

# Shape and efficiency of wood ant foraging networks

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**Abstract** We measured the shape of the foraging trail networks of 11 colonies of the wood ant *Formica aquilonia* (*Formica rufa* group). We characterized these networks in terms of their degree of branching and the angles between branches, as well as in terms of their efficiency. The measured networks were compared with idealized model networks built to optimize one of two components of efficiency, total length (i.e., total amount of trail) and route factor (i.e., average distance between nest and foraging site). The analysis shows that the networks built by the ants obtain a compromise between the two modes of efficiency. These results are largely independent of the size of the network or colony size. The ants' efficiency is comparable to that of networks built by humans but achieved without the benefit of centralized control.

**Keywords** Networks · Trunk trails · Ants · *Formica*

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## Introduction

Transport networks are observed at all levels of biological organization. Fungi (Bebber et al. 2007), slime molds (Nakagaki et al. 2004a, b), and human societies (Gastner and Newman 2006) all build networks that allow the movement of materials through their environment. One of the most striking examples of these transport networks are the trail systems formed and used by many different species of ants. Ants typically forage for food from a central nest, building a network of trails radiating out to nearby food sources. These networks are typically dendritic in form (Hölldobler and Möglich 1980; Hölldobler and Wilson 1990). Each trail starts from the nest as a single thick pathway out of the nest. This “trunk” splits first into thinner branches and then peters out as the distance from the nest increases into twigs, often barely distinguishable in the undergrowth.

While sharing this dendritic form, there are often between-species differences in the time for which trails persist and the mechanisms used in their construction. In army ant species (Schneirla 1971; Topoff 1984; Franks 1989), as well as in *Leptogenys processionalis* (Ganeshaiah and Veena 1991) and *Pheidologeton diversus* (Moffett 1988), swarm raid trails last for short periods of time (i.e., for a day or less) and result from strong positive feedback from recruitment pheromones. Other species like wood ants (Chauvin 1962; Rosengren and Sundström 1987), leaf-cutter ants (Weber 1972; Shepherd 1982; Vasconcellos 1990), and harvester ants (Hölldobler 1976; Hölldobler and Möglich 1980; Lopez et al. 1994; Detrain et al. 2000; Azcarate and Peco 2003) produce physical trails that can last from several weeks to months and in some cases endure the winter hibernation period (Weber 1972; Hölldobler and Möglich 1980; Rosengren and Sundström 1987; Fewell

1988). In addition to leaving pheromones, workers of these species clear trails of vegetation and debris and sometimes construct walls or tunnels around them (Shepherd 1982; Kenne and Dejean 1999; Anderson and McShea 2001) to form highways which allow large numbers of ants to travel quickly to food.

The short lasting raid patterns by the army ant (Deneubourg and Goss 1989; Franks et al. 1991) and the predatory ant *L. proccessionalis* (Ganeshaiah and Veena 1991) have been measured in detail. These raiding ants build exploratory networks which trade off between the cost of travel and the area over which they search for prey items. The networks tend to contract once resource items are located and foraging is then focused on the resource. Studies of permanent or semi-permanent trunk trails have been less detailed, despite the key role of these networks in sustaining the colony. Most empirical studies report measurements of the structure of only one or a few trails from one colony (Hölldobler and Möglich 1980; Rosengren and Sundström 1987) or concentrate on identifying the territory of different colonies rather than the trail structure (Elton 1932; Hölldobler and Möglich 1980). The size of territories–feeding areas and length of trails vary a lot between species (e.g., Pickles 1935, 1936, 1937, 1938; Brian 1955; Rosengren and Sundström 1991; Schlick-Steiner et al. 2006). In cases where there are data available on the structure of the trail networks, it is usually presented graphically without quantitative analysis of the properties of the networks.

Graph theory provides a rich framework to quantify network structures, identifying invariants in network topology and categorizing different classes of networks (Bollobas 1998; Newman 2003). For example, graph theory has been applied to street networks and underground ant nests to show that these networks achieve very high levels of directness of paths (how close paths are to the beeline distance) and robustness to random disconnections for a very small increase in total length in comparison to the shortest network possible (Latora and Marchiori 2001; Buhl et al. 2004, 2006; Cardillo et al. 2006; Bebbler et al. 2007). The networks built by the fungus *Phanerochaete velutina* or the slime mold *Physarum* between food sources have been studied in terms of their length and vulnerability to the breaking of one or more links (Nakagaki et al. 2000, 2004a,b; Bebbler et al. 2007). These studies have shown that even very simple organisms can produce highly efficient networks.

An early and central paradigm to the study of dendritic networks was the “Horton–Strahler” (Horton 1945; Strahler 1957) analysis. This method quantifies the ordering of branching and has led to the identification of empirical scaling relationships in the distribution of branching segments’ size and number in river networks of different sizes

(Dodds and Rothman 2000a, b, c), leaf patterns (Pelletier and Turcotte 2000), and even predatory ant trail patterns (Ganeshaiah and Veena 1991). However, in order for these metrics to provide interesting scaling properties, networks must have a degree of branching greater than that observed in most ant trunk trail networks; other branching numbering methods (e.g., the one used by Lopez et al (1994)), which do not allow the same scaling invariance analysis, must be used. Another key metric of network structure is the angle of branching at junctions in the network (Acosta et al. 1993). Branch order and angles are descriptive measures that are useful to characterize and differentiate network topologies; they do not however quantify the efficiency of networks.

