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# Local cost minimization in ant transport networks: from small-scale data to large-scale trade-offs

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Transport networks distribute resources and information in many human and biological systems. Their construction requires optimization and balance of conflicting criteria such as robustness against disruptions, transport efficiency and building cost. The colonies of the polydomous Australian meat ant *Iridomyrmex purpureus* are a striking example of such a decentralized network, consisting of trails that connect spatially separated nests. Here we study the rules that underlie network construction in these ants. We find that a simple model of network growth, which we call the minimum linking model (MLM), is sufficient to explain the growth of real ant colonies. For larger networks, the MLM shows a qualitative similarity with a Euclidean minimum spanning tree, prioritizing cost and efficiency over robustness. We introduce a variant of our model to show that a balance between cost, efficiency and robustness can be also reproduced at larger scales than ant colonies. Remarkably, such a balance is influenced by a parameter reflecting the specific features of the modelled transport system. The extended MLM could thus be a suitable source of inspiration for the construction of cheap and efficient transport networks with non-zero robustness, suggesting possible applications in the design of human-made networks.

## 1. Introduction

Transport networks are important in a wide range of applications from communication systems, through logistics and urban planning [1–6]. Most networks involve a trade-off between efficiency, cost and robustness. For example, efficient transport systems are those that allow direct travel between any two points in the network. However, acquiring high efficiency might require a lot of paths, making networks costly to build and possibly to maintain. Even when a low cost and efficient transportation network can be found, for example, by conveniently reducing the number of links until there is just one link per node, the resulting network is not likely to be robust. Indeed in this case, the failure of a single connection is enough to break the network into two parts, compromising transportation on a global level. As the simultaneous optimization of cost, robustness and efficiency is not possible, human transportation systems are carefully planned to obtain the best balance between these competing design criteria [5,7–10]. In nature, we can find many transport networks that are built without centralized planning. Examples include the vascular networks of vertebrates [11,12], the mycelial networks of fungi [13,14] and the trail networks of social insects [15,16]. Most of these have evolved to satisfy environmental and evolutionary constraints, often providing near-optimal solutions with similar trade-offs to human systems [13,17–19].

Some ant species build trails that connect multiple nests and food sources within the same colony (polydomy), providing a striking example of decentralized transport networks that allows the exchange of resources among spatially separated sites [20–23]. The best known and most widely studied example is the Argentine ant [16,22–24]. When observed under laboratory conditions, these ants connect their nests using a trail network which resembles a minimum

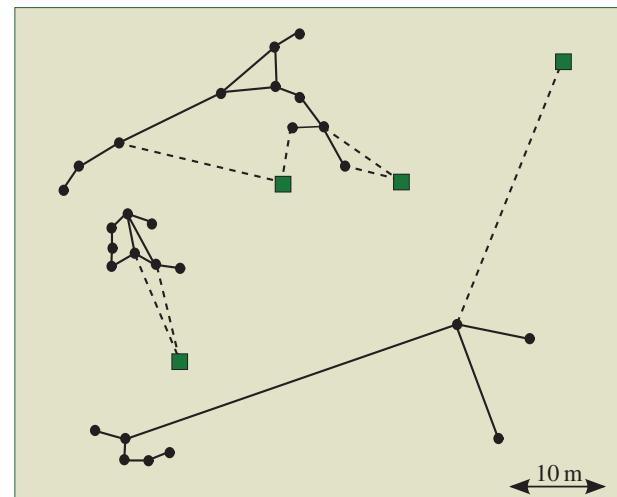
spanning tree (MST). The MST minimizes the total length of the network and thus its cost. [16,25]. In the field, Argentine ants appear to form more robust networks. For example, Heller *et al.* [23] show a trail map that has multiple trails between nest sites. In Argentine ants, network formation is based on pheromone deposition and evaporation; this simple process has inspired a number of optimization algorithms [26–28].

Cost minimization is only one of the optimization criteria that constrain the ants. As in human networks, several polydomous ant species face the problem of balancing efficiency, robustness and cost. Such balance differs for different ant species and seems to be linked to their mechanism of network formation [15,20,29]. However, little is known about how ants actually obtain a certain equilibrium among competing network design criteria. What are the building mechanisms that lead to an effective balance of topological properties? And can these be used as a source of inspiration for the design of human-built networks?

In this paper, we aim to identify simple and biologically plausible building rules for networks featuring trade-offs between robustness, cost and efficiency.

We start studying transport network construction and optimization in the Australian meat ant, *Iridomyrmex purpureus*. Meat ants live in underground nests covered by a mound of gravel, sand and bits of vegetation. Their main food source is honeydew, a sugary secretion they collect from aphids living on nearby trees. Meat ants are polydomous, therefore, their colonies consist of several nests and trees connected by physical trails and can stretch up to hundreds of metres. Such trail systems are actual transport networks where ants travel and transfer food, eggs and larvae between nests [20,21,30]. A graphical representation of some of these colonies can be found in figure 1 and was reconstructed from empirical data [20]. We chose meat ants because of two main features. First, their networks are made of two different kinds of nodes (trees and nests), resembling a large number of human transport networks constituted by sources and sinks [1,31]. Second, trails are quite large and kept clear of all vegetation, and thus are probably costly to build and maintain [20]. Here we assume that both building and maintenance costs will be proportional to the length of the trail (also following [25,32]). Although the proportion factor might not be the same, we cannot discard that trails will have a maintenance cost once built as, for example, ants will have to cut growing grass [30]. Recent analysis by Cook *et al.* [29] and Cabanes *et al.* [32] argue that meat ants' transport networks balance efficiency and cost without giving up robustness, rather than prioritizing any single design goal. These two facts make meat ant transportation networks particularly interesting for understanding network construction. Ideally, we would extract building rules by observing colonies as they develop under natural conditions. However, meat ant colonies are very slow growing and can take 60–80 years to mature [21,30]. Therefore, here we propose an alternative way to determine the building rules underlying network formation from the observation of a large set of colonies.

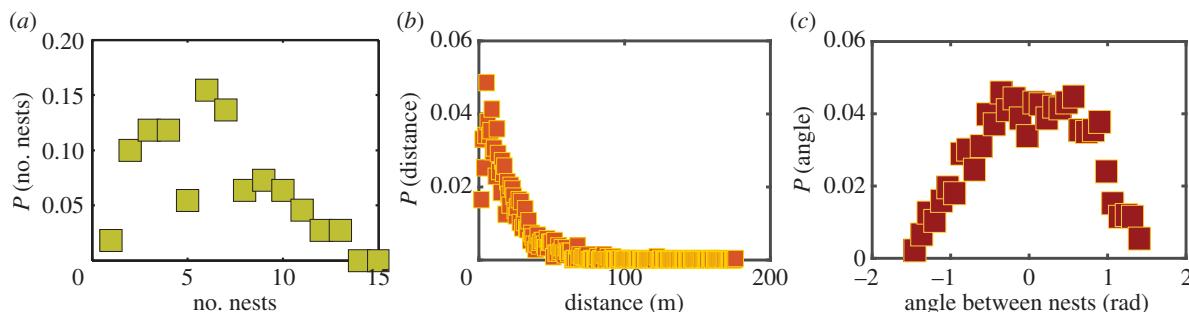
We focus on the growth of the ants' transport network through a data-driven modelling approach. We propose a model for the sequential addition of new vertices and edges, as is seen in both natural and human transport networks [33]. Our approach is similar to that taken in [1,34] and in contrast to other models that optimize transport



**Figure 1.** Graphical visualization of meat ants' colonies. The image shows three colonies of different size as detected through the GPS in [20]. Nests are represented by dots and trees by squares. Dashed lines are trails that connect the colony to trees and full lines represent trails between nests of the same colony. The scale is the same for all colonies as indicated at the bottom the figure. (Online version in colour.)

networks by rewiring an existing set of nodes [26,28,35,36]. Importantly, it is also consistent with how ants build their networks, starting with a single nest and building new ones as the ant population gets larger [30]. Note that we do not explicitly take into account the behaviour of individual ants. Instead, the global network building rules that we study here can be thought of as the result of underlying repeated local interactions between ants.

