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The impact of termites on soil sheeting properties is better explained by environmental factors than by their feeding and building strategies.

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Abstract

Termites are key soil bioturbators in tropical ecosystems. Apart from mound nests constructed by some advanced lineages, most of the species use their faeces, oral secretions, debris, or soil aggregates to protect themselves from predators and desiccation when they go out to forage. Although this soil 'sheeting' is considered to play a key role in soil functioning, the properties of these termite-made materials have been poorly studied. The few available data showed that sheeting properties are highly variable with positive, neutral or negative impacts on soil C and clay content, and consequently on soil aggregate stability. Therefore, the objective of this study was to determine the factors controlling the physical (particle size fractions and structural stability) and chemical (pH, electrical conductivity and carbon content) properties of soil sheeting produced by termite species encompassing all feeding and building categories using a dataset representative of an important diversity of biotopes coming from 21 countries from all continents colonized by termites. We showed that sheeting properties were explained by the properties of their environment, and especially by those of the bulk soil (linear relationships), followed in a lesser extent by the mean annual precipitation and biotope. Classic hypotheses related to termite feeding and building strategies were not hold by our analysis. However, the distinction of termites into fungus-growing and non-fungus growing species was useful when differentiating the impact of termites on soil electrical conductivity, C content, and structural stability. The large variability observed suggests the need to redefine termite functional groups based on their impacts on soil properties using a trait-based approach from morphological, anatomical and/or physiological traits.

Keywords. Feeding guilds, biostructures, ecosystem engineers, fungus-growing termites, bioturbation

1. Introduction

Soil bioturbation involves the modification and/or displacement of soil elements along the soil profile, including the production of biogenic soil aggregates (Wilkinson et al., 2009, Lavelle et al., 2020) and biopores such as tunnels or galleries (Bottinelli et al., 2015). This process is of primary importance in the soil system because it regulates key ecological functions such as those involved in the regulation of nutrient cycling and soil dynamics, the infiltration and diffusion of water in soil, and the resistance of soils to erosion.

In tropical soils, soil bioturbation is mainly carried out by earthworms and termites (Lavelle et al., 1997; Brussaard, 2012; Jouquet et al., 2016; Tuna et al., 2019). Unfortunately, little is known about termite biostructures (Jouquet et al., 2016), as previous literature has focused mostly on earthworms and described the specific biological, physical and chemical properties of earthworm casts compared with the surrounding environment (*e.g.*, Van Groenigen et al., 2019). Moreover, the little available termite literature has focused on their mounds (*e.g.*, Holt and Lepage, 2000; Abe et al., 2009; Mujinya et al., 2013; Jouquet et al., 2011), while there is a dearth of information on soil sheeting. Sheeting, also called mud tubes or covered runways (see Figure 1 as an illustration), is used by termites to cover their food or to forage on the ground and on the bark of trees and for protection from sunlight, drought and predators (Wood, 1988; Harit et al., 2017). Sheeting also helps termites to orientate by keeping them on the pheromone trail (Sillam-Dussès et al., 2005).

Soil sheeting is made of pellets of a few millimeters or aggregates that are glued together and constitute a cohesive soil layer. While small in size, soil sheeting can represent up to several tons ha^{-1} year^{-1} in some tropical ecosystems (*e.g.*, Wood, 1988; Mando, 1997; Rouland et al., 2003), a mass comparable to the amount of earthworm casts produced in temperate regions (Binet et al., 1997; Butt et al., 2015). However, while earthworm casts tend to influence soil fertility and resistance to soil erosion (Blanchart et al., 2004; Laossi et al., 2010; Van Groenigen et al., 2019), soil sheeting has variable effects, with positive, neutral or negative effects on soil C and clay contents, and consequently on soil aggregate stability and soil erosion (Diouf et al., 2006; Villenave et al., 2009; Harit et al., 2007; Jouquet et al., 2012). This extreme variability is likely related to the tendency of termites to alter the properties of their sheeting according to the properties of their environment (*e.g.*, precipitation and clay or C contents in soil) (Jouquet et al., 2015; Harit et al., 2017). However, these statements should be considered with caution, given the paucity of available data (n = 16 to 32 observations from only 24 studies in the meta-analysis carried out by Harit et al., 2017).

The regrouping of species into ecological guilds or functional groups is often used for understanding the influence of biological diversity on ecosystem functioning (Blondel, 2003; de Bello et al., 2010; Gerlach et al., 2013). Therefore, termite species are also commonly grouped into four groups (Groups I to IV) according to their feeding strategies, usually reflected by the structure of their gut and the degree of humification of their feeding substrates (Donovan et al., 2001; Davies et al., 2003; Palin et al., 2011; Dahlsjö et al., 2020). Termite species have also been grouped according to two different building strategies, which are related to the means used in soil construction with species using almost exclusively soil and saliva (*i.e.*, species from the fungus-growing termite group, all belonging to the Macrotermitinae subfamily) and those that incorporate a mixture of saliva, faeces and other non-digested material (*i.e.*, soil-feeding and wood and litter-feeding termites other than fungus-growing termites) (Holt & Lepage, 2000; Jouquet et al., 2011). Comparatively with other organisms (e.g., the utilization of the epigeic, anecic and endogeic earthworm functional categories), these feeding and building groups have rarely been used in the context of land use and/or environmental changes on termite diversity (*e.g.*, Ackerman et al., 2009; Palin et al., 2011; Liu et al., 2019). There is a need, therefore, to adopt relevant ecological indicators that give us a better understanding and prediction of the functional impacts of termites. Here, we examine the factors controlling the properties of soil sheeting produced by termite species across all feeding and building categories using a dataset of different termite biotopes from 21 countries from all continents colonized by termites. The main questions raised in this study are: what are the properties of soil sheeting? Are those properties controlled by the feeding or building strategies of termites, or as suggested by Harit et al. (2017), by the quality of the substrates covered by sheeting and/or the properties of their local environment?

2. Material and Methods

2.1. Study sites and sampling method

Soil sheeting and the surrounding bulk soil were sampled in 34 study sites from 19 countries (Figure 1, Table 1). We collected samples of visible soil sheeting covering leaf litter, fallen or standing branches or trees, and a sample of the surrounding bulk soil, about 2 m away, without visible evidence of bioturbation by termites or other invertebrates (2-5 cm depth; 3-5 samples, ~20-50 g composite). Termites were also sampled for taxonomic identification. We also used published data from 15 additional study sites from seven countries, resulting in a total of 49 sites and 21 countries.

2.2. Soil analyses

Soil samples were air-dried for several days before analysis. The total organic carbon concentrations (C) were measured using a SHIMADZU TOC V_{CSH} analyzer (model SSM-5000A). Calcareous soils were pre-treated with diluted HCl. Soils were sieved in water after soil organic matter (SOM) destruction using H_2O_2 and complete soil dispersion with Na-hexametaphosphate and ultrasonication. Three soil particle size classes were considered: sand > 50 µm, silt between 50 and 2 µm, and clay content for particles < 2 µm. Soil pH and electrical conductivity (EC) were determined in soil/water suspension (1:5 woil:water solution). The percentage of water stable aggregates > 5 mm corresponded to the percentage of soil aggregates > 200 µm that resisted to the immersion in 100 ml water during 10 min and after removal of the quantity of sand particles > 50 µm. For each variable, the properties of sheeting were compared to those of the bulk soil (in % relative to bulk soil) using the response ratio (R) as follow: $R = 100 \times (Vt / Vc)$, where V is the value of the response variable for termite sheeting (t) or for the bulk soil (c).

