

Accessibility in networks: A useful measure for understanding social insect nest architecture

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ABSTRACT

Networks and the associated tools from graph theory have now become well-established approaches to study natural as well as human-made systems. While early studies focused on topology and connectivity, the recent literature has acknowledged the importance of the dynamical properties of these networks. Here we focus on such a dynamic measure: accessibility. It characterizes for any given movement dynamics (such as random walks) the average number of nodes that can be reached in exactly h steps (out-accessibility), or the average number of nodes from which a given node can be reached (in-accessibility). This focus on dynamics makes accessibility particularly appropriate to study movement on networks and to detect complementary properties with respect to topology-based measurements such as betweenness centrality. We apply this measure to six nests of *Cubitermes* termites. Their mushroom-like 3D architectures consist of chambers and connecting tunnels that can be associated to nodes and edges in a communication network. Accessibilities turn out to be particularly low in the bottom part of the nests that link them to their underground tunneling network. We interpret this result in the context of anti-predator (ants) behavior and/or as a side effect of the global nest shape.

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1. Introduction

Efficient transportation of material and information is fundamental to maintaining the structure and organization of large biological systems. It is therefore not surprising that efficient transportation networks are found in biology from unicellular organisms [1] to fungi [2] to vascular and circulatory systems in higher organisms [3–6]. The efficiency of these networks is particularly amazing if we consider that they are produced in a completely distributed and self-organized process from the interactions of simple units, each with no direct “knowledge” of the global structure.

At a larger scale, an example of biological transportation networks is provided by the movement of animals across

space during their daily movements or seasonal migrations. In this case the network consists of the trails, galleries, rivers or corridors of vegetation on top of which the animals move. In this particular example of biological transportation network the scale – of the order of centimeters to kilometers – offers the additional advantage that both the structure of the network and the dynamics on top of it are easily observable, making such systems convenient for scientific investigation. Despite the recent interest in the network analysis of animal interaction networks (see e.g. [7–13]) and the recognition that patterns of social interactions are intrinsically related to patterns of movement (see e.g. [14]), only a few studies have analyzed explicitly spatial transportation networks built by animals (but see [15] and [16–18] for notable exceptions).

In this paper we focus on a particular class of transportation network, constituted by the interconnected cham-

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bers inside social insect nests. These nests are the result of the collective building activity of hundreds (in some cases even millions) of insects over several years [19]. As new structures are built and old ones are rearranged to meet the requirements of a growing colony, the final nest is likely to carry the remnants of this complex growth process. At the same time, at every stage of its growth the nest needs to be fully functional and provide essential features for the survival of the colony, such as protection from predators [20], a stable mechanical structure [21] and efficient movement of individuals during their routine activities [22].

In the study of social insect nest architecture it is often difficult to assess if a particular feature of a nest is a by-product of the building process, a necessity imposed by environmental or material constraints, or a useful characteristic which confers some selective advantage to the colony. This is all the more challenging because of the scarce amount of quantitative information available about the structure of social insect nests and about what the animals do in these structures [23]. Such a lack of knowledge is to a great extent related to the difficulties in observing the inner portions of the nests during development [24], as well as in describing their intrinsic geometric and topological complexity.

We have recently demonstrated that some termite nests can be represented as networks [25]. This representation paves the way for the application of the rich set of concepts and methods that have been developed in the ever evolving area of graph theory and analysis. For example, each ellipsoidal chamber of a nest of the termite genus *Cubitermes* can be mapped as the nodes of a network while the connecting tunnels between chambers can be mapped as the links between these nodes (Fig. 1). The analyses of these abstract networks with topological network indicators such as node degree, centrality measures or shortest path length have shown [25–27] that *Cubitermes* nests

have very sparse, tree-like networks (easy to defend) but that the few tunnels that exist are very well placed in order to shorten the distances between any two chambers.