The paper is structured as follows. We first propose a data-driven model of network growth based on the sequential addition of new nodes (nests) and links (connecting trails). The spatial distribution of nodes is taken from data [20], while we implement several possible mechanisms of connection for the new nodes. All these mechanisms are biologically plausible and could in principle produce spatial networks resembling the observed meat ant colonies. Comparing with empirical data, we identify a combination of rules reproducing some key global patterns and we name it the 'minimum linking model' (MLM). When we test the MLM on the relevant topological properties of transport networks (efficiency, robustness, cost), we find that we can reproduce the same balance characterizing meat ant networks at the same network size of about 15 nodes. We are also interested in the performance of the model when representing large man-made transport networks that may be composed of thousands of nodes [1,4]. We scale the MLM up to 2000 nodes, finding that the scaling of robustness, cost and efficiency with network size is qualitatively similar as in an MST. That is, the MLM is a dynamical prescription of local optimization having similar properties to the MST, which is usually computed by connecting a given set of nodes so to optimize global cost [37]. Thus at large scale, the transport networks grown with the MLM prescription feature a balance between efficiency and cost only, discarding robustness. In the last part of this work, we re-introduce a large-scale balance between all the considered design criteria by defining a local extension of the MLM (named 'local minimum linking model', LMLM). We show how the specific balance depends on the source nodes' catchment area, reflecting the supply–demand



**Figure 2.** Experimental distributions providing initial conditions and positional statistics for the model. We extracted the following three distributions from experimental data in [20] and used them to initiate the model: (a) distribution of the number of nests per colony; (b) distribution of distances between nests within a colony, independent of the existence of trails connecting them; (c) distribution of the angular distance between nests within a colony with respect to their closest tree, independent of connecting trails. (Online version in colour.)

relationship between sources and sinks. This allows us to make a more realistic parallel with typical source–sink transport networks, opening possible applications in the design and management of human transport networks.

## 2. Model and methods

### 2.1. Mechanisms of network growth

Meat ant colonies consist of a network of connections between two different kinds of nodes, trees and nests, with undirected links in the form of ant trails [20] (figure 1). The algorithm we now propose is a general mechanism for building a spatial network, but in what follows we will interchangeably use biological terms such as colony, nest, tree and trail and abstract terms as network, node and edge.

The aim of our methodology is to test various plausible mechanisms for colony network construction. Ant colonies observed in the field grow by budding a new nest from older ones [30]. Then the new nest is linked to the rest of the colony and possibly to a tree by a trail that is kept clear of any kind of vegetation. In order to investigate the process of linking nests to trails, we start by making a number of basic assumptions about where the nests are placed with respect to trees and older nests.

#### 2.1.1. Trees and initial territory

We assume a random distribution of trees in a square with the first nest (N1) placed in the centre of the square and connected to the closest tree. The density of trees in the surrounding square ( $0.002 \text{ trees m}^{-2}$ ) is compatible with that observed in [20]. This initial condition simulates how a new ant colony is founded, with the new queen landing and establishing a nest after the nuptial flight [30,38]. Also, it is in agreement with the observation that ants often build the shortest trail possible [20].

#### 2.1.2. Number of nests

The distribution of the number of nests per colony is taken directly from data previously collected by Wilgenburg [20] (figure 2a). In each simulation, we choose the eventual colony size from this distribution. We then add the nests one at a time, connecting them to the network at each time step.

#### 2.1.3. Placement of nests

On each time step, we choose a budding nest (BN) among the ones already belonging to the colony. A budding nest is

the nest from which ants start searching the surrounding territory for a suitable spot to build a new nest. Such a search typically starts due to overcrowding that is related, in turn, to the age of the nest and its maturity [30]. Thus in our model, the probability that nest  $i$  is a budding nest is proportional to its age  $T_i$ :

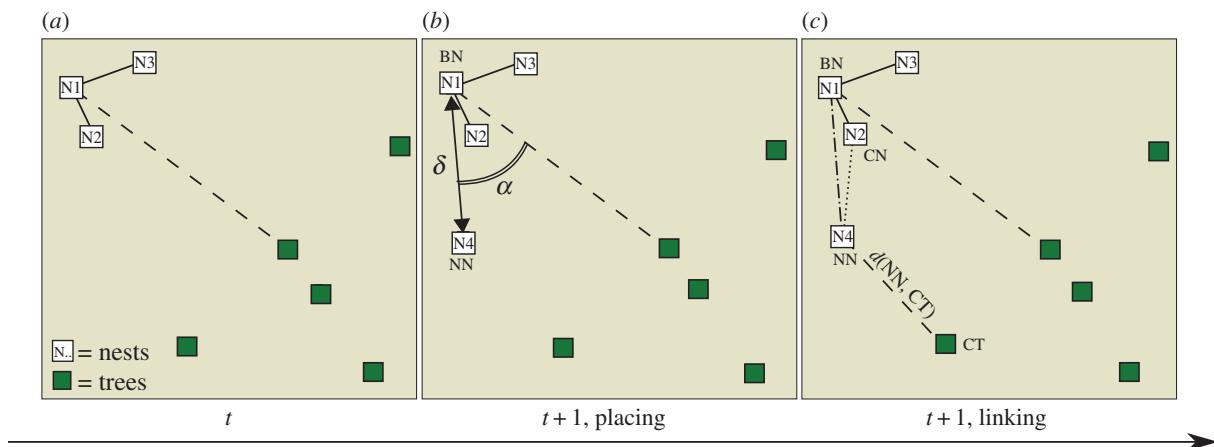
$$P_B(i) = \frac{T_i}{\sum_i T_i}. \quad (2.1)$$

Once the budding nest is selected, we determine the placement of a new nest from the experimental statistics. That is (1) the distribution of distances between nests within a colony, independent of the existence of trails connecting them (figure 2b); and (2) the distribution of the angles between nests within a colony with respect to their closest tree (figure 2c). To compute (2), we consider one nest belonging to a colony and we label it FN (focal nest). Then we find the FN's closest tree (CT), and all the nests that are closer to this tree than the focal nest, FN. Let  $k$  be the number of such nests, then we label them CN( $i$ ) (closer nests), with  $i = 1 \dots k$ . Finally, we compute the angle between the direction connecting FN with CT and FN with CN( $i$ ), for all  $i$ . The distribution (2) is computed over the angles obtained by iterating this procedure over all the nests belonging to each colony, treating them in turn as the focal nest (FN). This distribution implicitly represents physical and environmental constraints that ants have to account for while building their network. The computation algorithm follows from the empirical observation that meat ants tend to build new nests closer to food sources with respect to the rest of the colony [20,30]. The distributions described above do not contain any explicit constraint or information about the topology of ant transport networks. In numerical simulations, the position of the new nest (NN) with respect to the BN is then given by the polar coordinates  $(\delta, \alpha)$  (figure 3b).  $\delta$  is taken from the distance distribution (figure 2b) and  $\alpha$  from the angular distribution (figure 2c) and added to the direction connecting BN with its closest tree.