2.3 Potential controlling factors

Samples were described by three set of predictor variables, comprising environmental and ecological variables and ecological groups. Environmental variables included the type of substrate covered by sheeting (woody material, grass or leaves, compost or dung), the biotopes and the mean annual precipitation (MAP). Biotopes were determined from the habitats given in Table 1 and simplified into: laboratory conditions, cultivated or pastoral (agro-pastoral), parks, garden and urban trees (urban), tree plantations (planted), and less disturbed environments such as forests, savannahs and deserts (natural). Ecological variables were the size of the nest (estimated from the literature and differentiated into medium (nests < 1 m^3), large (1- 3 m^3) or very large (> 3 m^3)) and the ecological groups to which the species belong. Feeding strategy-based functional groups differentiated species belonging to the Groups I to III (G_{I}, for wood-feeding basal termites; G_{II}, for advanced termites feeding on dead wood, grass and leaf litter, including fungus-growing termites; and G_{III} for humus or soil-wood interface termites, Donovan et al. (2001)). Group IV species (*i.e.*, true soil-feeding termites) were excluded because they do not produce above-ground sheeting. Building strategy-based functional groups arranged termites into fungus-growing termites (FG) and non-fungus growing termites (non-FG) (Holt and Lepage, 2000; Jouquet et al., 2011).

2.4 Statistical analyses

Since the sampling effort was unbalanced with more replicates in some situations than in others, R values were averaged per species and per study site (n = 84 observations in total). Principal Component Analysis (PCA) were first used to assess differences in R values between feeding and building groups. Differences between groups were tested using Monte Carlo simulation tests. In addition, one-way ANOVA were performed to assess differences in R values between feeding and building groups. Prior to running ANOVA, data were tested for homogeneity of variance and normality. Kruskal-Wallis Chi² and Wilcoxon-Mann-Whitney U tests post-hoc planned pairwise comparisons were performed with a false discovery rate correction when parametric analysis of variance was impossible to use. The relative importance of the potential controlling variables explaining soil sheeting properties were measured from the whole dataset (n = 242 observations) and using the supervised machine learning algorithm Random Forest (ntree = 500, mtry = 2) (*e.g.*, Breiman, 2001). Importance of the predicting variables was given using the Gini impurity index (IncNodePutity) and results were displayed using a radar chart. Regarding the results from the random forest models, linear regressions and analysis of covariance (ANCOVA) were used to assess relationships between the properties of sheeting and those of the surrounding soil and with feeding or building groups as categorical independent variables. The slopes of regression lines were compared to y = x from the t test confidence interval and the offset function. Differences were considered significant only when *P* values were lower than 0.05. All statistical analyses and visualizations were carried out with R software using mainly “ade4”, “FactoMineR”, “Factoextra”, “randomForest”, “mlbench”, “caret” and “ggplot2” packages.

3. Results

3.1. Overall effect of termites

The impact of termites on soil sheeting properties, without differentiation into feeding or building groups, is shown in Figure 2. Relative termite effects (R values) were highly variable for EC, and the C, clay, silt and sand contents (mean coefficient of variation, CV = 0.54) in comparison with the percentage of water stable aggregates and the pH (CV = 0.25 and 0.08, respectively). The impact of termites was positive (R values were above 100%) for EC, and the C, clay and silt contents (t test, $P < 0.05$ in all cases). A neutral impact was measured for the pH and the percentage of stable aggregates (R = 100%, $P = 0.871$ and 0.655 for pH and stability, respectively). Finally, a negative impact was measured for the percentage of sand (R < 100%, $P = 0.035$).

3.2. Feeding vs. building strategies

The projection of the R values onto the first two axes of the PCA failed to differentiate either the three feeding groups (Figure 3a) or the two building groups (Figure 3b; Monte Carlo simulation test, $P > 0.05$). Additionally, ANOVA revealed significant differences between groups for stability only (Table 2), which was higher in non-FG (108 ± 23.6%, mean ± SE) than FG (79 ± 7.9%).

Random forest models carried out using the entire dataset explained 35, 68, 34, 77, 36, 53 and 76% of the variability for EC, pH, C, stability, sand, silt and clay, respectively. Properties of the bulk soil and MAP best explained the R values (Figure 4). The biotope was also an important predictor for the stability. Substrate type and ecological variables (*i.e.*, nest size, feeding and building functional groups) played only limited roles.

3.3. Relationship between sheeting and bulk soil properties

The impacts of termites on soil sheeting EC, aggregate stability and C content were the best explained by their building strategies (Table 3). We found different relationships between termite sheeting and bulk soil properties for different soil properties and feeding groups. For example, for FG termites, EC in sheeting was highly correlated with bulk soil, but not for non-FG termites. For aggregate stability, sheeting was highly correlated with bulk soil for non-FG, while the stability of sheeting was constant with 60% of water stable aggregates for FG termites (Figure 5b). Sheeting for non-FG termites was always enriched in C, but for FG termites, carbon enrichment only occurred when bulk soils had less than 2% C (Figure 5c).). Soil pH, sand, silt and clay contents of termite sheeting were all linearly related to the properties of the bulk soil, irrespective of termite feeding or building group (Figures 5e-g). Regression analyses indicated that soil pH was higher in termite sheeting below bulk soil pH of 6.6 and generally clay enriched. Sheeting was silt enriched at bulk soil silt levels < 21%.

3.4. Influence of MAP and biotopes on soil sheeting properties

No relationship could be measured between the relative effects of termites and MAP when termites were differentiated into feeding groups ($P > 0.05$ in all cases, data not shown). Conversely, a low but significant relationship was found between MAP and R_C when species were differentiated into FG and non-FG termites ($R^2 = 0.11$, $P = 0.048$, Figure 6) ($P > 0.05$ for all the other R values). A significant negative relationship was found between R_C and MAP for FG termites ($R^2 = 0.55$, $P < 0.001$). Although the influence of termites was mainly neutral or positive (*i.e.*, $R_C \geq 100$ %), the model suggested a negative effect of termites (i.e., $R_C < 100$ %) for MAP > 1500 mm year^{-1}. Regressions also evidenced a positive linear relationship between R_C and MAP for non-FG termites ($R^2 = 0.40$, $P < 0.001$) with a threshold measured at 500 mm year^{-1}. Biotopes did not significantly influence R values ($P > 0.05$ in all cases, Table 4).

4. Discussion

4.1. Relevance of the feeding and building functional groups

In this study, we focused on termite soil sheeting, which have been much less studied than termite mounds, and used a dataset representative of an important diversity of biotopes, from humid tropical forests in Vietnam and Colombia to arid and semi-arid environments in USA, Djibouti and Niger. A first striking result of this study is that the impact of termites on soil sheeting properties was highly variable with positive, neutral and negative values, indicating both increases and decreases in comparison with the bulk soil. Consequently, the PCA did not reveal clear trends using percent enrichment ratios (Figure 3), which raised the question of the value of feeding and building categories for understanding the functional impact of termites on soil sheeting properties.

