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The Topological Fortress of Termites

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Abstract. Termites are known for building some of the most elaborate architectures observed in the animal world. We here analyse some topological properties of three dimensional networks of galleries built by termites of the genus *Cubitermes*. These networks are extremely sparse, in spite of the fact that there is no building cost associated with higher connectivity. In addition, more "central" vertices (in term of betweenness or degree) are preferentially localised at spatial positions far from the external nest walls (more than in a null network model calibrated to exactly the same spatial arrangement of vertices). We argue that both sparseness and the particular spatial location of "central" vertices may be adaptive, because they provide an ecological advantage for nest defence against the attacks from other insects.

Keywords: spatial networks, social insects, morphogenesys, complex systems, patterns.

1 Introduction

Social insect societies have attracted much attention because of the complex level of coordination and organization of their collective activities. These allow them to perform complex tasks, such as finding the shortest path to a food source [9] and building elaborate nests [12]. These abilities do not result from planning or supervision, but emerge from the direct or indirect interactions between insects. Social insect colonies are cooperative distributed systems [18] that have known an extraordinary ecological success during the last 100 million years [13]. Understanding how social insect societies work can help us to design efficient artificial distributed systems that at some level of description share similar needs and constraints to those ruling social insect colonies.

Termites in particular are known for building some of the most amazing architectures observed in the animal world. The mounds built by some species can reach up to 6 meters of height against a size of the individual insect of the order of the millimeter[10]. Even when the nest is comparatively small in size,

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it can present an extremely complex form and internal organization [6]. The architectural refinement of these structures reflects their ecological importance. In fact, the nests protect insects from dessiccation, and contribute to maintain a stable internal environment [20,15,14]. The nest is also important for protecting insects from attacks by a variety of natural enemies. Because of their biomass, their chemical composition, the absence of a hard exoskeleton and their concentration in a single place, termites represent an interesting food resource for several predators [11].

A nest is also a network of interconnected chambers and galleries inside which all the displacements and the activities of insects take place. These networks are completely self-organized and emerge from the work of thousands to millions of individuals [19]. Because of their ecological importance, these networks may present particular topological properties.

Nests built by the termite genus *Cubitermes* are constructions made out of clay whose shape resembles that of a mushroom of 20-30 cm of height (figure 1-A). Inside, the nests are filled with chambers of similar size, interconnected by openings and short corridors, (visible in figure 1-B, where the nest is represented in a virtually cut reconstruction). The diameter of corridors is constant everywhere and just a little bit larger than the size of a "soldier" (soldiers are large termites of the same species specialized for defence).

Chambers and corridors in these nests can be mapped respectively into vertices and edges of a network. These are spatial networks, where each vertex occupies a precise position in the three-dimensional space, and edges are real physical connections. Each vertex in the network can be characterised by its topological properties in relation to the network (degree, centrality, belonging to a network motif), but also by the characteristics associated to its spatial position or arrangement. For instance figure 1-D colors in red the vertices identifying chambers adjacent to the external nest wall and in white the others. Henceforth

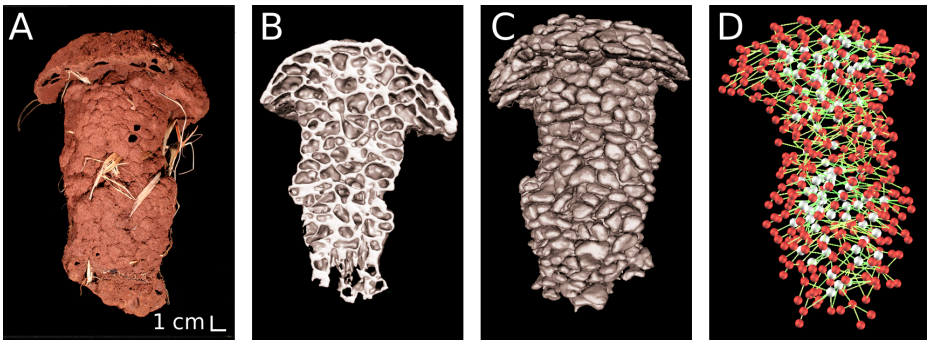

Fig. 1. A. Picture of one nest. B. Virtual cut of the nest. Chambers and corridors are clearly visible. C. Virtual cast of the same nest. Only the chambers and corridors are represented. D The connectivity network for the same nest. Each vertex corresponds to a chamber and each edge to a corridor. Nodes coloured in red indicate that the chamber is adjacent to the external nest surface.