#### 2.1.4. Linking schemes

We now test two different rules for connecting the new nest to the colony, and three rules to connect it to a tree. We assume that the new nest NN will make one and only one connection either to (i) BN: its budding nest or (ii) CN: its closest nest.

As in ant colonies only some nests are connected to trees, we propose three different criteria for building a connection



**Figure 3.** Illustration of the ants' network expansion model and the proposed wiring schemes. (a) Generic starting condition at time  $t$ . At time  $t + 1$ , the model adds a new nest (NN) and links it to the existing colony and possibly to a tree. (b) Positioning: extraction of a budding nest (BN) (equation (2.1)) and placement of the new nest at distance  $\delta$  and angular deviation  $\alpha$  extracted from the positional statistics in figure 2b and c. (c) Linking: connection of the new nest to the colony with two possible schemes: BN-linking (dotted-dashed line) or CN-linking (dotted line). We test three criteria for connecting NN to its closest tree CT (dashed line) depending on the distance  $D$  between NN and CT: (i) connect if  $D$  is the minimum over all the distances between CT and the other nests in the colony; (ii) connect if  $D$  is minimal over all the nest–tree distances; and (iii) connect if  $D$  is less than the distance between the NN and CN. (Online version in colour.)

**Table 1.** Summary of the main rules of the model and linking schemes.

rule	formula	description
choose the budding nest	$P_B(i) = T_i / \sum_j T_j$	the probability that a nest $i$ is a budding nest is proportional to its age $T_i$
link to the colony	BN	links NN to the budding nets
	CN	links NN to the closest nest
link to the closest tree if	$D < \min_N(d(CT, N))$	(1) $D$ is minimum compared with all distances between CT and the other nests in the colony
	$D < \min_{N,T}(d(T, N))$	(2) $D$ is a global minimum for all tree-colony distance
	$D < d(NN, CN)$	(3) $D$ is less than the distance between the new nest and its closest nest

between a new nest and its closest tree (CT). We do not possess information about the amount of resources provided by different trees, thus we assume that all trees are *a priori* equally likely to be linked. With such an assumption, in the model the cost and the advantage of annexing a tree depends only on its distance from the colony. Therefore, we compare the distance  $D = d(NN, CT)$  between a new nest and its closest tree to other relevant distances in the colony, establishing a connection in three (alternative) cases:

- (1)  $D$  is minimum compared with all distances between CT and the other nests in the colony, i.e.

$$D < \min_N(d(CT, N)); \quad (2.2)$$

- (2)  $D$  is a global minimum over all the distances between each nest and tree, independent of the existence of connections:

$$D < \min_{N,T}(d(T, N)); \quad (2.3)$$

- (3)  $D$  is less than the distance between the new nest and its closest nest:

$$D < d(NN, CN). \quad (2.4)$$

Connection scheme (1) is a local rule that tends to ensure a large number of trees per colony while minimizing the length of the trails needed to reach them. Scheme (2) establishes the least

possible number of trails, connecting to a food source only if it is globally the cheapest option. Rule (3) is a local criteria assessing the advantage of transporting resources from CT rather than transporting them from CN. Altogether we have six combinations (BN1, BN2, BN3, CN1, CN2, CN3) of linking rules that are biologically reasonable and give different final topologies. See table 1 for a summary.

## 2.2. Model selection through topological quantities

We determine which of the six models above (BN1, BN2, BN3, CN1, CN2, CN3) best reproduces empirical data using two quantities: the number of hubs within a colony and the number of trees per colony. Following [20], we define 'hub' as any point at which two or more trails intersect. In the model, hubs naturally arise as a consequence of nest placement and of the connection rules. We simulate 300 realizations for each of the six combinations of connection rules. We compute the distributions of the number of hubs and of the number of trees per colony and we compare them with the corresponding distributions for the 142 colonies in [20]. We use the distribution of hubs to determine the best nest-linking rule, and the tree distribution to find the best rule to link the new nest to a tree.

## 2.3. Model validation on the main transport networks design criteria

After selecting the model that best reproduces the distribution of the number of hubs and trees, we verify whether

it also reproduces the relevant topological properties of meat ant transport networks and the balance that characterizes them. Following [32], we consider robustness, efficiency and cost as the relevant and competing design goals in transport network construction [2,13]. Robustness is defined as the probability that the network remains connected under the removal of one random link. This definition can be interpreted as a particular case of reliability polynomial for vertex cancellation [39]. In the case of ants, robustness measures the resilience of the network against, for example, trail disruptions due to natural causes or to predation [40]. The efficiency of a graph  $G$  built on  $N$  nodes is defined following [41] and extended for spatial networks as

$$E(G) = \frac{1}{N(N-1)} \sum_{i \neq j \in G} \frac{d_{ij}^e}{d_{ij}}, \quad (2.5)$$

where  $i$  and  $j$  are nodes in  $G$ ,  $d_{ij}^e$  is their Euclidean distance and  $d_{ij}$  is the length of the shortest path connecting them on the network  $G$ . Efficiency represents how fast information and resources are exchanged over the network [29,41]. Finally, cost is defined as the total length of the trails connecting the network:

$$C(G) = \sum_{i \neq j \in G} d_{ij}. \quad (2.6)$$

As discussed in the introduction, meat ants build physical trails by removing all vegetation from them [20]. Here we make the simple assumption that the longer the trail, the wider the area to be cleared while building the trail and to keep clean afterwards. Accordingly, both the costs of building and maintaining a trail are proportional to its length [25,32]. As we do not have experimental evidence about the proportion factors, it is reasonable to directly use the total length of the trails as the main characterizing quantity for the total cost. To test our selection procedure, we compare the distributions of these three quantities for the 142 colonies in [20] with 300 realizations of the best model.

#### 2.4. Large-scale limit of the model

In this part of our work, we address the possible application of the selected model to the design of human transport networks requiring a balance between competing criteria. Man-made networks may be composed of thousands of nodes [1,4], thus we are interested in the large-scale behaviour of our model. Here we mainly focus on the evolution of topological quantities and their final balance with network size. We simulate the selected model up to 2000 nodes and, at different network sizes, we compute the average values of robustness, efficiency and cost over 300 instances of the model. As we do not have specific empirical data for large networks, we compare our model with the corresponding Euclidean MST. The MST, by definition, is the network of shortest length that connects a given set of nodes, optimizing cost at the expense of robustness [37]. At selected sizes, we use Prim's algorithm to build the MST connecting the existing nodes [42] and we compute the corresponding topological quantities. As regards the position of nodes, we follow the empirical distributions for distance and budding angle computed from [20] (figure 2b and c) together with the budding probability given by equation (2.1). As a consequence, the local density of nodes changes with the size of the network by construction. As older nodes are more likely to bud new ones, in particular, we expect the older,

central part of the network to be denser than the peripheral one. This spatial distribution is compatible, for example, with empirical observations on urban densities [43]. Sources are randomly distributed in a large territory in order to reproduce the average tree density used in the small-scale simulations.