Random forest models were useful for explaining a significant proportion of the variability in our enrichment ratios. They highlighted the importance of the environment for explaining R values and showed that, before being explained by the feeding and building group classifications, termite sheeting properties were explained by the properties of the bulk soil, thus confirming the study of Harit et al. (2017), and to lesser extent by the mean annual precipitation and biotopes. This was evidenced by the linear relationship between pH and the particle size distribution in termite sheeting with those measured in the bulk soil, without distinction between the feeding and building ecological groups (Figure 5d-g). Additionally, in line with the meta-analysis of Harit et al. (2017), the electrical conductivity, percentage of water stable aggregates, and C contents of termite sheeting were also linearly related to those of the bulk soil. However, we showed that distinguishing FG and non-FG termites was most useful to understand the impact of termites on soil sheeting properties. The same conclusion could be drawn from the influence of the mean annual precipitation on R_C, which was best explained by distinguishing between FG and non-FG termites. Therefore, we confirm both the major impact of environmental conditions, as suggested by Harit et al. (2007), and the usefulness of the classification proposed by Holt and Lepage (2000) and Jouquet et al. (2011) for understanding the functional impacts of termites on soil electrical conductivity, aggregate stability and C content.

4.2. Consequences on soil properties

Termites are considered intended engineers (Jouquet et al., 2006) and their nest constructions viewed as extended phenotypes (Turner, 2004) because mound architecture and its impact on soil properties reflect the interaction between termite ecological needs and the properties of their environment (*e.g.*, Korb and Linsenmair, 2000; Jouquet et al., 2006). The same reasoning has been used to explain the variability of their sheeting properties. Among soil properties, clay particles play a major role by cementing soil particles and are preferentially used by termites for building sheeting (Jouquet et al., 2007, 2015; Zacharia et al., 2017) because of the specific properties they confer to their constructions, such as providing a better microclimatic environment and stability (Obesrt et al., 2016; Jin et al., 2020). These results were confirmed in our study since termite sheeting were always impoverished in sand and always enriched in clay in comparison with the bulk soil. Therefore, these results suggest that termite effects will be critically important in sandy soils where a small incorporation of clay can have a significantly impact on soil functioning. They also confirm the importance of clay particles for termites (Harit et al., 2017) and the ability of termites to manipulate and select these particles from the bulk soil (Jouquet et al., 2002; Mujinya et al., 2013; Oberst et al., 2016).

In their review, Harit et al. (2017) also suggested that termites enrich their sheeting in C in poor soils but reduce it in soils where the C content exceeds 1%. Using a much larger dataset, our study shows that this relationship can be explained by the different building strategies of FG and non-FG termites. Non-FG termites tend to enrich the C content in soil sheeting in comparison with the bulk soil, mostly because their sheeting are made of soil and faeces (Wood, 1988). However, the positive impact of non-FG termites was more pronounced in more humid environments, as shown by the positive relationship between R_C and the mean annual precipitation. Conversely, linear regression suggests that FG termites, which only use soil and saliva during the molding of sheeting (Wood, 1988; Contour-Ansel et al., 2000), tend to enrich their constructions in C when the C content in the surrounding soil is less than 2% while they tend to reduce it above this threshold. This adaptation to the environment is also evidenced by the negative relationship between R_C and the mean annual precipitation. In our study, drylands had lower C contents than more humid environments and the linear regression suggests that positive impact of termites on sheeting C is mainly restricted to ecosystems with a mean annual precipitation < 1500 mm year^{-1}.

The lack of a linear relationship between EC in sheeting and in bulk soil for non-FG termites is likely to reflect the diversity of the feeding strategies, gut morphology and physiology of the species belonging to this group (Donovan et al., 2001). Conversely, the linear relationship between sheeting of FG termites and the bulk soil suggests that the incorporation of saliva has a limited impact on the electrical conductivity of sheeting, which was mainly influenced by the surrounding soil properties. Similarly, soil pH was only poorly impacted by termite activity. Because pH in the gut of non-FG termites can significantly differ from soil pH, particularly in the anterior hindgut of termites from the Termitidae family, where pH is alkaline (Brune, 2014), one could have expected a significant influence of the functional groups on sheeting pH. We consider that the absence of such effect could be explained by a short retention time in the gut.

The different building strategies of FG and non-FG termites also had an influence on the water stability of soil sheeting, which reflects the need for termites to control their environment and protect themselves against predators (Eggleton, 2010). The aggregate stability of FG sheeting was highly variable but contained in average ~60% of stable soil aggregates irrespective of the stability of bulk soil aggregates. Although our dataset does not allow us to pinpoint the mechanisms associated to the stability of soil aggregates, this result confirms an ability and/or the need of this functional group to control the properties of sheeting. This result also shows that the impact of FG termites is more important in environments characterized by low soil aggregate stability. This hypothesis is reinforced by the negative relationship between R_C and the mean annual precipitation, which suggests a more important incorporation of C in soil in drier environments, which are also often sandier, with a low C content and with a lower water stability (*i.e.*, in Niger and Djibouti) than in more humid environments. Conversely, non-FG termite sheeting was as stable as the bulk soil, suggesting a more limited ability or lower need of this group to build stable soil sheeting in comparison with FG termites.

An abundant literature describes the influence of land use type on termite functional and taxonomic diversity (Jones et al., 2003; Vaessen et al., 2011; Muvengwi et al., 2017; Liu et al., 2019). Our study shows that the impact of termites on sheeting properties is also influenced by biotope. This finding came out from the random forest models, especially for $R_{\mathrm{Stability}}$. However, no significant influence of the biotope type could be explained by our statistical analyses, most likely because of the low number of replicates per biotope and important above-mentioned variability. Therefore, more research is clearly needed to confirm that the impact of termites on soil properties, and especially on the stability of soil aggregates, varies depending on the biotope type.

5. Conclusion

Understanding the impact of biodiversity on soil functioning has become a key challenge, especially regarding its importance for the definition of sustainable agricultural practices (Brussaard et al., 2007; Bender et al., 2016; Bach et al., 2020; Tamburini et al., 2020). Because species identification skills are often lacking, species are commonly grouped into ecological or functional categories. The relevance of this approach is currently being debated with earthworms (*e.g.*, Van Groenigen et al., 2019; Bottinelli et al., 2020) but remains unexplored with termites. As suggested by Harris (1956), the ecological impact of termites is the outcome of several interacting forces: behavioral, material and climatic. However, it appears from this study that one termite's adage could be "tell me where you live and I'll tell you what you do". Before accounting for their feeding or building strategies, the impact of termites on soil sheeting properties is explained by the properties of their environment, particularly those of the bulk soil. Moreover, if the distinction between FG and non-FG termites is the most relevant, this study shows that there are major differences in the effects of termites that are not accounted for by a simple delineation between FG and non-FG. The large variability observed suggests the need to reshape or refine the groups using a trait-based approach from morphological, anatomical and physiological traits as it is commonly used for other organisms (Bottinelli et al., 2020).

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Author contributions

All authors have given approval to the final version of the manuscript. Pascal Jouquet coordinated the sampling design and analyses, and wrote the article with edits from all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Figure captions

Figure 1. World map showing the locations of the sampling sites. In red are samples collected by the consortium and in green are data coming from published articles (see table 1). An illustration of termite sheeting covering a tree is displayed (© IRD - Cristal Ricoy Martinez, 2020).