Information about the inner nest structure is particularly useful if one wants to compare nests from different species or from the same species but constructed under different environmental conditions. However, it is clear from recent network literature that more insights in the understanding of network functioning can be provided by the analysis of the dynamical processes that may take place on top of networks (see [28–30] for recent general surveys). The integration of the nest structure, its growth dynamics and the dynamical processes occurring within it is of fundamental importance for the understanding of real-world complex systems, whose very nature relies on the tight feed-back loop between form, dynamical properties and the growth of new forms. In the present paper, after a brief description of the structures of *Cubitermes* nests, we introduce the “accessibility” measure, which we apply to the characterization of dynamical processes that are likely to take place in *Cubitermes* networks. We will show in particular that this measure provides complementary information compared to the more traditional network indicators mentioned above, shedding new light on what might be happening in these nests.

Cubitermes nests consist of two parts: an underground (hypogeous) part, and a mushroom-shaped above ground (epigeous) part. The latter usually has no openings to the outside, while the former connects to an extensive foraging tunnel network [31,32]. The nests analyzed here comprise the epigeous structure and part of the hypogeous structure. For each nest we define three non-overlapping regions: the “bottleneck” region (B) through which the termites must pass when traveling between the epigeous part of the nest and the underground tunnel network, the central region (C) containing the chambers inside the nest that do not belong to B, and the surface region (S)

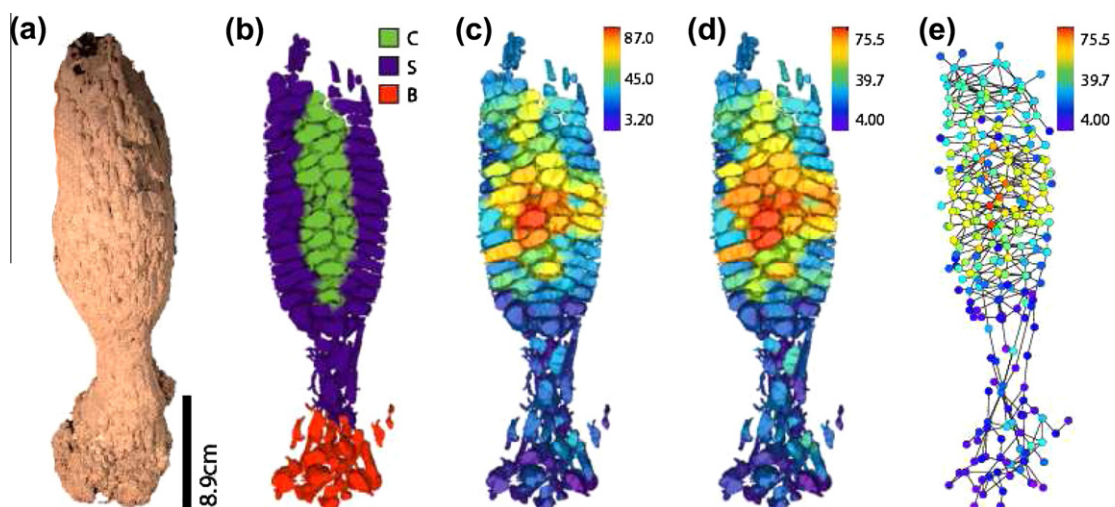


Fig. 1. Example of computed accessibilities for nest Cubi19 and $h = 4$, shown here in a virtual sagittal cut of the nest cast. (a) A photo of the complete above-ground part of the nest, its lowest part being anchored in the soil; (b) The three identified regions (C = central nodes, S = surface nodes, B = bottleneck nodes); (c) in-accessibility; (d) out-accessibility of the nodes seen in this cut; (e) Network representation of the whole nest in which the nodes' color correspond to their out-accessibility. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

containing the chambers that are adjacent to the outer wall of the nest (see Fig. 1).