#### 2.5. Local extension of the model

The final step in our work is to introduce a variation of the original source-linking rule in the large-scale simulations. The new connection scheme states that a link between a new nest (sink node) and its closest tree (source node) is established if their distance is minimal within a certain number of neighbouring nodes and their closest tree, independent of connections. We call the set of such nodes 'minimization neighbourhood',  $N_{\text{neigh}}$ , and we fix it to 20 nodes. With this choice, the introduced variation coincides with the original model on the typical size of an ant network. Thus, the new connection scheme can be seen as a 'local extension' of our original tree-linking rule. Such variation corresponds to the reasonable assumption that the resources provided by a source node can support only a finite amount of sink nodes. From the perspective of human-built networks, it is indeed the case for power plants, water stations or even schools and hospitals. We test the performances of the local version of the model simulating networks up to 2000 nodes and comparing the average values (computed from 300 realizations) of robustness, efficiency and cost with those obtained for the MST and with the original version of the model. Finally, we study the large-scale dependence of the balance between robustness, efficiency and cost as a function of the size of the minimization neighbourhood. We simulate the local version of the model for different neighbourhood sizes from  $N_{\text{neigh}} = 3$  to  $N_{\text{neigh}} = 100$ , and we observe change in the asymptotic (at  $N = 2000$ ) values of the relevant network properties.

### 3. Results and discussion

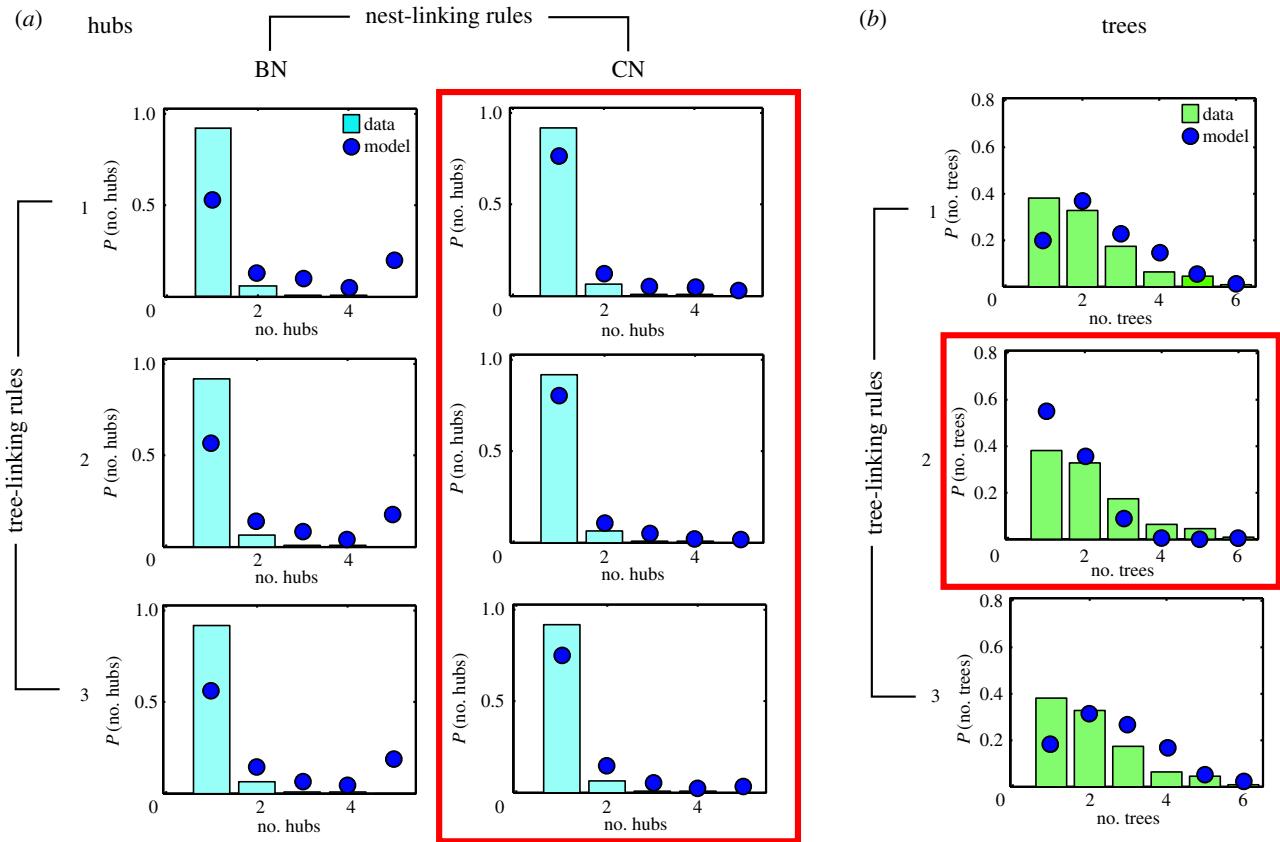
#### 3.1. Model selection: the 'minimum linking model'

The results of the comparison between data and the simulations of the different connection schemes are shown in figure 4. As shown in figure 4a, linking to the closest nest (CN) best reproduces the distribution of the number of hubs within a colony for all the three tree-linking rules. The number of hubs does not allow us to clearly choose between the rules to connect new nests to trees. The number of trees per colony depends only on how links to trees are established, thus in figure 4b we compare data and simulations only for the three tree-linking rules. The comparison shows that the distribution for the number of trees is reproduced only by rule (2), i.e. by linking the new nest to its closest tree only if their distance is minimal among all the nest-tree distances within the colony.

The combination of the linking rules that best reproduces data, CN2, is also the one that minimizes the total length of the trails over all the proposed schemes, thus we name it the MLM.

#### 3.2. Model validation on the design criteria of the main transport networks

Once we determined that the MLM is the model that best reproduces hubs and trees distributions out of the models proposed,



**Figure 4.** Selection of the MLM by comparison with empirical distributions. Histograms represent the empirical distributions, circles represent the model outcomes computed over 300 realizations. (a) The empirical distribution of the number of hubs per colony is compared with the distributions obtained simulating the six proposed linking schemes (CN and BN for the nests, columns; 1, 2, 3 for the trees, rows). The trend of the empirical distribution is reproduced only by linking the new nest to its closest nest (CN). (b) The empirical distribution of the number of trees per colony can be reproduced only by linking the new nest to its closest tree when their distance is minimal over all the nest–tree distances (rule 2). This distribution is independent of the nest-linking rules thus we show only the three cases for the tree-linking rules. The combination of the highlighted linking rules minimizes the total length of the trails over all the possible schemes defining the MLM. (Online version in colour.)

we check whether it also matches the relevant design criteria as observed in the meat ants' transport networks. In particular, we compare the model's distribution of robustness, efficiency and cost with the empirical ones (see Model and methods for the definitions). From this comparison, we see that the MLM produces the same key topological features of meat ants' transport networks (figure 5) and their characteristic balance. A graphical visualization of the simulated networks also shows that their structure is qualitatively similar to real ants' colonies as regards, for example, territorial extension and the presence of motifs such as triangular loops (cf. figures 1 and 6).