Figure 2. Boxplot representations of the response variables R (in % relative to bulk soil) for the clay content, electrical conductivity, carbon content, silt content, proportion of stable aggregates, pH and sand content.

Figure 3. Biplots showing the principal components analysis (PCA) from the response ratios for carbon (R_{C}), clay (R_{Clay}), electrical conductivity (R_{EC}), pH (R_{pH}), sand (R_{Sand}), silt (R_{Silt}) and stability ($R_{Stability}$) for sheeting made by termites belonging to Group I (circle), II (triangle) and III (square) (a) or to the fungus-growing (FG, circle) and non-fungus growing (non-FG, triangle) ecological groups (b). Large symbols represent the barycentres.

Figure 4. Linear regressions showing the influence of the properties of the surrounding soil on termite sheeting properties (electrical conductivity, 'EC'; aggregate stability, 'stability'; carbon content, 'C'; pH; and the sand, silt and clay contents). In orange: full dataset. In blue and red: data from fungus-growing termites (FG) and non-fungus-growing (non-FG) termites, respectively. Linear regressions are displayed in dashed lines while the bisecting line (y = x) is displayed in black.

Figure 6. Linear regressions showing the influence of mean annual precipitation (MAP, in mm $year^{-1}$) on R_{C} (in % relative to the bulk). In blue and red are data from fungus-growing termites (FG) and non-fungus-growing (non-FG) termites, respectively. Regression curves are displayed in dashed lines. The black line corresponds to R = 100 %, which represents the influence threshold above which termites have positive impacts and below which they have negative impacts.

