2021-04-27

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http://hdl.handle.net/10026.1/17299

ORIGINAL ARTICLE

bioTROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION · WILEY

Spatial structure of rainforest termites: Two matched pioneering cross-continental case studies

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Abstract

Termites are vital parts of the soil biota in tropical regions, but their spatial ecology is barely studied. Here, termites were surveyed in two one-hectare plots, to investigate spatial patterns of soil-dwelling termites in old growth rainforest. Ecological interactions tested were as follows: (1) environmental relationships; (2) termite feeding groups; and (3) termites and predatory ants. The studies were in Africa (Gabon, Ivindo) and in Asia (Malaysia, Sabah, Danum Valley). In both locations, the wood-feeding termites had an aggregated spatial structure at fine scales, while the humus-feeding termites had a continuous distribution. Environmental variables were similar, but only two associations were consistent across sites. Termite feeding groups along the humification gradient were consistently disassociated. Significant associations were detected between predatory ants and termites in both sites: however, their scale and direction differed. This shows that the termite-mediated ecosystem processes associated with wood- and humus-feeding termite were provided at similar spatial scales, but that for humus-feeding termites the intensity varied due to differences between the two plots. Competition at the functional level may be an important interaction, the nature of which is affected by resource availability, which is more limiting for wood-feeding termites. We hypothesize that predation by ants may be important, but the structure of these relationships varies between the two study plots. All of these preliminary patterns need to be tested in fully replicated studies, but future studies may be constrained due to the sampling effort being so great for even a single survey. Abstract in French is available with online material.

KEYWORDS
ants, diversity anomaly, feeding groups, spatial structure, termites

1 | INTRODUCTION

The ecology of tropical rain forests is poorly studied. The forests are generally distant from ecological institutes, they are often inaccessible, extraordinarily complex, hard to work in for long periods. This means that there is still a lot of baseline descriptive work that has not been done. It has been estimated, for example, that 50% of insect diversity is found in tropical rainforest (Stork, 2018), but most of this diversity is poorly understood. This is even true for social insects, especially ants and termites, which have an extraordinarily high biomass and ecological importance, especially in the tropics (Tuma et al., 2019), but where our knowledge is greater than for many other insects (e.g., parasitoids wasps).

Termites (Blattodea: Termitoidae) are "ecosystem engineers" (Bourguignon et al., 2017). The most important animal decomposers in the tropics (Cornwell et al., 2009; Griffiths et al., 2019), they

influence soil properties (Ashton et al., 2019) and are mediators of soil gas fluxes (Bignell & Eggleton, 2000; Collins, 1983; Watt et al., 1997; Wood & Sands, 1978; Yamada et al., 2005). Research on termite spatial ecology and ecosystem functions is biased toward grassy biomes (Bonachela et al., 2015; Gosling et al., 2016; Korb & Linsenmair, 2001; Pringle et al., 2010). In contrast, within equatorial rain forest soils, where termites are particularly diverse and abundant (Dahlsjö, Parr, Malhi, Rahman et al., 2014; Davies et al., 2003), we know little about their spatial structure and the ecosystem processes they mediate (e.g., Bourguignon et al., 2011; Bourguignon, Sobotnik et al., 2011; Donovan et al., 2007). We also lack critical information on the spatial scale of functional components of rain forest termites and therefore how they are contributing to ecosystem processes. We also have limited understanding of the evolutionary and ecological processes that may be supporting a high local species density (e.g., Bourguignon et al., 2015; Bourguignon et al., 2017).

Making generalities across continents is confounded by the termite global diversity anomaly (Dahlsjö, Parr, Malhi, Rahman et al., 2014; Davies et al., 2003). Regional species density varies enormously among the equatorial continental blocks for historical biogeographical reasons, while within broad biogeographical regions lowland closed-canopy forests have the highest species density (Jones & Eggleton, 2011).

In this paper, we present intensive data surveying two 1 ha plots, one each in Borneo and Gabon, examining (1) environmental associations, (2) between trophic group interactions, and (3) predator–prey interactions. As biogeographical evolutionary processes have had such a major effect on termite global diversity patterns, we considered whether the differences between sites could be explained by unique environmental conditions or by this strong historical footprint. Throughout, we emphasize that as there is no internal replication, so the findings are necessarily provisional, descriptive and hypothesis generating. Other studies will be needed to corroborate these patterns.

2 | METHODS

2.1 | Spatial sampling protocol and study sites

Our spatially explicit sampling protocol was designed to describe spatial patterns in samples from a local assemblage. The choice of grain size (area of the sampling unit), lag (spatial position of the pits), and extent (area of plot) were here based on recommendations from a previous spatially explicit termite study (Donovan et al., 2007) (see Appendix S1: S1). The grain consisted of a soil pit of 25 cm × 25 cm × 10 cm (depth), sampled at a lag of every 2 m × 2 m, to an extent of 96 m × 96 m (0.92 ha).

The African plot ("Ivindo") was in Ivindo National Park, Gabon (S 00° 10', E 12° 32'), and the S.E. Asian plot ("Danum") in Danum Valley Conservation Area, Borneo, Malaysia (N 4° 55', E 117° 49'). A single plot, with 2,304 soil pits per plot, was surveyed in each region. Each plot was as follows:

1. representative of termite generic-level richness typically found in lowland primary forest in each continent (with the partial exception of Ivindo that had no forest *Macrotermes*, which are intermittently abundant in other African [including Gabonese] rainforest areas); and

2. such that the influence of plot-scale habitat heterogeneity would be comparable between regions. Streams, gullies, and rocky outcrops were thus avoided, and the plot was in a relatively flat area. Other small-scale features that are typical of closed-canopy forest (e.g., animal trails and tree falls) were present in both plots.

