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Termite Assemblage Pattern and Niche Partitioning in a Tropical Forest Ecosystem

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ABSTRACT Termites are major plant decomposers in tropical forest ecosystems, but their cryptic nature poses an obstacle for studying their ecological roles in depth. In the current study, we quantified climatic and geographic information of 137 termite collection sites in the Kenting National Park, Taiwan, and described the ecological niches and assemblage patterns of 13 termite species of three families. Three major assemblage patterns are reported. First, the three termite families were found in most landcovering types with similar number of species, which indicated that each family played a unique role in the ecosystem. Second, average numbers of termite species were not different among collection sites, but the total number of termite species found in each landcovering type was different, which indicated that termite niche capacity in each small area was the same but some landcovering types were composed of diverse microhabitats to host more termite species. Third, termite species of every family showed distinct moisture preferences in their habitat choices. In addition to the three assemblage patterns, we found that niche size of the advanced termite family, Termitidae, was larger than that of the primitive termite families, Rhinotermitidae or Kalotermitidae. The broader choices of cellulosic materials as food sources may allow Termitidae to adapt to more diverse environments than exclusive wood feeders. Termite niche quantification could further be used to study termite pest adaption in urban areas, interspecific competition between native and invasive species, and plant decomposition processes.

KEY WORDS detritivore, niche segregation, niche size, congeneric competition, geographic information system

Termites are an important group of arthropods for wood decay and leaf litter decomposition (Wood and Sands 1978), which plays a major role in carbon mineralization and energy flow (Wood 1978). Termites are efficient lignocellulose digesters with diverse microbial symbionts in their guts and nests (Brune and Ohkuma 2011, Nobre et al. 2011). On a global scale, termite diversity is greatest in tropical areas and decreases with increasing latitude, and only a few termite genera are found beyond 40° latitude (Eggleton 2000). The biomass of termites in the tropics is abundant (Bignell and Eggleton 2000) and may account for as much as 10% of all animal life in these zones (Wilson 1992). Hence, termites comprise a great proportion of the food source for many predators (Wood and Sands 1978). Only a small proportion of termite species (104 of nearly 3,000 species, i.e., 3.5%; Krishna et al. 2013) are considered severe pests of wooden structures and furniture, but their global economic impact was estimated at US$40 billion per year in 2012 (Rust and Su 2012).

Because of their ecological and economic importance, termite biodiversity surveys have drawn some attention (Krishna and Weesner 1970, Jones et al. 2005). The most commonly used quantitative method for termite biodiversity surveys is the belt transect method, by which multiple 100 by 2 m areas in defined habitats are randomly selected, and in each subsampling unit (5 by 2 m), a 1-h collection effort is allocated for searching for termites in the upper layer of the soil, and to a height of 2 m above ground level (Jones and Eggleton 2000). The standardized transect method has been conducted in many Asian and African tropics, which provides data with a more complete species composition in various ecosystems than earlier nonsystematic methods, especially for soil-feeding termites (Gathorne-Hardy et al. 2001; Eggleton et al. 2002a,b; Jones et al. 2005). By analyzing the relationship between environmental factors and termite assemblages among ecosystems, the effects of altitude, precipitation, and anthropogenic disturbance on termite species composition was examined (Eggleton et al. 1996, 2002a; Gathorne-Hardy et al. 2001; Donovan et al. 2002).

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In addition to the short-term environmental factors, however, the difference of termite composition and diversity across continents or among distant ecosystems may have resulted from the historical dispersal pattern and evolution trends (Eggloton 2000).

To study the ecological roles of termites, they are typically classified into functional groups by their food sources and nesting structures (Abe 1987, Donovan et al. 2001, Eggleton and Tayasu 2001). The major food source categories included wood, litter, humus, and soil. Depending on the distance between food sources and nesting areas, termite's nesting styles were classified into 1) one-piece nesting type: termites feeding and nesting in one piece of wood; 2) intermediate nesting type: multiple nesting areas, some are within food sources and some are kept at distance from food sources; 3) separate nesting type: nesting area is excluded from food sources (Abe 1987, Eggleton and Tayasu 2001). The functional assemblage and evolution of termites have been studied by using these conceptualized nesting and feeding categories. Abe (1984) described termite fauna succession on the Krakatau Island after defaunation by a volcanic eruption. Abe (1980, 1987) showed the effect of the wood decay process on termite assemblage patterns among temperate, subtropical, and tropical forests throughout East Asia. Inward et al. (2007) described the phylogenetic relationships between the nesting and feeding groups, based on both molecular and morphological data. Evans et al. (2013) used termite ecological characteristics including nesting and feeding groups to explain their invasive potentials from native habitats to exotic areas.

Because all termites feed on wood or cellulose material, Abe (1987) hypothesized that the competitive relationship forced termites to evolve into various feeding types and nesting styles. If Abe's hypothesis is correct, the termite assemblages in a habitat should be formed by various feeding or nesting types to prevent competition. However, the interactions among termite species, feeding groups, or nesting groups in an ecosystem remain obscure and no quantitative study on termite niche partitioning is available. The challenges for field study of termite ecology include 1) cryptic behavior: termites very rarely expose themselves to open space, which impedes the direct observation of their behavior and interspecific interaction. They live within enclosed tunnel systems in wood and soils or shelter tubes constructed on the surface of trunk, grass, tree branches, and stones. Considerable effort is required to chop the wood, to dig the soil, and to search the environment for evidence to obtain termite samples (Jones et al. 2005). 2) Confusing taxonomic status: termite species description and identification was mainly based on the two morphologically distinct castes, soldier, and alate. Soldier caste composes a small portion of a colony, on average <5%, and alate is only available seasonally. Hence, many termite species descriptions do not include the complete caste series (Krishna et al. 2013), which poses an obstacle for correct identification and further ecological studies. 3) Insufficient environmental information: limited weather stations result in low resolution of environmental information in specific areas where termites are collected, which restrict the quantification of their ecological niche.

