *U* test to compare the depth of nodes adjacent to stones or thick roots with that of nodes adjacent to fibrous roots. If gallery systems had fewer than three nodes adjacent to stones, thick roots, or fibrous roots, the test was not conducted.

Results

Habitat environment and gallery structure

Five and seven subterranean gallery systems of *P. nitobei* (PN1–5, Table S1) and *S. mushae* (SM1–7, Table S2), respectively, were excavated. The sympatric distribution of these two species was observed at four of five study sites, namely Dakeng (PN1 and SM1), Huisun (PN4 and SM2), Fushan (SM6), and Tungmaoshan (SM7). When we excavated SM6 and SM7, some *P. nitobei* individuals were also observed. Because of the difficulty in tracing two close tunnel systems simultaneously, we prioritized excavating the *S. mushae* gallery systems at each location. *P. nitobei* was found in soil regions typically covered with fallen leaves, including broad and bamboo leaves (PN1), grass roots (PN2), and coniferous needles (PN3 and PN4). The study site of PN5, where no litter was present on top of the soil, was the only exception. The locations where we found *S. mushae* were also covered with plant debris, including leaves (SM1 and SM2), fallen dead trees (SM3), tree branches and leaves (SM4 and SM5), and decayed wood pieces (SM6 and SM7). More pieces of wood on top or in the soil were recorded at the sites where *S. mushae* was found than at those where *P. nitobei* was found. The soil color surrounding the gallery systems varied, with yellow (PN2 and SM6), yellowish brown (SM7), pale brown (PN3), brown (SM3, SM4, and SM5), deep brown (PN4, PN5, and SM2), and dark brown (PN1 and SM1) observed. No associated pattern between the soil color and termite species was observed.

P. nitobei and *S. mushae* were observed in flat, narrow, and irregular spaces beneath or around underground objects, including stones (Fig. 1a), thick roots (primary and secondary tree roots; Fig. 1b), wood pieces (Fig. 1c), and fibrous roots (tertiary tree roots and grass roots; Fig. 1d). In total, 90 nodes of *P. nitobei* and 64 nodes of *S. mushae* were observed. The simplest node comprised a few cells connected by a single tunnel (Fig. 1b), and the most complex nodes encompassed numerous cells connected by multiple tunnels (Fig. 1a). The width of the cells ranged from 8 to 12 mm and their estimated volume ranged from 1 to 5 cm^3. The internal surface of most cells was earthen, with no delicate modification. Only in a few nodes (15 of 90 *P. nitobei* nodes and 7 of 64 *S. mushae* nodes) was the internal surface of the cells covered with a black material with a smooth texture (Fig. 1a). Larvae, eggs, and reproductives were commonly observed in these plastered cells (Tables S1, S2).

Feeding and nesting sites

The forager proportion in the *P. nitobei* gallery systems was positively correlated with the occurrence of fibrous roots (coefficient = 0.24, $Z = 4.41$, $P < 0.001$; Fig. 3a; Table S3). This result indicated that nodes adjacent to fibrous roots are the feeding sites of *P. nitobei*. The forager proportion in the *S. mushae* gallery systems was positively correlated with the occurrence of wood (coefficient = 0.31, $Z = 4.73$, $P < 0.001$; Fig. 3b; Table S3). This result indicated that nodes associated with wood are the feeding sites of *S. mushae*.

The occurrence of *P. nitobei* larvae was positively correlated with that of thick roots and stones (thick roots: coefficient = 4.68, $Z = 2.89$, $P < 0.05$; stones: coefficient = 1.77, $Z = 2.68$, $P < 0.05$; Fig. 3a; Table S4). The occurrence of *P. nitobei* eggs was also positively correlated with that of thick roots (coefficient = 5.06, $Z = 3.06$, $P < 0.05$; Fig. 3a; Table S4). These results indicated that nodes adjacent to stones and thick roots are the nesting sites of *P. nitobei*. No association between the occurrence of nursed castes and that of underground objects in the *S. mushae* gallery systems was observed (Fig. 3b; Table S4), suggesting that the nesting sites of *S. mushae* are not at specific locations.

