Termitaria enhance soil and forest diversity in Deciduous Dipterocarp Forest, Northern Thailand

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Abstract

We characterised the soils and vegetation in 15 sets of four quadrats on and around mounds of *Macrotermes annandalei* (Isoptera, Macrotermitinae) on a plain of deep dystric clay over limestone in Deciduous Dipterocarp Forest in Northern Thailand. Termites have excavated the mounds from the deep calcareous substrate. The mound soils have darker subsoils, larger contents of clays and exchangeable cations, and higher pH values than the surrounding dystric clay loams. The thickets on the mounds are visually different from the surrounding Deciduous Dipterocarp Forest. They have few dipterocarps and are floristically similar to the regionally important Mixed Deciduous Forest. The clear visual differences are confirmed by floristic similarity, cluster, and canonical correspondence analyses for each of the tree, sapling and seedling size classes. The differences between the mound clays and surrounding red clay loams and the associations between soil and forest types are confirmed by '*t* tests' and the significant correlations of the soil base status with the main floristic axis of the canonical correspondence analyses. Soil variability due to termites and other agents of pedoturbation can significantly contribute to short-range floristic and structural diversity in some dry tropical forests.

Introduction

Spatial and temporal variations in the availability of abiotic resources, such as light, water, nutrients, root aeration and site stability, contribute to the high floristic and structural diversity of tropical forests. The soils of many tropical forests are intensively leached and substantially depleted of labile nutrients, especially P and the exchangeable cationic meso-nutrients K, Ca and Mg (Richards, 1996). Some of the variability of nutrient availability in tropical forest soils is systematically associated with lithological heterogeneity in soil parent materials (Baillie *et al.* 1987; Weemstra *et al.* 2020), and with slope position in catenary toposequences (Borden *et al.* 2020).

Soils are complex ecosystems, and host numerous and diverse fauna, the activities of which affect the local distributions and availabilities of abiotic resources. They spatially re-arrange the soil's solid components and modify pore systems, water retention and release characteristics, and the forms and availabilities of nutrients (Wood, 1988; Lee & Wood, 1971; Barros *et al.* 2001). The most important and widespread agents of faunal pedoturbation in tropical forests are earthworms (Goodnight & Goodnight,1956; Nemeth & Herrera, 1982) and termites (Nye, 1955; Gokhale *et al.* 1958; Donovan *et al.* 2001; Roose-Amsaleg *et al.* 2005; Tuma *et al.* 2019).

Termites considerably modify local soil patterns; both physically by the excavation of subsoil materials and construction of termitaria, and chemically by the concentration of nutrients through foraging and processing of litter from the surrounding forest. Termitaria are complex structures, and can include subterranean birth chambers for queens, fungal gardens and combs (Yamada *et al.* 2005); nurseries; and elaborate vanes and galleries for ventilation and thermoregulation. Above-ground, there are mounds and chimneys to enhance ventilation and also roofed protective walkways for foraging workers. The mounds and walkways are constructed from excavated soil particles and cemented with mixtures of saliva and clay (Lee & Wood, 1971; Jungerius *et al.* 1999; Korb, 2003). They are harder than the surrounding soils (Omo-Malaka, 1977; Jouquet *et al.* 2004), and have different capacities to adsorb, store and shed water (Mando *et al.* 1996; Konate *et al.* 1999; Sarr *et al.* 2001). Termites forage for litter from the

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surrounding forest, and termitaria tend to accumulate harvested nutrients, but are not as enriched with C, N and P as earthworm casts (Baillie *et al.* 2018). They usually have substantially higher pH, and exchangeable and total contents of cationic nutrients, especially Ca, than the surrounding soils (Arshad, 1981; Davies & Baillie, 1988).

Some savanna termites construct substantial towers with basal diameters of greater than 10 m. Their mounds often carry structurally distinct and floristically diverse vegetation, giving mosaics of dense wooded thickets in matrices of grassland or open woodland (Glover *et al.* 1964; Goodland, 1965; Dean *et al.* 1999; Holdo & McDowell, 2004; Loveridge & Moe, 2004; Joseph *et al.* 2013).Termite mounds in tropical forests are generally smaller than those in savannas, but they can still significantly increase short-range soil heterogeneity (Pendleton, 1941, 1942; Arshad, 1981; Davies & Baillie, 1988; Donovan *et al.* 2001; Obi & Ogununle, 2009).

The long-term forest ecological research plot in Deciduous Dipterocarp Forest at Mae Ping in northern Thailand is located on a colluvial plain of deep dystric red clay loams that is dotted with termitaria, the surface mounds of which range in diameter from 0.1 to 10 m. The larger mounds support moderately dense thickets, which are visually different from the more open surrounding forest. We here examine the extent to which the spatial variations in floristics and structures of the vegetation are associated with termitogenic soil heterogeneity (Beaudrot *et al.* 2011). The study attempts to clarify and quantify fortuitously observed phenomena, rather than test pre-ordained hypotheses.

Methods

Study site

The study site is the eastern 8 ha half of the 16 ha Mae Ping forest ecology plot, which is located in the Mae Ping National Park, Li district, Lamphun province, Northern Thailand, at 17° 37' N, 98° 50' E. The nearest meteorological station is at the Bhumibol Dam (17° 15' N., 98° 58' E), about 10 km to the south (Fig. 1), where the mean annual rainfall is about 1000 mm, with a marked dry season from December to May. Mean monthly temperatures are lowest in November-December, at about 22 – 24° C, and peak at about 30° C towards the end of the dry season in March – April (DNPWP, 2008).

The plot is located on the Shan-Thai terrane, which is a crustal segment that rifted off the Australasian part of Gondwanaland, migrated northwards, and sutured onto the Eurasian plate during the Palaeozoic (Rhodes *et al.* 2005; Hara, *et al.* 2010). The main bedrock under the plot is Devonian-Silurian limestone with subordinate quartzitic metasediments (DMR, 1983). The plot is moderately heterogenous with respect to geology, soils and ecology (Table 1), but our study is located wholly on the colluvial plain of deep, dystric red clay loam that covers the eastern half of the plot (Fig. 2).