2.2 | Biotic sampling and functional groups

Each soil pit was dug and hand-sorted for 10 min. When either termites or ants were encountered, a representative sample was collected and stored in 95% alcohol, this included varying individuals across helper castes. Individuals per pit were not counted, as this would have been too time consuming: individual colonies could not be identified in the field. Taxon abundance here refers to the number of pit encounters for an individual genus, a measure of relative generic frequency.

This sampling was extremely time consuming, even for just two plots. The surveys took approximately six investigator months to conduct in Ivindo, Gabon and four investigator months in Danum, Sabah, and Borneo (ten months in total).

Taxonomic identification of both termites and ants was to genus level (Appendix S1: S2). The high diversity of the Ivindo termites (especially of the taxonomically poorly known soldierless Apicotermitinae) meant that species-level identification was prohibitively time consuming in a three year project. Closely related species are thought to be ecologically and functionally more similar than distantly related (Slingsby & Verboom, 2006), and ecological interactions are phylogenetically conserved (Gómez et al., 2010).

Termite genera were assigned to feeding groups (FG) (Table 1) based on morphological characters of the worker that have been shown to indicate how far down the humification gradient termites are feeding (Donovan et al., 2001) (see Appendix S1: S2 for assignments). This classification has been questioned recently, particularly in relation to the soldierless Apicotermitinae (Bourguignon, Leponce et al., 2011; Bourguignon, Sobotnik et al., 2011) but still remains the most-used method and allows us to partition the data in a meaningful, if imperfect, way.

The summary list of genus-level feeding preferences in Brown (2000), and Ettema and Wardle (2002) was used to assign ant genera as predators and to the predatory ant group. Ant genera that are termitophages, as well as those defined as generalist predators and therefore likely to feed on termites, were assigned to this group (Appendix S1: S3). Other ants were classified as "non-predators."

TABLE 1 Feeding group classification in termites based on Donovan, Eggleton, and Bignell (2001) and Inward et al. (2007). Throughout, FGIII and FGIV feeding groups together are referred to as SOM ("Soil Organic Matter") feeders, while FGI +FGII are described as wood feeders, although some species feed on other substrates. FGI was too rare in our samples to be analyzed separately

Feeding group	Food consumed
FGI	Lower termite families (non-Termitidae families). These termites are all dead wood and/or grass feeders and have symbiont flagellates in their guts. They are infrequent in tropical rain forests
FGII	Consume a range of non-soil food material including dead wood, grass, leaf-litter, micro-epiphytes, and here include fungus-growing Macrotermitinae termites. They have no symbiont flagellates. FGI +FGII here are described as wood feeders
FGIII	Consume soil material with a high organic content, and wood material that is heavily decayed and has become soil-like, but still has recognizable fragments of plant material. Here, they are called humus feeders
FGIV	Consume heavily decomposed (=humified) mineral soil with low organic content (no visible fragments of plant material. Here, they are called soil feeders

Environmental measurements were recorded from every 2 m × 2 m sample point with three categories of environmental data: food availability/quality, soil properties, and understory vegetation (see Appendix S1: S4).

2.3 | SADIE red-blue spatial structure analysis

Spatial Analysis by Distance Indices (SADIE) is an ecological approach employed to assess the spatial structure in biotic and abiotic data (Perry et al., 1999; Winder et al., 2019). The method identifies areas where data is at random, or forms clustering in local neighborhoods of consistently large or small values, referred to as "patches" and "gaps," respectively. Here, a local cluster index was calculated for each sample point (I_{ij}); showing whether it contributes to a patch or gap. Sample points that have a value greater than the sample mean were assigned a positive cluster index (I_i) and contribute to a patch, while sample points that have a value less than the sample mean were assigned a negative cluster index (I_j) and contributed to a gap. The cluster indices were contoured by interpolation and mapped onto the plot space (Surfer v6.04; Golden Software Inc., Colorado, USA). Neighborhoods where $I_i > 1.5$ were identified as patches and indicated in red in mapped figures, and those where $I_j < -1.5$ are gaps are indicated in blue (Perry et al., 1999). An arrangement of random neighboring counts was assigned where $I_i < 1.5$ or $I_j > -1.5$ and indicated in white. A global index of aggregation I_a was calculated, which shows whether the overall spatial pattern was non-random ($I_a > 1$), accompanied by an overall gap (I_j) and patch (I_i) index. The significance of indices was tested by Monte Carlo procedures with 5999 randomizations, following (Perry et al., 1999).

SADIE analyses were performed on the following data sets: (1) the full termite assemblage (TA); (2) wood feeders, consisting of a pooled sample of FGI and FGII genera due to the extremely low encounter rate of FGI: they are similar in their feeding preferences (see Appendix S1: S2, S3); (3) humus feeders (FGIII), (4) soil feeders (FGIV) which were only recorded in Ivindo, and (5) predatory ants.

SADIE has also been used to analyze associations with environmental variables (e.g., Donovan et al., 2007; McGraw & Schlossberg, 2017). For this the data were normalized and transformed to create integer values (see Appendix S1:Table S4).

For each variable (biotic and environmental), the global index of aggregation (I_a) provided an indicator of spatial structure, that is, heterogeneity. The local cluster index values (I_{ij}) generated for each variable provided the spatial description used in subsequent pair-wise association tests, to assess spatial relationships (see Appendix S1: Table S4).

2.4 | Association tests from SADIE

Pairs of variables (here SADIE red-blue local spatial descriptors) may be positively associated, disassociated, or occur at random with respect to each other. Local spatial association was measured using the index χ_k. This is based on the similarity, measured at the kth unit (sample point), between the local cluster index values (I_{ij}) generated in the SADIE analysis, from any pair of variables (Perry & Dixon, 2002)), denoted z_{k1} and z_{k2} for the pair of indices. Positive values of χ_k arise from coincidences of patches ($I_i > 0$) or of gaps ($I_j < 0$) in a pair-wise analysis; termed "positive association." Negative χ_k values arise from coinciding "patch-gap" or "gap-patch" cluster types, termed "disassociation." Overall spatial association, X, was calculated as the mean of local values, $\chi = \Sigma_k \chi_k / n$, equivalent to the simple correlation coefficient between z_{k1} and z_{k2}. The significance of X was tested by randomizations, with values of z_k reassigned among the units, after allowance for small-scale spatial autocorrelation in either set of z_k to provide a probability value p_D (Dutilleul, 1993)).