Recently, Gastner and Newman (2006) proposed a number of basic statistical tools for studying the efficiency of tree-like networks with a central point. We can think of these transport networks as graphs, consisting of set of *vertices* (e.g., underground stations or food sources) joined by *edges* (e.g., railway track or ant trails) and all joined, possibly via a number of intermediate vertices (called a *path*), to some central vertex (e.g., a city center or an ants nest). Newman and Gastner state that an efficient transport network has two important properties. Firstly, the distance from each vertex to the central vertex should be relatively short. This property is characterized by the *route factor*, which is calculated by taking the average of the *path length* (sum of the length of the edges in the path) between each vertex and the central vertex divided by the direct Euclidean distance (i.e., the distance as the crow flies) between the two vertices. In terms of ant trails, a low route factor corresponds to a relatively short travel time between nest and food source. The second property of an efficient network is that its *total length* (the sum of all edge lengths) should be low.

The success of ant colonies that forage from a central nest, such as the wood ant species *Formica aquilonia* we study here, is likely to depend both on the length of the path home for foragers (i.e., low route factor) and the amount of trail that they need to maintain (i.e., low total length). Fewell (1988) showed that, for the harvester ant *Pogonomyrmex occidentalis*, vegetation structure has a profound effect on foraging costs because traveling through dense vegetation decreases speed and increases the Euclidian distance (stretching in the three-dimensional structure of vegetation) a forager must travel. In the leaf-cutter ant, *Atta colombica*, workers cut and pull on obstructions when their movement is restricted (Shepherd 1982). Since cleared trails require maintenance to keep them clear, there is a cost associated with having too much trail, but these trails are essential for the rapid transport of resources back to the nest.

Finding the network that minimizes total length of the edges connecting a set of vertices is a computationally

difficult problem, known as the Euclidean Steiner tree problem (Gilbert and Pollak 1968). It belongs to a class of problems known to be NP-complete (Garey and Johnson 1979). If an efficient algorithm were developed to solve the Steiner tree problem, it could be employed to solve a whole range of other computationally difficult problems. For this reason, it is thought unlikely that such an algorithm exists in a general setting, although finding nearly minimal networks in specific cases is usually possible. It is thus interesting to know whether an ant colony can “solve” such a problem, not only because the solution would act to increase the fitness of colony members but also because the decentralized algorithm employed by the ants could give us useful insight into how biological systems solve computationally difficult problems (Bonabeau et al. 2000; Dorigo and Stutzle 2004).

An additional problem faced in constructing transport networks is that route factor and total length almost inevitably conflict. For all but the simplest vertex distributions, the network that minimizes route factor and the network that minimizes total length look very different. The network that minimizes route factor has a star-like shape, with a direct edge between every vertex and the central vertex, typically leading to a very high total length. Conversely, networks that minimize total length tend to consist of clusters of triangles and long sprawling paths connecting nearby vertices while leading away from the central vertex, thus having large route factors (Fig. 1). However, while a single network can never be optimal in terms of total length and route factor, Gastner and Newman (2006) demonstrated that the transport networks constructed by humans are often close to optimal in both properties. While the construction of human networks may

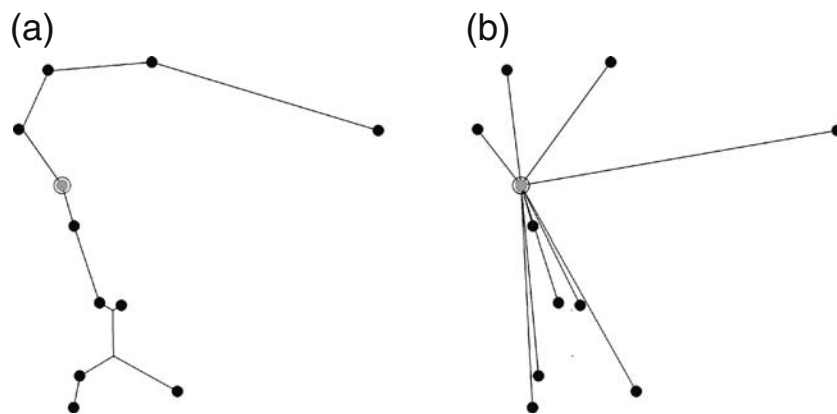
benefit from some form of central planning, individual ants have a limited ability to plan the overall shape of the network they construct. The question is thus whether ants also build efficient transport networks.

## Materials and methods

### Fieldwork

We characterized the trail networks of 11 colonies of the ant *F. aquilonia*, a member of the *Formica rufa* group of wood ants. Wood ants are an ideal study species since they build long-lasting nests, with clear trails spanning large areas. Fieldwork took place in Bäcksjön, 10 km north of Umeå, Västerbotten, Northern Sweden (grid reference: NS 63° 97 and EW 20° 24). Data collection took place during July and August 2005 (colonies 1 to 5) and 2006 (colonies 6 to 11). We returned to colonies 1 to 5 in 2006 to investigate whether the position of their trails had changed from 1 year to the next. The nests were located in areas of dense Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) trees and situated on relatively flat rocky ground, covered with undergrowth of bilberry (*Vaccinium myrtillus*) bushes and thick layers of moss.