Deep augering shows that the red clay loam reaches to below 3 m. The nature of the termitaria indicate that it is underlain by calcareous material, presumably derived from limestone. The soils are therefore bi-sequent, with a lithological discontinuity at several metres depth.

The plain drains southwards in shallow zero-order declivities (Strahler, 1957). Infiltration is slower than that suggested by the red soil colours, and there is some surface runoff. There are ephemeral puddles of standing water during heavy rain and there are scattered patches of green lichen (Supplementary Table S1).
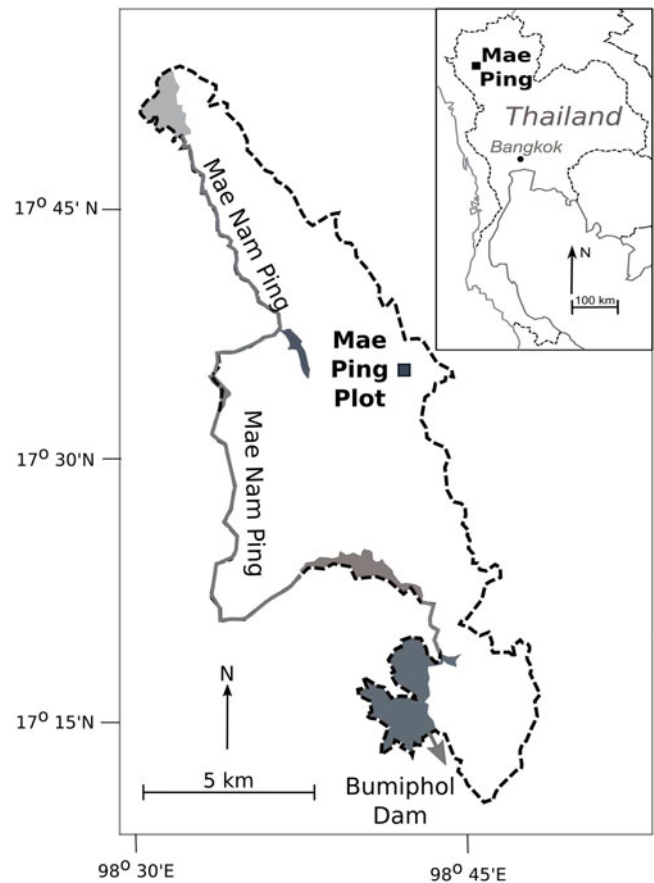

Figure 1. Location of Mae Ping Forest Ecology plot: Dashed line – Mae Ping National Park boundary Shaded – Mae Ping river, Bhumibol Dam, & other lakes; Solid square – Mae Ping Forest Ecology Plot.

Field methods

We characterised and sampled the vegetation and soils on 15 sets of four 10×10 m quadrats in the eastern 8 ha study site. Each set consisted of one quadrat on a large *Macrotermes annandalei* mound, with the other three at 10 m distance out in surrounding non-mound forest, located beyond the drip rings of the mound vegetation, and so as not to impinge on neighbouring mounds. The layout is constrained by the juxtaposition of the mounds and does not permit the characterisation of distance decay functions (Sileshi & Arshad, 2012). Tree density is higher on the mounds, and three quadrats in the surrounding forest were needed to give comparable numbers of stems in the mound and non-mound samples.

The mounds on the 8 ha study site were mapped by diameter classes of < 0.5 m, 0.5 – 1 m, and > 1 m (Fig. 2). Military caste termites were collected from each mound, preserved in 70% ethanol, and identified according to the Thailand Termite Classification (Sornuwat & Wongkhalung, 2004).

Trees with diameter at breast height (dbh = 1.3 m) > 4.5 cm were identified and measured for dbh in the 10×10 m quadrats. Saplings (height > 1.3 m, dbh < 4.5 cm) were identified in a 5 m $\times 5$ m sub-quadrat at the centre of each 10×10 m quadrat; and seedlings (height < 1.3 m) were identified in four 1 m $\times 1$ m mini-quadrats in each 10 m $\times 10$ m quadrat.

The topsoil (0–15 cm) at the centre of each quadrat was characterised in the field for Munsell colour and hand texture, and

Table 1. Land and forest types on Mae Ping 16 ha ecological research plot

| Map code (Fig. 2)	Geology	Topography	Soil	Deciduous Dipterocarp Forest variant
C	Deep colluvium	Gentle pediplain	Dominant red dystric fine loam – light clay with patches of dark calcareous clay in termite mounds	Medium canopy DDF with *Dipterocarpus tuberculatus* dominant and many *Shorea obtusa*
L	Limestone	Low hill with linear sharp fins and grikes	Bare limestone with dark eutric loam in grikes	Low-medium canopy DDF with *Shorea siamensis* dominant
M	Metargillite with subordinate quartzite	Low rise with quartz stones and few outcrops	Shallow stony dystric coarse loam	Low canopy DDF with *Dipterocarpus tuberculatus* dominant with many *Shorea obtusa* & some *Dipterocarpus obtusifolia*
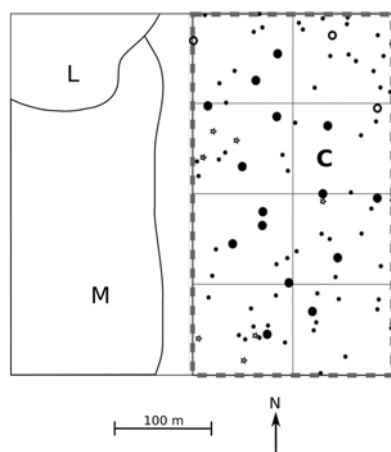
Figure 2. Land types, termite mounds, and sampling in the Mae Ping plot Dashed grey line – Termite study area C – Colluvial plain of deep, dystric red loam with dark calcareous clay on termite mounds L – Shallow eutric loam on limestone fins M – Shallow dystric loam on metargillite hillocks Large circle – Mound > 1 m diameter: Filled are sampled; open are unsampled Unsampled smaller mounds: Small circle 0.5 – 1 m diameter; Star < 0.5 m diameter.

tested for free carbonates with HCl. A disturbed topsoil sample from each quadrat was collected for analysis, with the samples from the three non-mound quadrats in each set bulked for analysis. Undisturbed cores of 100 ml volume were taken from 0 to 10 cm depth at the centre of each 10m x 10m quadrat for further physical analyses.