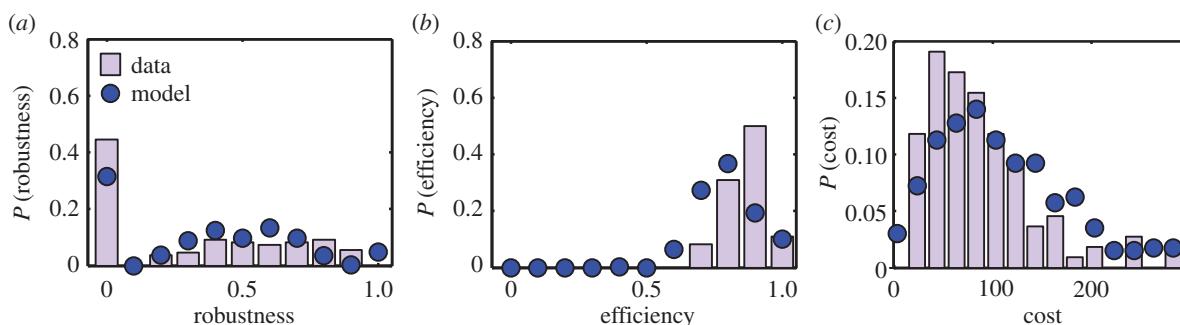
### 3.3. Large-scale limit of the model

We have shown that the MLM reproduces the meat ants' transport networks, balancing robustness, cost and efficiency through a simple prescription of local optimization. This is achieved on small networks of about 10–15 nodes, while human transport networks are typically larger, spanning from hundreds to thousands of nodes [1,4].

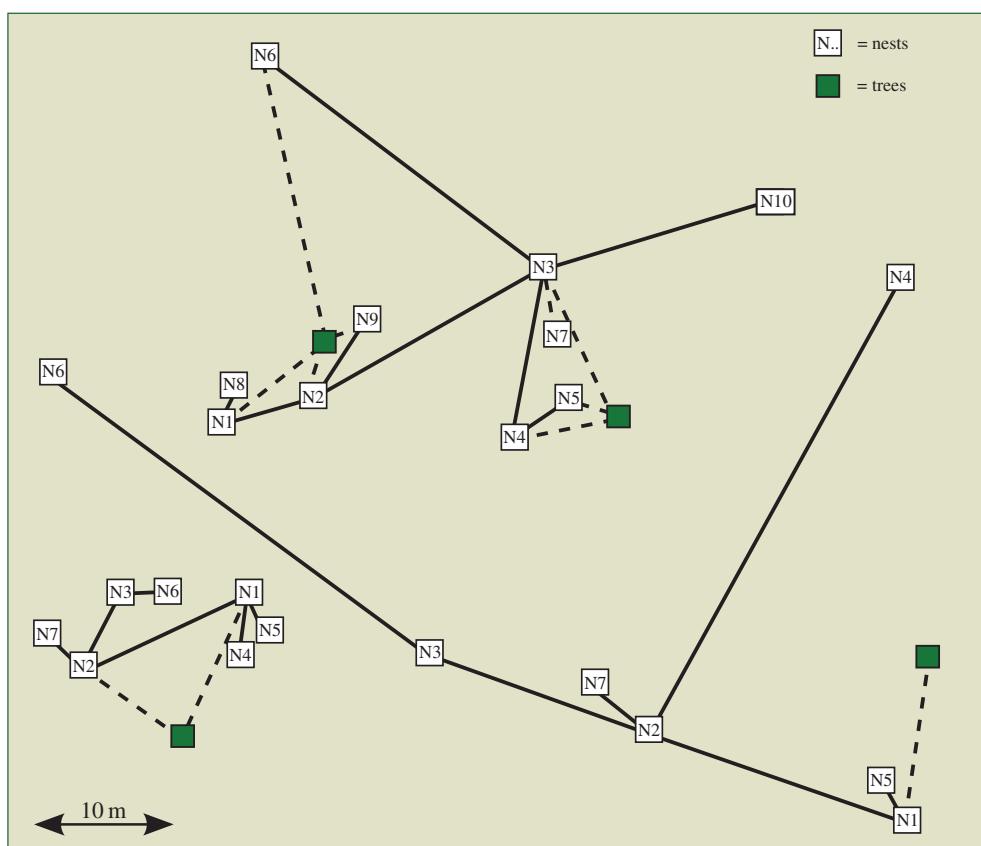
Large-scale simulations (up to 2000 nodes) show that the scaling of the MLM with network size is qualitatively similar to the one of an MST, albeit with some interesting differences. The first three plots in figure 7 compare the trends of the mean values of the MLM with the corresponding MST for robustness, efficiency and cost at increasing network size. The robustness of the MLM's networks tends to zero with

network size, approaching the value that is typical of an MST (figure 7a). Efficiency in the MLM is a monotonically decreasing function of the number of nodes as in the MST. However, initially it is smaller than the efficiency of an MST, and becomes larger after a certain critical network size  $N^*$  that we estimated to be 230 nodes (figure 7b). Fitting the average cost gives a power scaling  $C \sim N^\alpha$  for both models (figure 7c) with exponents  $\alpha_{\text{MLM}} = 0.71$  (s.e. = 0.03,  $R^2 = 0.99$ ) and  $\alpha_{\text{MST}} = 0.69$  (s.e. = 0.03,  $R^2 = 0.99$ ). The observed gap in the exponent  $\Delta\alpha = 0.02$  is within both standard errors, thus the difference in cost scaling is not particularly significant. Consistently, the ratio of the network's mean cost of the MLM over the MST shows a sharp increase at small sizes that slows down significantly as  $N$  gets larger than the critical size  $N^*$  estimated from efficiency (inset in figure 7c).

The drop in robustness can be explained by the sub-linear growth of the average number of connected trees (source nodes) per colony that is shown in figure 7d. By construction, the only way to have a closed path (also called loop) in our model is when two different nests cast a connection to the same tree. Therefore, the lack of connected trees at larger sizes causes the lack of loops, which number becomes almost constant near  $N^*$  (figure 7d). The presence of loops is fundamental for robustness, as they provide more than one path to go from one node to another, making the network more robust against the random removal of links. It is



**Figure 5.** Comparison between simulations of the MLM and experimental data for the distributions of robustness, cost and efficiency. Empirical data are represented by the histograms and the model is represented by circles with distributions computed over 300 realizations. Comparing (a) robustness, (b) efficiency (equation (2.5)) and (c) cost (equation (2.6)) shows that the networks grown according to the MLM possess the same key topological features of meat ant transport networks. (Online version in colour.)



**Figure 6.** Visualization of selected realizations of the MLM. The scale is the same for all networks as shown at the bottom of the main panel. The comparison with figure 1 shows that the MLM produces outputs that are also visually similar to real ant colonies. In particular, network size can span from a few up to a tens of metres being compatible with the size of real colonies. Also, the model reproduces typical motifs found in ants' colonies such as triangular loops. (Online version in colour.)

likely that increasing the number of loops would also increase the network's efficiency. In our model, loops confer robustness to the network by adding a little cost at small size, however, they do not seem to constitute a particular advantage for the efficiency of the network. At sizes  $N$  larger than  $N^*$ , the number of loops becomes constant while the network keeps growing, meaning that it becomes less and less likely to obtain a connected network by removing a random link. Accordingly, robustness tends to zero.