2.4.1 | Environmental relationships

The SADIE red-blue descriptions of the termite data sets (TA, FGII, FGIII, and FGIV) and the environmental variables that were significantly spatially structured ($I_a > 1$, $p > 0.05$) were used for pair-wise analysis of spatial association, to examine the global spatial relationships (X) between termites and environmental conditions.

2.4.2 | Biotic relationships

Positive spatial association may be due to some broad-scale indirect effect, such as an environmental variable selecting against the

TABLE 2 Local spatial relationships (χ_k): contour shades and symbols used in plots of association tests between biotic data

Local cluster index Patch: $I_i > 0$, Gap: $I_j < 0$			Local spatial index and contour color	Symbol where χ_k > upper or <lower percentile limits
Variable I	Variable II	Spatial relationship		
Patch	Patch	Positive Association	$\chi_k > 0$ Light gray	●
Gap	Gap			+
Patch	Gap	Disassociation	$\chi_k < 0$ Dark gray	O
Gap	Patch			X

TABLE 3 Generic richness and soil pit occupancy in Danum and Ivindo

	Number of genera		Percentage of occupied pits	
	Danum	Ivindo	Danum	Ivindo
Wood feeders (FGI)	3	1	<1	<1
Wood feeders (FGII)	10	7	20	20
Humus feeders (FGIII)	16	8	26	70
Soil feeders (FGIV)	0	29	0	53
Total Termites	29	43*	44	90
Predatory ants	17	12	22	29

Note: (*) Two genera have both humus feeder and soil feeder representatives based on enteric valve architecture (see methods).

TABLE 4 SADIE red-blue analyses summary statistics

	Danum			Ivindo		
	I_a	I_j	I_i	I_a	I_j	I_i
All termites	1.606***	−1.596***	1.538***	1.777***	−1.724***	1.663***
Wood feeders	1.706***	−1.792***	1.758***	1.617**	−1.619***	1.630***
Humus feeders	1.348*	−1.355**	1.351**	1.22	−1.233*	1.158
Soil feeders				2.022***	−2.050***	1.967***
Predatory ants	1.29*			1.57***		

Note: When $I_a > 1$ spatial pattern is non-random. *p* value ***≤0.001, **≤0.01, *≤0.05.
Abbreviations: I_a, Global index aggregation; I_i, Patch cluster index; I_j, Gap cluster index.

presence of both biotic groups, and therefore generating overlapping gaps. To consider just the localized interaction between biotic groups, from the SADIE spatial descriptions, "empty soil pit" sample points, that is, where the soil pit was not occupied by at least one of either ants or termites, were removed (Perry & Dixon, 2002). The association test was then carried out on these "occupied only" data sets. The following pair-wise biotic association analyses were performed: (a) wood feeders (FGI and FGII) and humus feeders (FGIII) (Danum and Ivindo), (b) humus feeders (FGIII, Danum and Ivindo) and soil feeders (FGIV) (Ivindo only, due to the absence of FGIV in Danum), and (c) Predatory ants and the full termite assemblage (both sites).

To examine the heterogeneity and magnitude of spatial relationships, plots were constructed of the local spatial index χ_k (Winder et al., 2019). These plots are the χ_k, value contoured by interpolation and mapped (Surfer v6.04; Golden Software Inc., Colorado, USA), where positive association ($\chi_k > 0$) and disassociation ($\chi_k < 0$) are distinguished by color categories (Table 2). Local positive association ($\chi_k > 0$) encompasses the co-occurrence of both patches and gaps. Similarly,

local disassociation ($\chi_k < 0$) encompasses the co-occurrence of "variable 1 gap" and "variable 2 patch," and the co-occurrence of "variable 1 patch" and "variable 2 gap." The local cluster index values (I_{ij}) from the SADIE red-blue analysis, distinguishes between these. At the sample points where χ_k, exceeded the lower and upper percentile limits adjusted for local spatial autocorrelation (i.e., significant local spatial associations), these four spatial relationships were identified and presented by various symbols within the contour plots (see Table 2).

3 | RESULTS

3.1 | Assemblage composition and abundance

Generic density was greatest in Ivindo, with a large number of soil-feeding genera, while there were more genera of wood feeders and humus feeders in Danum (Table 3). Termites occupied 90% of the pits in Ivindo with an extremely high occupancy level by humus

