Better tired than lost: turtle ant trail networks favor coherence over shortest paths

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Abstract

To create and maintain a backbone routing network is a basic challenge in many engineered and biological systems [1–3], from wireless sensor networks and robot swarms to neural circuits and blood circulation. Optimal routing in such networks often seeks to minimize transport delay [4–8], but routing decisions may be influenced by variability in the terrain [9–12]. Here we find that turtle ants build trail networks that emphasize coherence, keeping the ants together on the trail in a heterogeneous environment, rather than minimizing the distance travelled. The routing backbone of turtle ants (*Cephalotes goniodontus*), an arboreal species that forages in the

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tree canopy of tropical forests, connects many nests [13–15], using trail pheromone that the ants put down continuously, not just on the way back from a food source. Unlike species that forage on the ground, arboreal ants are constrained to travel within the vegetation network of branches and vines. We compared observed turtle ant trails with random, hypothetical trails in the same surrounding vegetation. Strikingly, the trails do not minimize distance travelled, but instead minimize the total number of nodes in the backbone, and favor nodes with 3d configurations that are easily reinforced with pheromone. Thus, rather than forming the shortest paths, turtle ants take advantage of natural variation in the environment to build coherent trails. This ensures that the nests and food sources stay connected, at the expense of longer travel time. This design principle may be beneficial in applications where distributed agents, such as swarms of robots, must coordinate using a communication backbone in complex environments to collectively solve a task, such as building a structure, searching for resources, or surveying terrain [16].

Introduction

The goal of a backbone routing network is to ensure that there is a path for any two devices on the network to communicate. In real-world systems, however, physical variation in the environment can affect the accuracy and rate of communication [9–12, 17–19]. Understanding the physical structure of the environment may improve the design of routing algorithms [16, 20–24], for example, by reducing the search space of possible routing paths and steering network construction away from parts of the terrain that are difficult to reach.

The 14,000 species of ants have evolved diverse distributed routing and search algorithms to search for, obtain, and distribute resources [25] in the diverse environments that they inhabit [26–29]. For example, species such as *Formica* and Argentine ants, which forage and build trails in a 2d-plane, have minimal constraints on trail geometry [30–32], and can minimize the distance travelled by forming trails with branch points that approximate Steiner trees [27, 33, 34], an NP-complete generalization of the minimal spanning tree concept. By contrast, many species operate

in 3d environments, such as arboreal turtle ants (*Cephalotes goniodontus*), which nest and forage in the tree canopy of tropical forests. Their trail networks are constrained by the topology of the vegetation because their paths must use only available stems and branches (Figure 1A).

A turtle ant colony creates a trail network to connect several nests, providing a routing backbone that must be maintained to allow resources to be distributed throughout the colony [13, 14]. Ants search off the backbone to find and create trails to ephemeral food sources. The colony modifies the trail from day to day, sometimes forming small alternative paths, or loops, of which one is eventually chosen. They repair the backbone in response to frequent changes in the vegetation caused by plant growth and ruptures created by wind or passing animals [14]. Each ant lays a pheromone trail as it walks along stems and branches, and at each junction, ants tend to choose the edge most reinforced by pheromone [15]. Turtle ants forage in tangled, variable vegetation (Figure 1A), providing an opportunity to learn how a natural biological system can build a routing backbone under diverse challenges.

Results

To test whether turtle ant networks minimize distance travelled, or instead optimize some other objective, we mapped the trail networks that connected nest sites and food sources of 3 colonies (Tejon 189, Tejon 446, Turtle Hill 460), for 10-15 days over the course of 6 weeks. We identified the nodes, i.e., junctions in the vegetation where an ant has a choice among more than one edge in the direction it is travelling, and the edges between the nodes, and we measured the length of each edge. To evaluate how the ants choose nodes and edges from the options provided by the surrounding vegetation, we mapped all nodes and edges up to 5 nodes away from each node used by the ants (Figure 1A-C).