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Figure 1

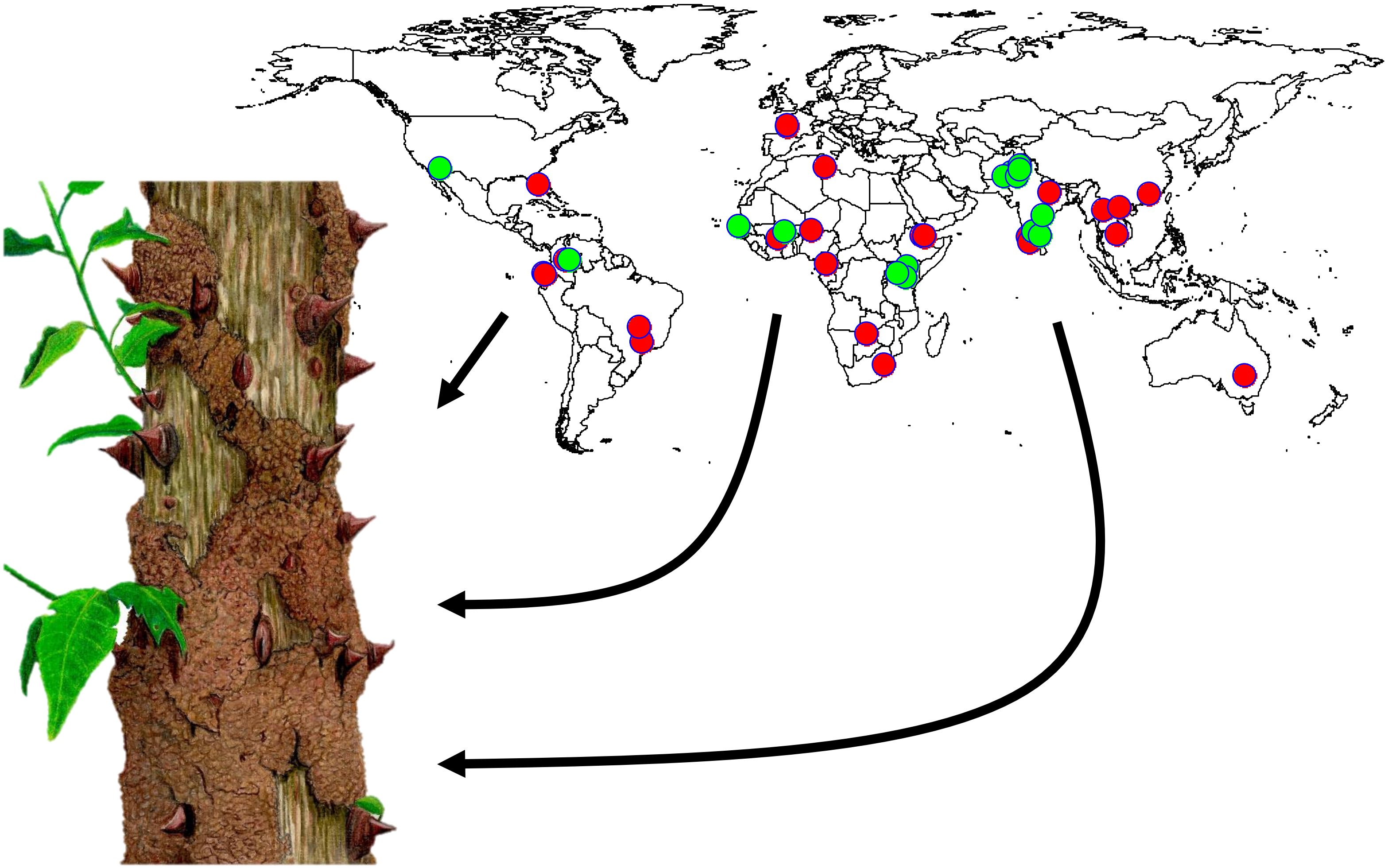


Figure 2

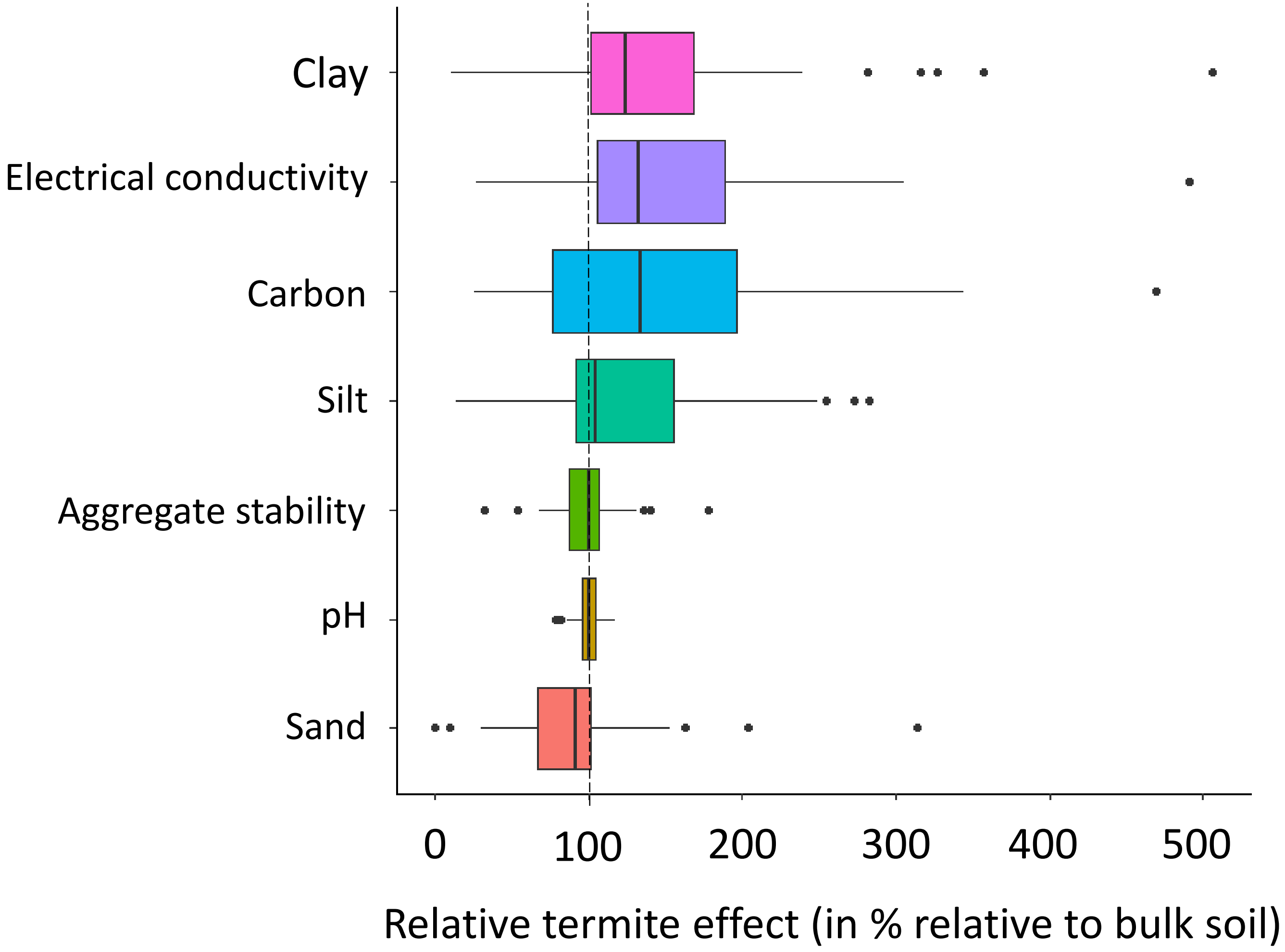

Clay
Electrical conductivity
Carbon
Silt
Aggregate stability
pH
Sand
0
100
200
300
400
500
Relative termite effect (in % relative to bulk soil)

Figure 3

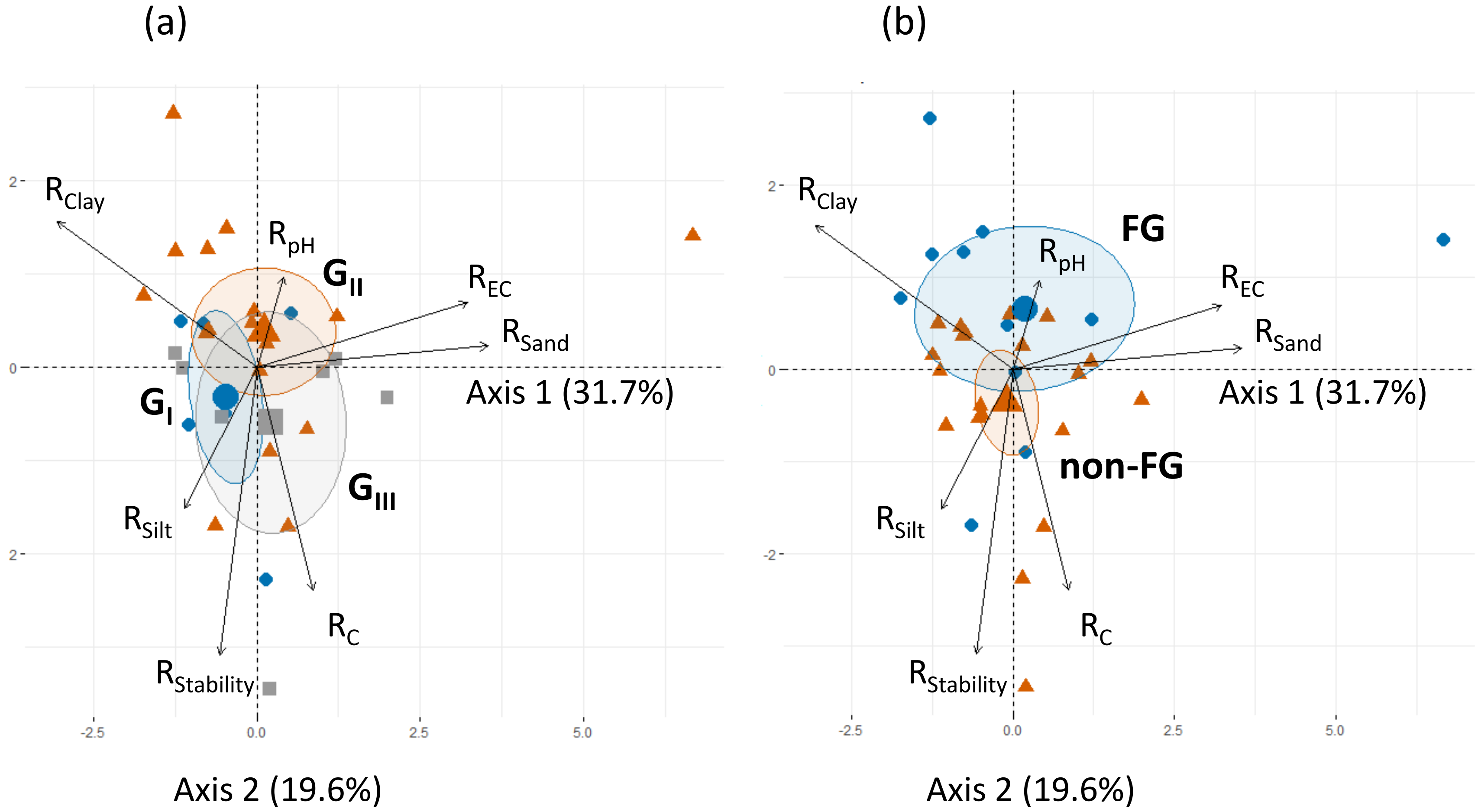

(a)
R_{Clay}
R_{pH}
G_{II}
R_{EC}
R_{Sand}
G_{I}
Axis 1 (31.7%)
G_{III}
R_{Silt}
R_{C}
$R_{Stability}$
2
0
2
-2.5
0.0
2.5
5.0
Axis 2 (19.6%)
(b)
R_{Clay}
FG
R_{pH}
R_{EC}
R_{Sand}
Axis 1 (31.7%)
non-FG
R_{Silt}
R_{C}
$R_{Stability}$
2
0
-2
-2.5
0.0
2.5
5.0
Axis 2 (19.6%)