FIGURE 1 SADIE red-blue plots, from Danum and Ivindo, for the full assemblage, and by feeding group. I_s, Global index of aggregation is included in each plot
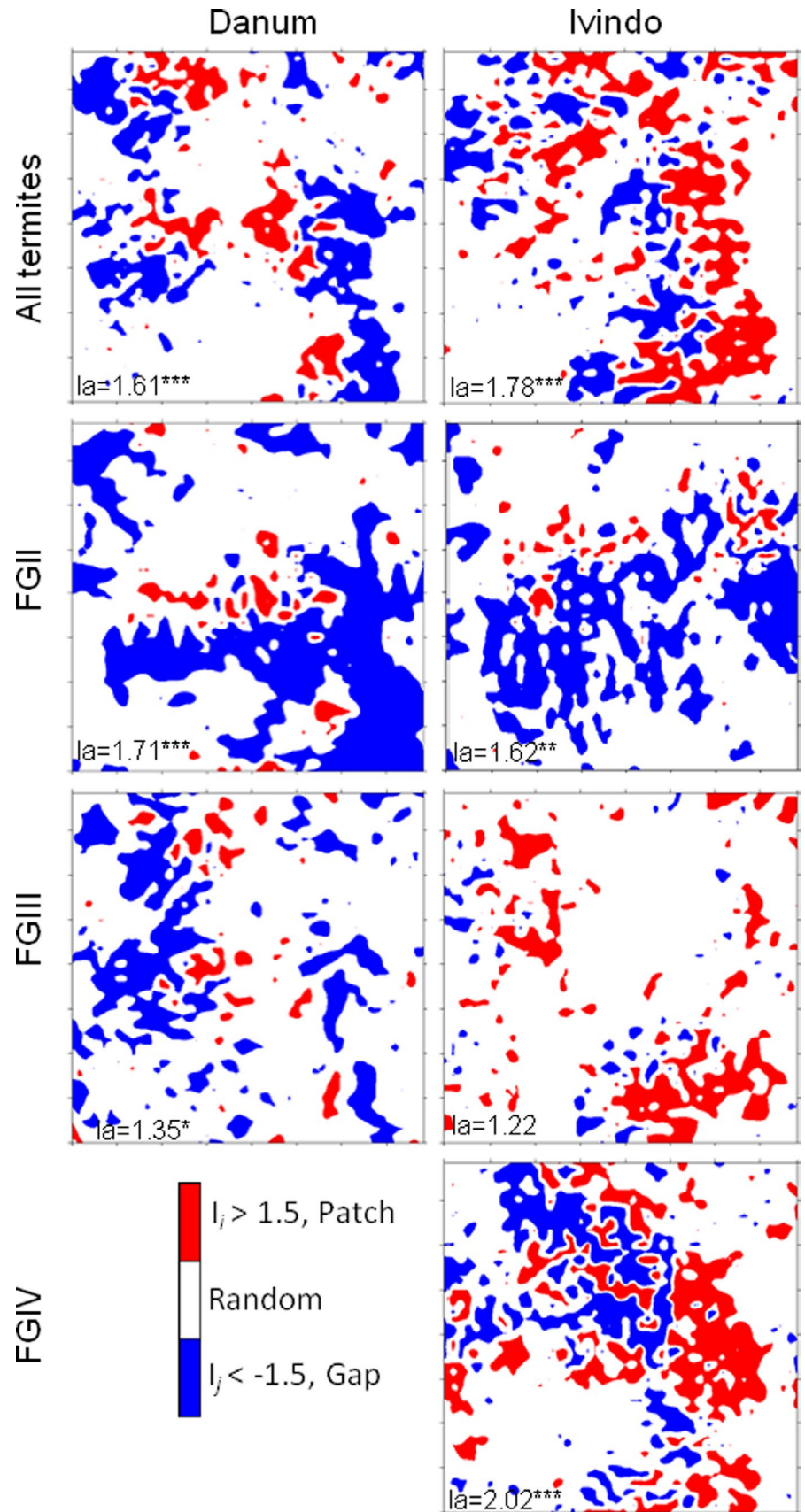
feeders (70% of pits). In Danum, termites occupied 44% of the soil pits, with humus-feeding termites having the highest occupancy (26%), but much lower than in Ivindo.

Occupancy rates were similar for wood feeders in the two sites, with FGI being negligibly low (<1% in both places).

3.2 | SADIE analyses

The termite assemblages in both sites were significantly spatially structured (I_a > 1.0, p < 0.05) considering both the global index and the gap and patch cluster indices (Table 4). Danum and Ivindo showed similar differences in spatial patterns for wood feeders and humus feeders. I_a values are consistently higher for wood feeders compared with humus feeders, reflecting wood feeders' patchier distribution compared with humus feeders, while the Ivindo humus feeder sample is statistically significant only for the gap and patch cluster index. The red-blue plots for each analysis illustrate how the significant patches and gaps are distributed across the plot (Figure 1). In Ivindo, wood feeder patches appear to be small and limited in area compared with the relatively larger and dominant patches and gaps for the soil feeders (FGIV).

3.3 | Environmental variables and associations

Soil pH, soil C_{tot}, and N had similar means and distributions in Danum and Ivindo, while the soils in Danum were wetter and less porous (Table 5). Danum had fewer sticks, while the leaf-litter layer and number of logs were similar in both sites (Table 5). There were more smaller trees in Danum compared with Ivindo, accompanied by a higher frequency of young trees (stems), while ground vegetation cover was lower (Table 5).

Environmental variables were all, apart from trees, significantly spatially structured (see Table 5). There were several significant associations between environmental variables and the termite groups, yet few are consistent across the two sites (see Table 6 and Appendix S1: S5 for full results). The only consistent associations in both sites were as follows: a positive association between wood-feeding termites and sticks, and a positive association between soil infiltration rates and SOM-feeding termites (FGIII +FGIV). All other associations were unique to each site, and sometimes opposing between sites (Table 6).

3.4 | Inter-feeding group associations

In Danum, 38% of sample points were retained for the "occupied-only" association analysis between wood feeders and humus feeders. This yielded a strongly disassociated global relationship (X = −0.467, p > 0.999). Disassociation dominates much of the plot as evidenced by the dark shading due to negative χ_k values (Figure 2a). Of the sample points that negatively exceeded the a_l, most are coinciding [wood feeder patch—humus feeder gap] points (open circles). The global disassociation is therefore largely due to an absence of humus feeders' from patches of wood feeders.

In the same analysis in Ivindo (76% of the complete data set, using occupied-only samples), the wood-feeding and humus-feeding termite assemblages were again globally disassociated (X = −0.144, p > 0.999). As in Danum, this disassociation is distributed across the plot, mostly comprised significant [wood feeder patch—humus feeder gap] co-occurrences (Figure 2b), and therefore also shows the absence of humus-feeding termites from patches of wood-feeding termites.