The total length of the network is not equivalent to the number of nodes traversed, as assumed in some ant colony optimization algorithms [35, 36] and other search algorithms [15, 37,

38], because the lengths of edges vary; the distance between one node and another ranges from less than a centimeter to more than a meter (Table 1). Thus, we could distinguish the goal of minimizing the length of the network from that of minimizing the number of junctions. In addition, nodes are not identical as is often assumed in graph-theoretical analyses, but rather are variable 3d structures, from a simple fork created by a branch in a plant, to a cluster of entwined vines and branches from different plants (Figure 2).

We hypothesized that the physical configuration of a junction influences how likely are successive ants to cross it the same way and to reinforce it with volatile trail pheromone. The ants have short antennae that detect pheromone only locally, so the transition from one edge through a node to another edge is reinforced rapidly only when successive ants make exactly the same transition (Figure 2). Each transition through a node (e.g., edge $u \rightarrow v$ through node v to edge $v \rightarrow w$) was assigned a transition index value by estimating, from the physical configuration of the node, how likely were successive ants passing from $u \rightarrow v$ to choose the same transition through v to a particular edge $v \rightarrow w$. Values of the transition index ranged from 1 to 4, with 1 likely to be detected and reinforced most quickly and 4 least quickly (Figure 2). A particular node v may have more than one transition index when there is more than one edge available to enter or exit v.

A trail network on one day is illustrated in Figure 1B–C. We modeled the network of vegetation as a directed, weighted graph, $G = (V_G, E_G)$, where each junction forms a node, and edges represent stems or branches that connect one node to another. Some nodes are designated as terminals, corresponding to the nests and food sources (see Methods). Both the ant trail network and the terminals change over time [14].

We considered three candidate objectives that the ants' decentralized trail routing and search algorithm may optimize: 1) Minimizing the average length of all edges, or the total edge length for a given number of nodes, which tests whether trail networks minimize the distance travelled; 2) Minimizing the total number of nodes, which tests whether trail networks minimize the number of decision points where ants could get lost; and 3) Minimizing the average transition index of all

nodes, which tests whether trail networks favor choices of nodes that are more rapidly reinforced, by minimizing the opportunities for successive ants to diverge toward different edges at a junction. We compared the extent to which each observed network on a given day optimized each objective, relative to a set of 100,000 random networks connecting the same terminals (see Methods).

The ants' networks minimized the transition index (Kruskall-Wallis test for differences among objectives, relative to random networks, $W = 31.718$, $p < 0.001$; Dunn test [39] for average transition index, $Z = 4.395$, $p < 0.001$) and minimized the total number of nodes (Dunn test, $Z = 5.247$, $p < 0.001$) rather than the distance travelled (Figure 3A). Because the total number of nodes and the total edge length are correlated ($R = 0.67$), we also tested whether random networks with the same number of nodes as the observed network differed in total length (see Methods). For all 3 colonies, the observed networks had total length similar to the random networks with the same number of nodes (Percentile 50% means that the observed is equal to random; 44.41% ± 37.54% for Tejon 189, 43.95% ± 29.24% for Tejon 446, and 36.91% ± 40.57% for Turtle Hill 460), indicating that like average edge length, the total edge length, or distance travelled in observed paths was not less than in random paths. There were no significant differences in the extent to which observed networks minimized the average transition index and total number of nodes (Dunn test, $Z = 0.852$, ns), compared to random networks. By forming trails that stay on the same plant [14], i.e., using nodes with transition indices of 1, ants are also led to resources at the edge of the canopy, such as flowers that provide nectar.

These results were robust to the removal of outlier values (see Methods), showing the same differences among objectives, relative to random networks, when we removed nodes with a high transition index (KW test, $H = 30.285$, $df = 2$, $p < 0.001$), when we omitted each of the 93 networks across all colony-days in a leave-one-out manner (KW-test, $H > 29$, $df = 2$, $p < 0.001$ in all cases), or when we omitted an observation made later than the others (KW-test, $H = 25.613$, $df = 2$, $p < 0.001$).