Most of the measures used in the literature to describe network properties depend on the notion of shortest path. For instance the topological efficiency [33] of a network with N nodes (used, e.g., in references [2,34]) is measured as $L = \frac{1}{N(N-1)} \sum_{v_i \neq v_j} 1/d(v_i, v_j)$ where $d(v_i, v_j)$ is the topological distance between nodes v_i and v_j ($1 \leq i, j \leq N$) along the shortest path. Betweenness centrality, defined as $BC(v) = \sum_{v_i \neq v_j} \frac{c_{ij}(v)}{c(v_i, v_j)}$, is another widely used network measure. It quantifies the number of shortest paths between any two nodes passing through a given edge or node v ($c(v_i, v_j)$ is the number of shortest paths between nodes v_i and v_j , and $c_{ij}(v)$ is the number of shortest path that pass through v). In the context of nest structure, however, these indices are of limited use because they rely on the knowledge of the whole network. We would prefer a measure that only uses the local topology around some node or edge. Also, the implicit assumption that animals move along the shortest path from one destination to another is in itself not trivial (though social insects can find optimal solutions in specific situations [35,36]). Foraging termites are known to be able to learn navigation in simple mazes [37] and to use optical, pheromonal, gravity and magnetic cues [38–40]. However nothing is known about their movement inside the nest, which is probably saturated with colony odors and packed with individuals (factors that complicate orientation). Rather, the movement of termites inside their nest may be more similar to a random walk, which should also apply to the predators that invade their nests. This lead us to apply a more appropriate measure which we called accessibility [41,42]. Accessibility is an estimate of the number of nodes that can be reached in exactly h steps after departing from a given node, a measurement henceforth called *out-accessibility*, as well as the number of nodes from which a reference node can be reached in h steps (*in-accessibility*). Such measurements are fundamentally related to several of the above mentioned constraints imposed on the nest topology. The local (h) range of accessibility also relates to the self-organized functioning of social insect colonies in which individuals base their behavior on locally available information [35].

The distinction between out- and in-accessibility actually makes a lot of sense in the context of termite societies. The lower part of the nest is special in that it links the above ground nest to the underground foraging tunnel network. Also, like many other termite species, *Cubitermes* have a single reproductive pair that move around freely in this nest part [19,43,44]. One may therefore wonder if this area has a particular accessibility pattern. For instance, if this area is shown to be a region with high in-accessibility and low out-accessibility, the royal couple could simply be found in this region more frequently because of the characteristics of the network, without showing a particular preference for that portion of the nest. On the other hand, high in- and out-accessibility might be favorable to the royal couple because they allow more efficient exchanges with the rest of the nest (arrival of food, nursery of eggs etc.).

Nest parts that are the first target of insect predator attacks (such as army ants) may have very low accessibilities in general. Conversely, isolated nodes of very high accessibility may be strategic defense points for *Cubitermes* soldiers that can block tunnels with their sclerotic heads.

2. Materials and methods

2.1. Accessibility

We approach the accessibility issue by considering a recently proposed measurement [41,42,45,46]. This measurement is defined with respect to the type of movement among the nodes. Here, we focus on simple random walks. From a current node with degree d , the next node is chosen with probability d^{-1} . The assumption of equal probability between edges makes sense in *Cubitermes* nests because all tunnels have a similar diameter (approximately the size of a soldier's head capsule, which is thought to be an adaptation for nest defense [47]).

As it was recently shown [42], the accessibilities, as defined in Eqs. (1) and (2), provide an estimate of the number of nodes that can be visited in exactly h steps. The value of h in Eqs. (1) and (2) defines the length of the random walk, and p_{ij}^h is the probability to reach node j from node i in exactly h steps.

$$A_h^{out}(i) = \exp \left[- \sum_{j=1}^N p_{ij}^h \log(p_{ij}^h) \right] \quad (1)$$

$$A_h^{in}(i) = \exp \left[- \sum_{j=1}^N \left(\frac{p_{ji}^h}{\sum_{r=1}^N p_{r,i}^h} \right) \log \left(\frac{p_{ji}^h}{\sum_{r=1}^N p_{r,i}^h} \right) \right] \quad (2)$$

The main motivation underlying the accessibility concept is illustrated in Fig. 2. In Fig. 2(a), the reference node 1 connects directly to 5 other nodes (2, 3, ..., 6). Displacement in one step from node 1 to its neighbors takes place with the respective probabilities $p_{1,2}^1, p_{1,3}^1, \dots, p_{1,6}^1$, which can be modulated by biological factors such as pheromone density, gallery width, or gravity (among others). In the simplest case where no modulation is considered, a neighbor is chosen at random (with probabilities equal to $d_1^{-1} = 0.2$ in this case). Now, assume we want to quantify the effectivity of visiting the neighboring nodes by an agent starting at node 1. If all probabilities are equal, all nodes can be visited within a minimum number of steps or period of time [42]. However, if the probabilities are higher for some nodes, most of the movements will end up at those nodes, while the other nodes will be rarely visited. Accessibility is defined in order to account for such effects. More specifically, it is defined so as to reach a maximum value in the case of equal probabilities, taking smaller values for other cases. In brief, accessibility inherently captures the fact that movement between nodes in a network can take place with varying probabilities in a manner that would not be captured by any other traditional complex network measurement.