A global disassociation was also found between occupied-only (88% of complete data set) spatial structures of the humus feeders

TABLE 5 Environmental variables: mean and standard deviation, with total counts for the plot in parentheses, index aggregation (I_a) for the environmental variables
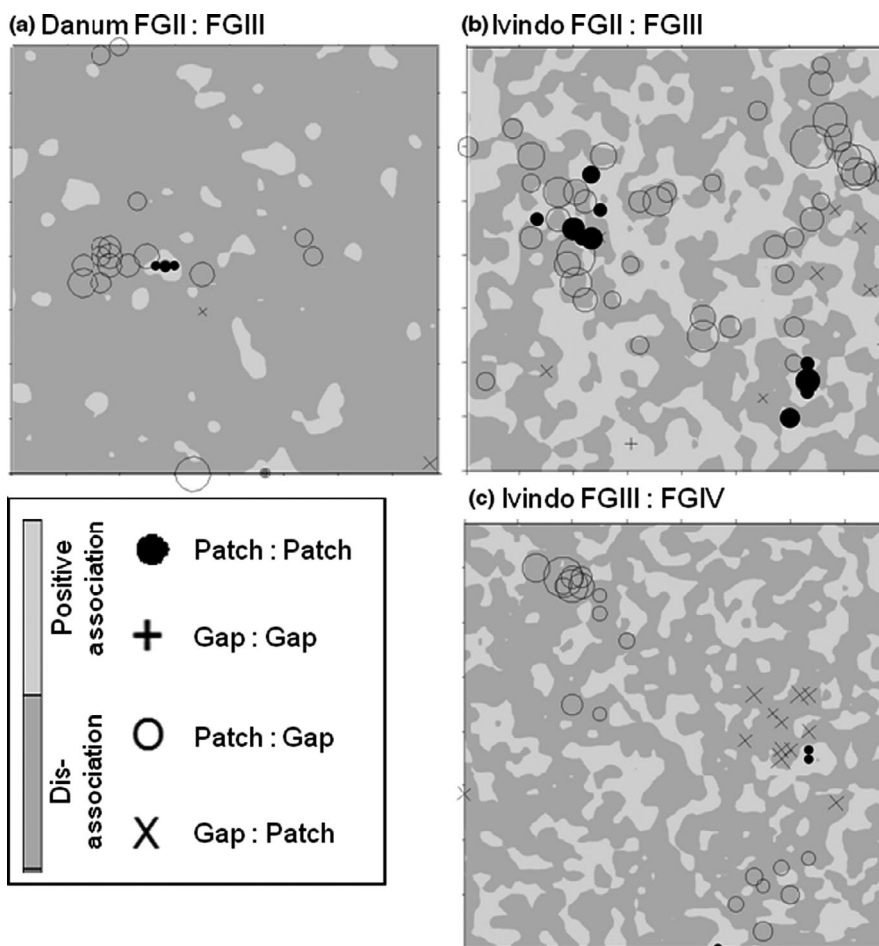
Category	Variable	Danum Mean ± SD per sample point	Ivindo Mean ± SD per sample point	Danum SADIE *Ia*	Ivindo SADIE *Ia*
Food material	Logs	0.21 ± 0.5 (488)	0.21 ± 0.5 (473)	1.602***	2.90***
	Sticks	2.37 ± 2.6 (5468)	2.6 ± 2.6 (6089)	3.769**	4.31***
	Leaf litter depth	1.2 ± 0.4	1.1 ± 0.4	2.156**	2.90***
	Soil C_{tot}	4.52 ± 2.02	4.09 ± 1.52	265.1***	4.68***
	Soil N	0.27 ± 0.12	0.29 ± 0.08	5.574***	2.55***
Soil properties	pH	4.0 ± 0.2	4.1 ± 0.3	4.303***	2.26***
	Infiltration rate	3.05 ± 4.36	4.83 ± 5.29	1.868***	254.29***
	Soil moisture	38.8 ± 6.3	25.5 ± 5.6	3.465***	7.33***
Vegetation	Trees	0.2 ± 0.4 (370)	0.1 ± 0.3 (224)	0.052	0.90
	Tree dbh.	22.8 ± 24.6	32.4 ± 24.4	NA	NA
	Stems	2.4 ± 1.9 (5547)	1.1 ± 1.0 (2495)	2.610***	2.68***
	Ground vegetation cover	17 ± 10	21 ± 16	2.317**	3.60***

Note: **, p < 0.01; ***, p < 0.005.

TABLE 6 Significant association results with termites. (see Appendix S1: S5 for full association results)

Variable	Danum only	Danum +Ivindo	Ivindo only
Stems	− ve all termites		+ ve all termites
Logs			+ ve soil feeders
			− ve humus feeders
	+ ve wood feeders		− ve wood feeders
Sticks		+ ve wood feeders	
Leaf litter depth	+ ve wood feeders		
Soil N	+ ve humus feeders		
	− ve wood feeders		
Soil moisture	− ve all termites		
Soil pH			+ ve humus feeders
Soil Porosity	− ve wood feeders	+ ve humus feeders (Danum) soil feeders (Ivindo)	

FIGURE 2 Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th a_u percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k. (a) Danum wood feeders (FGII) vs humus feeders (FGIII), a_l = −2.73, a_u = 2.71. (b) Ivindo wood feeders (FGII) vs humus feeders (FGIII), a_l = −2.800, a_u = 2.841. (c) Ivindo humus feeders (FGIII) vs soil feeders (FGIV), a_l = −2.522, a_u = 2.417

(a) Danum FGII : FGIII
(b) Ivindo FGII : FGIII
(c) Ivindo FGIII : FGIV

Positive association / Dis-association

● Patch : Patch
+ Gap : Gap
○ Patch : Gap
✕ Gap : Patch

and soil feeders in Ivindo (X = −0.256, p > 0.999). Here, the disassociation is due to two clusters of [humus feeder patch—soil feeder gap] co-occurrences (open circles) and one cluster of [humus feeder gap—soil feeder patch] co-occurrences (crosses) (Figure 2c). Unlike the wood feeder and humus feeder dissociation, which is represented by an absence of humus feeders from wood feeder areas, here, the two SOM-feeding groups appear equally dispersed away from "patches" of the other group (humus feeder patches are not,

however, significant, see Table 2). There is limited positive local association between any of the feeding groups.