Figure 4

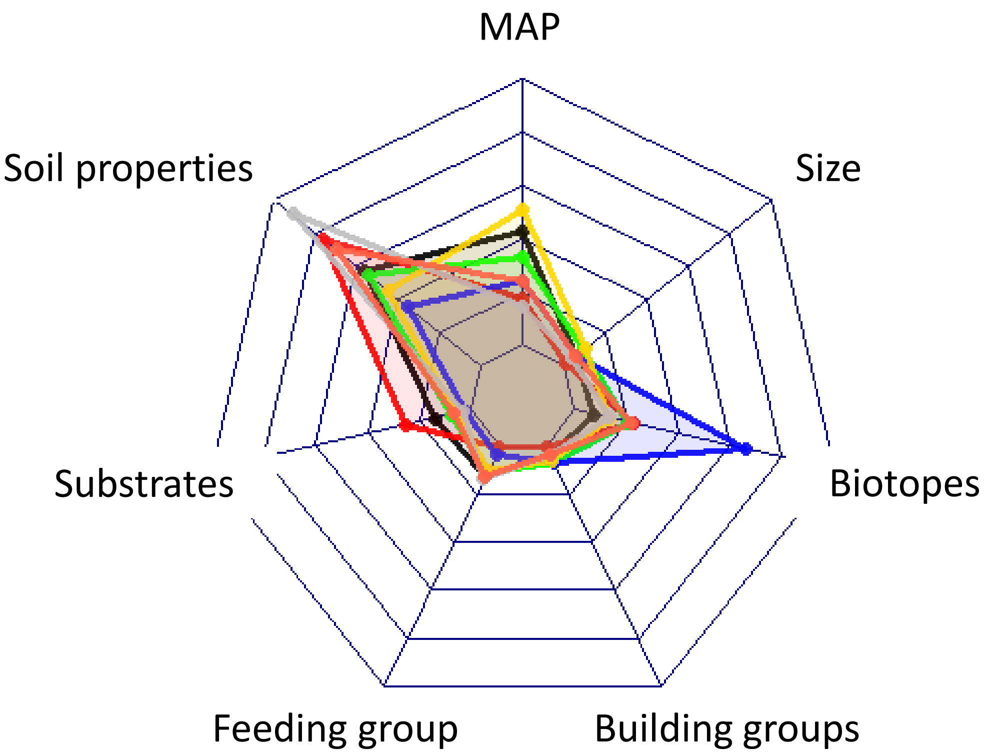

MAP
Size
Biotopes
Building groups
Feeding group
Substrates
Soil properties

Figure 5

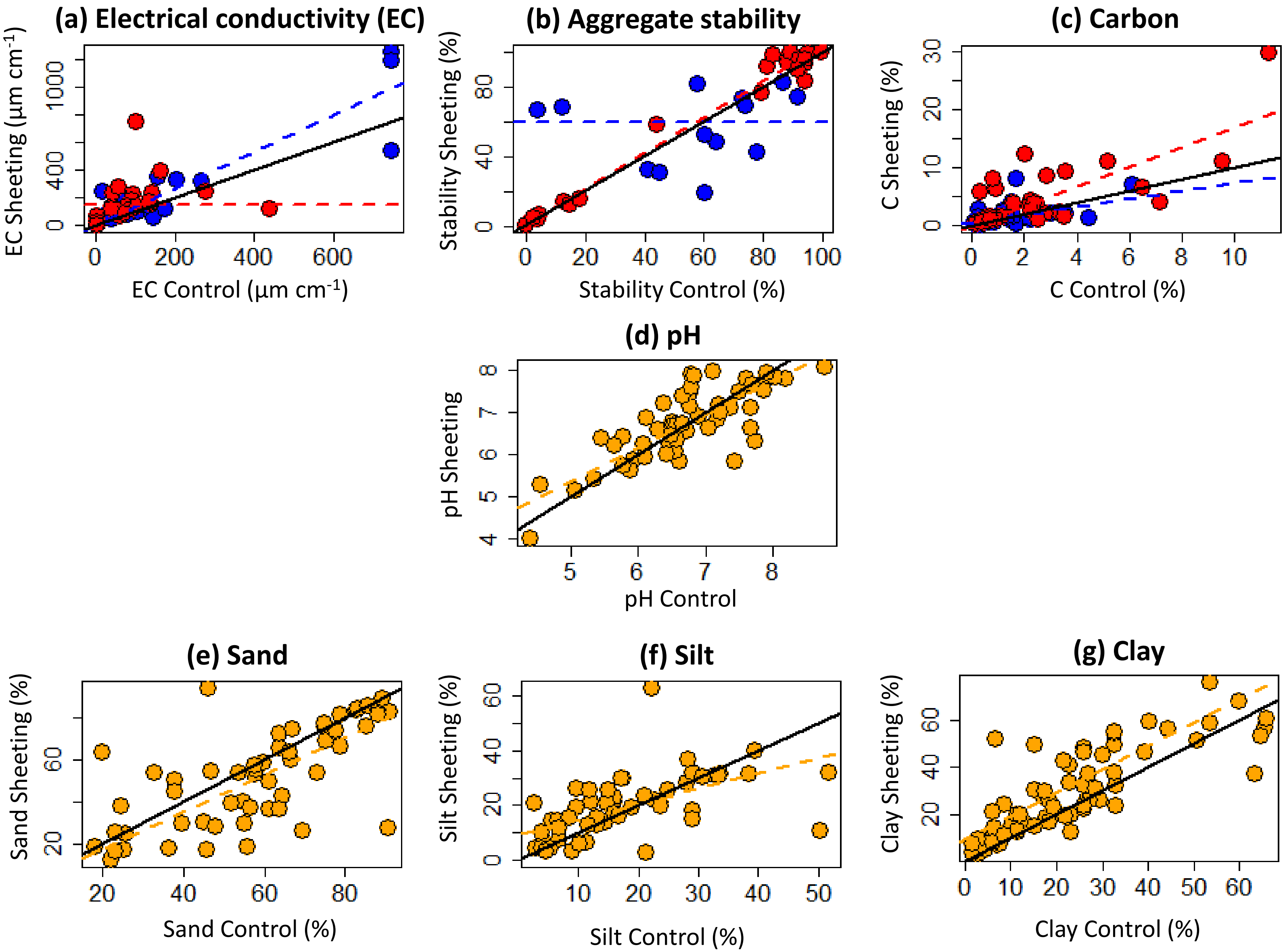
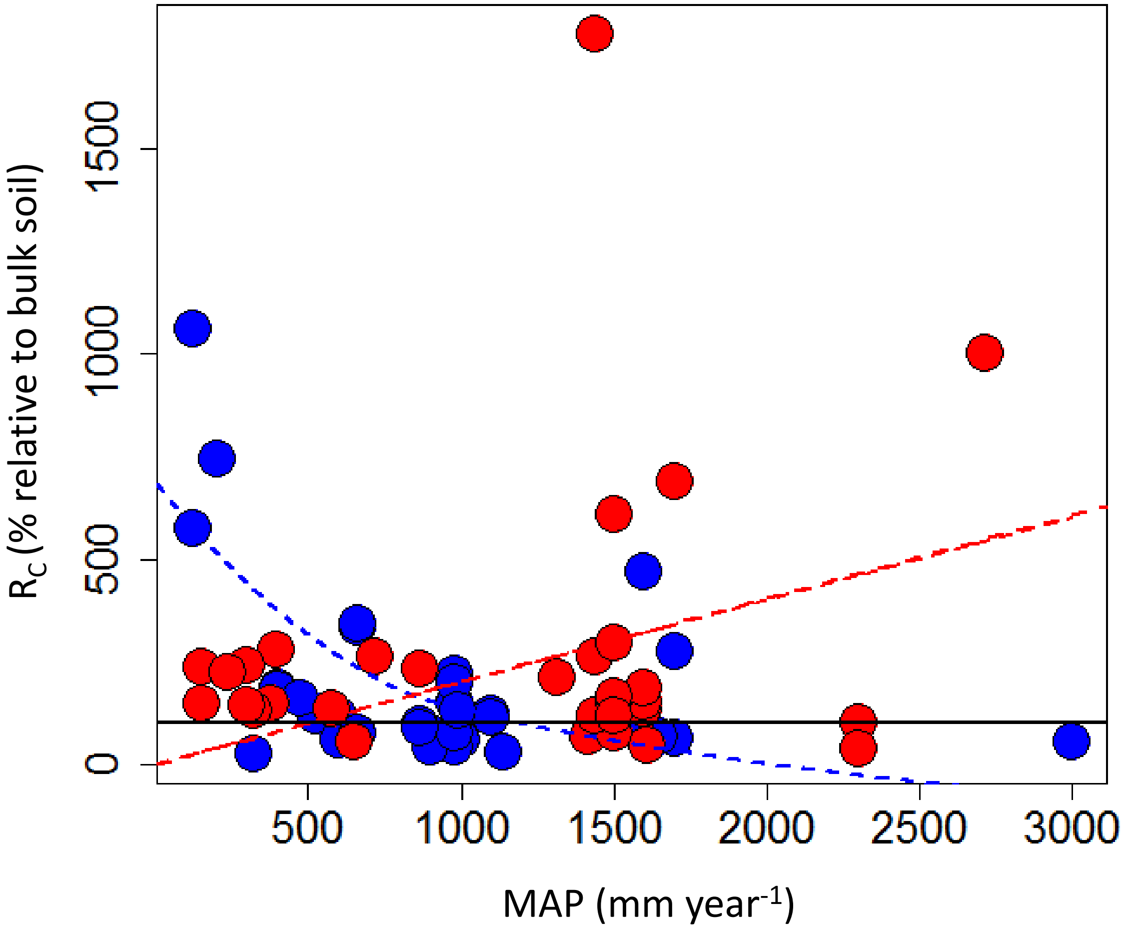