Soil analyses

Chemical
The disturbed topsoil samples were analysed at the Soil Analysis Laboratory, Department of Soil Science, Kasetsart University, Bangkok, by the following methods: (1) pH electrometrically in a 1:1 suspension of fresh soil in water; (2) organic C by Walkley-Black acid dichromate oxidation; (3) total N by micro-Kjeldahl distillation; (4) available P by Bray and Kurtz extraction and colourimetric assay; (5) exchangeable cations by leaching with 1M neutral ammonium acetate and assay by atomic adsorption spectrometry (AAS); (6) cation exchange capacity (CEC) by displacement of the sorbed NH_4^+ with excess NaCl, followed by distillation. Total cations and total P were extracted by digestion with concentrated sulphuric acid and a selenium catalyst, and assayed by AAS (cations) or colourimetry (P). (7) Total

micronutrients were extracted by digestion with nitric and perchloric acids and assayed by AAS. (8)

Physical
Soil particle size distributions in the disturbed samples were determined by hydrometer after organic matter removal with hydrogen peroxide, carbonate removal with HCl, and clay dispersion with sodium hexametaphosphate (Hesse, 1955).

The undisturbed core samples were analysed at the Department of Silviculture, Faculty of Forestry, Kasetsart University, Bangkok, for: (1) moisture content (MC) by loss in core weight after oven drying; (2) dry bulk density (BD) from core weight after drying; (3) particle density (PD) by pycnometer; (4) porosity is derived from the bulk and particle densities (i.e. porosity % = 100 (1 – (BD/PD)); and (5) saturated hydraulic conductivity (Ks).

Data analyses

Each species was characterised separately in each of the three size classes for: (1) relative frequency, as the percentage of quadrats on which the species occurs; (2) relative density, as the number of stems of a species as a percentage of the total stems of all species; and (3) relative basal area of trees, as the species basal area as a percentage of the total basal area of all tree species. A species' importance value index (IVI) was estimated as the sum of (relative frequency + relative density + relative basal area) (Curtis & McIntosh, 1951). The Sorensen index (W) of floristic similarity between quadrats A and B was estimated from the number of shared species relative to the total number of species, i.e. 2c/(a + b + 2c), where 'a' is the number of species found only on quadrat A, 'b' is the number of species found only on quadrat B, and 'c' is the number of species common to both (Sorensen, 1948). Species diversity was characterised by the Shannon-Wiener index, H (= Σ [(pi × ln(pi)] where *pi* is the relative density for each species). Floristic cluster analysis of quadrats was based on the Sorenson similarity index (Kent & Coker, 1994). Canonical Correspondence Analysis (CCA) segregated quadrats on floristic composition and also clarified environmental relationships (McCune & Mefford, 1999).

The laboratory analyses of the mound and non-mound topsoils were compared by 't tests'. The associations between quadrat floristics and topsoil properties were tested by Pearson and rank correlations of the soil variables with the main floristic CCA axis for each size class(Palmer, 1993; ter Braak & Verdonschot, 1993; Uurito et al. 2017). The stoichiometries of the exchangeable cations and pH were compared visually in Alvim (1978) roses.

Table 2. Termites in mounds on Mae Ping 8 ha study site

Termite species	Mound diameter (m)			Total
	<0.5	0.5 – 1	>1	
Macrotermes annandalei	7	56	18	81
Globitermes sulphureus	0	4	0	4
None (abandoned)_	0	4	0	4
Total	7	64	18	89

Table 3. Forest structure at Mae Ping

	Stems/ha by size class		
		Trees	
	Saplings	Small trees	Large trees
	Dbh < 4.5 cm	Dbh 4.5 – 10 cm	Dbh > 10 cm
Non-mound quadrats	246	105	187
Mound quadrats	980	107	94

Where Dbh = diameter at breast height (1.3 m).

Results

Termite mounds

We mapped and measured 89 termite mounds in the study area (Fig. 2), giving an approximate mean density of 11/ha (Table 2). This is equivalent to a mean inter-mound spacing of about 30 m. The actual spacing is variable and Fig. 2 shows that distances between adjacent large mounds range from 20 to 70 m. About three quarters (64) of the mounds were of intermediate size (diameter 0.5 – 1 m). Soldiers of the fungivorous species *Macrotermes annandalei* (Macrotermitinae) (Davies, 1997; Hyodo *et al.* 2003) were found in 81 mounds, including all 18 in the largest diameter class (>1 m).

Soldiers of *Globitermes sulphureus* (Amitermitinae) (Yamada *et al.* 2003, 2004) were found in four mounds of intermediate size. No termites were observed in four apparently abandoned mounds of intermediate size (Table 2).

The mounds of *Macrotermes annandalei* account for about 96% of the total soil volume excavated (Tuma *et al.* 2019). They have irregular profiles, with diameters of up to 10 m and heights of up to 2.5 m (Fig. 3). The few *Globitermes sulphureus* mounds are roughly cylindrical and do not attain great size, ranging in diameter and height from 40 cm to 1 m They are dome-topped and have near-vertical sides, which are not readily colonised by plants. They are formed of red clay loam that appears to have been excavated from the upper subsoil (Supplementary Figure S1).