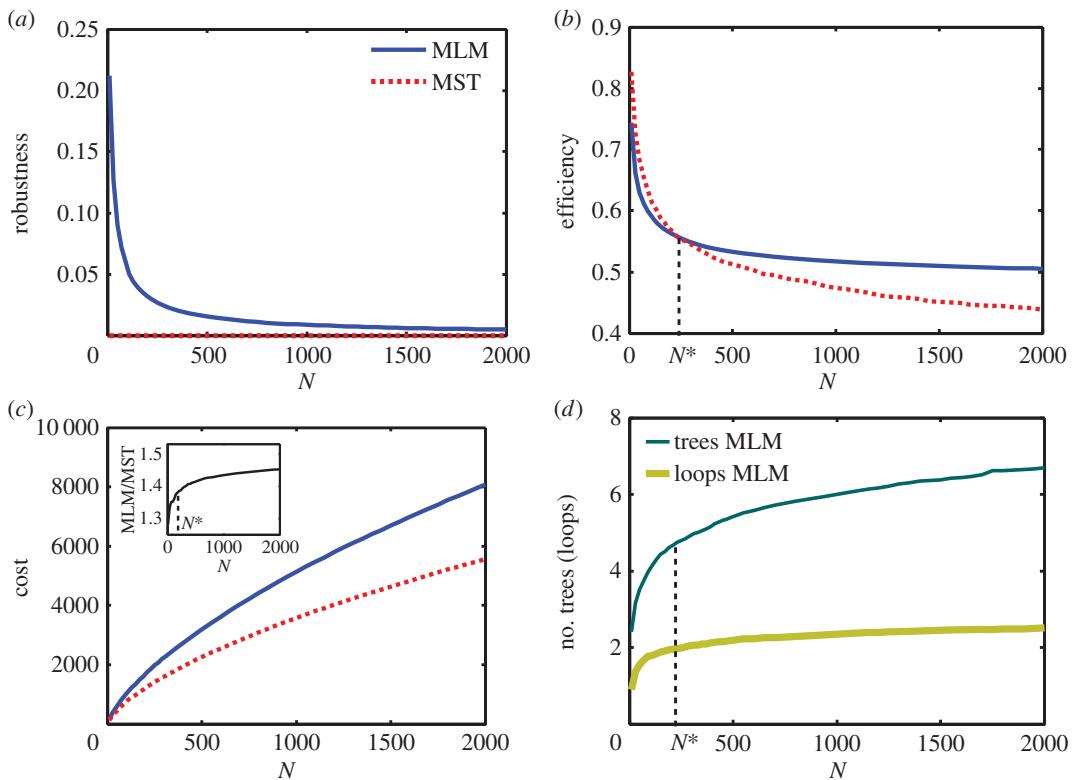
At large sizes, the MLM features higher values of efficiency and cost with respect to the MST, the latter being still compatible with an MST as shown above. This can be explained by the fact that the MLM links new nodes to their nearest neighbour but, as the network gets larger, it becomes more and more likely that new nodes fall closer to old nodes than their

previous nearest neighbour. This implies that the MLM features long-range links at large size, being more efficient than the corresponding MST, but not significantly more expensive.

Overall, the above results indicate that the MLM provides a dynamical framework for building networks that vary slightly from the MST, thereby balancing cost and efficiency at large scale.

### 3.4. Local extension of the model

In order to explore the model's potential in the framework of human-made transport networks, we introduced a local variation of the MLM where the tree-linking rule minimizes the distance  $D$  over a certain minimization neighbourhood  $N_{\text{neigh}}$  (see Model and methods for a detailed description). This



**Figure 7.** Large-scale behaviour of the MLM. Solid lines represent the average value of key topological features of the MLM as a function of network size. Dashed lines represent the scaling of the same quantities for the MST that was built at selected network size by rewiring the network's existing nodes. Mean values are averaged over 300 realizations. (a) Robustness: the MLM shows some robustness at small size that tends to zero with network size, reaching the typical value for the MST. (b) Efficiency: the MLM is less efficient than the corresponding MST at small size, while it is more efficient for sizes larger than a critical size  $N^* = 230$ . (c) Cost: in both MLM and MST, cost scales as a power law  $N^\alpha$  with similar exponents  $\alpha_{\text{MLM}} = 0.71$  and  $\alpha_{\text{MST}} = 0.69$ . (d) The average number of trees per colony and the number of loops (closed paths) grow sub-linearly with  $N$ , becoming almost constant after the critical size  $N^*$ . (Online version in colour.)

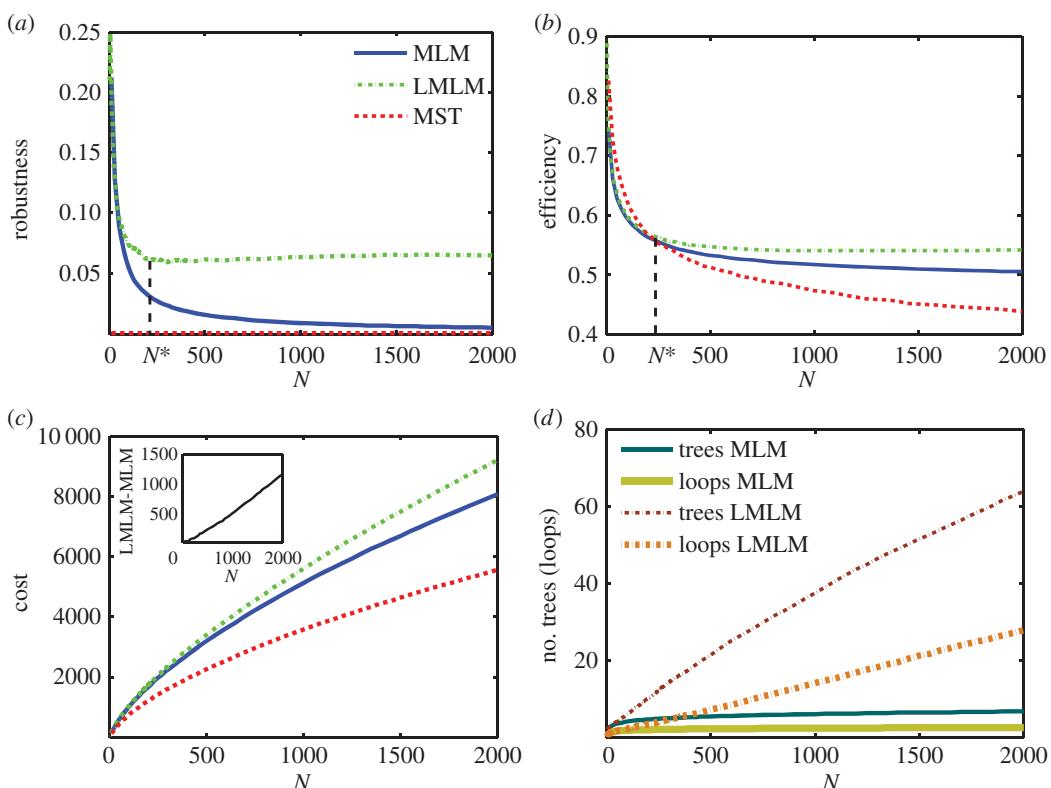
variation allows us to make a more realistic parallel with typical source–sinks transport networks. Indeed, it is reasonable to assume that a source node can support only a finite amount of sink nodes, such an amount constituting the minimization neighbourhood. As discussed below, it also makes it possible to build robust transport networks, reintroducing a balance between all the design criteria.

From now on we will refer to this variation as the LMLM.