we will call accordingly "internal" those vertices that are not adjacent to the external nest wall and "peripheral" the vertices that are adjacent to the external nest wall.

These attributes of a vertex only depend on the spatial position of the chamber, not on its topological localization inside the network. In the present paper we explore whether some network statistics correlate nevertheless with the internal or peripheral location of the vertices.

The rest of the paper is organized as follows. Section 2 presents our nest database and the segmentation process we developed to extract graphs from the tomographies of the nests. Section 3 introduces some indicators which characterize the properties of the nest transportation networks. In section 4 we define a null comparison model for networks with similar spatial constraints to those observed in our nests. Some strong effects of spatial embedding on network topology are described in section 5, while section 6 compares more directly some network properties of the real networks against the same properties in the null model. The results are discussed from an ecological viewpoint in section 7.

2 Network Extraction

Six *Cubitermes* nests were used. The nests, labeled M9, M10, M11, M12, M18 and M19 belonged to private or public collections (Natural History Museums of Paris and Toulouse) and originated from different locations in Central African Republic and Cameroon. One of the nests, M19, was still under construction when it was collected. This can be inferred from the fact that this nest still lacks the cap that is visible on top of all "complete" nests (old nests can also have more than one single cap, as is the case for nest M11 which has three caps).

Nests were imaged and reconstructed into 3-D virtual volumes using X-ray tomography with a medical scanner. For every nest, we extract its transportation network $G = (V, E)$ (fig 1.D). In this network, a vertex $v \in V$ represents a physical chamber and an edge $\{v_i, v_j\} \in E$ depicts a physical corridor between chambers v_i and v_j. We can reconstruct the network G as follows. "Cores" were defined as small empty regions located farther than about 1.5 mm from nest walls (internal or external). Given the narrow diameter of the corridors (less than ~ 0.5 mm in radius) these cores never belong to a corridor, but either to the space outside the nest or to a chamber. The chamber cores were identified as the network vertices. They were then concurrently dilated to progressively fill their surrounding empty space (stopping at walls). At some point, a dilated core also crams into its outgoing corridors and gets in touch with the others dilated cores coming from the other end of the corridor. In this case, an edge between the vertices was created, corresponding to the physical corridor.

To obtain the virtual network corresponding to the case when all physically adjacent chambers would be connected, the dilation of the same chamber cores was repeated in the pure 3D-space up to the complete space filling (neglecting now the nest walls). When two dilated cores got in touch, they were marked as adjacent. The results of this automatic segmentation were verified and manually corrected.

3 Network Measures

The topological properties of the graph G=(V,E) associated with a gallery network can be characterized by a variety of indicators [2]. We here focus on three features: the network sparseness, the communication efficiency and the betweenness centrality. Let us denote by k_i the degree of the vertex $v_i \in V$ defined by the number of edges incident to v_i. The average degree $\langle k \rangle = \sum k_i/N$ indicates the level of network sparseness (N is the total number of vertices).

We can also measure the patterns of connections involving more than one vertex. In particular we compute path length and betweenness centrality. Let d_{ij} be the number of edges on a shortest path between the vertices v_i and v_j i.e. a path between v_i and v_j with a minimum edge number. The average path length $< L >$ on G is defined as follows:

$$< L >= \frac{1}{N} \sum_{v_i, v_j \in V} d_{ij} \tag{1}$$

Average path length is a measure of network spread or compactness. For instance, networks with low $< L >$ can be efficiently navigated.