Vegetation

The density of large trees in the non-mound forest is moderate (Table 3). The canopy, at heights of 20 – 30 m, is almost closed in the wet season, but there is sufficient light at ground level to allow some cover of grasses, forbs, and a few sedges. The mound vegetation forms lower and denser thickets with a trebling of sapling density compared to the non-mound forest and an increase in the ratio of small: large trees from 0.56 to 1.14 (Table 3 and Fig. 3). The structural differences are paralleled in the floristic

composition. The commonest tree species in the non-mound forest is *Dipterocarpus tuberculatus,* with *Shorea obtusa* subordinate. Frequent non-dipterocarp trees include *Aporosa villosa, Quercus kerrii, Strychnos nux-blanda, Buchanania lanzan,* and *Symplocos racemosa.* The composition of the seedlings is similar, and is dominated by the same dipterocarps, but there is a greater range of non-dipterocarps (Table 4a). The intermediate sapling class contains some dipterocarps, similar to those in the trees, but is dominated by the non-dipterocarps *Anacolosa ilicoides* and *Dillenia obovata.*

The floristic composition of the vegetation on the termite mounds differs distinctly from the surrounding forest, for all size classes. There are few dipterocarps, and the common tree species include *Morinda coreia, Ziziphus cambodiana, Schleichera oleosa, Walsura villosa,* and *Siphonodon celastrineus* (Table 4b; Supplementary Table S2b).

The diversity and similarity indices (Table 5) confirm the floristic differences between the mound and non-mound vegetation, with few shared species and little similarity between the groups, especially for the trees. The differences are also clearest for the trees in the cluster analyses (Fig. 4a–4c). There are two main clusters for each of the non-mound and mound quadrats. The dipterocarps *Dipterocarpus tuberculatus* and *Shorea obtusa* dominate in both of the non-mound clusters, and these are differentiated on the non-dipterocarps. The commonest non-dipterocarps in the quadrats of cluster 1 are *Aporosa villosa, Quercus kerrii* and *Strychnos nux-blanda,* whereas *Symplocos racemosa* and *Dalbergia dongnaiensis* are important in cluster 2.

Frequent tree species in the quadrats of cluster 1 for the mound quadrats include *Morinda coreia, Antidesma ghaesembilla, Ziziphus cambodiana, Cassia fistula,* and *Grewia eriocarpa*., whereas *Schleichera oleosa, Walsura villosa, Siphonodon celastrineus,* and *Xantolis burmanica* are common trees in mound cluster 2. The separation between the non-mound and mound quadrats is complete for the seedlings but is less pronounced than for the larger size classes (Fig. 4c). The non-mound saplings are dipterocarp-poor and more diverse than the other size classes, but the sapling analysis still separates the two formations, with four clusters for the mound and five for the non-mound quadrats (Fig. 4b).

The Canonical Correspondence Analyses (CCA) confirms the clear floristic separation of mound and non-mound vegetation. The CCA patterns in the non-mound quadrats are similar for the trees and seedlings, with tight clustering on both axes (Fig. 5a & 5c). The wider spread for the saplings on both axes confirms that this size class is more diverse (Fig. 5b). The greater diversity of the mound vegetation gives wider spread on both axes.

Soils

The non-mound topsoils are brownish red clay loams with compound blocky structures breaking to crumb (Supplementary Table S1). The subsoils are bright red, friable light clays, at least 3.5 m deep. There are no mottles in the subsoils, but convoluted layers of brittle black manganiferous angular concretions occur at several depths. These soils are moderately acid and dystric, with base saturations in the topsoils of almost 50%, but the subsoils are more acid, with base saturations of less than 35%. All of the non-mound soils are inert to HCl and contain no free carbonates.

The mound soils are darker, with yellower Munsell hues, and lower chromas and values. Some contain enough free carbonates to effervesce slightly with HCl. They are clay textured throughout,

Figure 3. *Macrotermes annandalei* mound in Deciduous Dipterocarp Forest, Mae Ping.

crack more readily, and have blockier structures than the non-mound soils. Their subsoils are also darker and yellower, with predominant Munsell hues of 5YR to 10YR compared with 10R and 2.5 YR for the non-mound soils. However, organic darkening gives both groups overlapping ranges of brownish topsoil colours.

Chemically, the non-mound and mound topsoils differ little with respect to organic C and both available and total P (Table 6). The mound topsoils contain significantly more total N, but the difference is not substantial. However, the two sets differ substantially and significantly with respect to base status. pH values are at least a unit (i.e. ten-fold) higher in the mound topsoils, and this is accompanied by a highly significant doubling of base saturation. All of the main exchangeable cations are very significantly higher in the mounds, with K and Ca approximately quadrupled, and Mg and CEC doubled (Table 6). The stoichiometries of exchangeable cations are depicted in roses (Fig. 6). These are based on the idea of wind roses, and show nutrient proportions as well as quantities (Alvim, 1978). Comparison of the sizes of the polygons confirms the substantially larger contents of exchangeable cations in the mound soils. The two polygons are of different shape, the comparison of which shows how the proportions of cations vary between the sets. Enrichment of the mound soils with

Ca widens the Ca:Mg ratio from 2 to 4.5 (Table 6), but this is not thought to be sufficient to induce Mg deficiency (Osemwota *et al.* 2007; Baillie *et al.* 2018).

Some cations also show marked differences in their total, as well as exchangeable, contents (Table 6). Total Mg and Ca are significantly higher in the mound soils. Mean total Fe is substantially higher in the mound soils, but the high variability of Fe in the non-mound soils renders the difference non-significant. Totals of the micro-nutrients Zn and Cu are significantly higher in the mound soils, but total Mn contents are almost identical.

The laboratory soil particle size distributions confirm the field textures, with significantly higher clay and lower sand in the mound topsoils. The mound topsoils have significantly lower mean particle densities, but significantly higher bulk densities. This results in significantly lower overall porosities and contributes to significantly lower saturated hydraulic conductivities (Table 6).