The objective of the current study is to assess termite diversity and assemblage pattern, to quantify the ecological niches of termites, and to further investigate their potential interspecific interactions. The Kenting National Park resides in a tropical forest ecosystem, which provided multiple plant communities for our comparison studies. Our study carried out in this park, hence, circumvents the influence of different historical termite dispersal patterns among multiple ecosystems, a concern raised by a previous study (Eggleton 2000). Intensive termite collection at 137 locations in the park resulted in 672 termite colony samples, which provided us substantial numbers of locations for termite ecological niche description and comparison. Taxonomic study of the termite fauna collected was conducted in advance to provide dependable termite classification (Li et al. 2009a,b; 2011a, and H.F.L., unpublished data). To quantify the ecological niche of each termite species, the environmental information of respective collection sites was obtained by using a geographic information system. Habitat types were classified according to Chen's criterion (2009), using remote sensing techniques to delineate the dominant plant communities in the park.

Materials and Methods

Termite Sampling. Of the 17 recorded termite species in Taiwan, 15 are exclusively wood feeders or associated with wood to a certain degree (Li 2010). The other two species are humus feeders that feed on the organic rich upper layer of soil, usually found at the interface between soil and wood or soil and grass roots (Chiu 2014). Because the food sources of wood-feeding termites, including dead standing trees, dead branches of living trees, and wood laying on the ground, are scattered, a belt transect survey in a 200 m^2 area (Jones and Eggleton 2000) usually results in low termite encounter rate in Taiwan. To increase the collection efficiency, we increased the sampling area of the collection site to a 100-m-diameter scope (7,850 m^2). Surveys were conducted by—three to five experienced researchers with ~100-min collection time in total per location. With this survey protocol, termite assemblages of 137 locations in the Kenting National Park were obtained during 16–21 October 2008 and 23 June–2 July 2009. We surveyed the termite fauna through the most accessible roads and trails. Collection sites were at least 100 m apart from each other. Attention was paid to various termite food sources including 1) woody material: dead branches of living trees, dead standing trees, decomposed tree trunks on the ground; 2) soft plant material and debris: moss, grass, decomposed leaves, and cow dung; 3) soil: top soil with organic material, interface between soil and wood, and soil under stone. In addition to food sources, termite evidence such as mud tubes, mud shelters, and arboreal nests were also checked. In total, 672 termite colony samples were collected in the 137 locations (Fig. 1). Termite species were identified by using soldier and
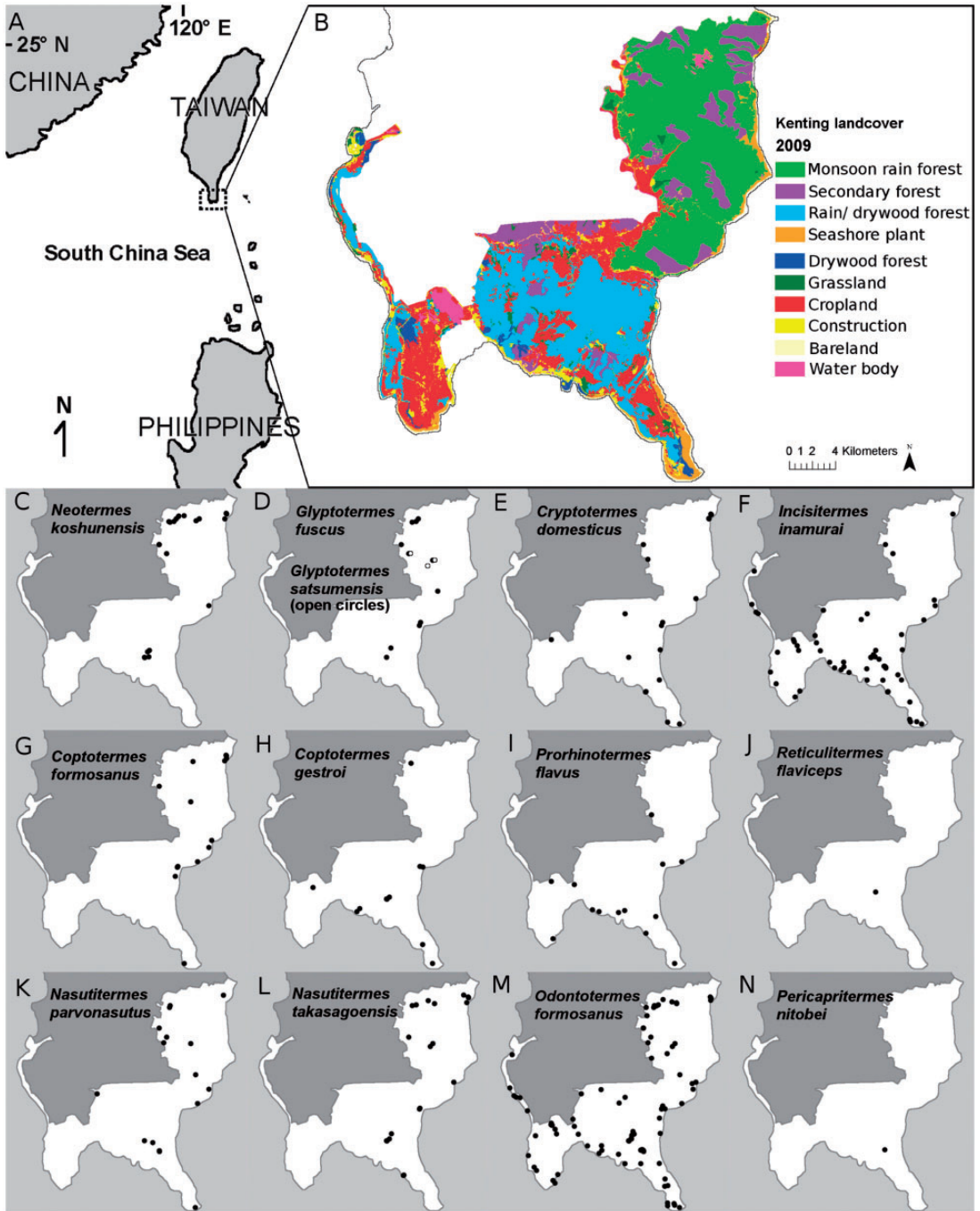
Fig. 1.   The Kenting National Park located at the southern tip of the Taiwan Island (A), and its vegetation was classified into 10 categories (B) by Chen 2009. Thirteen termite species were collected from 137 locations (closed circles), including five kalotermitids (C–F), four rhinotermitids (G–J), and four termitids (K–N).

alate morphology according to original descriptions (Table 1) and taxonomic redescription (Li et al. 2009a, 2011a). Molecular tools were used to identify cryptic species such as *Coptotermes* and *Reticulitermes* spp. (Li et al. 2009b, H.F.L., unpublished data). All

specimens were deposited in the National Chung Hsing University Termite Collection.