3.5 | Ant-termite associations

Global diversity patterns for ants show the same latitudinal hemispherical asymmetry (Dunn et al., 2009) but not the longitudinal
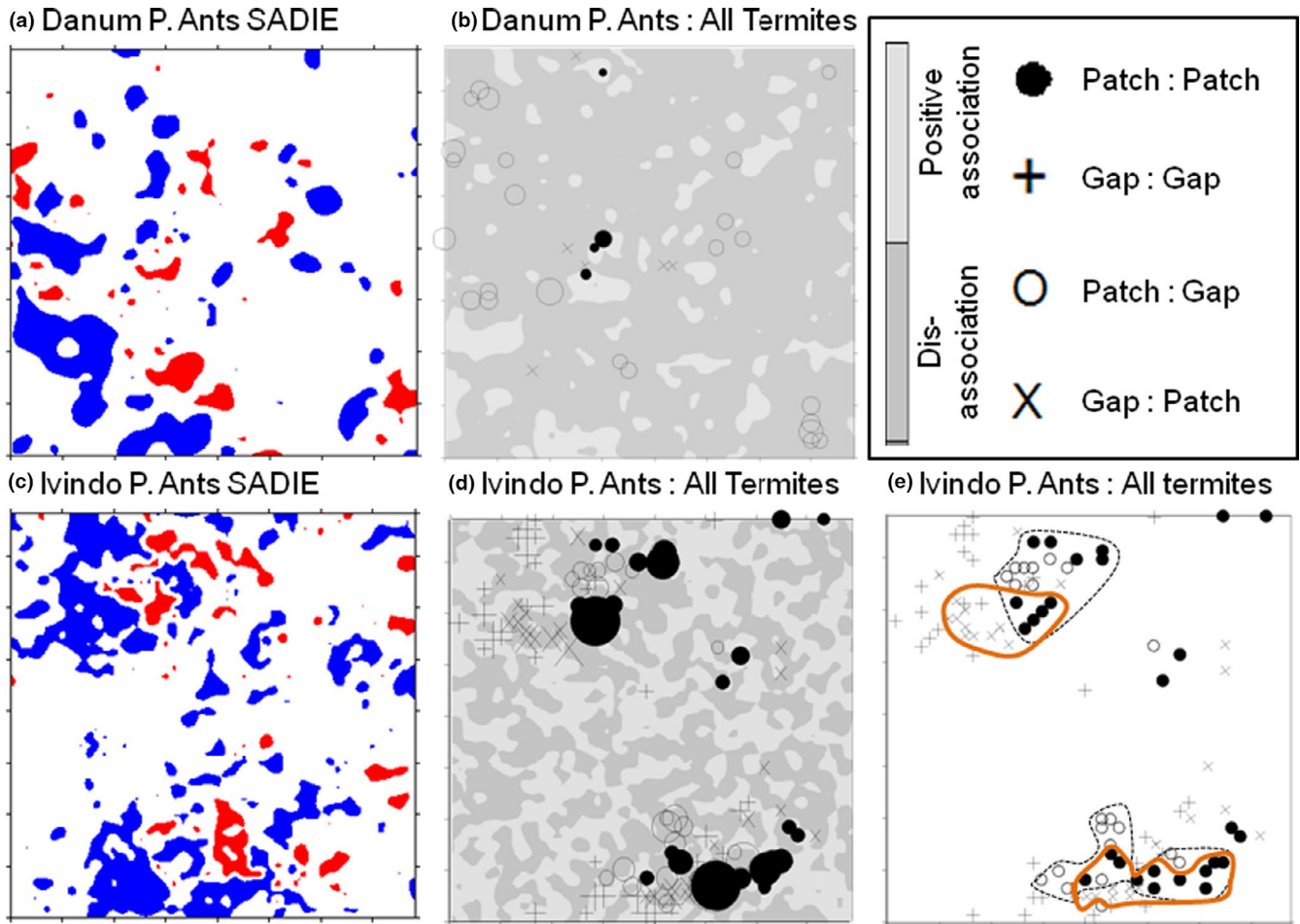
FIGURE 3 Association results of predatory ants (P. Ants) vs termite assemblage. (a) and (b) Danum. (c, d and e) Ivindo. (a) and (c) SADIE red-blue plot for predatory ants. (b) and (d) Local association index (χ_k) contour plots, with indices that exceeded the lower 5th (a_l) and upper 95th a_u percentile critical values, adjusted for spatial autocorrelation presented as symbols, where size represents the magnitude of χ_k. (b) Danum, a_l = −2.488, a_u = 2.443. (d) Ivindo, a_l = −2.560, a_u = 2.146. (e) Additional plot taken from Ivindo (d) presenting only the significant local associations; black line envelopes ant patches (black dot and open circle); orange line envelopes termite patches (black dot and X)

anomaly seen in termites. Most predatory ant genera were collected in both Danum and Ivindo (Appendix S1: S3), and genus-level richness and pit occupancy were similar in both sites (Tables 3 and 4, and Figure 3).

The Danum predatory ant assemblage was weakly spatially structured (I_a = 1.29, p < 0.05) with scattered patches and gaps (Figure 3a). Fifty percent of the sample points were retained for the occupied-only association analysis of the predatory ants/termite assemblage spatial patterns. The strong global disassociation (X = −0.398, p > 0.999) is broadly distributed across the plot. Most of the significant χ_k values are "ant patch - termite gap" co-occurrences (Figure 3b, open circles), and therefore the disassociation reflects an absence of termites from patches of predatory ants.