Normalized betweenness centrality $C_B(v)$ of vertex v is defined as follows:

$$C_B(v) = \frac{2}{(N-1)(N-2)} \sum_{v_i \neq v \neq v_j \in V} \frac{\sigma_{i,j}(v)}{\sigma_{i,j}} \tag{2}$$

where $\sigma_{i,j}$ is the number of shortest paths from v_i to v_j, and $\sigma_{i,j}(v)$ is the number of shortest paths from v_i to v_j that pass through v [1,3]. Vertices that have high betweenness centrality scores lie on important communication paths, and for this reason are important to guarantee fast displacements in the network.

Given the normalized betweenness centrality, one can compute the central point dominance [8], which is a measure of the maximum betweenness of any point in the graph: it will be 0 for complete graphs and 1 for "wheel" graphs (in which there is a central vertex that includes all shortest paths). Let v^* be the vertex with the largest betweenness centrality; then, the central point dominance is defined as

$$C'_B = \sum_{v_i \in \mathbf{V}} \frac{C_B(v^*) - C_B(v_i)}{N-1} \tag{3}$$

4 Definition and Generation of Random Spatial Networks

The chambers of Cubitermes nests completely fill the space without leaving significant gaps for the passage of long distance corridors. As a consequence, in the corresponding transportation network, connections exist only between vertices representing physically adjacent chambers. The classical models of random graphs [7] are not well-suited here for a null comparison test because they do

not take into account spatial constraints. We here propose a model which fits the physical specifities of the termite nests.

Let us define the Maximal Embedded Graph (MEG) as the network $G_M = (V, E_M)$ with the same set of vertices as in the gallery network G and where there is an edge $(v_i, v_j) \in E_M$ if chambers v_i and v_j are adjacent (separated by a single wall), independently whether they were also physically connected by a corridor or not. When there are no long distance connections between non-adjacent chambers (i.e. long chains in the associated graph), a MEG contains the whole edge set allowed by the constraints of the spatial embedding. Hence, all the possible networks compatible with these constraints can be generated as subgraphs of a MEG. We here restrict ourselves to graph spanners of G_M [16] i.e. connected graphs $G = (V, E_S)$ with the same vertex set V, and an edge set $E_S \subset E_M$ subset of E_M.

The topological assumptions required by our model have been checked in the real *Cubitermes* nests. There are no long-range connections in these nests; all the connections take place between physically adjacent chambers. In addition, the edges of the real nests are a subset of the MEG edges in the vast majority of the cases. These properties were verified for nests M9, M11, M12, M18 and M19; in each of these nests around 99% of the edges were also edges of the MEG. The remaining about 1% of the edges connected chambers adjacent at a corner, and for this reason these edges were not marked as adjacent by the automatic segmentation procedure. We added these edges to the MEG. Nest M10 displays a different behaviour because termites have built some long-range corridors on the external surface of the nest that link to distant chambers. For this reason, nest M10 was not used in some of the analyses.

For each nest of our corpus, we have compared its internal topological properties with those of 10000 random spanners of the MEG (for the same nest). These were obtained by first generating random spanning trees [17] of G_M, and then inserting additional edges (chosen with uniform probability among the edges in G_M) until we reach the same number of edges as in the observed gallery network G.

5 Effect of the Spatial Embedding on the Graph Average Degree

In *Cubitermes* networks, the maximum degree of the vertices is limited by the physical constraints: no vertex can have a higher degree than its associated degree in the MEG. Consequently, the average network degree is smaller than the average degree of G_M. Figure 2-A reports for the six nests of the corpus, the degree in the MEG and in the real network, showing that the average degree of real networks is significantly smaller than the average degree of G_M. This indicates that the strong maximum limit to vertex connectivity imposed by spatial embedding has hardly any effect on these networks. Indeed, real termite networks have connectivity near the percolation threshold, suggesting that these networks tend to minimize connectivity.