All three colonies tended to minimize the average transition index or total number of nodes

more than average length, as seen in the day-to-day changes in trails (Figure 3B–E). For example, in Tejon 189, trails on successive days (days 9 and 10) minimized average transition index, and decreased in number of nodes, while increasing in length (Figure 3B), and this continued from days 11 to 15 (Figure 3C). Similarly, in Tejon 446 (Figure 3D), trails minimized transition index but included longer average edge length on days 7 and 9. In Turtle Hill 460 (Figure 3E), there was a rupture on day 6 of a node leading to a 95 cm edge, one of the longest edges we measured. This edge was on the trail to a nest that could be reached only by using nodes with high transition index, leading to a high average. The initial decrease in average edge length was thus not due to a choice of shorter edges. Over time, however, the network shifted to include lower transition indices and fewer nodes (days 6 to 10), but increased in average edge length (days 10 to 14).

Turtle ants form loops in their paths, consisting of small, temporary alternative paths with the same start and end points, and typically all but one of these paths is pruned away [14]. We tested whether loops occur because trails tend to form along reinforced nodes. Such loops are often considered to decrease the efficiency of routing networks [1, 3]. Compared to randomly generated loops with the same start and end points, the observed loops tend to use rapidly reinforced nodes (i.e., nodes with low transition indices), and tend to minimize the number of nodes. We compared the centered ranks (see Methods) of the average transition index, number of nodes, and average edge length, of paths connecting the same two start and end points on each trail in observed and randomly generated loops. A negative value of centered rank indicates that an observed path has a low transition index compared to all of the random paths with the same start and end points. The mean (SD) of the centered rank in observed loops for average transition index was -1.59 (2.96); for number of nodes -1.88 (2.91) and for average edge length 0.44 (2.23); in all cases, significantly different from 0 (T-Test, $|T| > 3$, $p < 0.01$).

Discussion

The trail networks of arboreal ants show how evolution shapes biological distributed algorithms to respond to dynamic environments. Minimizing distance travelled is often considered the main problem in wireless routing or ant colony optimization [40–42], but turtle ants optimize coherence instead, which is an NP-hard problem (Supplementary Information). Like water flowing over a rocky stream bed, turtle ants tend to find trails most conducive to the flow of ants. By pruning away nodes they eliminate opportunities for ants to wander off the path, laying pheromone trail that can lead other ants also to leave the trail. While exploration is needed to find new resources [15], and connectivity of the vegetation is high (Table 1), the priority is to keep the ants together on the trail. Evolved algorithms, operating in the natural world, can take advantage of structure in the environment to reduce and more effectively search the space of possible routing paths, making it easier to coordinate distributed agents [16].

Methods

Observation of trail networks

The trail networks of 3 turtle ant colonies (Turtle Hill 460, Tejon 446, and Tejon 189) were observed between 06/20/18 and 08/03/18 at La Estación Biológica de Chamela in Jalisco, Mexico. Tejon 189 was observed for 10 days from 6/22/208–6/28/2018 and again on 07/01/2018, 7/04/2018 and 8/3/2018. Tejon 446 was observed for 11 days on 6/20/2018–6/28/2018 and again on 07/01/2018, 07/04/2018, and 08/03/2018; and Turtle Hill 460 was observed for 10 days from 06/21/2018–06/28/2018 and again on 07/02/2018, 07/05/2018, and 08/03/2018. Note that not every network was observed on each day.

The numbers of observation days were 10 for Tejon 189 and Turtle Hill 460, and 11 for Tejon 446, for a total of $93 = (10 + 10 + 11) \times 3$ observed networks.

Assigning directionality to edges

Experiments with marked ants show that ants tend to use particular routes from a nest [13], and tend not to turn around on the trail. To account for this, for all edges we defined a direction relative to one terminal; the outbound direction went away from it, and the inbound direction went towards it. We restricted the analysis to paths that proceed in the outbound direction.

Modeling the transition index as a line graph (Figure S1)

The transition index of a node describes the probability that successive ants will take the same transition from an edge (u, v) through node v to edge (v, w). Thus, a transition index involving node v depends on which incoming edge was used to reach v, and which outgoing edge was used to leave v.