Having introduced the main motivation for accessibility with respect to a specific situation involving only directly connected nodes, we now proceed to the more general case where the destination nodes are further away, in the sense

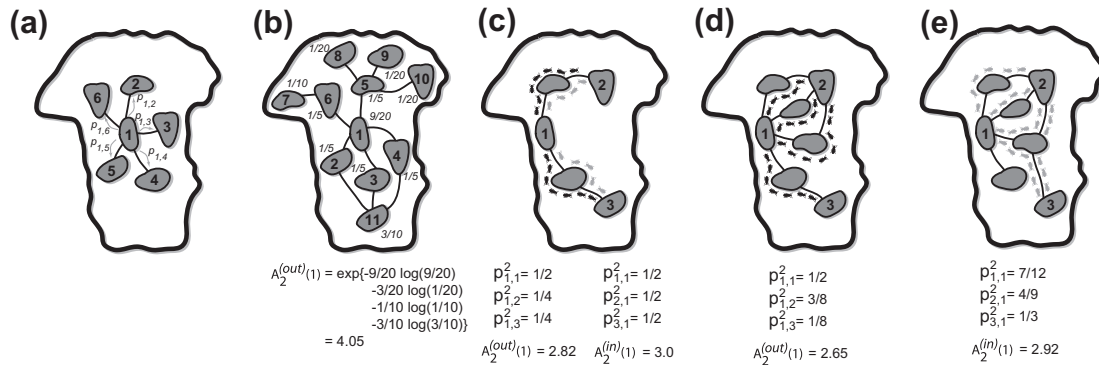


Fig. 2. Examples of accessibility calculation for network nodes in termite nests. (a) Illustration of how the chambers are mapped into nodes and the tunnels between chambers into edges. In this case, node 1 can access five other nodes in one step ($h = 1$). (b) In this example node 1 can reach five other nodes or itself after two steps ($h = 2$) of a standard random walk. The numbers correspond to the probabilities of reaching each of these nodes. Out-accessibility computation for this reference node is given in detail below the nest. (c) A simple case where the reference node 1 has a maximum in- and out-accessibility for $h = 2$. Termites leaving the reference node are marked in black, while termites arriving at the reference node are grey. (d) In this case the reference node has smaller out-accessibility than the maximum that can be obtained for two reachable nodes after two steps. (e) The reference node 1 has smaller in-accessibility than the maximum that can be obtained for a reference node that is reached from two nodes after two steps. The numbers below the nests in (c), (d) and (e) show the probabilities related to the reference node 1 as well as the final in- and out-accessibility values.

that they are reached after moving through two or more edges. This case is illustrated in Fig. 2(b), which also contains 5 destination nodes that are reachable by an agent in exactly two steps ($h = 2$) from the reference node 1. Let us assume that the probabilities of going through any link are identical. Even so, the different connectivity (e.g. number of paths) between the reference and destination nodes implies probabilities that are different. For instance, the probability of going from node 1 to 11 is $3/10$ while the probability of reaching node 8, 9 or 10 is only $1/20$ and the probability of coming back to node 1 is $9/20$. These different probabilities imply that some of the destination nodes will be reached most of the time, while others will rarely be accessed. This is quantified by the accessibility value of node 1, which is equal to 4.05 in this case. The above examples consider movements from the reference node to other reachable nodes. We will henceforth call this accessibility *out-accessibility* in order to distinguish it from the case in which the reference node acts as the destination after departing from other nodes, yielding the concept of *in-accessibility*.