The correlation between the forager proportion and occurrence of nursed castes in the *P. nitobei* gallery systems was significantly negative (coefficient = −3.55, $Z = -2.71$, $P < 0.01$; Table S5), indicating that the feeding and nesting sites of *P. nitobei* are separated. The correlation between the *S. mushae* forager proportion and occurrence of nursed castes was not significant (coefficient = −1.82, $Z = -1.49$, $P = 0.14$; Table S5), indicating that its feeding and nesting sites are not separated.

In the *P. nitobei* gallery systems, nodes adjacent to fibrous roots were located mostly at a depth of <6 cm and

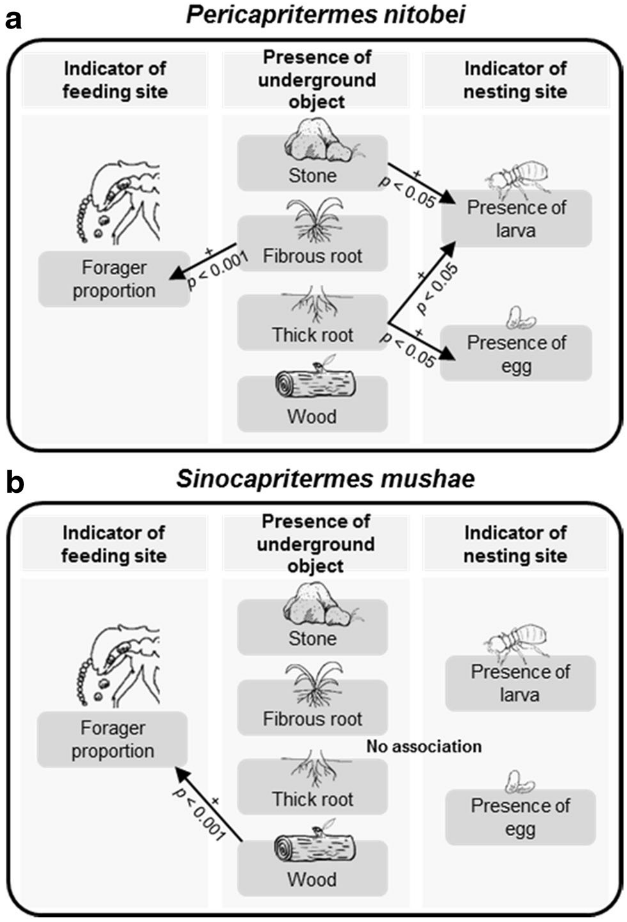

Fig. 3 Locating the feeding and nesting sites of *P. nitobei* (**a**) and *S. mushae* (**b**). Association between the forager proportion and occurrence of each underground object was analyzed using LME models. Association between the occurrence of nursed castes and that of each underground object was analyzed using GLMMs. Lines represent significant associations at $P \leq 0.05$. Pluses represent a positive correlation. Full models are presented in Table S3 and S4

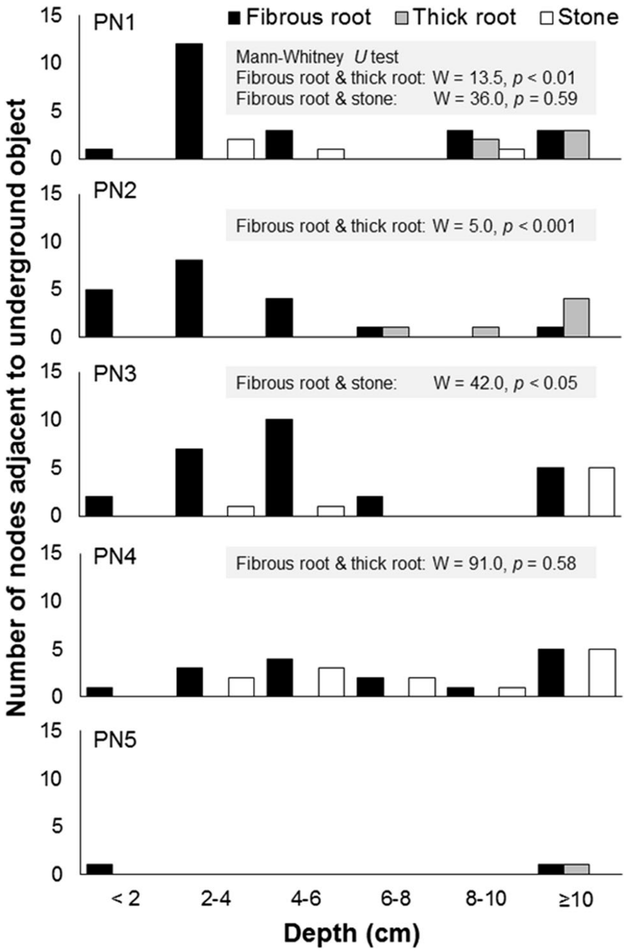

Fig. 4 Vertical distributions of feeding (fibrous root) and nesting sites (thick root and stone) of *P. nitobei*. Three of five subterranean gallery systems (PN1–5, Table S1) had nesting sites significantly deeper than feeding sites (Mann–Whitney *U* test)