Environmental Data and Vegetation Classification. The Kenting National Park occupies a terrestrial area of ~175 km². We used vector data of

Table 1. Termite species abundance, assemblage, and diversity in the Kenting National Park

Taxon	Monsoon rain forest	Rain or drywood forest mosaic	Secondary forest	Seashore plant community	Cropland	Grassland	Drywood forest	Bare land	Entire park
Kalotermitidae (dampwood and drywood feeding group)									
Neotermes koshunensis (Shiraki, 1909)	20 (8.6%)	16 (7.9%)	1 (1.7%)	0	0	3 (15.8%)	0	0	275 (40.9%)
Glyptotermes fuscus Oshima, 1912	13 (5.6%)	2 (1.0%)	0	0	0	0	0	0	40 (6.0%)
Glyptotermes satsumensis (Matsumura, 1907)	3 (1.3%)	0	0	0	0	0	0	0	15 (2.2%)
Cryptotermes domesticus (Haviland, 1898)	24 (10.3%)	16 (7.9%)	1 (1.7%)	8 (14.0%)	3 (3.8%)	0	0	0	3 (0.4%)
Incisitermes inamurai (Oshima, 1912)	10 (4.3%)	61 (30.0%)	17 (28.3%)	20 (35.1%)	38 (47.5%)	11 (57.9%)	3 (23.1%)	5 (62.5%)	52 (7.7%)
									165 (24.6%)
Rhinotermitidae (subterranean wood-feeding group)									
Coptotermes formosanus Shiraki, 1909	21 (9.1%)	4 (2.0%)	2 (3.3%)	1 (1.8%)	0	0	0	0	66 (9.8%)
Coptotermes gestroi (Wasmann, 1896)	2 (0.9%)	5 (2.5%)	6 (10.0%)	0	2 (2.5%)	0	1 (7.7%)	0	28 (4.2%)
Prorhinotermes flavus (Bugnion and Popoff, 1910)	1 (0.4%)	6 (3.0%)	2 (3.3%)	1 (1.8%)	4 (5.0%)	0	3 (23.1)	3 (37.5%)	16 (2.4%)
Reticulitermes flaviceps (Oshima, 1911)	0	2 (1.0%)	0	0	0	0	0	0	20 (3.0%)
									2 (0.3%)
Termitidae (Arboreal, fungus-growing, and humus-feeding group)									331 (49.3%)
Nasutitermes parvonasutus (Nawa, 1911)	24 (10.3%)	6 (3.0%)	3 (5.0%)	2 (3.5%)	0	0	0	0	35 (5.2%)
Nasutitermes takasagoensis (Nawa, 1911)	37 (15.9%)	16 (7.9%)	2 (3.3%)	4 (7.0%)	0	0	0	0	59 (8.8%)
Odontotermes formosanus (Shiraki, 1909)	77 (33.2%)	69 (34.0%)	25 (41.7%)	21 (36.8%)	33 (41.3%)	5 (26.3%)	6 (46.2%)	0	236 (35.1%)
Pericapritermes nitobei (Shiraki, 1909)	0	0	1 (1.7%)	0	0	0	0	0	1 (0.1%)
Total no. of samples	232	203	60	57	80	19	13	8	672
Total no. of species (Kalo-, Rhino-, Termitidae)[a]	11 (5, 3, 3)	11 (4, 4, 3)	10 (3, 3, 4)	7 (2, 2, 3)	5 (2, 2,1)	3 (2, 0, 1)	4 (1, 2, 1)	2 (1, 1, 0)	13 (5, 4, 4)
Total no. of collection sites	40	36	20	11	22	5	2	1	137
No. of species collected per site[b]	2.75 ± 1.66	2.44 ± 1.48	1.90 ± 1.12	2.09 ± 0.94	1.82 ± 0.80	1.60 ± 0.55	3.00 ± 1.41	2	2.30 ± 1.37
Shannon's diversity index	1.91	1.8	1.65	1.46	1.08	0.96	1.23	0.66	1.91
Shannon's equitability index	0.87	0.75	0.72	0.75	0.67	0.87	0.89	0.95	0.74

The number (%) of samples of each termite species collected in each landcovering type is shown.

[a]Species proportion of the three termite families in each landcovering type is not significantly different (chi-square test, Supp. Table 2 [online only]).

[b]Number of species collected per site (mean ± SE) among the eight landcovering types was not significantly different ($n = 137$; $F = 1.67$; $P = 0.12$; PROC GLM, SAS Institute 1985).

land cover type in the Park (Chen 2009), in which its vegetation types were classified into 10 categories by analyzing 2.5-m resolution satellite images that were reconfirmed with a field survey (Fig. 1). In the current study, we adopted Chen's landcovering classification, but the two categories, urban and water, were excluded because termites were neither collected in man-made structures nor bodies of water. Our land cover classes included monsoon rain forest, rain/drywood forest mosaic, secondary forest, seashore plant community, crop land, grassland, drywood forest, and bare land (Chen 2009). The landcovering type of each collection site is defined by the majority landcovering type in its 100-m-diameter searching scope using ArcGIS 9.3 (ESRI, Redlands, CA). To represent the termite fauna of the park quantitatively, the number of collection sites in each landcovering type is correlated with its area size (Supp Table 1 [online only]; $r = 0.96$, PROC CORR procedure, SAS Institute, 1985, Cary, NC). In addition to vegetation classification, we used seven 30 arc seconds (~1 km) resolution raster data sets to characterize sample locations: altitude, minimum temperature of the coldest month (MinT), maximum temperature of the warmest month (MaxT), and annual precipitation, obtained from WorldClim (www.world clim.org, Hijmans et al. 2005), and global aridity index and global potential evapotranspiration (Trabucco and Zomer 2009).