Soil – forest associations

The differences between the termite mounds and the surrounding forest are visually clear for both vegetation and soils. The

Table 4a. Main species in quadrats in non-mound forest, Mae Ping

Trees			Saplings			Seedlings		
Species	Frequency	IVI	Species	Frequency	IVI	Species	Frequency	IVI
Dipterocarpus tuberculatus	97	110.25	*Quercus kerrii*	12	39.88	*Dipterocarpus tuberculatus*	160	47.18
Shorea obtuse	58	55.03	*Anacolosa ilicoides*	11	33.76	*Shorea obtuse*	90	24.72
Aporosa villosa	36	29.82	*Symplocos racemosa*	10	33.25	*Symplocos racemosa*	80	23.97
Quercus kerrii	19	21.05	*Aporosa villosa*	5	21.35	*Dillenia obovata*	61	19.57
Strychnos nux-blanda	18	15.46	*Dillenia obovata*	5	20.79	*Gluta usitata*	47	11.21
Buchanania lanzan	11	10.63	*Terminalia chebula*	3	15.60	*Lophopetalum wallichii*	40	10.13
Symplocos racemosa	13	9.64	*Glocidion eriocarpum*	5	14.44	*Anacolosa ilicoides*	21	8.08
Dalbergia dongnaiensis	5	6.85	*Albizia odoratissima*	3	13.61	*Quercus kerrii*	23	7.61
Terminalia chebula	5	5.86	*Terminalia alata*	5	10.69	*Ochna interregima*	29	7.57
Lophopetalum wallichii	4	5.27	*Strychnos nux-vomica*	2	8.46	*Strychnos nux-vomica*	15	5.33
Terminalia alata	4	4.42	Unknown A	4	7.56	*Vaccinium sprengelii*	21	4.23
Bridelia retusa	3	3.96	*Buchanania lanzan*	1	6.97	*Vitex penduncularis*	17	3.88
Syzgium odoratum	3	3.34	*Wendlandia ternifolia*	3	6.34	Unknown D	9	2.43
Dioecescis erythroclada	3	2.98	*Dalbergia dongnaiensis*	2	6.26	*Dalbergia dongnaiensis*	2	2.40
Wendlandia ternifolia	2	2.63	*Crabidendron stellatum*	1	5.85	*Symplocos racemosa*	12	2.18

Table 4b. Main species in quadrats on termite mounds, Mae Ping

Trees			Saplings			Seedlings		
Species	Frequency	IVI	Species	Frequency	IVI	Species	Frequency	IVI
Walsura villosa	20	31.27	*Polyalthia cerasoides*	24	33.96	*Polyalthia cerasoides*	106	22.12
Terminalia alata	19	29.99	*Cassia fistula*	14	31.94	*Diospyros montana*	125	20.74
Schleichera oleosa	17	39.09	*Siphonodon celastrineus*	7	19.83	*Walsura villosa*	75	17.92
Morinda coreia	15	24.67	*Xantolis burmanica*	8	19.64	*Schleichera oleosa*	73	16.10
Lannea coromandelica	12	10.78	*Schleichera oleosa*	8	17.43	*Vagueria pubescens*	60	11.20
Antidesma ghaesembilla	9	14.84	*Grewia eriocarpa*	4	13.27	*Catunaregum spathulifolia*	40	8.31
Siphonodon celastrineus	7	9.09	*Walsura villosa*	3	11.17	*Dalbergia dongnaiensis*	37	6.45
Tamilnadia uliginosa	7	8.89	*Albizia odoratissima*	6	10.19	*Dalbergia cultrata*	40	5.90
Bridelia retusa	7	8.27	*Diospyros coaetanea*	4	8.76	*Melientha suavis*	26	5.72
Cassia fistula	7	6.53	*Lannea coromandelica*	4	8.23	*Tamilnadia uliginosa*	26	5.61
Ziziphus cambodiana	6	8.14	*Catunaregum spathulifolia*	3	8.17	*Vitex canescens*	27	5.50
Strychnos nux-blanda	6	7.51	*Dalbergia ovata*	5	8.00	*Antidesma ghaesembilla*	31	5.15
Grewia eriocarpa	5	6.35	*Diospyros montana*	7	7.04	*Ochna integerregima*	26	4.88
Vagueria pubescens	5	4.30	*Litsea grandis*	4	7.01	*Cassia fistula*	18	3.75
Dipterocarpus tuberculatus	4	14.01	*Croton hutchinsonianus*	5	6.98	*Terminalia alata*	19	3.69