those adjacent to stones or thick roots were generally located at a depth of >6 cm underground (Fig. 4; Table S1). Three of five gallery systems differed significantly in depth between nodes adjacent to fibrous roots and those adjacent to stones or thick roots (Fig. 4). These results indicated that the feeding and nesting sites of *P. nitobei* are separated vertically.

Discussion

This study revealed that the subterranean gallery systems of *P. nitobei* and *S. mushae* comprise clusters of small cells connected by tunnels, and no distinct nesting construction was observed, which conforms to the description of diffuse nests by Noirot (1970). However, *P. nitobei* was described as a mound-building species in Hong Kong (Crosland and Darlington 1997). This geographical variation in the nest structure also occurs in other termite species. For example, *Coptotermes lacteus* (Froggatt) builds mounds in most regions of Australia; however, it constructs subterranean nests in New South Wales and Southern Queensland (Gay and Calaby 1970). The *P. nitobei* species observed in Taiwan may differ from that observed in Hong Kong. To further understand how geographical differences affect the construction of nests by *P. nitobei*, confirming termite species and comparing multiple geographical and climatic factors between Taiwan and Hong Kong would be necessary.

In this study, we determined that the shape of nodes depends on the shape of adjacent underground objects. Nodes comprising only a few cells connected by one tunnel were adjacent to thick roots, whereas those with multiple tunnels and numerous cells were adjacent to stones. Termites likely utilize the surfaces of underground objects as excavation platforms and the shape of underground objects likely affects the shape of cells. The excavation behavior of soil-feeding termites must be observed further to understand the differences in cell formation among nodes.

The underground objects, stones, thick roots, wood pieces, and fibrous roots observed in the subterranean gallery systems in this study have been previously recorded in the gallery systems of other termite species; for example, pieces of wood and roots have been observed in the subterranean gallery systems of *C. formosanus* Shiraki (King and Spink 1969) and stones and roots have been observed in those of other soil-feeding termites (Krishna and Weesner 1970; Kirton and Cheng 2007). In addition, plastic man-made structures have been reported to be associated with the subterranean gallery systems of termites (Lenz et al. 2012). The reason that termites extend their galleries to diverse underground objects is not fully understood. We speculate that the density of underground objects in a given area and termite foraging preference may be factors. In this study, the subterranean gallery systems of *P. nitobei* and *S. mushae* were found sympatrically at most study sites and their gallery systems were mostly found in the topsoil. Hence, the chance of the two species encountering wood pieces, fibrous roots, thick roots, or stones during foraging should be the same. Therefore, the different occurrence of underground objects in the gallery systems of these species is likely due to their different foraging preferences. Fibrous roots are a carbon source for many soil-inhabiting invertebrates, such as earthworms (Curry and Schmidt 2007), nematodes, and many insect larvae (Bonkowski et al. 2009). Fibrous roots provide an interface between plants and soil, and the transportation of nutrients and energy occurs on the surface of these roots (Lavelle and Spain 2001). The exudates of fibrous roots can facilitate the growth of some symbiotic bacterial species, and the bacteria may attract bacterivorous protozoa and nematodes (Paterson 2003). Fibrous roots or organic matter accumulated in the rhizosphere have been considered potential carbon sources for soil-feeding termites (Brauman et al. 2000; Kirton and Cheng 2007). In this study, 93 % of nodes in the gallery systems of *P. nitobei* were adjacent to fibrous roots and significantly more foragers were found in these nodes (Fig. 3a), suggesting that *P. nitobei* foraging targets fibrous roots. Underground wood, such as tree roots and stumps, is a food source for many subterranean termites (King and Spink 1969; Apolinário and Martius 2004; Jasmi and Ahmad 2011). Several soil-feeding termites have been recorded feeding on the organic matter found at the wood–soil interface (Souza and Brown 1994; Eggleton et al. 1996). In the current study, the gallery systems of *P. nitobei* rarely reached underground wood; however, those of *S. mushae* frequently did. In six of the seven gallery systems of *S. mushae*, we found nodes adjacent to underground wood, with significantly more foragers in these nodes (Fig. 3b). This observation suggests that *S. mushae* is an intermediate feeder between wood and soil.

