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Termite transects from Buton Island, Sulawesi, have a low diversity compared with Sundaland sites

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Abstract

We used a standardised transect method to compare lowland forest termite assemblages in Buton Island, Sulawesi, with transects in Sundaland. The four Buton transects were extremely depauperate with species density ranging from 1 to 6 species, which is around 10% of the species density in 11 described Sundaland transects. Soil-feeding species were absent from the Buton transects but represent some 43% of species in the Sundaland transects. The Buton transects have relatively high soil pH (6.7–7.9), which may be associated with depauperate termite assemblages. Most termite genera recorded in Sulawesi are wood nesters that can raft in floating wood, which is probably how they arrived in Sulawesi. The Macrotermitinae (fungus-growers) do not raft and probably flew across serendipitously. Geographic isolation, both on Buton and in Sulawesi more generally, and Buton's underlying geology causing high soil pH, may account for the near-absence of soil-nesters and soil-feeders, none of which are known to raft.

The biogeographical area of Wallacea consists of a group of islands in the middle of the Indonesian archipelago, the largest of which is Sulawesi. Wallacea is recognised as a global biodiversity hotspot with high levels of endemism (Myers *et al.* 2000). It is separated by deep water from the Asian Sunda continental shelf to the West, and from the Australian Sahul continental shelf to the East and South. Sulawesi is geologically complex, consisting of diverse rock types including ultramafics, and soils which have relatively high pHs (Smith & Silver 1991).

Termites are the most important invertebrate decomposers in tropical rainforests. They are ecosystem engineers and deliver important ecosystem services (Bignell & Eggleton 2000). These services include decomposition, soil carbon and nitrogen mineralisation, soil bioturbation, and water availability (Ashton *et al.* 2019, Evans *et al.* 2011). Soil formation and conditioning processes, which are also services provided by termites, can be affected by atypical soil conditions (Holt & Lepage 2000). Furthermore, termite communities are strongly affected by biogeography (Davies *et al.* 2003) and soil type (Jones *et al.* 2010). It is therefore important to study the interaction of geographical position and geological influence on the ecology and diversity of termites.

The biogeographical region of Sundaland, on the Sunda Shelf, is Peninsular Malaysia, Borneo, Sumatra, Java and their associated islands. During the Quaternary, at the Lower Glacial Maxima, land bridges connected these islands allowing species to move freely within Sundaland (Voris 2000). However, Sundaland and Wallacea have never been connected because of an ocean trench which has an average depth of 2 km (Situmorang 1982). The Wallace Line runs between the islands of Borneo and the Sulawesi in the north, and Bali and Lombok in the south (Wallace 1863). It defines the eastern boundary of the Asiatic biota, leaving Sulawesi with a predominantly Australian biotic composition (Wilson & Moss 1999). The Makassar Strait separates Borneo from Sulawesi and is 100 km wide at its narrowest point. The Makassar Strait is a physical barrier to the colonisation of termites from Sundaland to Wallacea (i.e. west to east). It is not thought that many termites have colonised east to west (Arab *et al.*, 2017; Bourguignon *et al.*, 2017; Bourguignon *et al.*, 2016)

Here we present data on termite assemblages from Buton, an island in the archipelago of South East Sulawesi. The whole archipelago has never before been sampled quantitatively for termites, using a standardised method, although faunal inventories suggest that the assemblage is depauperate (Collins, 1984, Gathorne-Hardy *et al.*, 2000a). We compare the regional termite assemblages found across Sundaland with those found in Buton (Sulawesi) using transect data, taken with the same, comparable, termite sampling method (Jones & Eggleton 2000).