To establish the structure of each nest, all trails radiating out from the nest were marked out using bright plastic sticks. A stick was placed at every bend and junction and at every 30 cm along the trail. Once the trail became indistinguishable in the undergrowth it was followed no further. In order to identify the relative positions of each stick a 10×10 or 15×15 m grid was laid out using large wooden poles. The distance from each plastic stick (flag) to



**Fig. 1** Example of a Steiner tree **a** and a star graph **b** for a random set of vertices. The Steiner tree links all vertices (shown as *black circles*, except for the central vertex shown in *gray*) together for a minimal length; to achieve this, additional vertices can be added (two of them can be seen at the *bottom* of the figure where two branching points have been formed where no vertex was initially present). While the Steiner tree minimizes total length, it can create considerable circum-

volutions and detours from a beeline path, as can be seen when traveling from the central vertex (*gray circle*) to the vertex most on the right. The star graph, on the other hand, has no detours since it creates a direct edge linking each vertex to the central one; this, however, leads to a higher total length, which is particularly obvious in this example when comparing the lower part of the figure for the Steiner tree and the star graph

two poles from the grid was measured using either a laser distance measurer (Leica Disto Classic, accuracy  $\pm 3$  mm) or a 30-m tape measure. The width of the trail and the flow rate along the trail was measured at flag points at 1-m intervals along the trail. The position of any tree within 1 m of a trail was also recorded by measuring the distance from the trunk at breast height to two poles. Any tree with ants found on it over 1 m away was also recorded. The taxonomical group (Norway spruce, Scots pine, or birch (*Betula spp.*)), the number of ants on its base, and its circumference at breast height were recorded for each tree. In some cases, trails did not end at a specific tree but rather ended in aggregations of ants. At these aggregations, we counted the local number of ants and measured the aggregation positions.

The points generated by the measurement process can be categorized as being one of four types: we called the nest the *central vertex*, the trees and aggregations at the end of trails *resource vertices*, the points at which two trails join are *branch vertices* and intermediate points on the trail are *intermediate vertices*. Vertices were marked every 30 cm or whenever a branch occurred. The set of edges of the graph,  $E$ , are straight lines joining the vertices between which a trail was found. Whenever a resource vertex corresponded to a tree that was not directly linked to trail, an edge was created between this resource vertex and the nearest vertex belonging to a trail.

### Network efficiency

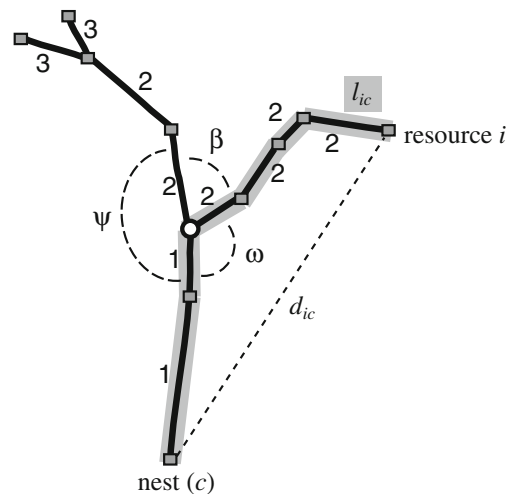
To analyze the efficiency of the trail networks, we adopted a similar approach as Gastner and Newman (2006). For each set of resource vertices (denoted by  $R$ ), we calculated the network with a route factor of 1, i.e., the star graph where every resource vertex is connected by a straight line to the central nest vertex (labeled  $c$ ). The route factor for a graph is given by

$$r = \frac{1}{|R|} \sum_{i \in R} \frac{l_{ic}}{d_{ic}}$$

Where  $l_{ic}$  is the path length from the resource vertex  $i$  to the central vertex  $c$  (i.e., the length of the trail an ant would walk from resource to the nest; see also Fig. 2) and  $d_{ic}$  is the Euclidean distance between resource vertex  $i$  and the central vertex  $c$  (i.e., the distance in the star graph, which has a route factor  $r=1$ ).

The total length is defined as the sum of the length of all the edges in the network, i.e.,

$$L = \sum_{(i,j) \in E} l_{ij}$$



**Fig. 2** Illustration of some trail network characteristics. An illustrative network composed of one trail with two branching points is shown. The trail is composed of a set of *vertices* (gray squares, corresponding to point of measurement) linked by *edges* (black lines). For each resource (here, we show one example of a resource  $i$ ), there exists a sequence of vertices (each consecutive pair of them linked by an edge) leading to the nest vertex 0; such as sequence is called a *path* (shown in gray). The *path length*  $l_{i0}$  corresponds to the sum of the length of all edge in the path, which differs from the Euclidean distance  $d_{i0}$  between resource  $i$  and nest if there is not a direct edge between these two vertices. Branching order is shown by the numbers standing next to each edge and is determined following the method of Lopez et al. (1994): starting from the nest with a value of 1, branching order is incremented by 1 for each branching point observed when moving along the trail and toward its distal dead-ends. The figure also shows angle measurements performed around branching points (here, one example is shown as a white circle). The segment of the lower order, here 1, is called the parent branch, while the two branches emerging from it (of higher order, here 2) are called daughter branches. The angle  $\beta$  between the first edges of the two daughter branches is called the branching angle, while the two other angles are called side angles,  $\psi$  and  $\omega$  being the largest and the smallest angles, respectively. The ratio of  $\omega$  to  $\psi$  is called symmetry coefficient