Biodiversity Index and Statistics. To describe termite species diversity, Shannon's diversity index is calculated as $H = -\sum_{i=1}^{n} P_i \ln P_i$, where P_i is the proportion of the termite species i relative to the total number of termite species, and Shannon's equitability index is calculated as $E_H = H / \ln S$, where S is the total number of termite species in the landcovering type. To test distribution equitability of the three termite families in each landcovering type, chi-square test was used. To determine if the landcovering type affects termite species niche capacity of each 100-m-diameter searching scope, number of termite species collected per location among the eight landcovering types were compared with the general linear model (PROC GLM, SAS Institute 1985).

To test if ecological niche differs among termite species, the environmental data of each collection location among associated termite species were compared by GLM procedure model at the $\alpha = 0.05$ level followed with Waller–Duncan K-ratio t-test grouping (SAS Institute 1985). To calculate niche breadth, the range of each environmental factor across the 137 collection sites was equally divided into 10 sections. Niche breadth of a termite species based on one environmental factor is calculated as $B = \left(\sum_{i=1}^{10} P_i^2 \right)^{-1}$, where P_i is the proportion of termite species found in the section i (Levins 1968). Because we divided the range of each environmental factor into 10 equal sections, the maximum niche breadth is 10 and minimum is 1. The niche size was calculated as the production of the seven niche breadths. To test if the niche sizes among the three termite families were the same, niche size of each termite species was analyzed with GLM procedure model followed with LSD grouping at the $\alpha = 0.05$ level (SAS

Institute 1985). To test if the niche breadths between every two species are the same, the seven niche breadths between every two species were compared by using paired t-test.

Results

Termite Diversity and Distribution. In total, 672 termite samples of 13 species were collected in this study, and 275 (40.9%), 66 (9.8%), and 331 (49.3%) belonged to three families, Kalotermitidae, Rhinotermitidae, and Termitidae, respectively (Table 1). Of the eight landcovering types, the number of termite species in the monsoon rain forest was the largest (11 species) and the number in the bare land was the smallest (2 species). Shannon's diversity index also shows that the highest and lowest termite diversity was found in the monsoon rain forest (1.91) and in the bare land (0.66), respectively. The Shannon's equitability index, ranging from 0.67 to 0.95, presents the balanced proportion of termite species in each landcovering type. Average number of termite species collected per site among the eight landcovering types ranged from 1.60 to 2.75, but were not significantly different ($n = 137$; $F = 1.67$; $P = 0.12$; Table 1), which indicated niche capacity of termite species of each collection site, a 100-m-diameter searching scope, was the same. In most landcovering types, all three termite families were found (Table 1), and the proportion of total species from each family was not different from one-third (chi-square test; Supp Table 2 [online only]), which indicates that the three termite families were equally distributed in each landcovering type.

Five kalotermitid species were found in the monsoon rain forest and their abundance ranged from 1.3 to 10.3% (Table 1). In the monsoon rain forest, species abundance among the five kalotermitids was more uniform than those of the other seven habitats (Table 1). *Neotermes koshunensis* (Shiraki) (Fig. 1C) and *Cryptotermes domesticus* (Haviland) (Fig. 1E) were the two most abundant kalotermitids in the monsoon rain forest. The *Incisitermes inamurai* (Oshima) (Fig. 1F) was rarer in the monsoon rain forest, but it was the most dominant kalotermitid in the entire Kenting National Park, constituting a quarter of the entire collection. The two *Glyptotermes* species (Fig. 1D) were found only in the monsoon rain forest and rain or drywood forest mosaic area.

Rhinotermitids were less commonly encountered than kalotermitids and termitids, which represented 9.8% of the entire collection (Table 1). *Coptotermes formosanus* Shiraki was most frequently found in the monsoon rain forest (Fig. 1G), and the cogeneric species, *Coptotermes gestroi* (Wasmann), was found mostly in the rain or drywood forest mosaic and secondary forest (Fig. 1H). *Prorhinotermes flavus* (Bugnion & Popoff) was found in all landcovering types except grassland (Fig. 1I), but its abundance was low in general and less than six samples were collected in each landcovering type (Table 1). *Reticulitermes flaviceps* Oshima was found only at one site in the rain or drywood forest mosaic area (Fig. 1J).

In total, 331 samples of four termitid species were collected, which was close to a half of the entire collection (49.3%; Table 1). The distribution of the two arboreal termite species, *Nasutitermes parvonasutus* (Nawa) and *Nasutitermes takasagoensis* (Nawa), were similar. They were most frequently found in the monsoon rain forest, and none were found in cropland, grassland, drywood forest, or bare land (Fig. 1K and 1L; Table 1). The fungus-growing termite, *Odontotermes formosanus* (Shiraki), was the most dominant termite species in the park, which accounted for 35.1% of all collections. Except for bare land, approximately one-third of the collection in each landcovering type was contributed by *O. formosanus* (Fig. 1M; Table 1). The humus-feeding termite *Pericapritermes nitobei* (Shiraki) was found only at one site in the secondary forest (Fig. 1N; Table 1).

Ecological Niche. The Kenting National Park, represented by the 137 collection locations, is generally a low land area (−2–336 m), close to the coast (5–7,316 m), warm in summer (maximum temperature: 29.3–31.2 °C), and in winter (minimum temperature: 15.2–17.3 °C), high precipitation (2,193–3,067 mm), high evapotranspiration (1,035–1,219 mm), and very humid (aridity index: 1.71–2.42; Table 2). Although the overall ranges of the seven environmental factors among all collection sites were small, the ecological niches of termite species were significantly different ($P < 0.0001$; Table 2).