Data were collected between June–July 2012 and June–August 2013 on Buton Island (longitude 123°12'E–122°33'E, latitude 005°44'S–004°21'S). Termites were sampled in four sites in Tropical Monsoon Forest (Whitten *et al.* 1987), using a standardised belt transect (100 m × 2 m) sampling protocol (Jones & Eggleton 2000). The protocol gives a measure of species density and relative abundance (number of encounters) per transect. One transect was run in each site, and six soil samples were collected along each transect to measure the pH of surface

Table 1. Species encounters in the four transects from Buton, as well as termites collected casually. No enc. = number of termite encounters. II(f) = fungus-growers, II(n) = non-fungus-growers

Species	Feeding group	T1	T2	T3	T4	Casual	No enc.
Schedorhinotermes medioobscuris	I	0	0	0	0	2	2
Hospitalitermes Sp A	II(n)	1	0	0	0	1	2
Nasutitermes Sp A	II(n)	1	0	0	17	1	19
Laccessititermes Sp A	II(n)	0	0	0	0	1	1
Bulbitermes? Sp A	II(n)	3	0	0	0	0	3
Bulbitermes? Sp B	II(n)	1	0	0	0	0	1
Microcerotermes serulla	II(n)	1	0	0	0	0	1
Odontotermes Sp A	II(f)	16	31	24	30	7	108
Total		23	31	24	47	12	137

soil (top 10 cm). Termites were identified at the Natural History Museum, London. The feeding group classification follows Donovan *et al.* (2001).

Transect 1 (T1) was in Kakanauwe Nature Reserve (122° 53’18”E, 05°10’12”S; c. 230 m a.s.l.). The site has a history of selective logging, and few big trees remain. The underlying geology is Wapulaka reef limestone, and there is little to no soil present due to the Quaternary coral protrusions. Mean soil pH was 7.9.

Transect 2 (T2) was near Bala Camp in Lambusango Forest Reserve (122°56’55”E, 05°17’44”S; c. 400 m a.s.l.). Although the area is within a Limited Production Forest, there was no evidence of recent selective logging or rattan harvesting. Soil was present in the form of lime-rich mud and clay due to the underlying Sampolakosa formations with chalks and marls. The soils were shallow with a mean pH of 6.9.

Transect 3 (T3) was near North Buton camp (123°09’24”E, 04° 41’10”S; c. 250 m a.s.l.). This site was undisturbed old growth forest, with a full canopy and trees up to 40 m in height. The soils were derived from the Tondo geological formation of clastic sediments made up of mafic and ultramafic rocks. The soils were shallow with a mean pH of 6.7.

Transect 4 (T4) was near Lapago camp, also in Lambusango Forest Reserve (122°50’49”E, 05°13’54”S; c. 225 m a.s.l.). The site had a history of selective logging. Some tall trees remain and there were gaps in the canopy. The soils were deeper than the other three sites, with a deep litter layer, and mean soil pH of 6.8. The soils were again predominantly limestone.

The results (Table 1; Figure 1) show that the termite assemblages have a distinctly lower species density (mean = 2.5 species, range = 1 to 6) compared with assemblages in Sundaland forest on non-ultramafic soils (species density mean = 29.9 species, range: 23 to 35). Relative abundance is also lower on Buton (mean = 31.3 encounters, range = 23 to 47) compared with the same Sundaland transects (mean = 93.3 encounters, range = 68 to 110) (Figure 1). The exceptions are the four Java transects, which have intermediate levels of species richness (Figure 1), probably because they are coastal forests (Gathorne-Hardy *et al.* 2000b). The Buton transects are most similar to the four ultramafic transects on Borneo (Figure 1), with mean species density = 8.5 species (range: 7 to 10) and mean relative abundance = 20 encounters (range: 18 to 23).

Functional diversity of the Buton assemblages was also greatly reduced, with 75% of the relative abundance being represented by one species of *Odontotermes* sp. (group-II fungus-growing wood-feeder), 24% being represented by non-fungus-growing group-II wood-feeders (*Microcerotermes serrula*, *Nasutitermes* sp. and two species of *Bulbitermes*) and a single encounter with *Hospitalitermes* sp. (group-II micro-epiphyte-feeder). This is in sharp contrast to the Sundaland transects (excluding ultramafic transects and the Java transects), which have a mean of 43% (range: 25% to 61%) group III and group IV soil-feeding species (Figure 1).