The Ivindo predatory ant assemblage is strongly spatially structured (I_a = 1.57, p < 0.001, Figure 3c). The global index of the occupied-only (termite and ants) association test (91% of complete data set) was non-significant (X = 0.004, p = 0.439). However,

inspection of the local association plot identifies two discrete clusters of significant local association values (χ_k values exceeding the a_l and a_u values). Each cluster is composed of all four types of associations (gap-gap, patch-patch, gap-patch, and patch-gap), which suggests a complex and potentially dynamic interaction between the predatory ants and termites at the scale of these clusters (Figure 3d and e). The lack of a significant global relationship is therefore due to both strong positive and negative interactions, occurring in two large clusters.

4 | DISCUSSION

4.1 | Occupancy and spatial patterns

Differences in termite occupancy rates between Ivindo and Danum probably reflect not only inevitable plot differences but also probably the global termite diversity anomaly (Dahlsjö, Parr, Malhi,

Rahman et al., 2014). Termites, particularly SOM-feeding termites (FG III and FG IV), are generally far more abundant in African forests than in Southeast Asian ones (see discussion in Davies et al., 2003). While occupancy and diversity differed quite dramatically, spatial patterns of wood-feeding and humus feeders were consistent between our two study sites and agree with a previous study from Danum (Donovan et al., 2007). Wood feeders are heterogeneously distributed with small aggregations and larger gaps, while humus feeders are more continuously distributed with diffuse gaps and clusters. These spatial patterns appear robust between the two regions and times suggesting the hypothesis that these may be the typical patterns at the scale we have studied, although only future replicated studies will corroborate this hypothesis. The trend from patchy to homogenous along the humification gradient does not, however, hold for true soil feeders (thought to feed lower down the humification gradient), which were found to be heterogeneously distributed with significant aggregations in Ivindo (Table 4, Figure 1). Soil feeder diversity is extremely low in Asian compared with African forests (Dahlsjö, Parr, Malhi, Rahman et al., 2014; Davies et al., 2003), and explains why they were not detected in the Danum plot.

4.2 | Environmental relationships

Environmental associations were mostly site specific, with some due to differences in general environmental conditions (Tables 5 and 6). For instance, the higher soil moisture at Danum may explain the negative association with termites, where soils tend to saturate more frequently here due to the higher rainfall (mean annual rainfall in Danum is approximately twice that in Ivindo). There were also several associations in each site that cannot be explained by differences in environment. For example, the opposing associations between FGs and logs (Table 6), despite logs being present in similar abundances in both sites (Table 5).

Two environmental associations were consistent between sites. Wood-feeding termites were positively associated with their food source (sticks in both sites, and leaf-litter and logs in Danum). Wood feeder food is patchy and finite, and so a more restricted resource (Brauman et al., 2000). This may drive a strong association with patches of available food. A positive association between humus feeders and soil N or C was only detected in Danum. Although this could reflect selection of soil-rich patches, it is difficult to tease out cause and effect of this association, particularly in only two studies. Ordination analyses of the environmental variables (reported in Scholtz, [2010]) showed that the broad-scale patterns in soil C and N were associated with the gentle slopes in both plots, as in other fine-scale studies of soil properties (e.g., Tsui et al., 2004). For termites, the overall heterogeneity in soil C and N is probably less important than the availability of the proteinaceous fractions in highly stable humic substances, which soil-feeding termites selectively digest (Ji et al., 2000). Meanwhile, vegetation structure decomposed logs and abandoned termite mounds create organic-rich patches in the soil profile that some species respond to

(Bourguignon, Leponce et al., 2011; Bourguignon, Sobotnik et al., 2011; Davies et al., 2003). However, a study on *Anoplotermes*-group soil-feeding termites showed that strictly soil-feeding termites were not selecting nutrient-rich patches in bare soil (Bourguignon, Drouet et al., 2015). At fine scales, soil-associated termites deplete soil C and N (Dahlsjö et al., 2014), while also working the soil and influencing the distribution of nutrients patches (Jouquet et al., 2011). We conclude that termites that consume soil in our plots may not be greatly affected by the dominant patterns in soil C and N. The associations detected in Danum may even reflect the point-scale effect of termites on soil nutrient distribution.

Soil porosity was positively associated with soil-associated groups in both sites (humus feeders in Danum and soil feeders in Ivindo). Again, we hypothesize that the termite communities could be the cause of this association, as the micro-aggregates produced in termite-worked soil have been shown to improve soil microstructure and porosity (Mando et al., 1996).

4.3 | Inter-feeding group relation

A spatial signature of competition is spatial separation (Levings & Traniello, 1981; Traniello & Levings, 1986). An "asymmetric" spatial disassociation was consistently detected between wood feeders and humus feeders. While this may be driven by a competitive interaction due to some shared resource, the dissociations could arise from differences in environmental preferences (Valckx et al., 2009).

The SOM-feeding termites were consistently absent from patches of wood-feeding termites in both sites. If heterogeneity in resource availability is more limiting for wood-feeding termites (Brauman et al., 2000), they may defend their space in the soil profile to access this resource. This could drive local exclusion of SOM-feeding termites, which are themselves less restricted by resource availability. In a previous study on spatial relationships from an assemblage in Danum, an aggregation was detected between the wood- and soil-associated groups (Donovan et al., 2007). Therefore, given this difference, and although here the patterns appear robust between sites, repeated surveys will be necessary to determine their consistency.

In Ivindo, the SOM-feeding groups were "symmetrically" disassociated, with humus feeders being absent from soil feeder patches and vice versa. The only opposing environmental association was with logs (Table 6; negative with humus feeders and positive with soil feeders). The majority of termite abundance is found in the top 20 cm of the soil profile (Inoue et al., 2001), and therefore if vertical stratification in the soil is restricted, space in the upper soil profile may be limiting. The high diversity in soil systems may be due to low levels of competitive interactions, within a compact and continuous soil matrix (Ettema & Wardle, 2002), with competition considered to be a weak ecological force in soil organisms generally (Bardgett et al., 2005). In soil macrofaunal groups, particularly it may, however, be a stronger ecological force, with numerous examples in earthworms and ants (Levings & Traniello, 1981; Traniello & Levings, 1986) and at

the intra-specific level in termites (e.g. Bourguignon, Leponce et al., 2011; Bourguignon, Sobotnik et al., 2011). Soil feeders were found to be strongly aggregated, while humus feeders were less patchy but essentially occupied the soil's entire horizontal profile. These levels of occupancy in the soil profile may be illustrating competition for space.