Several mechanisms of termite trophic niche partitioning have been reported. Niches could be segregated on the basis of feeding on various carbon sources, such as wood, plant roots, lichens, litter, and grass (Maki 1920; Duncan and Hewitt 1989; Miura and Matsumoto 1998a, b). The trophic niches of wood-feeding termites could be further classified on the basis of wood hardness (Behr et al. 1972), wood size (Evans et al. 2005), or the wood of a particular tree species (Smythe and Carter 1970a, b). In this study, we observed that the subterranean gallery systems of the two soil-feeding termite species are located proximally; hence, frequent interaction between these two species is likely. Feeding on two carbon sources, such as soil under plant roots or wood, could be the trophic niche partitioning mechanism of the species. Our observations partially support the hypothesis proposed by Bourguignon et al. (2009) that soil-feeding termites select species-specific food items in soil; however, they do not support the supposition that niche partitioning is achieved by "feeding on organic matter with different humification degrees."

The occurrence of larvae and eggs in the gallery system of *P. nitobei* was significantly correlated with that of thick roots and stones. The thick roots and stones likely protected the nursed castes. Stones may also provide stable humidity (Nobel et al. 1992) and a suitable shelter for soil invertebrates (Goldsbrough et al. 2003). Crosland and Darlington (1997) proposed that a place containing larvae should have a stable food supply and good protection. In this study, we found that all nodes adjacent to stones contained fibrous roots (Table S1); therefore, keeping larvae in nodes under stones seems to be the optimal means of providing them protection and food. More than 83 % of nodes in the gallery systems of *S. mushae* were adjacent to stones, thick roots, or wood (Table S2), which generally provided protection to all castes; hence, gathering near one of these objects seems unnecessary for nursed castes. Less than 41 % of nodes in the gallery systems of *P. nitobei* were adjacent to stones or thick roots (Table S1); hence, gathering of nursed castes under these objects was more obvious in *P. nitobei* than in *S. mushae*.

We found that *P. nitobei* had specific feeding and nesting sites (Fig. 3a). Its nesting sites were located deeper in the soil than its feeding sites (Fig. 4). Based on the classification proposed by Abe (1987), *P. nitobei* is having a separate life type. *S. mushae* has specific feeding sites but not specific nesting sites (Fig. 3b). The nesting and feeding sites of the species partially overlap; hence, *S. mushae* is having an intermediate life type. This current study demonstrated that, in contrast to the findings of Noirot and Darlington (2000), neither of the soil-feeding termites can be classified as having a one-piece life type. The feeding and nesting sites of primitive termite species feeding on large but scattered food sources, such as wood, tree stumps, and tree branches, usually overlap (Krishna and Weesner 1970). Termite species that feed on small but widely distributed food sources, such as lichens (Miura and Matsumoto 1998a, b), grass (Duncan and Hewitt 1989), and litter (Krishna and Weesner 1970), commonly have well-defined nesting sites separated from their food source. Our study supports this pattern. *P. nitobei* feeds on widely distributed humus in the rhizosphere and has a separate life type. *S. mushae* feeds on humus under scattered but long-lasting wood and has an intermediate life type. The distribution and type of food sources are likely the major selection forces for the life type evolution of soil-feeding termites.