To model the transition index, we used the line graph of G, where $L_G = (V_L, G_L)$. The nodes

$V_L = E_G$, and the edges $E_L = \{((x, y), (y, z)) | (x, y), (y, z) \in E_G\}$. The line graph creates a node for each edge in G and connects two nodes if they correspond to two adjacent edges in G. Every edge in the line graph denotes a transition in the original graph; traversing the edge $((u, v), (v, w)) \in L_G$ corresponds to starting at u, going to v, crossing the junction at v, and then going to w. We assign every edge in L a transition index. The line graph is used to compare the observed and random networks, as described below.

Generating random trail networks

We compared the observed trail networks to random trail networks based on their average edge length, total number of nodes, and average transition index. The random trail networks may include loops, as do the observed networks.

We generated random trail networks as follows:

1. **Input:** Graph $G = (V_G, E_G)$, terminals $X \subseteq V_G$
2. Create an empty graph R, add a random terminal $x \in X$ to R.
3. Choose a random terminal $x' \in X$ that has not already been added to R.
4. Perform a random walk on G that starts at x' and stops when it touches any node in R.
5. Add all edges and nodes touched by the random walk to R.
6. Repeat steps 3–5 until all terminals have been added to R.

Comparing observed and random networks

To compare the observed and random networks, we computed for each network, using the line graph, the following three objectives: 1) Average edge length: the average length of all edges

in the network; 2) Total nodes: the total number of nodes in the network; and 3) Average transition index: the average transition index over all transitions in the network.

For each objective, we computed a value of φ_{ants} for the observed network and $\varphi_1, \varphi_2, \ldots, \varphi_n$ for n random networks. We measured the similarity between the observed network and the random networks for that objective as the percentage of random networks that have a lower value for the objective:

$$100 \times \frac{|\{\varphi_i | \varphi_i \leq \varphi_{\text{ants}}\}|}{n}. \tag{1}$$

An observed network is most like a random network if its similarity score is 50; lower scores indicate that the observed network optimizes the objective much better than random, and higher scores indicate much worse. This percentile-based approach is unit-less, making it possible to compare performance for objectives that differ in the range of values.

We considered each observation day independently. For each colony (Tejon 189, Tejon 446, Turtle Hill 460), and for each objective (average length, total nodes, and average transition index), we computed the similarity of each observed network to 100,000 random networks that connected the same set of terminals, using Equation (1). Because the total number of nodes and the total edge length are correlated, we tested whether there was a statistically significant difference in total length between random and observed paths that had the same number of nodes. For each observation of one colony on one day, we found all the random networks that had the same number of nodes as the observed network (98 for Tejon 189, 785 for Tejon 446, 121 for Turtle Hill. We then found the total lengths of all of these networks, and used the percentile measure as above to evaluate the similarity of the total lengths of each observed network to the random networks with the same number of nodes.

To test the null hypothesis that all objectives have the same similarity to random networks we used the non-parametric Kruskal-Wallis one-factor ANOVA test [43]. We then applied post hoc Dunn's non-parametric tests, using a Bonferroni correction for multiple comparisons, with a

significance threshold of $p = 0.05$.

Effect of outliers on the results

To test the robustness of our results, we removed outliers in several ways, and performed the same Kruskal-Wallis tests as above. First, we removed the small number of nodes with a transition index of 4 (5 in Tejon 189, 1 in Tejon 446, and 3 in Turtle Hill 460). Second, we omitted each of the 93 networks across all colony-days, using a leave-one-out analysis. Third, we excluded the final day of observation in August 2018, which was about a month after the July observations.

Loops

We compared the average transition index and number of nodes in observed loops with randomly generated loops in the vegetation. A loop was defined as two or more outbound paths that start and end at the same source and target nodes. For each observed loop, we computed all possible paths in the vegetation between the corresponding source and target nodes. We ranked all paths based on the average transition index of the path, and compared this to the rank of the average transition index of the paths used by the ants. We repeated the same measure for total number of nodes and average edge length.