The analysis of environmental factors of collection sites (Table 2) showed that the five kalotermitids could be clearly separated into two groups, dampwood termites, including *N. koshunensis*, *Glyptotermes fuscus* Oshima, and *Glyptotermes satsumensis* (Matsumura), and drywood termites, including *Cr. domesticus* and *I. inamurai* (Fig. 2). The dampwood termites were generally found in the locations with higher altitude, further away from coast, lower temperature, more precipitation, and higher humidity with higher evapotranspiration than those of drywood termites (Table 2). The niche size of the dampwood termite, *N. koshunensis*, in the Park was restricted by its preference of cooler areas (MaxT, 29.9 °C; B_{maxT}, 2.3; MinT, 15.9 °C; B_{minT}, 2.7) with high precipitation (2,853 mm; $B_{precipitation}$, 2.7), and a humid environment (Aridity index, 2.24; $B_{aridity\ index}$, 2.9; Tables 2 and 3). The niche size of *G. fuscus* is larger than the other four kalotermitid species (Table 3), indicating that the Park is generally a suitable habitat for *G. fuscus*. The niche of the congeneric species, *G. satsumensis*, is much smaller than that of *G. fuscus* (Table 3). Based on analysis of the seven environmental factors, the niches of the three dampwood termites were similar and the only difference was found between *N. koshunensis* and *G. satsumensis* on the MaxT and MinT factors (Tables 2 and 3), but their niche breadths were significantly different (Tables 3 and 4), which also resulted in different niche sizes (Table 3). The drywood termite, *Cr. domesticus*, was mostly found near the coast (1,579.1 m) and in lower areas (52.7 m; Table 2), these two factors ($B_{distance-to-coast}$, 2.0; $B_{altitude}$, 2.6; Table 3) restricted its niche size. The other drywood termite, *I. inamurai*, was found in

Table 2. Termite ecological niche description based on seven environmental factors in the Kenting National Park

Taxon	No. of locations	Altitude (m)	Distance to coast (m)	MaxT (°C)	MinT (°C)	Precipitation (mm)	Evapotranspiration (mm)	Aridity index
Kalotermitidae								
Neotermes koshunensis	25	190.6 ± 86.2 a	3481.9 ± 2245.7 abc	29.9 ± 0.2 f	15.9 ± 0.3 e	2853.2 ± 200.9 a	1149.7 ± 32.3 a	2.24 ± 0.15 a
Glyptotermes fuscus	11	144.8 ± 77.9 ab	3579.1 ± 2444.7 ab	30.1 ± 0.4 ef	16.1 ± 0.5 ed	2789.2 ± 210.7 ab	1142.4 ± 25.3 a	2.18 ± 0.17 a
Glyptotermes satsumensis	3	143.7 ± 61.7 abc	4934.7 ± 1453.5 a	30.3 ± 0.1 bcde	16.3 ± 0.0 cd	2926.7 ± 12.7 a	1157.7 ± 9.2 a	2.20 ± 0.02 a
Cryptotermes domesticus	19	52.7 ± 53.2 de	1579.1 ± 2429.0 de	30.5 ± 0.5 abc	16.6 ± 0.5 bc	2634.7 ± 291.8 bcd	1135.1 ± 50.6 ab	2.05 ± 0.22 bcd
Incisitermes inamurai	65	82.4 ± 76.7 de	1614.3 ± 1781.4 de	30.6 ± 0.5 ab	16.7 ± 0.5 ab	2464.2 ± 205.7 e	1095.2 ± 39.8 c	1.92 ± 0.17 de
Rhinotermitidae								
Coptotermes formosanus	20	99.3 ± 90.6 bcde	2080.1 ± 2493.0 cde	30.2 ± 0.5 cde	16.2 ± 0.6 cd	2782.3 ± 267.2 ab	1153.5 ± 38.5 a	2.18 ± 0.20 ab
Coptotermes gestroi	11	104.5 ± 102.5 bcd	1747.2 ± 1802.8 de	30.6 ± 0.6 abc	16.7 ± 0.6 ab	2474.8 ± 220.2 de	1099.6 ± 34.8 c	1.93 ± 0.18 de
Prorhinotermes flavus	14	38.6 ± 24.9 e	1074.6 ± 1454.2 e	30.9 ± 0.2 a	17.0 ± 0.2 a	2396.2 ± 137.5 e	1090.9 ± 35.8 c	1.86 ± 0.12 e
Reticulitermes flaviceps	1	274	2767.5	29.8~	16.0	2617	1113	2.06
Termitidae								
Nasutitermes parvonasutus	17	112.9 ± 59.5 bcd	3128.3 ± 2657.2 bcd	30.4 ± 0.4 bcd	16.4 ± 0.5 bcd	2688.1 ± 232 abc	1139.1 ± 33.0 ab	2.11 ± 0.18 abc
Nasutitermes takasagoensis	26	139.2 ± 94.5 abc	2631.2 ± 2112.9 bcde	30.2 ± 0.5 def	16.2 ± 0.5 de	2776.6 ± 246.7 ab	1147.7 ± 38.5 a	2.17 ± 0.19 ab
Odontotermes formosanus	102	101.0 ± 88.9 bcd	2255.9 ± 2144.1 bcde	30.5 ± 0.5 bcd	16.5 ± 0.5 bc	2563.9 ± 260.6 cde	1111.9 ± 46.4 bc	2.00 ± 0.21 cd
Pericapritermes nitobei	1	157	1682.5	30.5	16.7	2496	1114	1.96
Range		−2 ~ 336	4.8 ~ 7316.1	29.3 ~ 31.2	15.2 ~ 17.3	2193 ~ 3067	1035 ~ 1219	1.71 ~ 2.42
F value		5.75	3.62	8.13	9.32	10.39	8.79	10.65
P value		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

The total number of collection sites is 137, and environmental factors of locations associated with each species are shown below. For each environmental factor, means followed by the same letter are not significant different at the $\alpha = 0.05$ level (PROC GLM followed by Waller–Duncan K-ratio t-test, SAS Institute 1985). *R. flaviceps* and *Pe. nitobei* were excluded from analysis because they were only collected at a single location each.