Table 5. Floristic diversity and similarity, Mae Ping

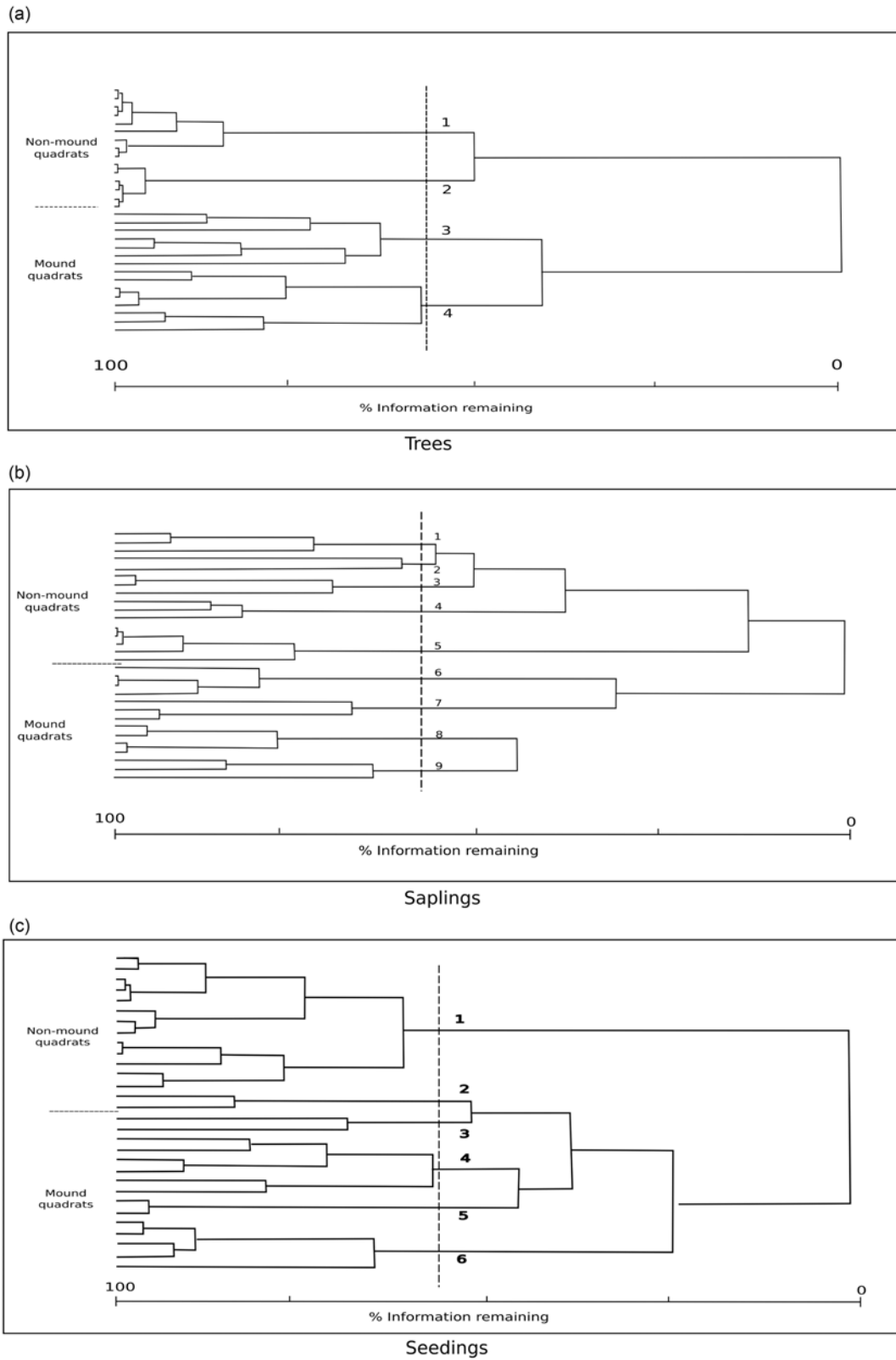|	Number of species			Shannon- Wiener Diversity index		
	Non-mound	Mound	Species shared	Non-mound	Mound	Similarity index
Tree	24	44	7	1.62 ± 0.44	2.04 ± 0.26	20.59
Sapling	29	28	8	1.05 ± 0.58	1.16 ± 0629	28.07
Seedling	29	46	13	1.65 ± 0.39	1.66 ± 0.30	32.91

Figure 4. Floristic cluster analyses of quadrats at Mae Ping (a) Trees (b) Saplings (c) Seedlings.

Table 6. Comparison of non-mound and mound topsoils

	Non-mound (mean ± SD)	Mound (mean ± SD)	't test' of difference
(a) Chemical			
pH	5.3 ± 0.2	6.4 ± 0.2	***
Organic carbon (%)	2.8 ± 0.7	2.8 ± 0.6	ns
Available. P (mg kg^{-1})	5.9 ± 4.5	5.8 ± 3.4	ns
Exch. K (cmol$^+$.kg^{-1})	0.3 ± 0.1	1.3 ± 0.4	***
Exch. Ca (cmol$^+$.kg^{-1})	3.1 ± 1.4	13.2 ± 4.3	***
Exch. Mg (cmol$^+$.kg^{-1})	1.5 ± 0.4	3.0 ± 0.7	***
CEC. (cmol$^+$.kg^{-1})	10.8 ± 2.4	19.1 ± 2.5	***
Total exchangeable bases	4.9 ± 1.8	17.3 ± 4.3	***
Base saturation (%)	44.9 ± 8.4	87.1 ± 19.7	***
Total N (%)	0.1 ± 0.02	0.1 ± 0.02	***
Total P (%)	0.05 ± 0.01	0.05 ± 0.01	ns
Total K (%)	0.91 ± 1.0	1.0 ± 0.5	ns
Total Ca (%)	0.1 ± 0.2	0.2 ± 0.2	*
Total Mg (%)	0.1 ± 0.05	0.2 ± 0.05	***
Total Zn (mg kg^{-1})	64.6 ± 27.9	110.6 ± 33.9	***
Total Mn (mg kg^{-1})	1319 ± 1578	1297 ± 1309	ns
Total Fe (mg kg^{-1})	19691 ± 5393	29791 ± 911	ns
Total Cu (mg kg^{-1})	18.7 ± 5.8	30.9 ± 12.2	**
Sand (%)	53.7 ± 7.0	39.5 ± 2.6	***
Silt (%)	30.3 ± 5.5	27.5 ± 3.4	ns
Clay (%)	16.0 ± 3.2	33.0 ± 3.9	***
Bulk density (g/cm3)	1.3 ± 0.1	1.3 ± 0.1	*
Particle density (g/cm3)	2.7 ± 0.1	2.6 ± 0.1	**
Porosity (%)	52.7 ± 3.2	47.4 ± 4.0	***
Soil moisture (%)	18.2 ± 2.9	19.3 ± 2.3	ns
Saturated hydraulic conductivity (Ks) (cm/sec)	0.04 ± 0.03	0.02 ± 0.01	*

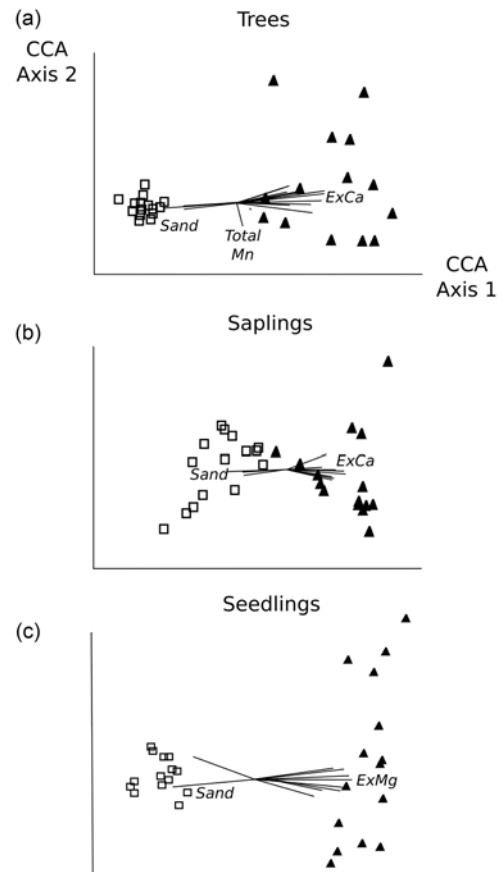***$p < 0.001$;**$p < 0.01$;*$p < 0.05$; ns $p > 0.05$.