Some of the shortfall may be due to the transect method not sampling arboreal termites. This would be especially true of the Kalotermitidae, which feed and nest on dead branches still attached to trees in the canopy. However, we have no data on kalotermitid distribution in any of the sites (Sundaland or Sulawesi) and so we cannot say anything about these inaccessible groups. There have been two previous published accounts of termites from Sulawesi (Kemner 1934; Gathorne-Hardy *et al.* 2000a), and these data, albeit limited and collected casually, also suggests that the island has a relatively low termite diversity. In total, only 41 species from 18 genera are known from Sulawesi, and only one species is a soil-feeder (Gathorne-Hardy *et al.* 2000a). In contrast, at least 226 described species from 48 genera are known from Sundaland, of which 27% are group III or group IV soil-feeders. (Gathorne-Hardy, 2004). Mark Collins, a very experienced termite collector, carried out intensive sampling in lowland rainforest in Dumoga-Bone National Park, North Sulawesi, and found only 22 species (see Gathorne-Hardy *et al.* 2000a). However, in a similar sampling programme in Mulu National Park in Borneo, Collins (1984) found 59 species in the lowland forest. In other intensive sampling programmes in lowland forest in Sundaland, 95 species were found in Danum Valley in Sabah, Malaysian Borneo, and 80 species were

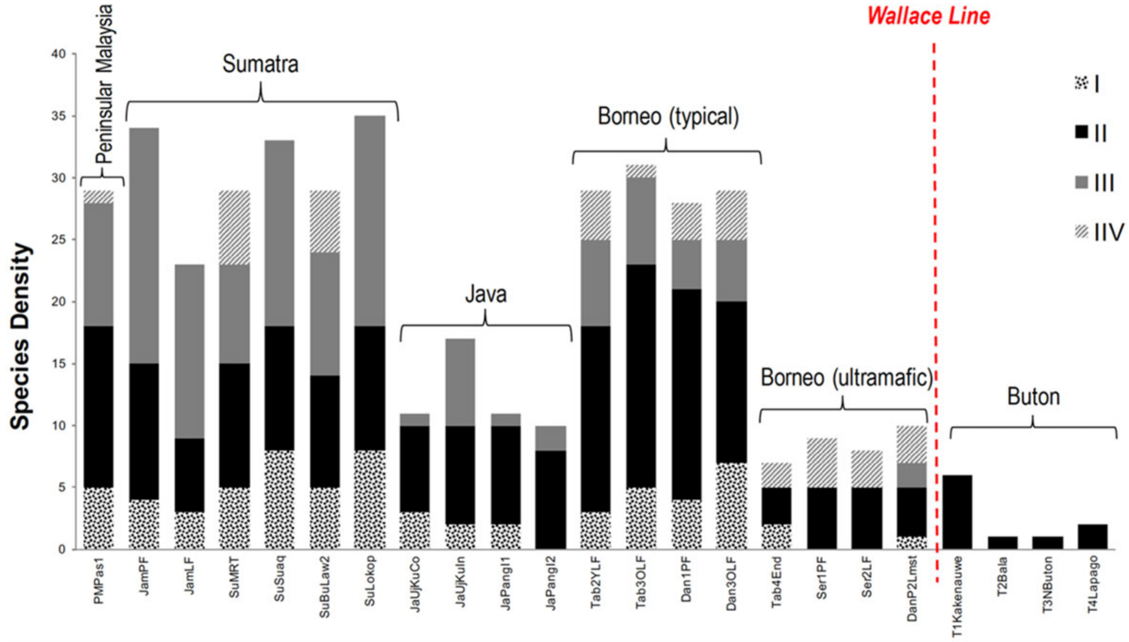

Figure 1. Termite species density from transect in lowland forest across Sundaland and Sulawesi. Species density from each site is categorised into four feeding groups (Donovan *et al.* 2001). Tab4End, Ser1PF, SER2LF and DanP2Lmst are atypical assemblages present on ultramafic-derived soils in Borneo (Jones *et al.* 2010). Other sites codes are from Gathorne-Hardy *et al.* 2002.

found in Pasoh Forest Reserve in Peninsular Malaysia (Jones & Eggleton 2000). The transect method and these other intensive sampling programmes are designed to collect all feeding groups from all terrestrial microhabitats.

