The organization of strong links in complex networks

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Many complex systems reveal a small-world topology, which allows simultaneously local and global efficiency in the interaction between system constituents. Here, we report the results of a comprehensive study that investigates the relation between the clustering properties in such small-world systems and the strength of interactions between its constituents, quantified by the link weight. For brain, gene, social and language networks, we find a local integrative weight organization in which strong links preferentially occur between nodes with overlapping neighbourhoods; we relate this to global robustness of the clustering to removal of the weakest links. Furthermore, we identify local learning rules that establish integrative networks and improve network traffic in response to past traffic failures. Our findings identify a general organization for complex systems that strikes a balance between efficient local and global communication in their strong interactions, while allowing for robust, exploratory development of weak interactions.

Many complex systems reveal a small-world topology, which allows simultaneously local and global efficiency in the interaction between system constituents. Here, we report the results of a comprehensive study that investigates the relation between the clustering properties in such small-world systems and the strength of interactions between its constituents, quantified by the link weight. For brain, gene, social and language networks, we find a local integrative weight organization in which strong links preferentially occur between nodes with overlapping neighbourhoods; we relate this to global robustness of the clustering to removal of the weakest links. Furthermore, we identify local learning rules that establish integrative networks and improve network traffic in response to past traffic failures. Our findings identify a general organization for complex systems that strikes a balance between efficient local and global communication in their strong interactions, while allowing for robust, exploratory development of weak interactions.

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In the seminal work by Granovetter\(24,25\), it is stated that “the degree of overlap of two individuals’ friendship networks varies directly with the strength of their tie to one another”. Thus, strong links are found between nodes with highly overlapping neighbourhoods, a principle that was recently confirmed in mobile phone communications\(26\). Here we extend this finding to other complex networks, in particular brain, gene, and human interaction networks. On the other hand, some real networks and network models exhibit the opposite behaviour, where strong links tend to connect non-overlapping neighbourhoods.

We analyse the relationship between clustering and the weights, both locally and globally, in small-world networks. We assign to each link a local measure of clustering, the link clustering coefficient, \(C_l\), defined using the relative neighbourhood overlap,

\[
C_l = \frac{n_C}{n_T}
\]

where \(n_C\) is the number of common neighbours and \(n_T\) is the total number of neighbouring nodes, excluding the end nodes (Fig. 1a).

For directed networks, we use outgoing links for neighbourhood definition if not stated otherwise (see Supplementary Information). For undirected networks, \(C_l\) is equivalent to the edge clustering coefficient\(14,28\), but normalized differently.

We quantify the relationship between \(C_l\) and link weight, \(w\), using the correlation coefficient, \(R_{C_l}\). As \(R_{C_l}\) reveals only the linear trend, we also visualize the dependence of the average excess link clustering, \(\Delta C_l\), on weight rank (rank 1 being the smallest weight). In Fig. 1c, results are shown for three functional networks derived from neuronal avalanche activity in two different types of organotypic neuronal culture and in the pre-motor cortex in awake macaque monkeys\(14\). In these networks, weights represent the spontaneous propagation of neuronal activity between different nodes, that is, sites in the neural tissue\(18\). The steep positive trend we observe and the positive value of \(R_{C_l}\) demonstrate that activity propagates preferentially between nodes with highly overlapping neighbourhoods.

Similar results are obtained for networks of the structural and functional organization of the human cerebral cortex\(9\) (Fig. 1d), both describing the connectivity between \(\sim\)1,000 cortical regions of interest (nodes) distributed over 66 functional cortical areas. The weights in these two networks represent axonal fibre density, identified using diffusion spectrum imaging (DSI), and the correlation strength, derived from the ‘resting state’ cortical activity using functional magnetic resonance imaging\(8\) (fMRI), respectively. In Fig. 1e, we show similar results for gene regulation networks derived from human and mouse gene expression data\(29\). The weights in these networks measure the degree of regulation between two genes. To have computationally manageable link analysis, links lower than a threshold of 0.08 were discarded. We point out that similar results are obtained for gene sub-networks containing a smaller and randomly chosen subset of the original nodes (Supplementary Fig. S1). A comparable weight organization is also observed for gene sub-networks containing a smaller and randomly chosen subset of the original nodes (Supplementary Fig. S1).