We computed the centered rank of each path used by the ants as follows: We ranked n available paths in the vegetation, by the average transition index of nodes in the path, total number of nodes in the path, or average length of edges in the path. The ranks of the paths are $1, 2, 3, \ldots n$, and the median rank is $r_m = (n + 1)/2$. For each observed path, we computed its centered rank by subtracting the median rank from that path's rank. Using average transition index as an example, the centered rank is 0 when the observed loop had the same average transition index as the median random loop, negative when the observed loop has a lower average transition index, and positive when the observed loop has a higher average transition index. We performed a similar analysis for

total number of nodes and average edge length.

Connectivity

To calculate the connectivity of the vegetation (Table 1), we estimated how many nodes are required for an ant that leaves the trail to return to the trail. For each edge (u, v) connecting a node on the trail to a node off the trail, we found the length, in number of nodes, of the path with fewest nodes from v back to a node on the trail. We measured connectivity as the smallest number of nodes in a path back to the trail, averaged over all edges (u, v) leading off the trail on all days.

Data Availability Statement

All data collected and analyzed are available from the corresponding author on reasonable request. Python code is available at: `https://github.com/DiODeProject/SteinerAnts`.

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Author Contributions

AC: data analysis, computational modeling, manuscript preparation. JM: computational modeling, manuscript preparation. CA: data collection, manuscript preparation. SN: data analysis, computational modeling, manuscript preparation. DMG: data collection, data analysis, computational modeling, and manuscript preparation.

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	Tejon 189		Tejon 446		Turtle Hill 460	
	Available	**Used**	**Available**	**Used**	**Available**	**Used**
Edge Length (cm)	10698	20.71 ± 6.21	7615	13.46 ± 0.74	14696	39.97 ± 9.43
Total Nodes	217	43.5 ± 9.43	196	36.09 ± 3.81	202	54.0 ± 17.93
Transition Index	1.60	1.31 ± 0.06	1.70	1.44 ± 0.13	1.48	1.44 ± 0.10
Connectivity	—	3.75 ± 0.23	—	4.00 ± 0.24	—	4.46 ± 0.95

Table 1: **Comparison of networks and vegetation in the three colonies observed** Values for 'Available' are for all of the vegetation mapped. Values for 'Used' are means, averaged over observation days, for each colony's network (n = 10 for Tejon 189 and Turtle Hill 460, and n = 11 for Tejon 446). Connectivity is a measure of the smallest number of nodes needed to get back to the trail, from an edge off the trail, averaged over all edges that lead off the trail (see Methods).