Fig. 2(c)–(e) illustrate three cases of interest regarding the use of accessibility to investigate movement in termite nests, where node 1 is always taken as the reference point. In Fig. 2(c), after two steps, one will have the same

probability (0.25) of reaching nodes 2 or 3, but a probability of $1/2$ of reaching node 1. Therefore the out-accessibility of node 1 for two steps is 2.82. The network shown in Fig. 2(d) has more paths between nodes 1 and 2, though node 1 is still reached with probability $1/2$, node 2 is now reached with probability $3/8$, while node 3 will be found only $1/8$ of the time. This asymmetry is quantified completely in terms of the out-accessibility of node 1, which is now 2.64 instead of 2.83 in the case of Fig. 2(c).

The concept of in-accessibility is now illustrated in Fig. 2(c) and (e). First, in Fig. 2(c), node 1 can be reached from nodes 1, 2 and 3 with equal probabilities, assuming movements of two steps. Consequently, the value of in-accessibility is maximum and equal to 3. In the analogous situation shown in Fig. 2(e), node 1 can also be reached from nodes 1, 2 and 3 after two steps, but the probabilities are now different ($7/12$, $4/9$ and $1/3$, respectively), yielding an in-accessibility of 2.92 according to Eq. (2).

It is common to use h inside the interval $[1, \ell]$, where ℓ is the mean shortest topological distance between any two nodes of the network and corresponds to its characteristic topological scale. In the present case we choose for each nest $h = \ell/2$ (see Table 1).

Table 1

Parameters chosen for each nest and the resulting statistics for each part B, S or C: the “habitat” (hab.) of the nest is either Forest (F) or Savannah (S), “% in B” is the percentage of lowest nodes attributed to the bottleneck part B, ℓ the mean length of the shortest topological paths, h the length of the random walks, $\langle k \rangle$ the average node degree, N the number of nodes, A^{in} and A^{out} average \pm sem in- and out-accessibility respectively.

Sample	hab.	% in B (%)	ℓ	h	$\langle k \rangle, N_B$	$\langle k \rangle, N_S$	$\langle k \rangle, N_C$	$\langle A_B^{in} \rangle$	$\langle A_B^{out} \rangle$	$\langle A_S^{in} \rangle$	$\langle A_S^{out} \rangle$	$\langle A_C^{in} \rangle$	$\langle A_C^{out} \rangle$
Cubi09	S	15	8.5	4	(2.29, 75)	(2.28, 344)	(4.49, 88)	12.7 ± 0.9	12.4 ± 0.7	15.5 ± 0.6	16.1 ± 0.5	29.6 ± 2.0	27.5 ± 1.7
Cubi10	F	15	16.9	8	(2.12, 51)	(1.83, 274)	(4.54, 24)	11.4 ± 0.6	10.3 ± 0.4	11.9 ± 0.3	10.9 ± 0.3	14.1 ± 1.3	11.6 ± 1.2
Cubi11	F	15	9.1	4	(1.90, 38)	(2.13, 211)	(3.45, 11)	6.9 ± 0.5	6.8 ± 0.5	9.4 ± 0.4	8.9 ± 0.3	13.1 ± 1.4	11.5 ± 1.2
Cubi12	F	7	8.1	4	(1.79, 14)	(2.36, 160)	(7.00, 9)	5.6 ± 0.5	5.5 ± 0.4	15.2 ± 0.6	14.5 ± 0.5	28.6 ± 2.8	23.2 ± 2.9
Cubi18	S	15	8.4	4	(2.34, 44)	(2.21, 219)	(4.04, 24)	9.3 ± 1.0	8.9 ± 0.8	11.4 ± 0.5	11.4 ± 0.4	17.8 ± 1.4	15.9 ± 1.3
Cubi19	F	15	7.9	4	(2.59, 41)	(2.97, 206)	(7.43, 21)	12.4 ± 1.1	12.1 ± 0.9	24.7 ± 0.9	24.1 ± 0.7	43.4 ± 3.0	38.4 ± 2.4
Mean values					(2.24, 44)	(2.30, 236)	(5.16, 30)	9.7	9.3	14.7	14.3	24.4	21.3

