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Topological efficiency in three-dimensional gallery networks of termite nests

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ABSTRACT

Transport networks are a key component of human and natural societies that enable efficient communication at a low cost. Here, we study the topological efficiency of the three-dimensional networks of galleries in termite nests and how spatial constraints affect the organisation of these networks. *Cubitermes* termite nests have far better than random transportation efficiency, but they do not reach theoretical optimal performance. We rather suggest a multiobjective process where a number of additional requirements, such as resilience to external attacks and the presence of spatial constraints, limit the ability of the system to achieve maximal transportation performance.

1. Introduction

Animals and humans move across the space following preferential paths. These are the trails, tracks, roads, rails and air routes that compose large transportation networks.

In human built transportation networks, planning and design take an active part in shaping the final network topology. On the contrary, animal built networks grow out of the merging and intersection of individual paths formed by individuals that in general do not possess a global knowledge of the whole structure. For this reason animal transportation networks are particularly interesting, because they are completely self-organised [1].

Transportation networks are spatial networks, that is, networks where the probability for two vertices to be connected is function of their relative distance [2] (see also Ref. [3] for review). Spatial planar networks have received much attention in recent literature because of their capability to describe human transportation systems and street patterns [4–9]. Human built transportation networks, sometimes deviate from planarity in the sense that vertices all lie on a 2-dimensional plane, but edges are not constrained to connect to spatial "neighbours". This is the case, for instance, of the world-wide air transportation network [10,11], the physical internet wiring [12], or wireless networks.

In order to understand the properties of a particular real world transportation network, papers typically compute many network estimators. On the theoretical ground they usually address the question 'what is the optimal transportation network given a set of constraints and a particular objective of optimisation?'. Comparing the properties of the real world networks with the "optimal" network model, it is possible to make hypotheses about which factors have shaped the real network topology.

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Typical examples of optimal networks include *minimum spanning trees* (MST, the network that connects all the vertices at the minimum total cost), *shortest path spanning trees* (the spanning trees with minimum distance between its root and any other vertex), and spanning trees minimising the average or maximum distance between all pairs of vertices (respectively the *minimum average stretch spanning tree* MAST and the *minimum maximum stretch spanning tree* MMST). Usually, however, complex real world networks grow under the effect of multiple forces and multiple constraints. In order to evaluate the performance of these networks, more complex optimality criteria have been considered.

In general one can distinguish between rooted transportation networks (where all the flows originate from a single source or are directed toward a single sink) and unrooted, distributed networks where resources are exchanged between many vertices. In the context of rooted networks Banavar et al. [13] study transportation networks that provide a route from a root vertex (the source) to all the L^D sites uniformly distributed in a D-dimensional space. In this context, they describe a class of efficient networks that minimise the total flow over all the edges $\sum_{\forall e_{ij}} |I(e_{ij})|$ (where $|I(e_{ij})|$ is the magnitude of flow on the edge e_{ij}). In this model, networks can have loops. However, if no local constraint is imposed on the carrying capacity of individual edges, the optimal networks are trees [14]. Gastner and Newman [9] use a model of network generation that minimises both distance from the root and the total length of edges to simulate the properties of four real world transportation networks.

Urban street patterns are unrooted distributed networks with all vertices having similar importance. Buhl et al. [6] and Cardillo et al. [7] have studied the cost and robustness of urban streets networks comparing them with two extreme models: the Minimum Spanning Tree and the Greedy Triangulation (the planar network with the highest number of edges and low total cost).

In many cases, the relevant properties of unrooted transportation networks have been well reproduced by optimisation models that minimise an average network quantity. The exact measure to be minimised changes in different studies, but in general it basically involves a measure of distance that can be combined with additional parameters and constraints. Colizza et al. [15] study optimal networks minimising two parameters: average path length and traffic congestion (this latter assumed to be proportional to vertex degree). These authors show that a variety of networks can be generated simply varying a control parameter, so as to give more importance to either path length or congestion. Gastner and Newman [16] minimise edge "effective length", where the "effective length" of an edge is a weighted average between its topological and Euclidean distances. The optimisation is performed under the constraint that the total cost of the network must not exceed a given value. Depending on the values of the control parameter, this model can simulate different classes of networks ranging from networks resembling urban street patterns to networks more similar to the air transportation network. In Barthelemy and Flammini [17] optimal traffic networks result from minimisation of an average cost function along all the shortest paths. The cost here is proportional to the length of the edge and inversely proportional to the traffic (it is assumed that the more traffic there is along an edge, the easier it will be to find a fast connection).

However, minimisation of an average quantity is not necessary to reproduce some characteristics of human transportation networks. For instance, Barthelemy and Flammini [18] show that some of the peculiar properties of urban street patterns are well described by a local growth model where new vertices are connected to the existing network through the cheapest connections.

Animal built transportation networks have received less attention in the literature, in part because of the lack of accurate characterisations of real world networks. Animal transportation networks have important ecological and biological functions. They favour animal orientation [19,20] and regulate interactions between individuals, communities or species [21,22]. It is likely that the topology of such networks has been shaped by selective pressures associated to the above functions.

Most animal displacements follow paths and trails *on the ground* that are well described by planar networks. Buhl et al. [23] describe an underground system of galleries excavated by ants that is also well represented by a planar network (though here the planarity is somehow imposed by experimental constraints).

However, there exist also animal transportation networks that are 3-dimensional. One of these is the gallery system inside the nests of termites. Termites are known for building huge and extremely complex nests [24,25]. In most cases the nests do not simply result from the repetition of local patterns, but present a coherent global organisation.

The nests of African termites of the Macrotermitinae subfamily in particular have attracted much attention in the literature [26–32]. Termites of this subfamily build mounds that are up to six metres high and house millions of insects, each less than 1 cm in length. Inside the mounds, the termites accumulate plant material that they use to grow a particular genus of mushrooms (*Termitomyces*), used as food by the colony. The fungi and termites together have a high metabolism, and produce abundant CO_2 and heat. Many studies have shown that the particular form of the mound and the inner air channels contribute to maintain the optimal levels of temperature and CO_2 necessary to the colony.

Phenomena such as thermoregulation and ventilation represent important examples of adaptive properties of termite nests, but they are likely to be ecologically important functions only for big colonies of fungus growing termites. Nevertheless, other aspects of nests built by all termite species are worth emphasising. In particular, we consider here the fact that inside the nests of almost all termite species are huge networks of galleries and chambers that span the three dimensions. These are one of the rare described examples of 3D transportation networks. Their topological properties are also likely to be extremely relevant for the ecology and the survival of the termite colony. In fact termites spend most of their life inside a single network, comprising the galleries inside the nest and other subterranean galleries that connect the nest to the foraging sites [25].