When setting the neighbourhood size to  $N_{\text{neigh}} = 20$ , the LMLM features an improvement in robustness and efficiency against a further increase in cost with respect to both the MST and our initial model. In figure 8, we compare the average values of robustness, efficiency and cost obtained by the three considered models (LMLM, MLM, MST). Robustness in the LMLM converges to a non-zero value estimated around 0.064, staying stably larger than for the MST and the MLM. This means that, in the modified model, the chance of obtaining a disconnected network under a random link removal is still high (93%), but consistently different from 100%. Efficiency in the LMLM shows the same initial decrease as observed in the MLM, intersecting both the MLM and the MST at the critical size  $N^*$  (estimated to 230 nodes, see the previous section). After the intersection at  $N^*$  it seems to tend to an asymptotic value, remaining significantly higher than in the MST and in the original MLM (figure 8b). The average cost for the local MLM scales as  $N^\alpha$  with fitted exponent  $\alpha_{\text{LMLM}} = 0.76$  (s.e. = 0.05,  $R^2 = 0.99$ ; figure 8c). The increase in the scaling exponent results in a

linear growth of the cost difference of the two models (inset in figure 8c). Although the LMLM is growing faster than in the initial MLM,  $\alpha_{\text{LMLM}}$  is within the standard deviation of the fit for  $\alpha_{\text{MLM}}$ , while it is no longer compatible with the scaling exponent of the MST. Figure 8d shows that the average number of trees and loops per colony increases almost linearly with the size of the network. The linear growth in the number of loops explains the asymptotic convergence observed in the topological quantities, in particular the achievement of a constant non-zero value of robustness.

Our initial choice for the size of the minimization neighbourhood ( $N_{\text{neigh}} = 20$ ) was motivated by the conservation of the correspondence between LMLM and MLM for typical ant network sizes (where  $N < 15$ ). However, this is not the only possible choice. In figure 9, we show how the neighbourhood size influences the trends of the relevant network design criteria and their asymptotic balance. As expected, the size of the local neighbourhood is directly related to the value of robustness through the number of loops, also influencing the value of cost and efficiency. In figure 9a, we report the trend of the mean value of the key design criteria with network size  $N$  for increasing size of the minimization neighbourhood from  $N_{\text{neigh}} = 3$  to  $N_{\text{neigh}} = 100$ . Interestingly, for  $N_{\text{neigh}} = 3$  robustness is an increasing function of network size. This corresponds to a linear increase in cost with the number of nodes. To compare with the former trends in cost, now the scaling is a power law with  $\alpha_{N_{\text{neigh}}=3} = 1$ , leading to very expensive networks compared with the MLM ( $\alpha_{\text{MLM}} = 0.71$ ). Efficiency also is higher for smaller



**Figure 8.** Large-scale behaviour of the LMLM and comparison with the original MLM and the MST. The first three panels in the figure show the comparison between the mean values given by the three analysed models (LMLM dotted-dashed lines, the original MLM full lines and the MST dashed lines) at increasing network size. The fourth panel shows the comparison between MLM and LMLM as regards the scaling of the number of loops and trees per colony. Mean values are averaged over 300 realizations and the MST is built by rewiring the nodes of each network grown with the MLM at selected network sizes. (a) Robustness in the LMLM converges to a non-zero value estimated around 0.064 and remains stably larger than in the MLM and MST. (b) Efficiency of the LMLM decreases like the MLM until  $N^*$  (230 nodes), then tends to an asymptotic value that is larger than in the original MLM. (c) Cost grows as a power law  $N^\alpha$  with fitted exponent  $\alpha_{\text{LMLM}} = 0.76$ , resulting in a linear growth of the cost difference of the two models (inset). (d) The average number of trees per colony appears to increase linearly with the size of the network, being compatible with the asymptotic behaviour of the key topological quantities. (Online version in colour.)

minimization neighbourhoods but its trend is not substantially affected by  $N_{\text{neigh}}$ . In particular, figure 9b shows that at large network size ( $N = 2000$ ) high values of robustness (up to 0.7) can be obtained for small neighbourhood size, but require an almost a sixfold increase in the total cost with respect to the MLM (approximated with  $N_{\text{neigh}} = 100$ ). As already noted, the variation in the asymptotic value of efficiency is not as wide as for robustness.

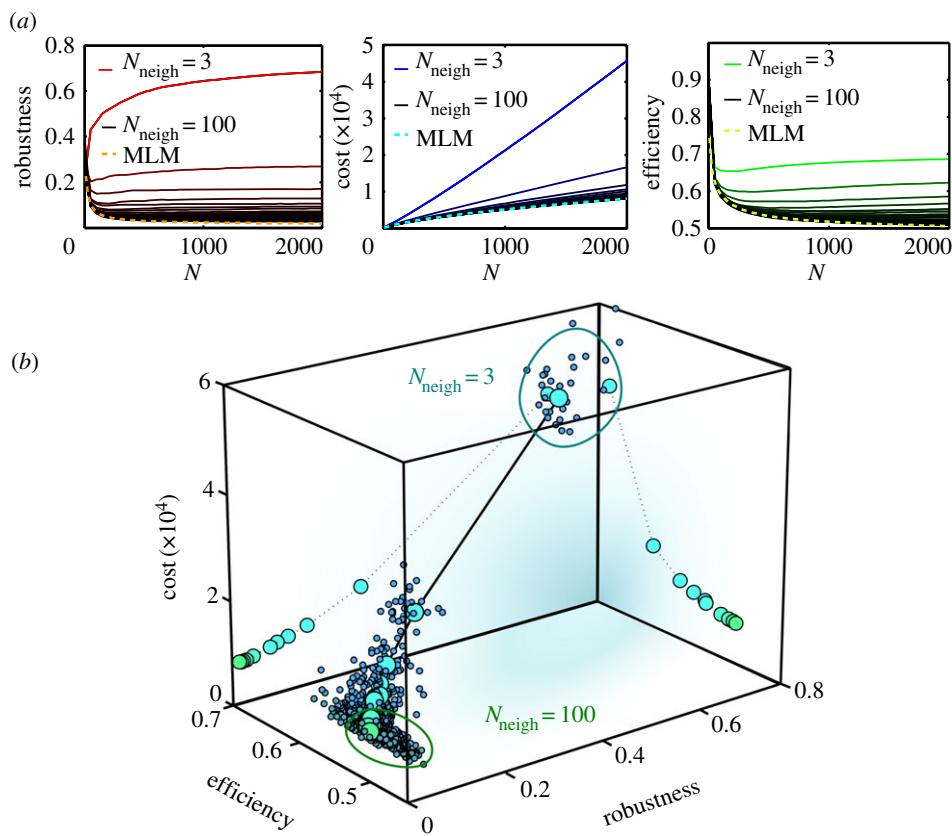
Overall, our analysis indicates that the local version of the MLM provides a prescription for building transport networks that balance all the key topological properties at each network size. Remarkably, the point of equilibrium can be tuned by changing one parameter: the size of the minimization neighbourhood. This new parameter can be chosen according to the features of the modelled system. For example, in a certain transport network each source node might be able to serve a maximum number of sinks. Setting the size of the minimization neighbourhood accordingly, one could predict what balance could be reached using the LMLM prescription.