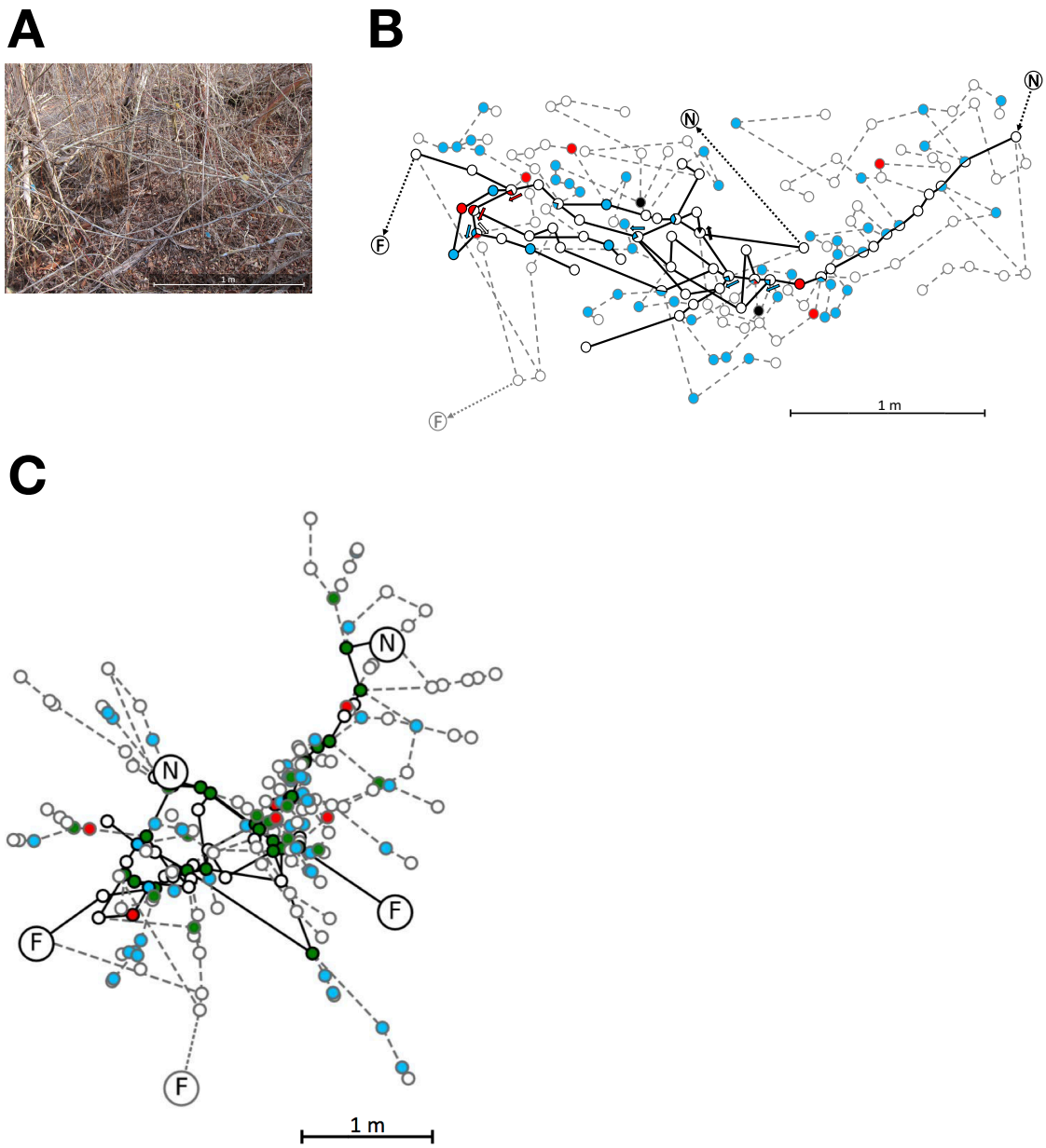

Figure 1: **Turtle ant vegetation.** A) The network mapped in B and C was in this vegetation, photographed in the dry season; after rain the branches have leaves. B) Schematic illustration of part of the trail network for Tejon 189 on day 9. Edge lengths are scaled to measured distance but actual location is not represented here. N represents a nest, F represents a food source. Circles represent nodes. The color of a node represents the transition index (TI) from the preceding edge to the following one: TI1, open circles; TI2, blue; TI3, red; TI4, black. Where there is a choice of more than one edge in the indicated direction, TI is represented with a pie chart, and arrows show which transition has the TI represented by the arrow's color. Solid lines represent edges used on that day; dashed lines represent edges not used that day. The figure shows 166 of the 217 nodes mapped in the surrounding vegetation. C) Map of all 217 nodes for Tejon 189 on day 9. Symbols as in B. Because of the large size of the network, all those with more than one TI are colored green.