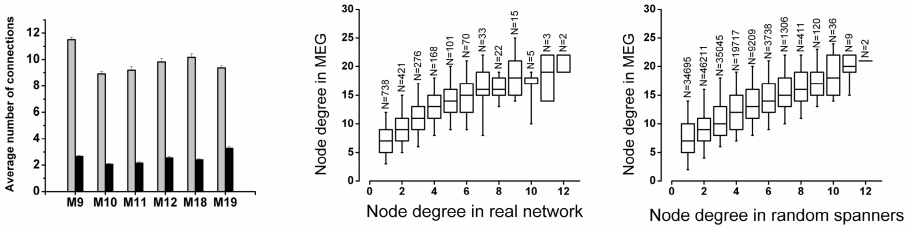

Fig. 2. Left graph: Average degree ($\pm SE$) in G_M (gray) and in real networks (black). Middle graph: For all vertices in the six nests, the degree of the vertex in G_M is binned according to the degree of the same vertex in the real network, in the abscissae. Right graph: The same as in the middle graph, but for the vertices of random spanners of each nest. The reported data for the random spanners are computed on a subset of 100 spanners for each nest.

However, spatial embedding can affect connectivity indirectly. For instance the degree of each vertex in the real network could correlate with its degree in the MEG. This is actually observed in our networks: figure 2-B bins together all the vertices with the same degree in the real networks (here, vertices from different nests are not differentiated) and reports a box-plot of the corresponding degree in G_M. The two are clearly correlated. If the vertices in G were simply a random sample from the vertices in G_M, a similar result should be found also for random spanners. The same statistics is reported for random spanners of G_M of each of the five nests in fig 2-C. The correlation of vertex degree with the degree in G_M is similar. However, real networks have a higher proportion of nodes with high degree (10 or more) than random spanners (see numbers N in the label associated to each box).

6 Effect of the Spatial Embedding on the Network Centrality

The correlation of the vertex degrees in real networks and in the corresponding G_Ss suggests that external vertices (representing chambers adjacent to the external nest surface, see page 167) should have lower degree than internal vertices, for the sole effect of spatial constraints. This tendency should be shared both by real networks and random spanners. However, we wonder if the same tendency is stronger in real networks than in random spanners. In order to investigate this issue, for each nest, we have computed two indicators for each vertex : (1) the ratio k^* between the degree the vertex has in the real nest and its average degree for 10000 random spanners of G_M defined on the same nest, (2) the ratio C_B^* between its betweenness centrality in the real nest and its average betweenness centrality for the random spanners. Internal and peripheral vertices are binned separately. If real networks do not particularly tend to segregate central vertices (in the network) across space, this ratio should be similar for both internal and

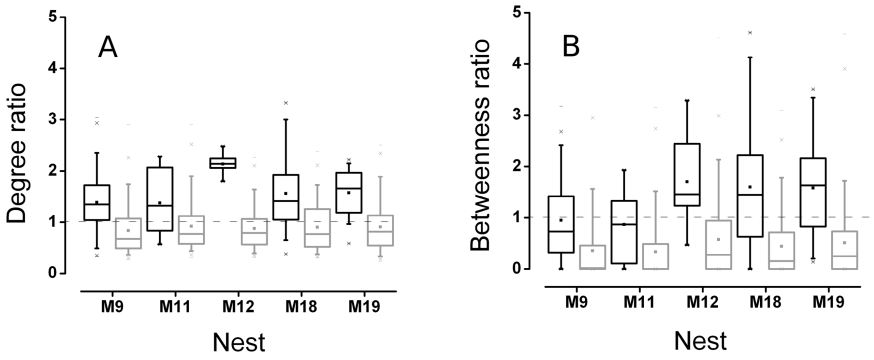

Fig. 3. Left. box plots representing the ratio, for each vertex, of the degree that the vertex has in the real network of galleries and its average degree in the spanners. In black: internal vertices; in gray, peripheral vertices. Right. the same as in the left layer, but with ratios of betweenness. The dashed line represents the expected ratio of 1 if there were no differences between internal and peripheral vertices.

peripheral vertices. Figure 3-A reports the distribution of the ratio k^* associated with the degree for internal and peripheral chambers in the five nests. In all the nests this ratio is higher in internal than in peripheral vertices. Higher degree does not necessarily correlate with a higher betweenness. Figure 3-B reports the distribution of the ratio C_B^* associated with the betweenness centrality. Again, the ratio is always higher in internal than in peripheral vertices.