2.2. *Cubitermes* biology and nest description

The genus *Cubitermes* gathers several species of soil-feeding termites that are found throughout equatorial and tropical Africa. Their club- or mushroom-like nests (see Fig. 1) are 20–100 cm high and made of clay. Their high density in certain areas makes them an impressive feature of many African Savannah's or forests. Our dataset consists of six previously published networks of *Cubitermes* spp. nests [25] that originate from either Savannah (nests Cubi09 and –18) or forest regions (nests Cubi10, –11, –12 and –19) of the Central African Republic and Cameroon. Unfortunately only one nest has been identified to the species level (Cubi12, *Cubitermes fungifaber*), for the other nests we only know the genus. However, attributing a nest to a particular species is quite a difficult task because (1) the mound can host many other termite species in addition or replacement to the one that built it [48] and (2) the nest morphological trait is not sufficiently specific to discriminate nests built by different species [49]. The latter argument actually makes an analysis at the genus level meaningful; we would not expect any topological differences between different *Cubitermes* species.

According to [50] the number of individuals in a nest is proportional to its external surface area (or to the volume to the power of 2/3). From this relationship and the estimated parameter values in [50] it is possible to estimate a population of 600–1300 individuals for the nests used in the present paper (see Table 1 in [25]). Nest construction takes place over a short time period, usually a couple of weeks. Growth occurs by addition of new material at the top of the nest (new caps) or by adding additional columns, but never by a widening of the existing structures [32,44,49,51]. Once built, the different parts of the nest are not modified. The nests analyzed here are all mature, fully grown nests with the possible exception of nest C19 [25].

It is assumed that *Cubitermes* nests provide shelter against flooding during the rainy season (where underground galleries can become inundated). Particular adaptations include the cap that protects the porous walls in the lower part of the nest against heavy rains, thus facilitating diffusive gas exchange [51]. *Cubitermes* species actually live in areas that are frequently flooded, supposedly to gain some advantage against predation by ants which are one of their most important natural enemies [52,53]. There are no openings towards the outside and when they exist they occur through erosions (heavy rain) or when the sexual morphs leave the nest for their nuptial flight. In this case small predators such as Dorylinae army ants can gain access to the internal chambers and prey on termites. Other ants dig themselves underground galleries and can find termite tunnels by chance and enter into the nest (Josens G. Pers Commun). Since these termites stand no chance of survival in a direct confrontation with ants, their defense strategy consists of moving deeper into the nest while soldier termites block the corridors with their large sclerotic heads [47,53]. Soldiers actually only make up approximately 1% of the population, which is well below average in termites [54]. There is indirect evidence of these termites making diurnal vertical migrations [44] with the highest densities

in the lower nest part. The royal couple have head sizes systematically below the soldiers' head sizes [55]. Thus they can freely move around in the nest. When excavating a nest the reproductive individuals were found mostly in the lower nest parts where one can also find most larvae, while the higher nest parts contain mostly workers [43,44].

The nests studied in this paper were labeled with the same numbered code as in [25] to identify them (cubi09, –10, –11, –12, –18 and –19). These nests were imaged [25] using X-ray tomography with a Somatom Sensation 16 medical scanner, and reconstructed into a series of virtual cuts (inter-slice distance 0.5 mm, slice thickness 1 mm, pixel resolution in the range 0.3–0.6 mm).

The bottom region of each sample was defined based on samples cubi10 and cubi19, where the bottleneck part is clearly identifiable as the part below the lowest diameter (see Fig. 1). It represents on average 15% of the total of chambers in the nest. An exception is the nest cubi12 that has a very small bottom part. We therefore chose for this nest only the lowest 7% of the chambers as the bottleneck part. This region is of particular interest because the mentioned diurnal vertical migration passes necessarily across this region.

2.3. Data acquisition and network extraction

The internal transportation network of the nests were reconstructed as described in [27]. First, the “core” of each chamber was detected by identifying image regions of distances greater than ≈ 1.5 mm from (internal and external) nest walls. Given the narrow diameter of the corridors (less than ~ 0.5 mm in radius) these regions either belong to a chamber or to the space outside the nest, but never to a corridor. These chamber cores were identified as the network vertices. They were then concurrently dilated to progressively fill their surrounding empty space. In subsequent dilation steps, each core filled all the empty space inside the chamber in which it is located (stopping at walls) and crammed into the corridors that open on that chamber. When one dilating chamber core was in contact with the other dilated core coming from the other end of the corridor, an edge between the vertices was created, corresponding to the physical corridor. In a final step the cores were dilated through the chamber walls, and spatial neighborhood was established when they encountered the core coming from another chamber.