Figure 5. Canonical Correspondence Analyses (CCA) with soil correlations at Mae Ping (a) Trees (b) Saplings (c) Seedlings Open rectangle – Quadrat in non-mound forest; Filled triangle – Quadrat on termite mound; Lines – Pearson correlations of topsoil variable with CCA axis 1.

associations between soils and vegetation are confirmed by the soil '*t* tests' (Table 6) and by the canonical correspondence (CCA) analyses (Fig. 5a–5c). The soil base status variables are correlated with CCA Axis 1 for all three size classes (Table 7). Total manganese differs in that it is aligned subparallel to Axis 2 in the tree CCA (Fig. 5a). This accords with the almost identical mean total Mn values for the two groups and the non-significant '*t* test' for Mn (Table 6).

Discussion

Forest

The non-mound forest is Deciduous Dipterocarp Forest (DDF), a formation that is adapted to seasonal moisture stress and frequent fires. It is widespread in the drier parts of northern Thailand, Upper Myanmar and northern Kampuchea (Bunyavejchewin *et al.* 2011; Wohlfahrt *et al.* 2014; Nguyen & Baker 2016). Its seasonally

open canopy and significant ground cover provide some grazing for large herbivores, such as elephants and ungulates. The main dipterocarps in the 20–30 m tall canopy are *Dipterocarpus obtusifolius, D. tuberculatus*, *Shorea siamensis* and *S. obtusa,* the proportions of which vary locally (Table 3 & Supplementary Table S2a; Fig. 4a). There are three DDF subtypes within the 16-hectare plot at Mae Ping, on different bedrock and soils (Table 1 and Fig. 2). The scarcity of dipterocarp saplings in the non-mound quadrats on the 8 ha study site may be due to a poor supply of seeds in the recent past, as the dipterocarps flower and fruit irregularly and gregariously. Prolonged droughts and the scarcity of bare sites suitable for germination may also be involved (Nguyen & Baker, 2016).

The mound vegetation is more typical of Mixed Deciduous Forest (MDF), a fire-adapted formation with few or no dipterocarps that is often associated with calcareous lithologies and is widespread in seasonal climates in northern Thailand and adjacent countries (Marod *et al.* 1999; Bunyavejchewin *et al.* 2011). Neither of the canopy species that normally differentiate the main MDF sub-types, i.e. *Tectona grandis* and *Lagerstroemia calyculata,* (Bunyavejchewin, 1983), were recorded on the mound quadrats. This may be because the stands are only as old as the mounds, and have yet to acquire the canopy composition f mature MDF. However, the floristic correspondence of the mound vegetation with lower canopy and ground layers of typical MDF is clear.

Table 7. Correlations of topsoil variables against CCA axes 1 and 2 for different size classes

	CCA Axis 1		CCA Axis 2	
	R	Tau	R	Tau
Tree CCA				
pH	−0.909	−0.600	−0.178	−0.082
Total N	−0.727	−0.577	0.029	0.032
Total P	0.322	0.168	0.114	0.064
Total K	−0.073	−0.129	0.172	0.009
Clay	−0.903	−0.565	−0.151	−0.030
Silt	0.314	0.161	0.102	0.012
Sand	0.780	0.527	0.104	0.019
Sapling CCA				
pH	0.903	0.737	−0.060	−0.082
Total N	0.672	0.504	0.000	0.086
Total P	−0.249	−0.143	0.238	0.168
Total K	−0.130	0.055	0.053	0.139
Clay	0.896	0.621	0.043	0.054
Silt	−0.176	−0.086	0.104	0.175
Sand	−0.846	−0.626	−0.100	−0.089
Seedling CCA				
pH	−0.917	−0.610	0.070	−0.040
Total N	−0.704	−0.558	−0.081	−0.120
Total P	0.391	0.204	0.274	0.198
Total K	−0.047	−0.162	−0.099	−0.069
Clay	−0.949	−0.714	−0.073	−0.045
Silt	0.414	0.319	0.064	0.027
Sand	0.775	0.509	0.043	0.065
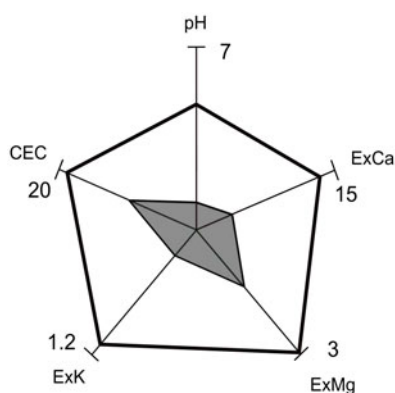
Figure 6. Stoichiometric roses of exchangeable cations and pH in Mae Ping topsoils
Shaded inner: Non-mound topsoil Clear outer: Mound topsoil All scales, except pH, are linear.

Soils

The contrast between the two sets of soils is enhanced by the lithological discontinuity in the regolith. The non-mound soils are developed in deep dystric colluvium several metres deep, whereas the larger mounds include calcareous materials that have been excavated from the limestone contact. The lithological difference means that the two groups of soils develop along separate pedogenic trajectories and qualify for different high-level taxa in the international soil classification systems. The non-mound soils are Acric Ferralsols in the *World Reference Base* (IUSS, 2022) and Rhodic Kandiudoxes in the USDA *Soil Taxonomy* (Soil Survey Staff, 2022). The mound soils are Provertic Cambisols in the *World Reference Base* and Vertic Eutrodepts in *Soil Taxonomy*.