Table 1 reports some additional statistics of real gallery networks, and of the random spanners for the same nest. Average path lengths in real networks are shorter than in random spanners with the same average degree, indicating that some optimization process is at work in termite gallery networks, which makes these networks more efficient than random networks.

7 Discussion: An Ecological Perspective

Networks of chambers and galleries inside termite nests are one of the few described examples of 3D self-organized spatial networks.

These networks are extremely sparse. In general, network sparseness is not an advantageous feature because it decreases the efficiency of displacement, increases the likelihood of traffic jams and decreases robustness to random failures or occlusions.

As a candidate rationale, the sparseness may result from a cost associated with adding new edges. In termite networks of galleries however, it is unlikely that there is such a building cost. First it is sufficient to dig a hole in a thin wall to obtain a new connection. Second, one of the nests, M19 which appeared to be still under construction has more connections (higher average degree in table 1) than the other nests. This indicates that the final topology is probably

Table 1. The table reports some descriptors of the real networks of galleries for nests M9, M11, M12, M18 and M19 (RN). The same descriptors are also reported (together with standard errors) for 10000 random spanners of the same nests (rand). V: number of vertices; E: number of edges; <k>: average node degre; <L>: characteristic path length; <bet>: average node betweenness; betmax: maximum betweenness; CPD: central point dominance.

nest	V	E	<k>	<L>	<bet>	betmax	CPD
M9-RN	507	676	2.67	8.51	0.015	0.22	0.20
M9-rand	507	676	2.67	11.18±0.42	0.020±0.001	0.27±0.06	0.25±0.06
M11-RN	260	280	2.15	9.11	0.031	0.48	0.45
M11-rand	260	280	2.15	15.66±1.56	0.057±0.006	0.52±0.04	0.47±0.04
M12-RN	183	233	2.55	8.19	0.040	0.36	0.33
M12-rand	183	233	2.55	9.92±0.65	0.049±0.004	0.40±0.07	0.35±0.06
M18-RN	287	342	2.38	8.40	0.026	0.32	0.30
M18-rand	287	342	2.38	11.00±0.69	0.035±0.002	0.34±0.07	0.31±0.07
M19-RN	268	437	3.26	7.89	0.026	0.35	0.33
M19-rand	268	437	3.26	9.47±0.38	0.032±0.001	0.31±0.05	0.28±0.05

reached by removing already existing connections, implying that the cost would be associated rather with edge removal than edge addition.

A better explanation of the sparseness of these networks could be their importance for defence. *Cubitermes* termites (like several other termite genera) are often attacked by ants that prey on the nests [5,11]. The reaction of *Cubitermes subarquatus* in response to attacks by the ant *Centromyrmex bequaerti* is accurately described [4]. In a first phase, if the ants find access to one chamber, each corridor leading from that chamber to other chambers of the nest is defended by a "soldier" termite. It is widely believed that the particular diameter of the galleries, exactly the size of a soldier, is an adaptive feature evolved to maximize the success of defence. Soldiers have specialized jaws and phragmotic heads (large heads that in some termite and ant species are be used to plug the nest entrance; Gr. $\phi\rho\alpha\gamma\mu o\varsigma \simeq fence, barrier$) that can effectively block narrow termite tunnels against ant entry. An additional defence strategy followed by termites consists in setting back to intact parts of the nest and plugging with earth the galleries that are still open to the invaded part.

The very low connectivity of the gallery network could hence present an high adaptive defence value, since it is often sufficient to close a single corridor to isolate an individual chamber, or a great part of the nest from outside. If this holds true, then the connectivity should be even sparser at the periphery of the nest (where defence ought to be the more efficient) than in the central part of the nest (where transportation ougth to be the prime concern). This hypothesis is clearly supported in the present case.

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