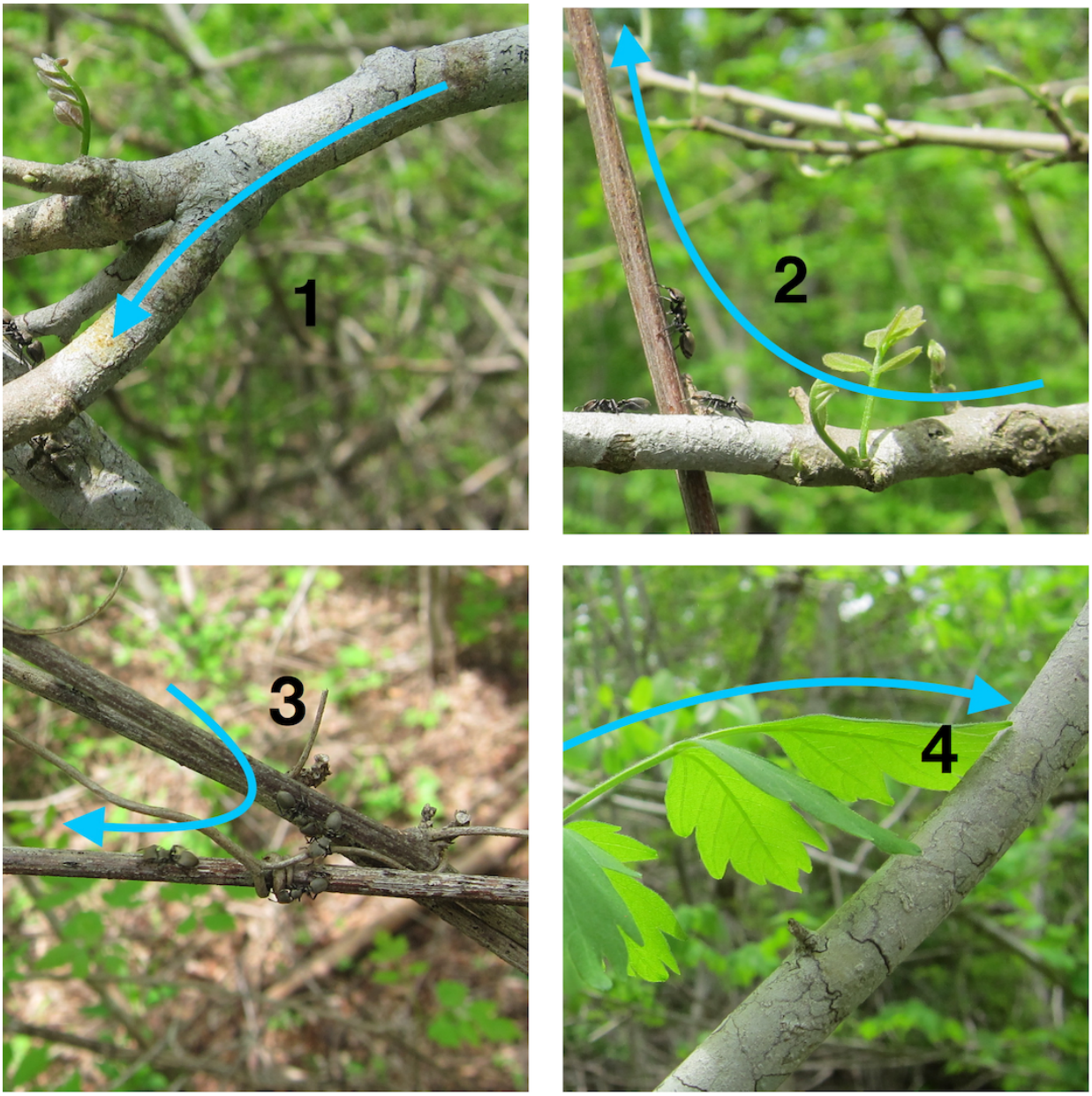

Figure 2: **Transition indices.** The photos show examples of nodes of transition index (TI) 1 (upper left): a node linking two edges on the same plant; TI 2 (upper right): a node that links one plant to another along a trajectory through a node that is likely to be the same for successive ants; TI 3 (lower left): a node that links one plant to another plant with more than one possible trajectory through the node; TI 4 (lower right): a node that links one plant to another with many possible trajectories that can easily be changed by conditions such as the wind.