Table 3. Niche breadth and niche size of termite species in the Kenting National Park

Taxon	$B_{altitude}$	$B_{distance-to-coast}$	B_{maxT}	B_{minT}	$B_{precipitation}$	$B_{evapotranspiration}$	$B_{aridity\ index}$	Niche size
Kalotermitidae								
Neotermes koshunensis	6.3	6.2	2.3	2.7	2.7	3.1	2.9	5,888
Glyptotermes fuscus	7.1	6.4	3.5	4.8	5.8	3.9	5.3	91,520
Glyptotermes satsumensis	3.0	3.0	1.0	1.0	1.0	1.8	1.8	29
Cryptotermes domesticus	2.6	2.0	5.6	4.3	6.8	6.3	6.3	33,795
Incisitermes inamurai	4.2	3.7	5.1	5.1	6.1	5.1	6.3	79,219
Rhinotermitidae								
Coptotermes formosanus	4.3	2.9	5.9	4.3	5.1	4.7	5.3	40,191
Coptotermes gestroi	2.7	2.8	3.3	3.1	3.9	4.5	3.9	5,293
Prorhinotermes flavus	2.6	2.6	3.2	3	4.3	5.2	4.1	5,949
Reticulitermes flaviceps	1	1	1	1	1	1	1	1
Termitidae								
Nasutitermes parvonasutus	5.1	5.5	6.7	5.1	7.8	4.9	7	256,429
Nasutitermes takasagoensis	7.5	5	4.3	3.7	4.4	3.9	4.6	47,095
Odontotermes formosanus	5.8	5	6.9	6.2	7.5	5.9	8	439,179
Pericapritermes nitobei	1	1	1	1	1	1	1	1

Niche size is the product of the seven niche breadths. The niche sizes of the three termite families, excluding *R. flaviceps* and *Pe. nitobei*, were analyzed with a general linear model ($F = 4.81$; $P = 0.04$; PROC GLM, SAS Institute 1985). The niche size of Termitidae is significantly larger than those of Rhinotermitidae and Kalotermitidae, but no significant difference was found between the latter two.

Table 4. Comparison of termite ecological niches based on environmental factors (above diagonal, data shown in Table 2) and niche breadth (below diagonal, data shown in Table 3) in the Kenting National Park

	1	2	3	4	5	6	7	8	9	10	11	12	13
Kalotermitidae													
1 *Neotermes koshunensis*		NS	S	S	S	S	S	S	-	S	S	S	-
2 *Glyptotermes fuscus*	S		NS	S	S	S	S	S	-	NS	NS	S	-
3 *Glyptotermes satsumensis*	S	S		S	S	S	S	S	-	S	S	S	-
4 *Cryptotermes domesticus*	NS	NS	S		S	NS	S	S	-	NS	S	NS	-
5 *Incisitermes inamurai*	NS	NS	S	NS		S	NS	NS	-	S	S	NS	-
Rhinotermitidae													
6 *Coptotermes formosanus*	NS	NS	S	NS	NS		S	S	-	NS	NS	S	-
7 *Coptotermes gestroi*	NS	S	S	S	S	S		S	-	S	S	NS	-
8 *Prorhinotermes flavus*	NS	NS	S	S	S	S	NS		-	S	S	S	-
9 *Reticulitermes flaviceps*	S	S	NS	S	S	S	S	S		-	-	-	-
Termitidae													
10 *Nasutitermes parvonasutus*	NS	NS	S	NS	S	S	S	S	S		NS	NS	-
11 *Nasutitermes takasagoensis*	S	NS	S	NS	NS	NS	NS	NS	S	NS		S	-
12 *Odontotermes formosanus*	S	NS	S	S	S	S	S	S	S	NS	NS		-
13 *Pericapritermes nitobei*	S	S	NS	S	S	S	S	S	-	S	S	S	

For environmental factor analysis, NS, no significant difference among all seven environmental factors; S, one or more environmental factors are significantly different. For niche breadth analysis, the seven niche breadths were compared by using paired *t*-test between every two species. NS, no significant difference; S, significant difference. The rectangles with dotted lines indicate intrafamily comparison.

even drier places than those of *Cr. domesticus*, where the precipitation and evapotranspiration was significantly lower than the habitats of the other four kalotermitids (Table 2). The niche breadths of the two drywood termites were not significantly different (Table 4).

Rhinotermitids were generally found near the coast and low elevation areas (Fig. 1G-1J; Table 2), with these two environmental factors restricted their niche sizes (Table 3). The four rhinotermitids could be also divided into two groups, damp subterranean termites, including *C. formosanus* and *R. flaviceps*, and dry subterranean termites, including *C. gestroi* and *P. flavus*

(Fig. 2). The damp subterranean termite, *C. formosanus*, was found in areas with lower minimum temperature in winter (16.2 °C), higher precipitation (2,782.3 mm), higher evapotranspiration (1,153.5 mm), and a higher aridity index (2.18) than the locations associated with the two dry subterranean termites (Table 2). *R. flaviceps* was encountered only at one location where the environmental factors were similar to those of *C. formosanus* (Table 2). The two dry subterranean termites were found at the warm and dry areas near the coast (Table 2). The only difference between the two dry subterranean termites was that *C. gestroi* was found at higher elevations than *P. flavus*
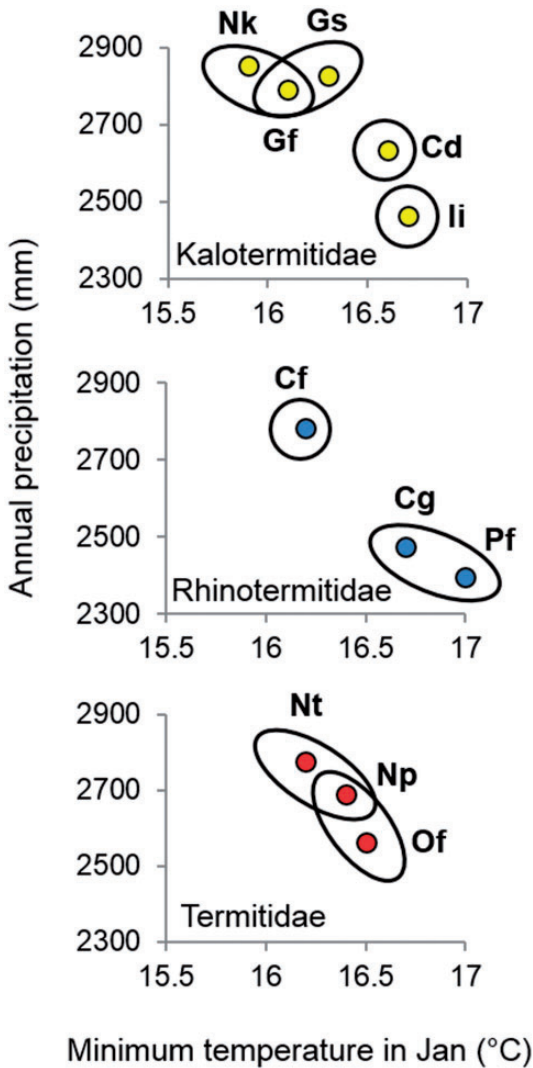
Fig. 2. The ecological niche grouping based on minimum temperature in January and annual precipitation. The species names are abbreviated based on the first letter of their genus and species names. Niche of the species in the same circle were not significantly different based on minimum temperature and annual precipitation.