We calculated the Steiner tree for the set containing all resource vertices and the central vertex, i.e.,  $R \cup \{c\}$ . The Steiner tree for a particular set of resource vertices is the network (or set of edges) such that the total length is minimized. In constructing this tree, it is permissible to add extra vertices, i.e., branch vertices that reduce the total length. We chose to calculate the Steiner tree rather than the minimum spanning tree (MST) used by Gastner and Newman because ant trails clearly have a number of branching points that do not occur at resource vertices (and the MST does not allow the addition of new vertices). While the Steiner tree is a more realistic model of ant trails, it is not as straightforward to calculate as the minimum spanning tree (which can be calculated by a simple and quick algorithm for adding edges (Kruskal 1956; Cheriton and Tarjan 1976)). We used a modified version of a custom algorithm developed by Bob Bell (available at



<http://www.css.taylor.edu/~bbell/steiner/>), giving similar results to the Geosteiner algorithm (Warme et al. 1998). Since finding the Steiner tree is such a computationally difficult problem, we cannot guarantee that the tree we have found is optimal for any particular set of vertices, and we thus refer to the trees as approximate Steiner trees.

To assess the relative position of ant networks between the two extreme cases of the Steiner trees and Star graphs, we define the length efficiency  $L^*$  and the route efficiency  $r^*$  as follows:

$$L^* = \frac{L_{\text{star}} - L_{\text{ant}}}{L_{\text{star}} - L_{\text{steiner}}}, \text{ and } r^* = \frac{r_{\text{steiner}} - r_{\text{ant}}}{r_{\text{steiner}} - r_{\text{star}}},$$

where  $L_{\text{star}}$ ,  $L_{\text{steiner}}$ , and  $L_{\text{ant}}$  are the total length for the star graph, approximate Steiner tree, and ant network, respectively, and  $r_{\text{star}}$ ,  $r_{\text{steiner}}$ , and  $r_{\text{ant}}$  the route factor for the star graph (always equal to 1), approximate Steiner tree, and ant network, respectively. Therefore, a value of  $L^*=1$  indicates an ant network that is as short as a Steiner tree, i.e., extremely efficient in term of length minimization, while with a value of  $L^*=0$ , the network would be as long as a Star graph. Similarly,  $r^*=1$  indicates a network with the same route factor as the Star graph, i.e., extremely efficient in term of route directness, while  $r^*=0$  indicates a route factor as high as the one of a Steiner tree.

#### Branching order and angles

Branching order was calculated following the method described by Lopez et al. (1994), where starting from the nest site with a value of 1, branching order is incremented by 1 for each branching point observed when moving along the trails and toward their distal dead-ends (Fig. 2). For example, a “Y”-shaped trail has got one initial sub-trail of order 1 and the two new branches have a branching order of 2. A trail branching order is the highest branching order observed among all its sub-components.

For each branching point, we measured the branching angle as the angle formed between the branching vertex and the two first vertices on each daughter branch (Fig. 2). The two other angles, the side angles, are the one formed between the first vertex on each daughter branch and the last vertex before the bifurcation on the main trail from which the branches are originated. The symmetry coefficient corresponds to the ratio between the smallest and the largest side angle.

#### Statistical tests

All statistical tests were performed using SPSS 15.0 for Windows. Kolmogorov–Smirnov tests were used to assess whether distributions were normal and the Levene tests were used to test the homogeneity of variance.