3. Results

Table 1 summarizes the data obtained for the six nests. If the bottleneck region was a simple extension of the central nest part, one would expect the average node degree in region B (that contains chambers adjacent to the outer nest wall and chambers completely surrounded by other chambers) to be between those observed in regions S and C. However, we found that the average degree of nodes in region B is the same as in region S (generalized linear mixed effect model with a Poisson error structure, $p = 0.688$), which indicates some peculiar features for this region.

Fig. 3 shows a sagittal cut of each of the six nests with the B region highlighted. For each nest we calculated the values of in- and out-accessibilities performing 10^6 random walks for each node. The plot of in- versus out-accessibility for all network nodes (Fig. 3) shows a very high correlation between the two measures, with (Pearson) correlation coefficients ranging from 0.95 to 0.97. The high correlation between in- and out-accessibility might actually be linked to the observation that chambers do not serve a fixed purpose but that their utilization changes dynamically, e.g., as a function of the outside temperature and humidity [31]. Note also that the individual node accessibilities vary a lot between the nodes of the same region (Fig. 3) without any clear outliers. It is therefore difficult to identify particular nodes that can fulfill a special function.

The B nodes are generally in the lower left corner of the graphs in Fig. 3 and the C nodes in the higher right part. This confirms the specificity of the B region found in the node degree analysis. To test the statistical significance of this difference we computed the mean accessibility of each node. Next, we compared them between any two regions by fitting a linear mixed effect model (with region nested in each nest) with or without the region effect and tested the significance of the difference by percentiles with random permutations of the regions inside a nest. All these comparisons were highly significant ($p < 0.001$). The bot-

tleneck nodes are therefore generally characterized by low accessibility (consistent with the anti-predator adaptation discussed in the introduction).

One might think that (mean) accessibility is redundant with betweenness centrality (a measure of the importance of a node with respect to the total network). The two measures are actually only weakly correlated, with coefficients ranging from 0.44 to 0.70. Accessibility, which is based on local dynamics, can therefore be used as a complementary measure for network characterization.

Although very little is known about termite movement inside the nest, it is important to note that the results described above are based on standard random walks. However, as stated above, there is some biological evidence that termites know at least from where they come and that they probably avoid going back along the same node. This would suggest that termites would move without using the same node twice. We therefore also computed accessibilities for such self-avoiding random walks, with termites that get stuck before making h steps either simply left stuck or removed from the simulations. In addition, it is also known that termite movement might be gravity-oriented [37,38]. In order to test how this hypothesis could affect our findings, we use a fourth type of random walk that takes into account the edges orientation. This is done by assuming the following rule: the probability of going from i to j is given by $p_{ij} \sim \arcsin(\theta_{ij})$, where θ_{ij} corresponds to