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References

Abe T (1987) Evolution of life types in termites. In: Kawano S, Connell JH, Hidaka T (eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, pp 125–148

Apolinário FE, Martius C (2004) Ecological role of termites (Insecta, Isoptera) in tree trunks in central Amazonian rain forests. For Ecol Manage 194:23–28

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://cran.r-project.org/package=lme4

Behr EA, Behr CT, Wilson LF (1972) Influence of wood hardness on feeding by the Eastern subterranean termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitadae). Ann Entomol Soc Amer 65:457–460

Bonkowski M, Villenave C, Griffiths B (2009) Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots. Plant Soil 321:213–233

Bourguignon T, Sobotnik J, Lepoint G, Martin JM, Roisin Y (2009) Niche differentiation among neotropical soldierless soil-feeding termites revealed by stable isotope ratios. Soil Biol Biochem 41:2038–2043

Bourguignon T, Sobotnik J, Lepoint G, Martin JM, Hardy OJ, Dejean A, Roisin Y (2011) Feeding ecology and phylogenetic structure of a complex neotropical termite assemblage, revealed by nitrogen stable isotope ratios. Ecol Entomol 36:261–269

Brauman A (2000) Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: a review. Eur J Soil Biol 36:117–125

Brauman A, Bignell DE, Tayasu I (2000) Soil-feeding termites: biology, microbial associations and digestive mechanisms. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 233–259

Chahartaghi M, Langel R, Scheu S, Ruess L (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biol Biochem 37:1718–1725

Chiu C-I (2014) Structures and functions of subterranean gallery systems of two soil-feeding termites. Dissertation, National Chung Hsing University, Taichung, Taiwan

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

Crosland MWJ, Darlington JPEC (1997) The relationship between the primary and a subsidiary nest of *Pericapritermes nitobei* (Isoptera, Termitidae, Termitinae) in Hong Kong. Sociobiology 29:263–268

Curry JP, Schmidt O (2007) The feeding ecology of earthworms—a review. Pedobiologia 50:463–477

Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. Ecol Entomol 26:356–366

Duncan FD, Hewitt PH (1989) Observations on the foraging behaviour of the harvester termite, *Hodotermes mossambicus* (Hagen) (Isoptera: Hodotermitidae). Bull Ent Res 79:631–642

Eggleton P, Bignell DE (1997) Secondary occupation of epigeal termite (Isoptera) mounds by other termites in the Mbalmayo Forest Reserve, southern Cameroon, and its biological significance. J Afr Zool 111:489–498

Eggleton P, Bignell DE, Sands WA, Mawdsley NA, Lawton JH, Wood TG, Bignell NC (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Phil Trans R Soc Lond B 351:51–68

Evans TA, Lai JCS, Toledano E, McDowall L, Rakotonarivo S, Lenz M (2005) Termites assess wood size by using vibration signals. P Natl Acad Sci USA 102:3732–3737

Garnier-Sillam E, Harry M (1995) Distribution of humic compounds in mounds of some soil-feeding termite species of tropical rainforests: its influence on soil structure stability. Insect Soc 42:167–185

Gay FJ, Calaby JH (1970) Termites of the Australian region. In: Krishna K, Weesner FM (eds) Biology of termites, vol 2. Academic Press, New York, pp 393–448

Goldsbrough CL, Hochuli DF, Shine R (2003) Invertebrate biodiversity under hot rocks: habitat use by the fauna of sandstone outcrops in the Sydney region. Biol Conserv 109:85–93

Haverty M, Nutting W (1975) A simulation of wood consumption by the subterranean termite *Heterotermes aureus* (Snyder), in an Arizona desert Grassland. Insect Soc 22:93–102

Hishi T, Hyodo F, Saitoh S, Takeda H (2007) The feeding habits of collembola along decomposition gradients using stable carbon and nitrogen isotope analyses. Soil Biol Biochem 39:1820–1823

Hsueh W-J (1998) Development of castes in *Capritermes*, *Sinocapritermes*, and *Nasutitermes* in Taiwan. Dissertation, National Taiwan University, Taipei, Taiwan

Inoue T, Takematsu Y, Hyodo F, Sugimoto A, Yamada A, Klangkaew C, Kirtibutr N, Abe T (2001) The abundance and biomass of subterranean termites (Isoptera) in a dry evergreen forest of northeast Thailand. Sociobiology 37:41–52

Inward DJG, Vogler AP, Eggleton P (2007) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. Mol Phylogenet Evol 44:953–967

Jasmi AH, Ahmad AH (2011) Termite incidence on an *Araucaria* plantation forest in Teluk Bahang, Penang. Insects 2:469–474

Jones DT, Eggleton P (2011) Global biogeography of termites: a compilation of sources. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer, Heidelberg, pp 477–498

King EG, Spink WT (1969) Foraging galleries of the Formosan subterranean termite, *Coptotermes formosanus*, in Louisiana. Ann Entomol Soc Amer 62:536–542