## Results

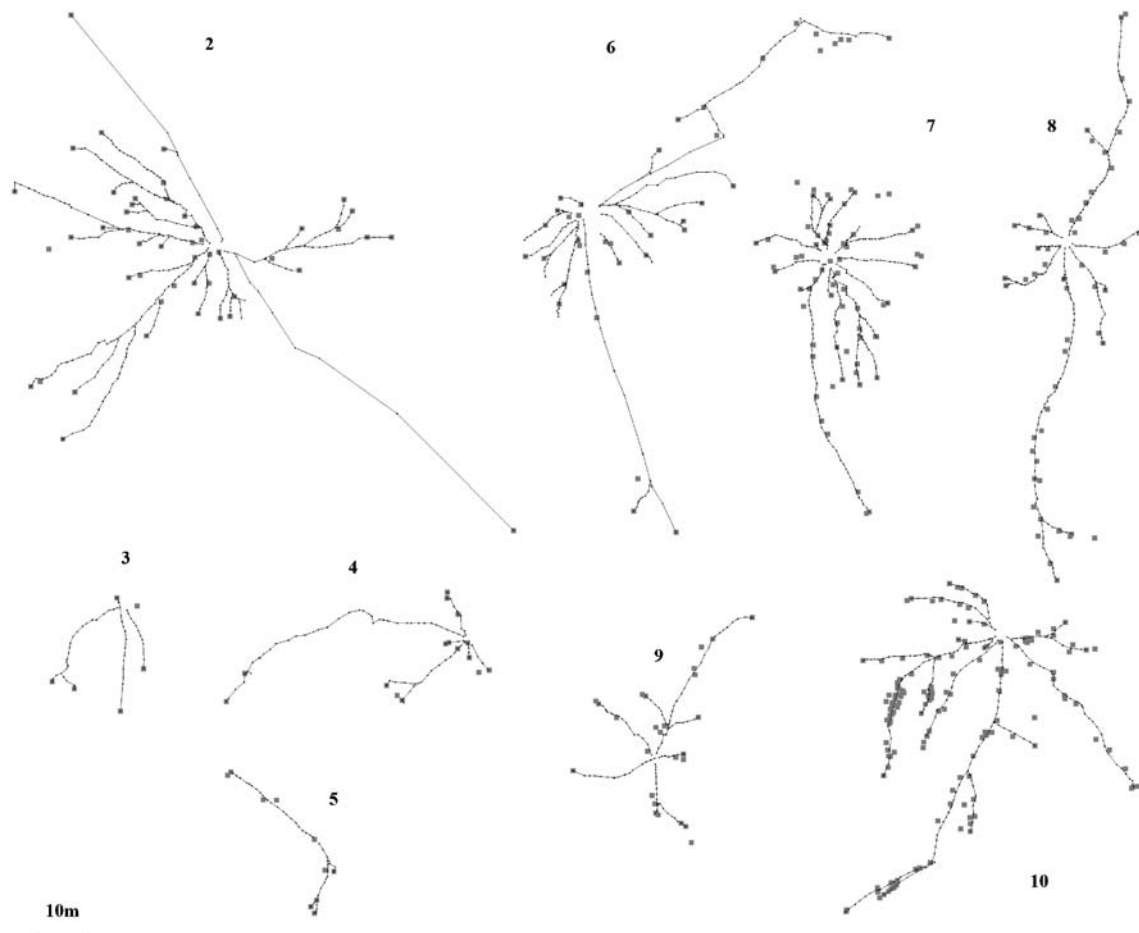
Figure 3 shows nine of the measured trail networks while Fig. 4a,d shows the remaining two. They were composed of  $5.82 (\pm 2.04 \text{ SD})$  independent trails on average, each leading to 23.09 trees on average ( $\pm 20.51 \text{ SD}$ ; see Table 1). The trails led almost exclusively to Norway spruce trees, the exceptions being a small number of birch trees. There were no trails to Scots pine trees, despite there being large numbers of these trees within the area covered by networks. Not all Norway spruce trees within the foraging area were exploited by the ants, however, with a large number having no or very few ants visiting them. The trails of colonies 1 to 5 changed very little from 1 year to the next. We found only one new trail (by colony 2) in 2006 that we had not observed in 2005.

#### Network efficiency

Figure 4 compares two of the ant trail networks to their respective star graph and approximate Steiner tree models. The star graphs are clearly different from real ant networks, with paths to nearby trees being linked to branches from a common trail. The real trail networks also appear somewhat different from their corresponding approximate Steiner tree, which have no clear trunk trails or an obvious central route vertex. The results seen in Fig. 4 are typical for the star graphs and Steiner trees of the other trail networks.

Table 1 presents the total length of the empirical trail networks and their respective star graphs and Steiner trees. On average, the ants' networks ( $\langle L_{\text{ant}} \rangle = 343.98 \text{ m} \pm 269.98 \text{ SD}$ ) were only slightly longer than the Steiner trees ( $\langle L_{\text{steiner}} \rangle = 223.5 \text{ m} \pm 153.57 \text{ SD}$ ) and much shorter than star graphs ( $\langle L_{\text{star}} \rangle = 1,313.91 \text{ m} \pm 1,398.50 \text{ SD}$ ), and their length efficiency  $L^* = 0.810 \pm 0.198$  indicates a length efficiency nearer to that of the Steiner graph than the star graph. There were significant differences in the total network length between ant networks, Steiner trees, and Star graphs (analysis of variance (ANOVA):  $F_{2, 30} = 5.619$ ,  $p = 0.008$ ); more precisely, post hoc tests (Tukey) showed no significant difference between ant networks and Steiner trees (mean difference = 143.3,  $p = 0.914$ ) but a significant difference for both of these groups with the star graphs (mean difference with ant networks = 1,090.4,  $p = 0.031$ ; mean difference with Steiner trees = 1,090.4,  $p = 0.012$ ).