4.4 | Predator–prey interactions

Soldier termites show remarkable adaptations for defense (Prestwich, 1984), and adaptation to predation pressure appears to have been continuous throughout their evolutionary history (Scholtz et al., 2008). There are numerous studies that document ant predation on termites, from specialized "termitophagous" predation (e.g., Bayliss & Fielding, 2002, to opportunistic generalist predation, for example, Tuma et al., 2019). This is considered a key trophic interaction in rain forests, as termites and ants constitute a large proportion of animal biomass in rain forests, particularly in the soil (Tuma et al., 2019).

The spatial associations found in both sites suggest there are important interactions, however, the nature of these associations differed (Figure 3b and d). Assuming they were not due to some habitat variable or competitive exclusion, there are some tentative hypotheses can be suggested. The absence of termites from small, isolated patches of predatory ants in Danum (Figure 3b), suggests that ants may predate termites opportunistically in the soil profile, causing temporary depletion at fine-scale contact points.

In Ivindo, the graduated overlap of termite and ant patches and gaps (Figure 3d) suggests that predatory ants are specifically targeting termite patches. This is supported by gut-contents analysis of the predatory ants collected from the Ivindo plot in this study, showing that some ant species were feeding on more than one termite taxa (Fayle et al., 2015). One of the few community-level predator–prey studies (Leponce et al., 1999) reported a range of ant-termite interactions between ants and arboreal nesting termites, including co-existence, intensive high-impact, and opportunistic but low-impact predation. It may be that the "predation clusters" in Ivindo represent a similar range of taxon-specific predator–prey interactions.

A plausible, although at this stage, tentative explanation for a targeted predation strategy in Africa and an opportunistic one in Asia is the regional differences in termite biomass (Dahlsjö, Parr, Malhi, Rahman et al., 2014); in African soils, termites may be a more reliable source of food. Notably, density-dependent mortality can promote species co-existence by influencing relative abundances and spatial distributions (He & Legendre, 2002), and therefore may be a factor in maintaining high diversity in African forests. If predation rates are high, termite recovery and colony re-establishment must also be very rapid (see Gathorne-Hardy et al., 2006).

4.5 | Implications for ecosystem function

Identifying generalities is valuable in efforts to extrapolate the links between soil biodiversity and ecosystem function, such as nutrient

cycling under increasing climate change pressure (e.g., Nielsen et al., 2011). From a management perspective, understanding the differences is as important as emphasizing the generalities. We acknowledge that our low replication means it is impossible to draw statistically robust conclusions about biogeographical generalities. However, the surveys are extremely time consuming, a single survey plot requires approximately six months for field collection and taxonomic identification. More replicated surveys are needed, but it will be enormously expensive in time and resources to allow sufficient replication to test these hypotheses properly.

The feeding-group spatial patterns observed here show the possible scales at which termites provide ecosystem services, such as nitrogen and carbon mineralization (Griffiths et al., 2019; Ji & Brune, 2006; Ji et al., 2000; Yamada et al., 2005), soil heterogeneity (Ashton et al., 2019; Donovan, Eggleton, & Bignell, 2001; Donovan et al., 2001), and pedogenesis (Holt & Lepage, 2000). Wood-feeding termites appear to be structured at fine scales in both the Africa plot and Asia plots, although the large foraging extent reported for fungus-growing termites (e.g., Acda & Cabangon, 2013) means they probably have a wide but heterogenous influence on leaf-litter turn-over. While humus-feeding termites are distributed throughout the soil, the magnitude of provided services may well be far greater in Africa due to their higher abundance (Eggleton et al., 1999).

We found it paradoxical that soil feeders, which consume the most uniformly distributed food resource, highly humified (bare) soil, were found to have a *more* heterogeneous structure than humus feeders, which we expected would be responding to a patchier food availability. There are four plausible explanations as follows: (1) environmental factor(s) apart from food availability, (2) intra-feeding group resource partitioning that generate a fine scale "trophic cascade" and therefore aggregation (although evidence suggests this not to be the case in termites feeding on bare soil (Bourguignon, Drouet et al., 2015), or (3) cooperation against predation leads to aggregation, as seen in mixed-species foraging mammals on the African plains or mixed-species flocks of birds, and (4) many soil-feeding termites eat the mound material of other soil-feeding mound builders, and this may be contributing to the aggregation. Although soil feeders are present in low numbers in Asia, their complete absence from the Danum study plot suggests that their functional contribution (e.g., nitrogen mineralization and provision of ammonia [Ji & Brune, 2006]) there will be marginal compared with African forests.

Overall, this study shows the spatial complexity of soil-inhabiting termites and provides some preliminary findings of differences between biogeographical regions. Whether these findings represent repeated general patterns of assemblage structure cannot be assessed using just two data points, but it has suggested hypotheses that can be tested and does show the major difference between the spatial structure of termites in African forests and Southeast Asian forests. The distribution of true soil-feeding termites in Gabon but not in Sabah is a well-established finding, and this seems to have a major role in the spatial structures explored here. It remains to be seen whether the ant-termite interaction

and the environment-distribution findings can be generalized. However, this study does serve to underline the importance of large-scale biogeographical patterns in termite distributions and ecology.

AUTHOR CONTRIBUTIONS

OS, PE, and MK conceived and developed the ideas behind the paper. OS sampled the data and did all the analyses. All authors helped with the writing and final editing of the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad. cz8w9gj38 (Scholtz et al. 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.