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language networks, consisting of the Reuters News 9/11 network (N = 13,300) and the directed words free-association network (N = 10,600), in which weights represent the co-occurrences of words in news articles and the number of subjects that associate a source word to a target word, respectively, $R_{C_L}$ is positive, but with small $ΔC_L$ (Fig. 1g).

These results demonstrate that the local weighting rule relating the neighbourhood overlap and the strength of the links, first observed in social networks\(^{24,25}\), has a more general validity, and is found to hold strongly in the above-mentioned biological and social networks. A number of other networks, however, show a less positive, or even negative, trend between neighbourhood overlap and link strength. The anatomically well-characterized neural network of the worm Caenorhabditis elegans (C. elegans, Fig. 1h) shows a negligible trend, with $R_{C_L} ≈ 0$. Regarding transportation networks (Fig. 1i), we find positive $R_{C_L}$ for traffic between 500 US airports, and negative $R_{C_L}$ for the US Airways (US Air) transportation network\(^{21,18}\), that is, strong links preferentially occur between non-overlapping neighbourhoods, indicating that strong routes connect airports that preferentially serve different destinations. Similarly, physics author collaboration networks (Fig. 1j), in which weights reflect the number of papers co-authored normalized by the number of authors for each paper, exhibit negative $R_{C_L}$. (For detailed properties of all networks see Supplementary Information and Table SI therein.)

For convenience, we define a weight organization with significantly positive $R_{C_L}$ as integrative, because of the tendency of strong links to connect nodes with overlapping neighbourhoods (Fig. 1b, left). Conversely, networks with negative $R_{C_L}$, in which strong links connect non-overlapping neighbourhoods, are...
defined as dispersive (Fig. 1b, right). Zero $R_{C_{ij}}$ defines neutral weight organization.

**Robustness of clustering in integrative networks**

The importance of network robustness to a loss of nodes or links has been emphasized in various studies\(^{30,31}\). Here, we explore the relationship between the integrative weight organization, a local network property, and the robustness of the average node clustering coefficient, $C$, to the loss of weak links, a global network property. More specifically, we use pruning analysis to characterize the change in the network on successive removal of the weakest (bottom-pruning), or strongest (top-pruning) links. For the neuronal avalanche networks described above, we find that, even when a large fraction $f$ of the weakest links is removed, the excess clustering remains high and fairly constant, that is, invariant (Fig. 2a; solid lines). In contrast, removing even a small fraction of the strongest links readily destroys clustering in avalanche networks (Fig. 2a; dashed lines). Similar results are found for other integrative networks, such as the brain, gene, social and language networks (Fig. 2b–f). In contrast, the opposite trend for $\Delta C$ is found for dispersive networks such as the US Air transportation network (Fig. 2g), which is robust to top-pruning but not bottom-pruning. We quantify the difference in constancy of $\Delta C$ between bottom-pruning and top-pruning by the measure $M$, which ranges between $-1$ and $1$ (see Methods). It is positive for networks in which $\Delta C$ is more invariant to bottom-pruning than top-pruning and negative when the opposite is true. $M$ is zero or small for networks, such as collaboration networks (Fig. 2h), that show no robustness or pruning asymmetry.

**Basic models of weight-clustering relationships**

To fully appreciate the particular weight–clustering organization shown in Figs 1 and 2, we first compare it with the case where weights are independent of any topological features. Therefore, the correlation $R_{C_{ij}}$ is zero and $\Delta C_{ij}$ shows no trend with respect to link rank. We show analytically in Methods that for independent weights $\Delta C$ decreases linearly for either pruning direction from the initial value, $\Delta C_{0}$, to zero, namely $\Delta C(f) = \Delta C_{0}(1-f)$, and consequently $M = 0$. Indeed, in simulations for the directed Ozk–Hunt–Ott growing network (OHO (ref. 32); see Supplementary Information) and Watts–Newman (WN; ref. 33) network with randomly assigned weights, $\Delta C_{ij}$ is flat and $\Delta C$ decays linearly to zero for both top-pruning and bottom-pruning (Fig. 2a).

Next, we compare our results with so-called Class II networks\(^{19}\), in which weights are positively correlated with node degrees. An example is the global airline network\(^{18}\), for which the link weights are related to the end node

$$w_{ij} \sim (k_{i} \cdot k_{j})^{\theta} \quad (1)$$

with $\theta = 0.5 \pm 0.1$. Implementing equation (1) in OHO and WN topologies results in networks which are robust to the loss of their strongest but not weakest links, and in which traffic occurs preferentially between non-overlapping neighbourhoods (Fig. 2b). Thus, $\Delta C_{ij}$ decreases with higher $w$, $R_{C_{ij}}$ is negative, and $\Delta C$ remains high for top-pruning but not for bottom-pruning, yielding negative $M$.