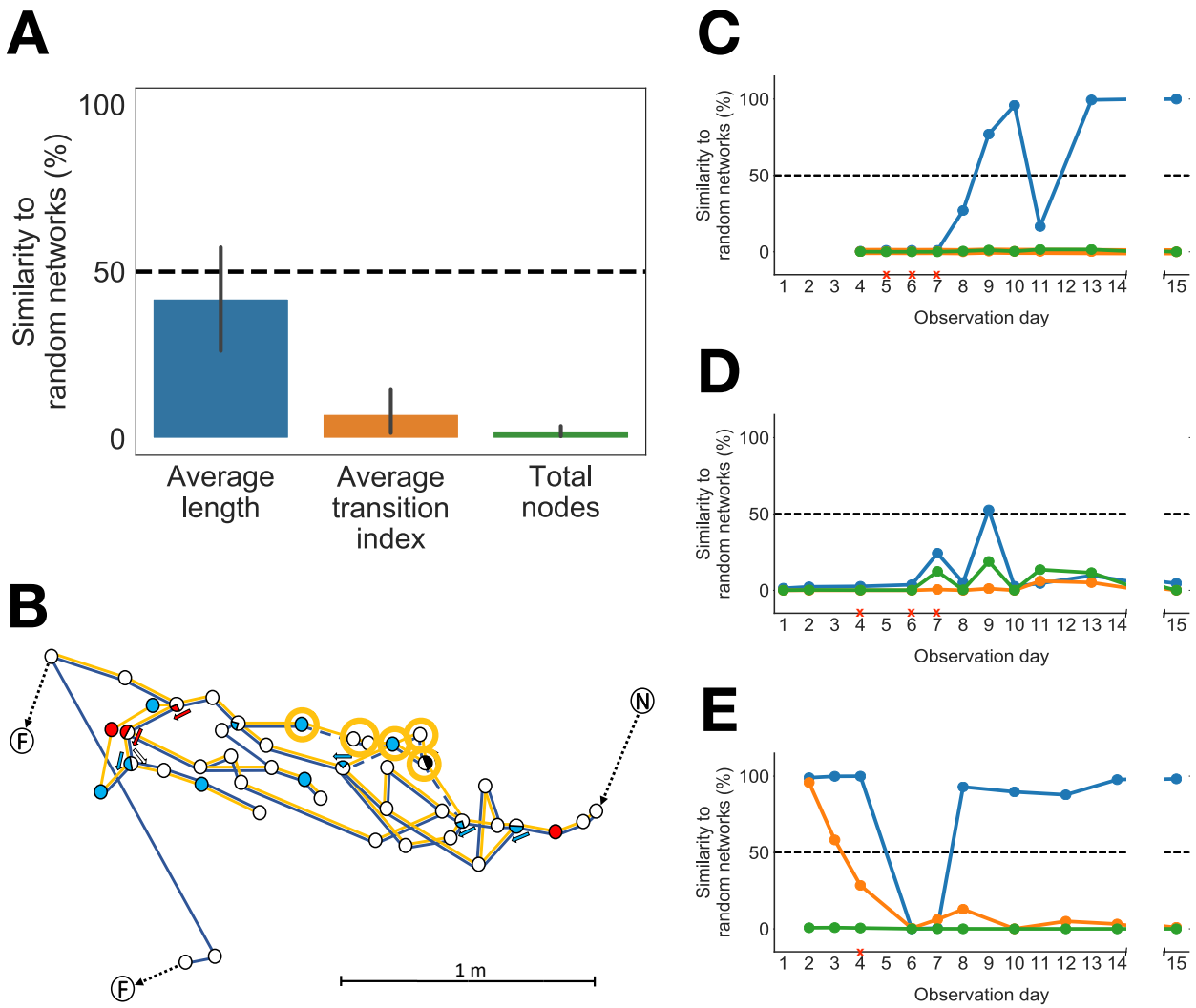

Figure 3: **Comparison of random and observed networks.** A) Similarity of observed and random networks measured as mean percentile. A value of 50 (dashed line) indicates that the observed network was similar to the random networks; the lower the value, the better the observed networks minimized the objective relative to the random networks. Error bars show standard error of the mean. B) Change in trails in Tejon 189. Symbols for transition index are the same as in Fig. 1B. Solid yellow lines show trails used on day 9; Solid blue lines show trails used on day 10; yellow circles and dashed blue lines show trails linking the 6 nodes that were used on day 9 but not on day 10. C-E Day to day changes in similarity to random for each objective. Blue represents average edge length, Orange average transition index, green, total number of nodes. 'X' indicates one or more ruptured edges on that day. C, Tejon 189, D, Tejon 446, E, Turtle Hill 460 .

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