(a) Electrical conductivity (EC)
EC Sheeting (µm cm^{-1})
0
400
1000
0
200
400
600
EC Control (µm cm^{-1})
(b) Aggregate stability
Stability Sheeting (%)
0
40
80
0
20
40
60
80
100
Stability Control (%)
(c) Carbon
C Sheeting (%)
0
10
20
30
0
2
4
6
8
10
C Control (%)
(d) pH
pH Sheeting
4
5
6
7
8
5
6
7
8
pH Control
(e) Sand
Sand Sheeting (%)
20
60
20
40
60
80
Sand Control (%)
(f) Silt
Silt Sheeting (%)
0
20
40
60
10
20
30
40
50
Silt Control (%)
(g) Clay
Clay Sheeting (%)
20
40
60
0
10
20
30
40
50
60
Clay Control (%)

Figure 6



R_C (% relative to bulk soil)
0
500
1000
1500
500
1000
1500
2000
2500
3000
MAP (mm year^{-1})

The impact of termites on soil sheeting properties is better explained by environmental factors than by their feeding and building strategies.

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TABLES

Table 1. Information about the sampling sites: location (country), GPS coordinates, habitat with in parenthesis the biotope type, Mean Annual Precipitation, MAP), and reference of the articles when data were previously published.

Location	Coordinates	Species	Habitat	MAP (mm)	References
Australia	31°32′02″S, 145°25′23″E	*Drepanotermes* sp.	Bush (natural)	236	
Botswana	18°44′18″S, 24°21′54″E	*Macrotermes michaelseni*	Savannah (natural)	600	
Brazil	21°07′48″S, 47°50′55″W	*Heterotermes* sp., *Neocapritermes* sp., *Embiratermes* sp. *Procornitermes araujoi*, *Vecocitermes* sp., *Syntermes* sp.	Urban park (urban)	1500	
	16°23′S, 48°56′W	*Nasutitermes* sp.. *Diversitermes* sp.	Gallery forest (natural)	1440	
		Anoplotermes sp., *Nasutitermes* sp., *Diversitermes* sp.. *Nasutitermes* sp.	Semi-deciduous forest (natural)	1440	
		Armitermes sp. or *Silvestritermes* sp.	Cerrado (natural)	1440	
Burkina Faso	11°13′25″N, 4°20′58″W	*Macrotermes* sp., *Odontotermes* sp.,	Savannah (natural)	1000	
	13°19′12″N, 2°13′12″W	*Macrotermes* sp.	Cultivated land (agro-pastoral)	660	Kaiser et al., 2017
Cambodia	12°21′09″N, 104°28′28″E	*Coptotermes* sp., *Globitermes globosus*, *Odontotermes* sp., *Macrotermes gilvus*	Cultivated land (agro-pastoral)	1700	
Cameroon	3°14′03″N, 11°16′54″E	*Microcerotermes* sp., *Nasutitermes* sp., Termitinae sp., *Odontotermes* sp., *Anoplotermes* sp.	Secondary forest (natural)	866	
China	24°59′21″N, 115°03′10″E	Nasutitermitinae sp.	Semi-deciduous forest (natural)	1609	
Colombia	4°37′N, 71°19′W	*Ruptitermes* sp.	Savanna (natural)	2300	Decaëns et al., 2001 Hedde et al., 2015
	4°49′48″N, 72°53′40″W	*Microcerotermes cf. exiguus*, *Nasutitermes* sp., *Nasutitermes similis*	Eucalyptus plantation (planted)	2714	
Djibouti	11°45′15″N, 42°41′17″E	*Macrotermes* sp.	Forest National Park (natural)	120	
	11°31′51″N, 42°51′26″E	*Macrotermes* sp.	Pastoral area (agro-pastoral)	120	
	11°41′07″N, 42°06′20″E	*Macrotermes* sp.	Pastoral area (agro-pastoral)	120	
Ecuador	0°00′01″S, 79°15′36″W	*Microcerotermes* sp., *Nasutitermes* sp.	Palm tree plantation (planted)	1600	
	4°04′48″S, 79°12′00″W	*Embiratermes* sp.	Primary forest (natural)	923	
	0°18′08″S, 79°03′16″W	*Embiratermes* sp.	Secondary forest (natural)	1317	
France	45°57′45″N, 1°18′29″W	*Reticulitermes flavipes*	Tree plantation (planted)	650	
	45°56′54″N, 1°04′59″E	*Reticulitermes* sp.	Private garden (urban)	720	
India	11°33′56″N, 76°32′47″E	*Odontotermes* spp.	Private park (urban)	980	
	11°26′24″N, 76°15′36″E	*Odontotermes* spp.	Secondary forest (natural)	980	
	12°00′25″N, 79°48′43″E	*Odontotermes brunneus*, *Hypothermes obscuriceps*	Secondary forest (natural)	1100	
	13°01′19″N, 77°34′02″E	*Odontotermes* spp.	Secondary forest (natural)	980	
	12°00′25″N, 79°48′43″E	*Odontotermes* sp., *Macrotermes* sp., *Hypotermes* sp.	Cultivated land (agro-pastoral)	1140	Lejoly et al., 2019