To study further the local interaction of clustering and weights in integrative networks, we create a weighting model in which the link
Strength of the weak links is their randomness
Granovetter’s work on the ‘strength of weak ties’ and recent work on mobile phone communication demonstrate that weak links serve a cohesive function in complex networks more than strong links. This could reflect a specific, targeted organization for weak links that is missed by our definition of integrative, neutral and dispersive networks. To quantify the cohesiveness of the network and its dependence on link weight, we study the reduction in the relative giant component, rGC, during bottom-pruning and top-pruning for our real networks in Fig. 1. To test whether the observed cohesiveness arises from targeted weight organization, we compare the change in rGC for both pruning directions with that obtained when pruning links randomly. In Fig. 5a, we show for the fMRI brain and human gene networks that removal of weak links (bottom-pruning) reduces rGC faster than random controls, in line with the targeted, non-random organization of strong links outlined in the previous sections. In contrast, the change in rGC when pruning from the top does not differ much from random removal of links. We quantify the area between the random control and each pruning direction and show that these findings are true for most integrative networks (Fig. 5b) and were also observed recently for financial networks. We conclude that the cohesive character of weak links in most real-world networks simply reflects their random nature, rather than targeted placement, further supporting our emphasis on weight organization based on strong links.

Local learning rules create integrative networks
Highly clustered neighbourhoods with strong links, as found in integrative networks, are known to trap the flow of information, hence the ‘strength of weak’ ties in increasing global efficiency in communication. Integrative networks can potentially alleviate such neighbourhood trapping without relying on the random organization for weak links, because having strong links in such clustered neighbourhoods can only increase a chance of escape. We demonstrate this using a dynamical model in which local learning rules adaptively change weights in response to past traffic. Using an OHO topology with random weight assignments, traffic is initiated at a randomly selected node and directed probabilistically to future nodes with link weights linearly scaled into probabilities of node activation. This establishes a critical branching process dynamics in which one active node leads on average to one active node in the near future. These dynamics serve as a good model for the propagation of avalanche activity in brain networks or other stochastic traffic which neither grows exponentially nor terminates prematurely. Thus, sequences of activated nodes can span many cascading steps, but nodes can only be active once within a cascade and remain refractory until the cascade ends. This behaviour is observed experimentally for neuronal avalanches in brain networks and, in general, restricts our exploration to non-cyclical network traffic. After each cascade, the weights of the links between nodes

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We study the learning of integrative and dispersive weight organization further by tracking the properties of the cascade termination nodes. As expected, initially, cascades tend to end in neighbourhoods of highly clustered nodes quantified by the high correlation between the clustering coefficient of a node and frequency of its participation in cascade termination, $R_{C_{TN}}$ (Fig. 6e). Importantly, the last-step learning, instead of exploring alternative routes in the network, directs more future traffic to failure sites by specifically increasing weights for links pointing to terminating nodes in highly clustered neighbourhoods. This eventually makes those nodes passable for traffic (Fig. 6e, arrowheads) while retaining the integrative weight organization (Fig. 6c–e). This improvement in flow is absent in dispersive networks, where clustered neighbourhoods remain cascade termination points throughout learning (Fig. 6f). This finding is extended to supercritical branching process dynamics, where one node on average activates more than one future node, whereas cascades in subcritical dynamics fail to reach clustered neighbourhoods sufficiently often (Fig. 4). Similar results are obtained using the WN network topology (data not shown).

**Comparison with other weighted network models**

We examined several network growth models (GM) with evolving weights. The first two models were originally introduced for networks with preferential attachment\cite{17,34,35} producing scale-free networks with no excess clustering. Thus, we apply the same weight assignment schemes to OHO growing network topologies to obtain networks with no excess clustering. Thus, we apply the same weight assignment schemes to OHO growing network topologies to obtain networks with preferential attachment. The first two models were originally introduced for networks with preferential attachment\cite{17,34,35} producing scale-free networks with no excess clustering. Thus, we apply the same weight assignment schemes to OHO growing network topologies to obtain networks with no excess clustering.