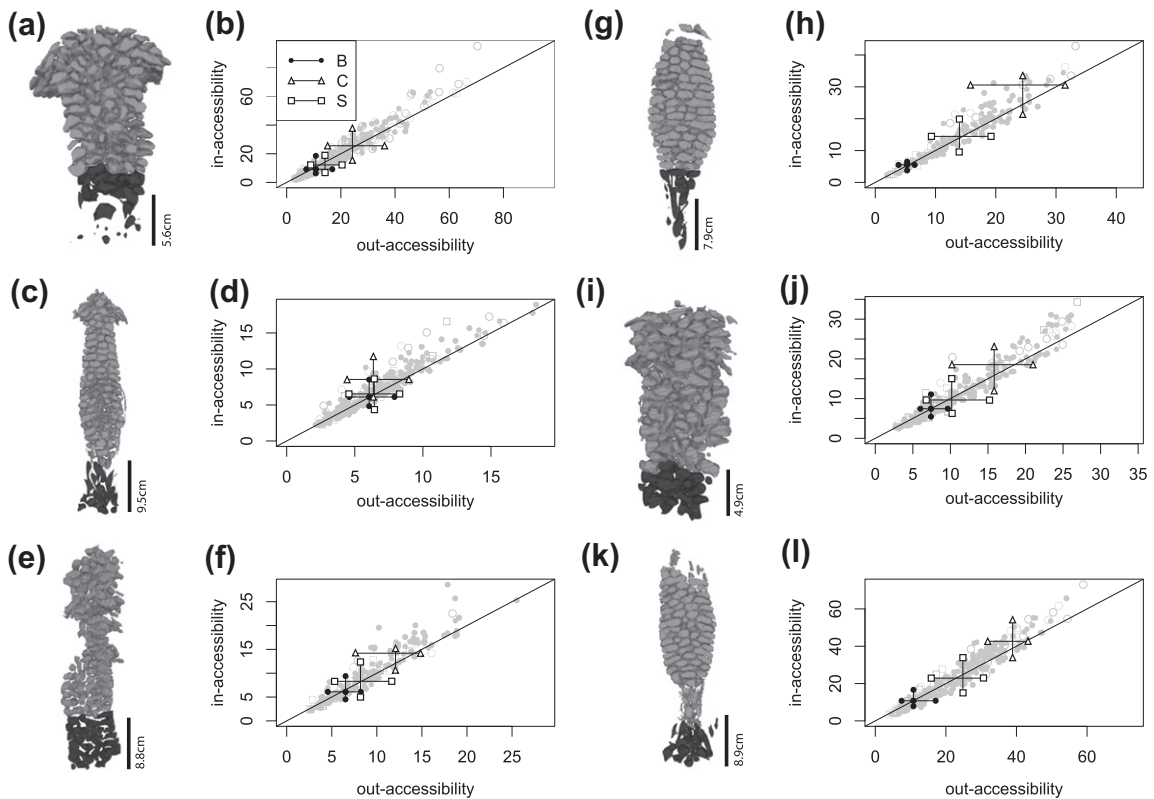


Fig. 3. Graphical summary of the six nests and the respective accessibility analyses. Each nest is represented by a sagittal cut through the virtual reconstruction of nest chambers and tunnels (dark regions correspond to the bottleneck regions) and a plot of A^{in} versus A^{out} . Each region B, C or S is summarized by its 1st, 2nd (median) and 3rd quartile for both in- and out-accessibility. The black line has a slope of 1.

the angle between the edge (i,j) and the xy plane. The results of the simulations with these types of random walk are summarized in [Supplementary electronic material](#). We found again that in- and out- accessibilities were highly correlated. The three regions also showed the same differences in mean accessibilities as in [Fig. 3](#). The major conclusions of the present work are therefore independent of the chosen type of random walk.

4. Discussion

Accessibility is a measure to characterize nodes in a network based on local dynamics. Therefore, it is well adapted to networks that have emerged through self-organized local dynamics such as those found in social insects. It is only weakly correlated with a related measure, betweenness centrality, that is computed from the global network. We have addressed in the present paper the comparison between in- and out-accessibility and the application of these measurements to study the networks of termite nests of the genus *Cubitermes*.

Our analysis has shown that the bottleneck regions of the analyzed *Cubitermes* nests are special: their accessibility is significantly lower than in the rest of the nest. The existing literature [53] describes attacks by ants to damaged nests or to nests that have been opened to give access to the sexual morphs before the nuptial flights. Ants enter the nest from the broken part. However, ants can also attack intact termite nests, entering through the underground galleries (Dejean A, Josens G. *Pers Commun*). In both cases the low accessibility of the bottleneck part of the nest could be an adaptation to slow down the predators' progression in the nest.

Future field work could shed more light on the functional significance of our findings, in particular if one had the chance to observe predator attacks on *Cubitermes* nests. Perna et al. [26] have already found that termite nest networks have lower average shortest paths than the corresponding random spanners. The present results show that they may also be adapted against an invasion through the bottleneck region. This is coherent with Valverde et al. [56] who found that these *Cubitermes* nests have a connectivity close to the percolation threshold, which is another way to slow down the spread of invading predators. Termites, with their ability to build pheromone trails, could bypass such restrictions in their own nest. Accessibility measures naturally take into account both topology and dynamics at local scale, with the dynamics being adaptable to specific movements, which is readily suited to study a large number of biological transportation networks, ranging from galleries and trails of larger animals, to the intracellular transportation of molecules along the cytoskeleton, to the spreading of genetic traits and diseases in populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.chaos.2012.11.003>.

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