(Table 2). The four rhinotermitids showed distinct niche characteristics from each other and varying niche breadths (Tables 2–4). At most collection sites where Rhinotermitidae were present (38 of 42), only one rhinotermitid species was collected.

Species within Kalotermitidae and Rhinotermitidae can be divided into two distinct groups: one preferring dry and the other preferring wet habitats. This pattern was also observed in species within Termitidae (Fig. 2). The fungus-growing termite, *O. formosanus*, was found in locations with higher MinT, lower precipitation, lower evapotranspiration, and a lower aridity index compared with the locations associated with the arboreal termite, *Na. takasagoensis* (Table 2). *Na.*

parvonasutus was found in both dry and humid environments and, hence, its ecological niche was not significantly different from those of *O. formosanus* and *Na. takasagoensis* (Tables 2 and 4). The fungus-growing termite and two *Nasutitermes* spp. were found in various landcovering types and, hence, the overall niche breadth across the seven environmental factors was large (Table 3), and niche breadths among these three termitids were not significantly different (Table 4).

Because *Pe. nitobei* and *R. flaviceps* were found only at one location each, they were excluded from niche size analysis. The niche sizes of the other 11 termite species among three families in the Park were significantly different ($F = 4.81$; $P = 0.04$). The niche size of Termitidae was significantly larger than that of Rhinotermitidae and Kalotermitidae, and no difference was found between the latter two (Table 3).

Discussion

Termite fauna in the Kenting National Park was studied by several researchers (Shiraki 1909, Nawa 1911, Oshima 1912, Tu 1955, Chu et al. 1986, Tsai and Chen 2003), and 11 termite species were recorded previously. The Kenting National Park was the type locality of five termite species, including *N. koshunensis*, *G. fuscus*, *I. inamurai*, *Na. parvonasutus*, and *Na. takasagoensis*. However, these previous collections were not found in any research institutes for further taxonomic and ecological studies. Our current collection has contributed to taxonomic redescriptions (Li et al. 2009a, 2011a), and two species, *G. satsumensis* and *Pr. flavus* (= *Pr. japonicus*) have been recorded in the park for the first time. So far, 13 of the 17 Taiwanese termite species were found in the Park, which indicates that the Kenting National Park has the highest termite diversity in Taiwan. The distribution of the four nonrecorded species in the Park and the three rarely found species may be restricted by the warm temperature and soil with low organic material. The Park is located in the low elevation tropics, and thus species adapted to cool temperatures may not survive easily. The temperate genus, *Reticulitermes*, was encountered only twice in this study. *Hodotermopsis sjostedti* Holmgren and *Nasutitermes kinoshitae* (Hozawa), previously found in high-elevation mountainous areas in Taiwan (Hozawa 1915, Tsai 2003, H.F.L., unpublished data), were not found in the Park. *G. satsumensis* distributed from southern Japan (Matsumura 1907), Ryukyu Islands (Ikehara 1957), to mountainous areas of Taiwan was found only at three locations in the Park (Fig. 1D). In addition to temperature, limited organic material in the soil surface may restrict the occurrence of humus-feeding termites, *Pe. nitobei* and *Sinocapritermes mushae* (Oshima & Maki). A previous study has shown that these two humus-feeding termites were usually found in soil with high organic matter ranging from 6 to16% (Chiu 2014), but the organic matter in the Park was lower, ranging from 0.74 to 5.79% (Chen and Chen 1984).

In each collection site, we allocated the same collection time, which resulted in a similar number of termite species per site. We speculated that each collection

site, a 100-m-diameter scope, provided similar number of niches for termites, but the niche diversity among each landcovering type is substantially different. For example, on the park scale, the monsoon rain forest is likely to be composed of more microhabitats for termites than the cropland. In addition to the diversity of microhabitats, the limited number of termite species in each site may also result from interspecific competition.