#### 4. Conclusion and outlook

In this paper, we have used a selection procedure based on data to find the model that, out of the set we tested, best reproduces the main topological features of meat ant transport networks (figure 5) and the spatial structure of colonies (figures 1 and 6). In terms of network models, it would be difficult to imagine

other simple, local and biologically plausible building rules that could be tested in this framework. Another approach, for example, through an individual-based model, would be to provide single-ant rules of motion. This would, however, require a totally different dataset in order to be tested. Such an approach would provide a specific tool tailored on meat ants that would be difficult to apply to other biological networks. Our procedure could be used both to extract the construction rules underlying network formation of other polydomous ants and to understand the emergence of topological patterns observed in other living systems. Given the increasing interest in studying the formation and topology of animal transportation networks [13–15,19,29], our methodology constitutes a way to infer the growth process of the network when observing it directly is difficult or costly. Using the same prescription on different biological networks would also allow for comparisons between different connection strategies across different species and systems. Do all polydomous ants, for example, use the same connection rules, and if not, which ecological and behavioural factors lead to the use of a particular rule?

In the case of meat ants, we found that the only plausible model matching the data was the MLM. This model turns out to be based on simple and biologically plausible rules, with local cost optimization as the key. Remarkably, the model constructs transport networks featuring a balance among global fundamental design criteria. Although our model gives insights into the formation process of ant networks, it is not based on direct observation as it would take



**Figure 9.** Dependence of the balance between design criteria on the size of the minimization neighbourhood (a) solid lines represent the mean values of the key design criteria with network size  $N$  at increasing size of the minimization neighbourhood from  $N_{\text{neigh}} = 3$  (top), to  $N_{\text{neigh}} = 100$  (bottom). Dashed lines represent the MLM. For  $N_{\text{neigh}} = 3$  robustness is an increasing function of  $N$ . This corresponds to a linear increase of cost with the number of nodes ( $\alpha_{N_{\text{neigh}}=3} = 1$ ), leading to very expensive networks compared with the MLM ( $\alpha_{\text{MLM}} = 0.71$ ). (b) Evolution of the balance between cost, efficiency and robustness at  $N = 2000$  from  $N_{\text{neigh}} = 3$  (top) to  $N_{\text{neigh}} = 100$  (bottom). Small circles represent individual simulations and large circles the average values. The full line in the three-dimensional plot represents the evolution of the average value of the equilibrium point between cost, efficiency and robustness. Dotted lines represent the cost-robustness and cost-efficiency balance (projected from the full one).  $N_{\text{neigh}} = 3$  gives high asymptotic values of robustness (up to 0.7) but require almost a sixfold increase in the total cost with respect to the lower values for  $N_{\text{neigh}} = 100$ . In both panels efficiency is higher for smaller minimization neighbourhood but its trend is not substantially affected by  $N_{\text{neigh}}$ . (Online version in colour.)

decades to observe the establishment of a new nest and the connecting trails [38,44]. However, the model could suggest experiments that would shed light on meat ant behaviour. For example, our model can be used to predict how ant trail networks are reconstructed after a disruption such as the loss of a nest or the blocking of a trail. Manipulative field experiments could then confirm or refute the models predictions. Another interesting experiment would be to change the substrate meat ants move through while building their trail network. This would change the cost of constructing the network and could lead to different topologies and building strategies. It might also allow us to distinguish between building cost and maintenance cost of a trail, leading to a better understanding of how cost is relevant to network construction.

Scaling up to large networks, our focus is on understanding the global network features emerging from a rule of local minimization. At this stage, the model is abstracted from its initial biological meaning and we are mainly interested in the evolution of topological quantities and their balance point. Is there anything that we can learn from ants and apply it to a different system such as human transportation or distribution networks? When simulated for a large number of nodes, the MLM produces networks that, on average, feature a balance between efficiency and total cost at the expenses of robustness. Cost, in particular, is comparable with that obtained via MST, meaning that the increase in efficiency is almost

effortless. Robustness, however, tends to zero at increasing size, increasing the probability that the network will break into two after a small failure. When designing transport networks, robustness plays a fundamental role and is highly desirable [8,10]. However, the drop in robustness with network size is still interesting from a biological perspective and might explain why we do not observe colonies larger than 15 nests (see the size distribution in figure 2a). The model seems to suggest that the construction strategy adopted by meat ants cannot balance cost and robustness when a colony becomes too big. It might be that a colony requires a minimum value of robustness because of, for example, territorial competition with other colonies or resistance to predation. Thus, the optimal strategy might be to keep the colony smaller than a certain size by either splitting it or by establishing a new colony in another area through a nuptial flight. Future field-work could test our prediction by studying the relationship between colony size and splitting events in wild colonies.

In order for the MLM to be more suitable for informing human transport networks, it would need to include robustness as well as high efficiency and low cost. Moreover, it is not completely realistic to assume that a source node could provide for any arbitrary number of sink nodes. To address this, we have introduced a local variant of our model to relax the condition of cost minimization for the source-linking rule. In particular, we require that the cost of linking a new node to a

source is minimal over a neighbourhood of 20 nodes, called the minimization neighbourhood. This is equivalent to setting the catchment area of the sources to 20 sink nodes. The new model is significantly more expensive with respect to the cheapest possible option of an MST, but at large scale it performs better as regards robustness and efficiency. Therefore, the introduced variant re-establishes the sought after balance between all the considered topological properties. Remarkably, such equilibrium can be tuned by making the size of the minimization neighbourhood a parameter of the model. In particular, for a very small minimization neighbourhood it is possible to make robustness increase with network size. This parameter represents the sources' catchment area and thus is suited to reflect the features of the specific modelled transport network.

The LMLM seems very reasonable if thought of in a real-world situation such as the construction of a supply network or urban planning. For example, building a new suburb requires connections not only to the existing urban network but also to public services (schools, supermarkets, power plants). In this case, the size of the minimization neighbourhood could be tuned to reflect the typical local need for resources of the system under consideration. Then the model could advise whether it is convenient to build a connection to an existing source or if it is enough for the new area to access services through the existing network. Conversely, the model could predict the final robustness of the network obtained by minimizing connections cost, given the source–sink relationship characterizing the considered system. A further use of the extended MLM could be as a rebuilding prescription in case of disruption of links or nodes. Indeed, we argue that using our model to reconstruct part of a damaged transport network would be locally cheap, preserving efficiency and robustness on a global level. Our local variant could therefore be a suitable source of inspiration for the construction of robust and efficient transport networks characterized by a sources–sinks duality. Moreover, the dynamical nature of the MLM and of its local version fits the growing, evolutive aspect characterizing most human-made networks [37].

A similar model of local optimization was proposed and partially analysed by Fabrikant *et al.* [45] in the framework of the growth of the Internet. The analysis of Fabrikant *et al.* did not include sources, but introduced the mechanism of local cost minimization as a linking prescription, naming the resulting model 'dynamical MST'. Quantifying the actual difference between the dynamical MST or, equivalently, the sourceless MLM, with the actual MST would be an interesting theoretical challenge, giving an insight into the broader topic of the definition of topological distance between graphs. It might also be a useful analysis for the problem of the MST dynamical update, i.e. how to recompute the MST efficiently when adding new nodes [46]. It may well be that the ant construction model can give insights into these much larger networks, and that similar design principles are used in both cases.

## 5. Materials

In this paper, we refer to the maps of ant trail networks collected by Wilgenburg *et al.* [20] in the field in Australia in 2002. Such data are comprised of 142 trail networks maps where the coordinates of nests and trees were obtained with the aid of a GPS and the existence of connections between them recorded by hand and through aerial photography [20]. Simulations are performed using the software MATLAB.

**Authors' contributions.** A.B., T.L. and D.T.J.S. designed the study, developed the methodology and drafted the manuscript; A.B. implemented the model and performed numerical simulations and data analysis; E.v.W. collected and provided the data [20].

**Competing interests.** We declare we have no competing interests.

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