The average route factor of the empirical networks was only  $1.133 \pm 0.072$  (a low value close to 1 which is the route factor of star graphs, by definition), compared to an average route factor of  $1.402 (\pm 0.18)$  for the approximate Steiner trees (ANOVA:  $F_{1,20} = 21.613$ ,  $p < 0.001$ ). The value  $r^* = 0.623 \pm 0.203$  indicates route efficiency nearer to that of the star graph than the Steiner tree. Furthermore, the efficiency of ant networks was not significantly influenced by their



**Fig. 3** Trail networks of the wood ant *F. aquilonia* and exploited resources, studied at Bäcksjön, Sweden. The figure shows the trail networks produced by all the ant colonies studied (excepted colonies 1 and 11 shown on Fig. 2). Trails are indicated by the solid lines, with each black circle indicating a point of measurement. The nest is

situated at the convergence of all trails. Gray squares indicate resource vertices (mainly trees) that stand at the end or on the side of the trails. The colony number is given next to each trail network and also corresponds to the number indicated in Table 1

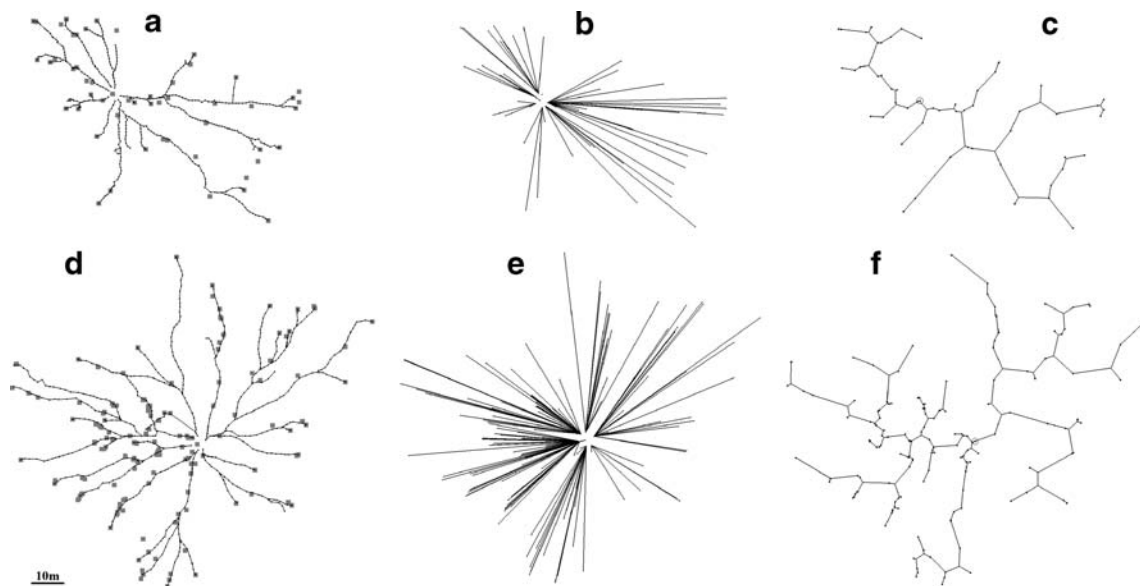
total length (Pearson  $r=0.223$ ,  $N=11$ ,  $p=0.510$  for the length efficiency;  $r=-0.437$ ,  $N=11$ ,  $p=0.179$  for the route efficiency) or the number of trees visited (Pearson  $r=0.402$ ,  $N=11$ ,  $p=0.220$  for the length efficiency;  $r=-0.399$ ,  $N=11$ ,  $p=0.224$  for the route efficiency). Thus, ant networks were always closer to Steiner trees in terms of total length, while they were always closer to Star graphs in term of the directness of their routes to food sources.

#### Branching order and angles

The networks have a clear dendritic structure, repeatedly branching as the trails become further away from the nest. There is a strong variability in the length and degree of branching reached by trails (Fig. 5). The median trail length from the nest to the end of a path was 27.97 m and median branching order was only 2. However, the maximum trail length was 279.63 m with nine successive branchings. Overall, the distribution of trail

branching order (the maximum number of successive branching points along the paths going from the nest to the ends of a trail) was highly skewed, similar to that observed in harvester ants (Lopez et al. 1994). There was a strong correlation between branching order and total trail length (Pearson  $r=0.839$ ;  $N=64$ ;  $p<0.001$ ). Within a trail, the length of trail segments (sub-trail length) that link an end of the trail to a branching point or two successive branchings is highly variable as well, following a lognormal distribution [one sample K-S goodness-of-fit test for a normal distribution, performed on log-transformed data:  $Z=0.875$ ,  $N=304$ ,  $p=0.428$ ; geometrical mean  $\mu=6.775$  m<sup>x</sup>/1.7; <sup>x</sup>/ denotes multiplicative standard deviation, following Limpert et al. (2001)] similar to that observed in harvester ants (Lopez et al. 1994).

Figure 6 shows a distribution of branching angles, the mean $\pm$ standard deviation for these angles taken over all networks was  $49.33^\circ\pm 29.9$  ( $N=116$ ). The ratio between the two other angles (between each daughter branch and the



**Fig. 4** Two examples of ant trail networks (**a, d**, same representation as in Fig. 1), their corresponding star graphs (**b, e**) that connect each resource by a direct edge to nest entrances, and approximate Steiner

trees (**c, f**) which connect all resources (small plain circles) to the nest (indicated by the larger black circle) by minimizing to the total length