Most termites found in the Kenting National Park were wood-feeding species representing three families, Kalotermitidae, Rhinotermitidae, and Termitidae. They are also the three major termite families that composed of 96.8% of all living termite species in the world (15.5, 10.7, and 70.6%, respectively; Krishna et al. 2013). Even though termites in the Park are mostly wood feeders, the food sizes they preferred, distribution of their food, and their foraging strategies were distinctly different. Kalotermitids were found in large pieces of wood such as rotten logs on the ground, dead branches of living trees, or dead standing trees. The distribution of these large pieces of wood was generally scattered in the Park. Kalotermitids infested wood most likely through seasonal dispersal flights as described by Nutting (1969). An incipient colony was founded by a pair of alates, the future king and queen. All individuals of a kalotermid colony feed and nest in a single piece of wood, this is known as a one-piece nesting type termite (Abe 1987). The wood serves as both shelter and a food source (Noirot 1970). The colony size can be up to several thousand individuals (Nutting 1969). When the piece of wood is exhausted, most pseudergates may molt into alates and fly out for searching another piece of wood. In addition to kalotermitids, we found rhinotermitids inhabiting large pieces of wood as well. No king and queen were found in the wood, but satellite nests built in tree trunks and stumps were observed. Previous study showed rhinotermitid species nest in the soil and build extensive subterranean tunnels to connect food sources, which is referred to as the intermediate nesting type (Abe 1987). This foraging strategy allows rhinotermitids to access more food sources than kalotermitids. Hence, the colony size could be up to several million individuals. The termitid species found in the park feed on various cellulose materials, including fallen leaves, twigs, logs, grasses, mosses, fungi, excretions of herbivore animals, and humus. Although termitids were also found in the same large pieces of wood as kalotermitids and rhinotermitids, they were able to utilize scattered and smaller resources by connecting them with various mud tubes on the surfaces of tree trunks, branches, stone, fallen leaves, and excavated subterranean tunnels. Their nesting sites are also diverse, such as subterranean nests of O. formosanus, arboreal nests of Na. takasagoensis, and within-wood nests of Na. parvonasutus. Previous studies showed that the termitids usually build central nests at distance from their food sources, i.e., separate nesting type (Abe 1987), but the two Nasutitermes spp. found in this study build their nests directly on or in their food sources.

In the current study, numbers of species of Kalotermitidae, Rhinotermitidae, and Termitidae were similar in each land covering type (Fig. 3), which indicated
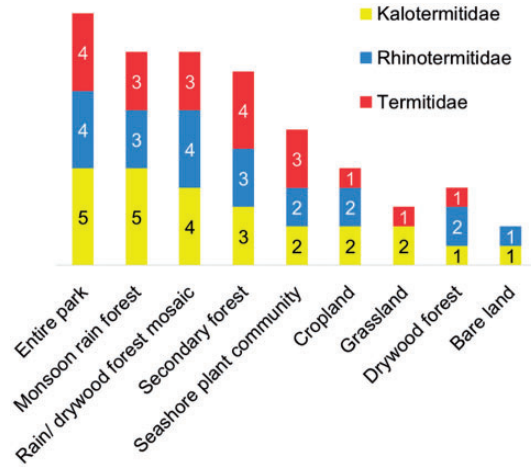

Fig. 3.   Termite species composition in each landcovering type in Kenting National Park.

that the three families have distinct ecological functions separating them from each other. In addition to natural habitats, the same three families, represented by Cr. domesticus, C. formosanus, C. gestroi, R. flaviceps, and O. formosanus, were also observed in the urban environment of Taiwan (Li et al. 2011b). Wood is the major food of both lower termite families, Kalotermitidae and Rhinotermitidae, and both of them have gut flagellates to assist wood digestion (Bignell 2011). Because kalotermids searched for new wood by alate dispersal flights, and rhinotermids foraged for new wood sources through the excavation of subterranean tunnels by the worker caste, the different spatial distribution of the pieces of wood may have contributed to their niche partitioning. The wood volume under and above ground are similar in general (Mauseth 2003), and, hence, both lower termite families have similar amounts of wood available to them in an ecosystem. The higher termite, Termitidae, feed on various cellulose materials with the help of gut bacteria and fungi symbionts (Bignell 2011). The availability of more varieties of cellulose sources may allow higher termites to adapt to a larger variety of environments than lower termites, as indicated by the niche size analysis (Table 3). By comparing the environmental data of collection sites between each termite species pair (Table 4, above diagonal), we found inconsistent results between lower and higher termites (Supp Table 3 [online only]). The habitats of lower termite species were quite different from each other. The niches of most lower termite species could be differentiated by one or more environmental factors (Supp Table 3 [online only]). However, the climatic and geographic data of collection sites between higher termite species or between higher and lower termites were not always different. We speculated that the different food sources between lower and higher termites or within higher termites is the major factor for their niche partitioning. On the other hand, the lower termite has similar food sources, and climatic and geographic factors are perhaps more significant for niche partitioning.

On a global scale, the distribution of termites is restricted by low temperature and low precipitation. In the current study, temperature and precipitation were also the two most influential environmental factors for their niche partitioning (Fig. 3). Termite species of the three families all showed the dry and wet habitat patterns. In addition to environmental factors, the interspecific competition was considered an important factor for termite distribution (Levings and Adams 1984, Jones and Trosset 1991, Li et al. 2010), but most evidence was based on laboratory experiments. In the current study, the distribution of the three pairs of congeneric species provided us with field data to test if interspecific competition is an important factor for termite niche partitioning. For the two *Nasutitermes* spp., no environmental factor of their collection sites was significantly different (Table 4), but they were found together only at four locations. A similar situation was observed in the two *Glyptotermes* spp. that were collected only once at the same location. The interspecific competition between these congeneric species may affect their distribution. On the other hand, the two *Coptotermes* spp. had significantly different environmental niches (Table 4). The global distribution of the two *Coptotermes* spp. is distinctly different. *C. gestroi* is found in the tropics but *C. formosanus* occurs in warm temperate areas. Their current sympatric distributions including South Taiwan, South Florida, and Hawaii represent recent introductions on the part of one or both species (Weesner 1965, Scheffrahn and Su 2005, Li et al. 2009b). The current study shows the two species are found in significantly different environments, which indicates that the interspecific competition may not play an important role for their niche segregation, as previously predicted by laboratory experiments (Li et al. 2010).

Studies of termite functional diversity provide an insight into plant decomposition of an ecosystem because termites require stable and large amounts of cellulosic materials to support the long-living colony with numerous individuals. In the current study, we discovered three termite assemblage patterns, 1) termite species niche capacity is similar in each 100-m-diameter scope of an ecosystem, 2) each landcovering type provides a niche for the all three families evenly, and 3) termite species of the three termite families can be divided into two distinct groups with one preferring dry and the other preferring wet habitats. Further studies on food source composition and interspecific competition would provide a better understanding of niche partitioning of these termites in the ecosystem.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

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