What factors are responsible for the low termite species density and the absence of soil-feeding termites seen on Sulawesi? These data are all from an island off the coast of Sulawesi, so island size and isolation may contribute to the low diversity found here, although this effect may be attenuated by Buton being a continental rather than a volcanic island and having most of the biotic elements found in mainland Sulawesi. (Michaux, 2010)

Generally, in order to colonise the Sulawesi region from Borneo, termites must disperse either by rafting in wood or they must fly over the 100-km-wide Makassar Strait. The chance of rafting to Sulawesi is reduced by the strong southbound oceanic current that passes through the Makassar Strait, called the Indonesian Throughflow, which is known to carry dead trees that are washed out of rivers on the East coast of Borneo southwards passed Sulawesi (Susanto *et al.* 2012). However, of the 18 termite genera listed from Sulawesi (Gathorne-Hardy *et al.* 2000a), 16 nest in wood, and most of those are widely distributed globally and are known to raft in floating wood (Abe 1984, Gathorne-Hardy *et al.* 2000b). The soil-nesting genus *Pericapritermes* has been recorded in Sulawesi, but it has been observed nesting in dead wood (Gathorne-Hardy *et al.* 2000a), so it may also have the ability to raft.

Dispersal from Borneo to Sulawesi by flying is difficult because the alates (winged reproductives) of most termite species are poor fliers and usually land within a few hundreds of metres of their natal nest (Abe 1984, Gathorne-Hardy *et al.* 2000b). Longer distances tend to be achieved only when alates are carried by strong air currents. However, the wind patterns associated with the Indonesian Throughflow are more likely to carry any alates south rather than east towards Sulawesi. This may account for the near-absence of soil-nesting termites recorded from Sulawesi, as rafting is not a possibility for these species. The one exception is the obligate soil-nesting species *Odontotermes* sp. which dominates all the Buton transects. This species may have flown from Borneo, as African *Microtermes* are known to have flown 300 km across the Mozambique Channel to colonise Madagascar (Aanen & Eggleton 2005; Nobre *et al.*, 2009).

Termites in Sundaland have been well studied (e.g. Gathorne-Hardy, 2004). In Sundaland, termites are most abundant and diverse in lowland forests (< 400 m elevation; Gathorne-Hardy *et al.* 2001) on soils with relatively low pH (range: 3.7 to 4.7; Jones *et al.* 2010). However, forests on ultramafic-derived soils in Borneo, which have higher soil pH (range: 5.4 to 6.4) and higher concentrations of Ca, Mg, N, Cr, Co, Cu and Zn, have termite assemblages with low species density (< 35%), low relative abundance (< 30%) and a near-absence of soil-feeding species compared with assemblages in forests in Borneo on non-ultramafic soils (Jones *et al.* 2010). They had an extremely low diversity of Rhinotermitidae and the non-fungus-growing taxa, which are mostly wood-feeders (Jones *et al.* 2010). Their low diversity in these sites is not due to any restrictions on dispersal by flight but may be associated with the soil conditions. These sites also have high concentrations of metals, and therefore three possible mechanisms may explain the depauperate assemblages on these ultramafic soils: 1) high soil pH (as shown in other studies, (Lavelle *et al.* 1995). disrupting termite gut physiology; 2) metal toxicity; and 3) microbial interactions with metals (Jones *et al.* 2010). The soil pH at the four Buton sites (range: pH 6.7 to 7.9) is considerably higher than the soil pH at the four ultramafic transects (range: 5.4 to 6.4) (Jones *et al.* 2010), suggesting that the negative impact of higher soil pH on termites may be even greater in Sulawesi. Therefore, those termite groups that are vulnerable to high soil pH and that do disperse from Borneo across the Makassar Strait by rafting or flight may be less likely to survive due to the effect of the higher soil pH.

Overall, we conclude that the low species diversity and functional diversity of the termite fauna of Buton is caused by a combination of a number of factors: particularly biogeographical position and soil chemistry. First, dispersal across the Wallace Line is difficult for non-rafting termites due to the unlikely chance of alates flying 100 km across the Makassar Strait. Second, termites that do arrive in Sulawesi may have reduced chances of colony establishment and survival due to the high pH of the soils in many parts of Sulawesi. To quantify the impact of these factors on termite diversity, sampling at other sites in Sulawesi is recommended, especially in forests with lower soil pH.

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