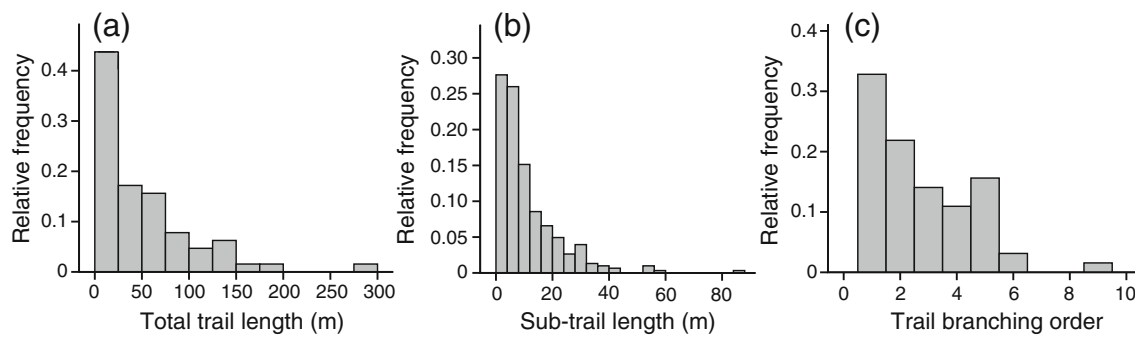
parent branch, the ratio being the smallest of these two angles over the other one) has an average value of 0.8127 ( $\pm 0.15$ ), indicating predominantly symmetric branching (Fig. 6b). The distribution is however skewed due to a small number of asymmetric branches, where one of the daughter branches is in the same direction as and the other is perpendicular to the parent branch (Fig. 6c). The largest

branching angles seemed to occur when trails branched on some heterogeneity in the environment, for example on a log. Two of the measured networks were found in areas where there were man-made paths or tracks. In these cases, the human paths were incorporated into the network, providing straight trails stretching over relatively long distances (e.g., colony 2 in Fig. 1).

**Table 1** Characteristics of 11 *F. aquilonia* trail networks observed at Bäcksjön, Sweden, compared to approximate Steiner trees and star graphs

Colony	Trees	Trails	Branching points	Total length				Route factor		
				Steiner graph	Ant trails	Star graph	Length efficiency	Ant trails	Steiner graph	Route efficiency
1	21	7	24	288.51	447.12	1,302.09	0.843	1.108	1.363	0.702
2	23	7	22	350.12	565.37	1,050.23	0.692	1.079	1.655	0.860
3	1	3	1	44.39	69.04	78.74	0.287	1.069	1.318	0.723
4	5	6	1	84.17	119.19	205.96	0.712	1.060	1.156	0.460
5	5	2	2	48.91	49.22	124.86	0.996	1.074	1.177	0.529
6	18	9	12	231.69	378.70	1,003.73	0.810	1.154	1.676	0.791
7	31	8	8	204.41	310.15	949.75	0.858	1.136	1.596	0.753
8	22	6	6	214.85	259.47	1,451.75	0.964	1.098	1.414	0.727
9	8	5	2	110.98	132.64	342.50	0.906	1.129	1.254	0.421
10	57	5	11	323.96	492.46	3,939.16	0.953	1.118	1.410	0.710
11	63	6	30	555.97	960.44	4,004.26	0.883	1.357	1.408	0.174
Mean	23.09	5.82	10.82	223.50	343.98	1,313.91	0.810	1.126	1.402	0.623
SD	20.51	2.04	10.23	153.57	269.98	1,398.50	0.198	0.083	0.178	0.203

The table shows the number of trees (within 1-m distance from the trails), independent trails, and branching points for each colony studied. The total length, shown for each ant trail network, and the corresponding approximate Steiner trees and Star graphs were calculated by adding the length of all edges in the graphs. The route factor was calculated for the approximate Steiner tree and the ant trail network (the route factor for the star graph is always 1). The length and route efficiency shows where the ant trail network stands between the approximate Steiner trees and the star graphs (see text for details)



**Fig. 5** Distribution of the trail network component size and branching ordering. The figure shows the distribution of total trail length **(a)**, a trail corresponding to any trail system connecting one nest entrance to a number of resources, which can be achieved with non-branched to highly branched patterns; **(b)** shows the distribution of sub-trail length, corresponding to the trail segments linking successive trail ends and/or

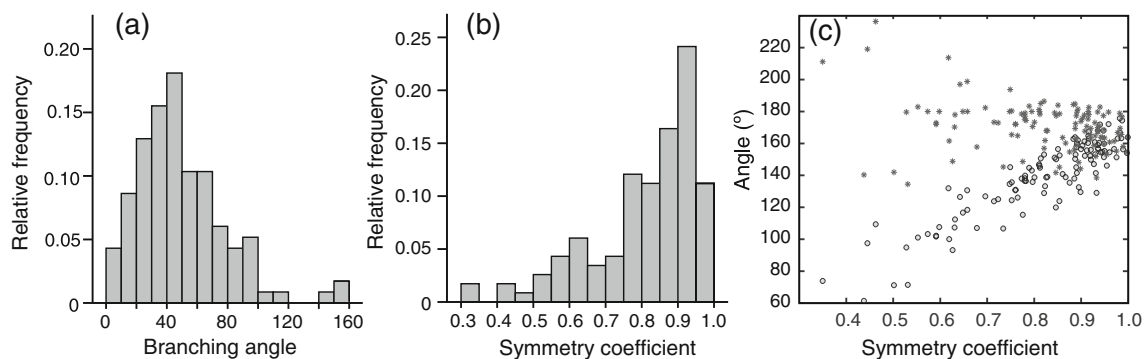
branching points; **(c)** shows the distribution of trail branching order. Here, the branching order corresponds to the number of successive branching vertices present along a path linking the nest end of a trail to one of its dead-ends. The branching order of the trail corresponds to the highest branching order observed among all of its paths