Kirton LG, Cheng S (2007) Ring-barking and root debarking of dipterocarp saplings by termites in an enrichment planting site in Malaysia. J Trop For Sci 19:67–72

Kovoor J (1967) Etude radiographique du transit intestinal chez un Termite supérieur. Experientia 23:820–821

Krishna K (1961) A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). Bull Am Mus Nat Hist 122:303–408

Krishna K, Weesner FM (1970) The biology of termites. Academic Press, New York

Lavelle P, Spain AV (2001) Soil ecology. Kluwer Academics Publishers, Dordrecht

Legendre F, Whiting MF, Bordereau C, Cancello EM, Evans TA, Grandcolas P (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: Implications for the evolution of the worker and pseudergate castes, and foraging behaviors. Mol Phylogenet Evol 48:615–627

Lenz M, Creffield JW, Evans TA, Kard B, Vongkaluang C, Sornnuwat Y, Lee CY, Yoshimura T, Tsunoda K (2012) Resistance of polyamide and polyethylene cable sheathings to termites in Australia, Thailand, USA, Malaysia and Japan: a comparison of four field assessment methods. Int Biodeter Biodegr 66:53–62

Maki M (1920) Termite and rice. Taiwan Noziho 14:36 **(in Japanese)**

Miura T, Matsumoto T (1998a) Foraging organization of the open-air processional lichenfeeding termite *Hospitalitermes* (Isoptera, Termitidae) in Borneo. Insect Soc 45:17–32

Miura T, Matsumoto T (1998b) Open-air litter foraging in the nasute termite *Longipeditermes longipes* (Isoptera: Termitidae). J Ins Beh 11:179–189

Nobel PS, Miller PM, Graham EA (1992) Influence of rocks on soil-temperature, soil-water potential, and rooting patterns for desert succulents. Oecologia 92:90–96

Noirot C (1970) The nests of termites. In: Krishna K, Weesner FM (eds) Biology of termites, vol 2. Academic Press, New York, pp 73–125

Noirot C, Darlington JPEC (2000) Termite nests: architecture, regulation and defence. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbiosis, ecology. Kluwer Academic Publishers, Dordrecht, pp 121–139

Paterson E (2003) Importance of rhizodeposition in the coupling of plant and microbial productivity. Eur J Soil Sci 54:741–750

R Development Core Team (2013) R: a language and environment for statistical computing computer program, version 3.0.2. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Schneider K, Migge S, Norton RA, Scheu S, Langel R, Reineking A, Maraun M (2004) Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (15 N/14 N). Soil Biol Biochem 36:1769–1774

Schuurman G (2005) Decomposition rates and termite assemblage composition in semiarid Africa. Ecology 86:1236–1249

Shellman-Reeve JS (1997) The spectrum of eusociality in termites. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, pp 52–93

Sleaford F, Bignell DE, Eggleton P (1996) A pilot analysis of gut contents in termites from the Mbalmayo Forest Reserve, Cameroon. Ecol Entomol 21:279–288

Smythe RV, Carter FL (1970a) Survival and behavior of three subterranean termite species in sawdust of eleven wood species. Ann Entomol Soc Amer 63:847–850

Smythe RV, Carter FL (1970b) Feeding responses to sound wood by *Coptotermes formosanus*, *Reticulitermes flavipes* and *R. virginicus* (Isoptera: Rhinotermitidae). Ann Entomol Soc Amer 63:841–847

Souza OFF, Brown VK (1994) Effects of habitat fragmentation on Amazonian termite communities. J Trop Ecol 10:197–206

Takamura K (2001) Effects of termite exclusion on decay of heavy and light hardwood in a tropical rain forest of Peninsular Malaysia. J Trop Ecol 17:541–548

Tayasu I, Abe T, Eggleton P, Bignell DE (1997) Nitrogen and carbon isotope ratios in termites: an indicator trophic habit along the gradient from wood-feeding to soil-feeding. Ecol Entomol 22:343–351

Tsai CC (2003) A taxonomic study of termite (Isoptera) from Taiwan. Dissertation, Tunghai University, Taichung, Taiwan

Tu TC (1954) Ecological supplement to a Formosan termite, *Capritermes* (*Capreitermes*) *nitobei* (Shiraki). J Formos Med Assoc 53:225–235 **(in Chinese)**