Clay contents increase with depth in the non-mound soils (Supplementary Table S1), although mostly not enough to qualify the subsoils as argic or argillic horizons *sensu stricto*. The finer textures of the mound topsoils could just be due to indiscriminate excavation of clay-enriched subsoil material. However, termite selectivity for particle size may contribute to the higher clay contents in the mound topsoils, as many termites are selective in their choice of particles for excavation and construction, with coarse sand particles carried by their mandibles and finer in their crops (Stoops, 1964; Abe, *et al.* 2009). The lower total porosities and hydraulic conductivities of the mound soils are unexpected, because the ventilation macro-voids should increase overall porosity. Micromorphological analysis might show that the low values are due to dense packing in the construction process. They contrast with findings that overall porosity increases in savanna termitaria (e.g. Konate *et al.* 1999). The consequently low infiltration and high surface runoff of the Mae Ping mounds are consistent with the lichen mats and morphological indicators of surface puddling.

Hard rounded gravels of concretionary manganese dioxide (MnO_2) are common in tropical forest subsoils. The red non-mound clay loams at Mae Ping have abnormally high contents of free MnO_2, distributed in convoluted layers of concretions that are unusually angular and brittle (Supplementary Table S1). MnO_2 concretions are often associated with fluctuating soil aeration, but the matrices of the non-mound subsoils are bright red and unmottled, and the profiles appear to be freely drained. Similar concretions have been seen in unmottled red clays over limestone in other tropical biomes, such as forest in Belize (Baillie *et al.* 1993), savanna in Tanzania (AHT, 1980), and semi-desert in Jordan (HTS, 1994), suggesting that a calcareous input into the soil parent material, and consequently elevated pH, base and Ca status, may be implicated in their formation.

Total Mn is unique among the cations assayed at Mae Ping, in that there is no difference observed between the calcareous mound and non-calcareous non-mound topsoils (Table 2). Also, total Mn is weakly correlated with CCA Axis 2, unlike the basic cations which are correlated with Axis 1 (Fig. 5a). The effect of soil Mn on the forest at Mae Ping is unclear. Manganese has been identified as a possible micronutrient but it can be toxic at high concentrations. It has been associated with P mobilisation and uptake, and can have complex interactions with cationic nutrients, especially Ca (Le Mare, 1977; Hall & Huang 2017; Zemunik *et al.* 2020).

The termites forage and import surface litter from surrounding areas for consumption by their symbiotic fungi. The consequently intense metabolic activity has been reported to increase subsoil temperatures, and the partial pressures of CO_2, methane and other respiratory products in the soil atmosphere (Seiler *et al.* 1984).

Forest – soil associations

The distributions of the contrasting DDF and MDF-like thickets in the study area are clearly associated with the soil differences. As in

many tropical forests, it is not possible to determine definitively which soil attributes most influence forest pattern, because many are highly inter-correlated. Soil processes and attributes that might be affected by the higher pH, bases and Ca in the mound soils include: lability of Al; stimulation of microbial activity; interactions with Mn; stoichiometric suppression of K and Mg by copious Ca uptake; and possibly sequestration or solubilisation of P (Baillie *et al.* 2018). Unusually for tropical forests, both available and total phosphorus are insignificant as differentiae at Mae Ping (Vitousek & Sanford, 1986).

Pedoturbation and forest diversification

The lithological discontinuity and the excavation of distinctly calcareous regolith material enhances the contrast in base status between the mound and non-mound soils. However, this trend is also apparent in tropical forest termite mounds derived from lithologically uniform regoliths (Davies & Baillie, 1988), because weathering rock C horizons often have higher base status than overlying leached subsoil B horizons (Baillie, 1996).

The termitogenic importation of substrate cations into the mound topsoils increases the amounts available for active biological cycling. This counters the climatogenic trend towards topsoil dystrophication by downward leaching of soil bases. Upward translocation by termite excavation can modify or retard other leaching-driven pedological processes, such as argilluviation, mineral weathering and desilication (Baillie, 1996).

Although widespread and important, termites are not the only agents of pedoturbation that renew soil diversity and counter leaching-driven dystrophication in tropical forests. Excavation and modification of forest soils by earthworms has been noted in forests on skarn rocks in western Thailand (Pendleton, 1941, 1942; Goodnight & Goodnight, 1956; Nemeth & Herrera, 1982; Baillie *et al.* 2018; Van Groenigen *et al.* 2019). Other pedoturbation agents include: pangolins (Shrestra *et al.* 2021), megapodes (Machincote *et al.* 2004; Karawita *et al.* 2018), wasps, cicadas (Tuma *et al.* 2019), mud lobsters (Hossain *et al.* 2019); ants (Green *et al.* 1999); and wild boar (Ickes *et al.* 2005). Landslides and treefall also excavate soils and chemically replenish mineral nutrients by exposing fresh regolith to weathering (Heineman *et al.* 2015).

Conclusion

Our results indicate that the floors of some dry tropical forests are mosaics of stable dystric soils interspersed with patches that have been rejuvenated by termite pedoturbation. This pattern somewhat mirrors the spatial mosaic of mature canopy and gaps in the forest canopy above. Termite pedoturbation also occurs in moist and evergreen forests (Baillie, 1996). The rejuvenation alters the edaphic conditions for the forest with respect to soil structure, root aeration, moisture dynamics, quantities and availability of nutrients, and mechanical stability for the root environment. At Mae Ping these changes are sufficient to significantly influence the local structural and floristic diversity of the forest. Pedoturbation and soil diversity, both as an instantaneous condition and as a set of ongoing processes, need to be accommodated at a range of spatial scales in comprehensive paradigms of tropical forest dynamics.

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