## Discussion

The route factor and the total length provide two useful measures of transport network efficiency. For the trail networks of *F. aquilonia* studied here, both of these factors were small. In particular, the route factor for the real networks was significantly lower than that for the network that minimizes total length, and the total length for the real networks was lower than that of the network that minimizes route factor. Comparison to human networks allows us to put the efficiency of ant networks in a wider context. The average route factor of 1.13 found in the ants was equal to that of the most efficient human transport network in Gastner and Newman's (2006) study of four different rail, gas, and sewage networks. Even the largest ant network has a route factor that lies well within the range (1.13 to 1.59) found for human networks. Ants are able to achieve route factors comparable to that of humans without the benefit of centralized planning. The average total length for the ants divided by the total length for the approximate Steiner tree

(Gastner and Newman's edge length factor) was  $1.45 \pm 0.22$ , range 1.01 to 1.73, and lies within the range of edge length factors for human networks (1.12 to 1.63).

There has been a great deal of theoretical interest in mechanisms of network growth, to which our observations provide valuable data. Gastner and Newman proposed two models of network growth based on adding edges one by one, each time choosing a new vertex to join to the network based on it minimizing a distance criterion. These models work well at producing networks that look like human transport networks and the ant networks we present here. However, the model assumes a central planner which assesses all available unconnected vertices and decides to link the one which minimizes the desired criteria. Such a central planner is not present in ants and networks instead arise from the repeated interactions of large numbers of individuals. For example, Rosengren and Sundström (1987) observed that at the start of the spring season the wood ants leave the nest in synchronized bursts and move all over the ground and climb most of the trees within a radius of 30 m



**Fig. 6** Characteristics of the ant trail network branching points. The figure shows the distribution of the branching angle **(a)** and the symmetry coefficient **(b)** of branching points, corresponding to the ratio between the smaller and the larger of the two other angles on the side of the

bifurcation. The two side angles, the largest one indicated by *asterisk* and the smallest by a *circle*, are shown **(c)** as a function of the symmetry coefficient



from the nest. Through this exploration, ants presumably find new and old food sources and pick up old trails which are then re-enforced. Various cellular automata models have shown how dendritic structures can emerge from interactions between pheromone laying and following individuals (Deneubourg and Goss 1989; Edelstein-Keshet et al. 1995). It would be interesting to compare the route factor and edge length factor of these models to those of the networks we have studied here in order to assess the plausibility of these mechanisms in explaining how networks are formed.

A major clue to the mechanisms behind network construction is found in the branching angle. Here, we found a trail branching angle of  $49.33^\circ \pm 29.9$ . This is close to, though slightly smaller than, the branching angles observed in leaf-cutter ants ( $55.6^\circ \pm 12.8$ ) and harvester ants ( $51.6^\circ \pm 16.7$ ; Acosta et al. 1993), as well as from Pharaohs' ants ( $53.4^\circ \pm 13.8$ ; Jackson et al. 2004). Several other topological measures such as the sub-trail–link length, tree order, and branching angle distributions are close not only to other trunk trail ant species such as harvester ants but also to other biological networks such as neuronal dendrites and rhizomatous plants (Ganeshaiah and Veena 1991; Lopez et al. 1994). This may be taken to suggest either a common mechanism in the way these networks are constructed or a universality in the properties of these networks which is mechanism independent.

Acosta et al. (1993) provide an intuitive argument for how branches arise in trails. They argue that when a forager finds a resource at a point perpendicular to an established trail it returns to the established trail leaving pheromone as it goes. This forager and subsequent foragers, which have followed the pheromone to the resource, will have a tendency to walk towards the nest thus diverting the newly formed trail such that the branching angle decreases. A computer simulation model which formalizes this argument is the active walker model (Helbing et al. 1997; Schweitzer et al. 1997). These models show that when trails are not particularly attractive, possibly because the environment offers little walking resistance, then star-like links between resources and nest will form. On the other hand, if the trail is attractive, by providing travel at lower walking resistance, then branching structures begin to form. In general, the branching angle should depend on the attractiveness of the trail with higher environment resistance leading to more branching. Again, work is needed to compare this model against our dataset.

It is important when we think about mechanisms for network growth, be it in ant, human, or other networks, that we do not consider the environment as merely a static entity for which a network solution is constructed. A large proportion of Norway spruce trees within the range of the trail networks are not visited by the ants. Wood ants have a

symbiotic relationship with the aphids that live in these trees: aphids support ants with honeydew while the ants nurse and protect the aphids. If the ants are not present in a particular tree, the aphids are subject to heavy predation and quickly drop in numbers and these trees become less attractive to the ants. There is thus positive feedback such that areas with trails attract the development of more trails. A similar process is probably at work in human urbanization. The construction of a railway or gas line to a particular place not only supplies that area but stimulates further economic development there and motivates further construction in this area. Network construction is a dynamic process that simultaneously optimizes for and changes the environment in which it occurs.

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