	13°04′33″N, 77°34′34″E	*Odontotermes wallonensis, O. redemanni, O. ceylonicus,* *O. horni, O. obesus*	Cultivated land (agro-pastoral)	980	Kalidash, 1986, Basappa, 1984 Basappa & Rajagopal, 1990 Kumar et al., 1991
	11°56′N, 79°53′E	*Hypotermes obscuriceps*	Laboratory conditions (laboratory)		Harit et al., 2017
	25°19′41″N, 82°58′21″E	*Odontotermes* sp.	Secondary forest (natural)	322	
	17°93’N, 80°83′E	*Odontotermes obesus*	Forest (natural)	990	Nageswara et al., 2013
Kenya	1°05′37″S, 36°54′21″E	*Odontotermes badius*	Coffee state (planted)	869	Robinson, 1958
	2°18′N, 37°00′E	*Odontotermes* sp.	Bushland (natural)	200	Bagine, 1984
	0°04′12″N, 34°14′24″E	*Pseudacanthotermes* sp., *Macrotermes* sp.	Cultivated land (agro-pastoral)	1580	Kihara et al., 2015
Niger	13°32′13″N, 6°37′45″E	Macrotermitinae sp.	Agro-pastoral (agro-pastoral)	525	
Pakistan	31°31′N, 71°04″E	*Anacanthotermes macrocephalus*	Cultivated land (agro-pastoral)	395	Sheikh and Kayani, 1982
	30°15′N, 68°25″E	*Anacanthotermes vagans*	Tree plantation (planted)	378	Sheikh and Kayani, 1982
	30°31′N, 72°43″E	*Coptotermes heimi*	Cultivated land (agro-pastoral)	320	Sheikh and Kayani, 1982
	33°55′N, 73°25″E	*Heterotermes indicola*	Tree plantation (planted)	1600	Sheikh and Kayani, 1982
	32°50′N, 73°45″E	*Amitermes belli*	Tree plantation (planted)	576	Sheikh and Kayani, 1982
Senegal	14°55′N, 16°49′W	*Odontotermes* sp.	Cultivated land (agro-pastoral)	475	
	14°46′59″N, 16°56′02″W	*Odontotermes nilensis, Ancistrotermes guineensis*	Cultivated land (agro-pastoral)	400	Mora et al., 2003
South Africa	29°36′06″S, 30°21′07″E	*Macrotermes* sp.	Park (urban)	665	
Thailand	19°38′54″N, 100°17′19″E	*Odontotermes* sp., *Microtermes* sp.	Rubber tree (agro-pastoral)	1000	
Tunisia	33°17′39″N, 10°47′04″E	*Anacanthotermes sp.* (most likely *A. ochraceus*)	Bush land (natural)	150	
USA	27°32′23″N, 81°11′59″W	*Coptotermes gestroi*	Laboratory (laboratory)		
	32°55′04″N, 112°40′12″W	*Heterotermes aureus, Gnathamitermes perplexus*	Desert (natural)	300	Nutting et al., 1987
Vietnam	20°34′15″N, 105°17′26″E	Macrotermitinae sp.	Secondary forest (natural)	1650	

Table 2. Results from the ANOVA (*F* and *P*-values) or Kruskal-Wallis Chi^2 test testing the influence of the ecological groups (feeding vs. building groups) on the response ratio (R) for the different soil properties (electrical conductivity (EC), pH, carbon content (C), percentage of water stable aggregates (stability), and sand, silt and clay contents). Bold letters indicate significant results ($P < 0.05$).

	R_{EC}	R_{pH}	R_{C}	$R_{Stability}$	R_{Sand}	R_{Silt}	R_{Clay}
Feeding groups (I, II or III)	*Chi*^{2} = 0.90 *P* = 0.638	$F_{2,51}$ = 0.25 *P* = 0.782	*Chi*^{2} = 0.87 *P* = 0.647	*Chi*^{2} = 3.79 *P* = 0.150	*Chi*^{2} = 0.92 *P* = 0.631	*Chi*^{2} = 6.12 *P* = 0.057	*Chi*^{2} = 3.51 *P* = 0.173
Building groups (FG vs. NFG)	*Chi*^{2} = 0.57 *P* = 0.448	$F_{1,52}$ = 0.01 *P* = 0.956	*Chi*^{2} = 3.51 *P* = 0.061	*Chi*^{2} = 4.31 ***P* = 0.038**	*Chi*^{2} = 2.33 *P* = 0.127	*Chi*^{2} = 1.06 *P* = 0.302	*Chi*^{2} = 0.24 *P* = 0.623

Table 3. Results of the linear models testing the influence of the initial soil properties (X) on termite sheeting properties (Y) and for the whole dataset ("all", no differentiation between groups) or for the different feeding (I to III) or building (fungus-growing, "FG" vs. non fungus-growing, "non-FG") ecological groups. Only most significant models (ANCOVA testing differences in slope and/or intercept) and models considering the whole dataset without differentiation between functional groups are displayed.

	Functional Groups		Models	
Electrical conductivity (EC, µS cm^{-1})	All		$R^2 = 0.76$, $P < 0.001$	Y = 1.27 X
	Building	G_{FG}:	$R^2 = 0.88$, $P < 0.001$	Y = 1.32 X
		G_{NFG}:	$R^2 = 0.01$, $P = 0.987$	Y = 149.5
pH	All		$R^2 = 0.66$, $P < 0.001$	Y = 1.33 + 0.80 X
Carbon (C, %)	All		$R^2 = 0.68$, $P < 0.001$	Y = 1.50 X
	Building	$G_{II\ FG}$:	$R^2 = 0.27$, $P < 0.001$	Y = 0.70 + 0.66 X
		$G_{II\ NFG}$:	$R^2 = 0.72$, $P = 0.003$	Y = 1.69 X
Stability (%)	All		$R^2 = 0.93$, P < 0.001	Y = 0.98 X
	Building	G_{FG}:	$R^2 = 0.08$, $P = 0.325$	Y = 59.58
		G_{NFG}:	$R^2 = 0.99$, $P < 0.001$	Y = X
Sand (%)	All		$R^2 = 0.91$, $P < 0.001$	Y = 0.88 X
Silt (%)	All		$R^2 = 0.33$, $P = 0.314$	Y = 9.48 + 0.55 X
Clay (%)	All		$R^2 = 0.66$, $P < 0.001$	Y = 5.40 + X

Table 4. Results from the ANOVA (*F* and *P*-values) or Kruskal-Wallis Chi² test testing the influence of the biotope type (laboratory conditions or natural, planted, agro-pastoral or urban ecosystems) on the response ratio (R) for the different soil properties (electrical conductivity (EC), pH, carbon concentrations (C), stability, sand, silt and clay.

R_{EC}	R_{pH}	R_{C}	$R_{Stability}$	R_{Sand}	R_{Silt}	R_{Clay}
$Chi^2 = 3.97$	$F_{4,51} = 1.09$	$Chi^2 = 3.51$	$F_{4,29} = 0.75$	$F_{4,56} = 1.81$	$Chi^2 = 4.14$	$Chi^2 = 4.32$
$P = 0.409$	$P = 0.373$	$P = 0.480$	$P = 0.568$	$P = 0.139$	$P = 0.387$	$P = 0.364$