**Figure 4** Summary plot of $M$ versus $R_{C_{TN}}$ for all the networks analysed in the present study. Brain, gene, social and language networks are integrative, with brain and gene networks exhibiting among the highest positive values of $M$ and $R_{C_{TN}}$. We note that only models OHO II and GM1 achieve high dispersive characteristics, whereas natural networks such as airline and collaboration networks range from weakly dispersive to neutral. For further description of the simulated networks see the main text.

**Figure 5** The cohesive nature of weak links is grounded in their random organization. a, The relative giant component, rGC, in fMRI brain and human gene 1 networks decays faster for top-pruning than for randomized weight controls. In contrast, rGC changes similarly to randomized weight controls for top-pruning. b, Summary plots of the differences in the area under the curve of rGC for bottom-pruning and top-pruning compared against randomized weight controls for all real-world networks. The small difference for integrative networks with top-pruning indicates random organization of weak links. Conversely, the large difference for bottom-pruning indicates targeted, non-random organization of strong links. The error bars represent the s.e. among $n = 10$ replicates.
Figure 6 | Adaptive implementation of integrative and dispersive weight organization. a, An initial random (that is, neutral) weight assignment (before) changes into integrative (after) during last step learning (10⁶ cascades; OHO topology; N = 60; n = 5 realizations; see also Supplementary Table S1). b, Learning only at the first step (second step) results in neutral (dispersive) weight organization. c,d, Temporal progression of M and $R_{CL}$ during last-step learning (solid black), at any particular step conditional on it being also the last step (coloured solid), all-step learning (dashed black) and at any particular step (coloured dashed). Learning at every first through to fifth cascade step, if this step is also the last in the cascade, results in integrative networks. Learning at every first step (A1; red dashed) maintains neutral networks, whereas dispersive networks emerge for later steps (A2–A5). e, Last step learning enables cascades to break through the traffic traps that exist in clustered neighbourhoods during early stages of learning. Temporal progression of $R_{CTN}$ for corresponding last, L1, . . . , L5 step learning in c–d. f, In dispersive networks clustered neighbourhoods continue to stall traffic throughout learning. The same key applies to all plots from c–f. Error bars indicate the s.e.

Discussion
Here we identify two important properties of weighted complex networks that are based on the interactions between the clustering and the weights. Earlier findings by Granovetter and others have related neighbourhood overlap to link weights between nodes in social networks, suggesting that the interaction between two people positively correlates with the number of the friends they share. We extend its validity to other complex networks, in particular, biological and human interaction networks, using the relationship between weights and the link clustering, $C_L$, but also find opposite behaviour in other networks (US Air transportation network, physics collaboration networks). Hence, on the basis of the local correlations between the clustering and weights, two types of networks can be distinguished, integrative and dispersive (Fig. 1b), which capture the targeted organization of strong links that emerges from a random network of weak links. Other local measures of clustering lead to a similar distinction, as demonstrated using the correlations of actual weights with the weighting model based on the clustering coefficient of nodes (see equation (2), Supplementary Fig. S9a). The division into integrative and dispersive networks requires that a common interpretation of weights is used for all networks, as any inverse transformation of weights would switch the classification. Here we presume that link weights quantify traffic, flow, intensity, or any other measure of increased communication or interaction between a pair of nodes.
We also find that integrative networks exhibit a high invariance of their clustering properties to the removal of weak links. A network with high $M$ might have functional advantages during growth and development, as it allows the rewiring and dynamical exploration of new, weak connections without undermining the network’s functionality, which is embedded in the clustering of its strong links. For example, during cortex development, weak neuronal connections are constantly formed, removed or strengthened, depending on the activity that occurs between neurons. Integrative weight organization potentially enables neural systems to acquire new memories without detrimentally affecting the old ones stored in strong connections. We note that the integrative and robust weight organization depends primarily on the weighting model and cannot be explained by purely topological measures. We tabulated many of the topological properties of the observed networks, but none of them correlated significantly with high $R_{\text{C}}$ or $M$. For example, there was no correlation between the assortativity and $R_{\text{C}}$ or $M$ ($R = 0.13$ and $R = -0.05$, respectively) across all real-world networks.

The general question arises as to which degree a local integrative rule, measured by $R_{\text{C}}$, generates the desired global network characteristics, such as invariance to loss of weak links, measured by $M$, or the weighted measure of modularity $Q$ (ref. 38). For the networks and simulations in this study, a positive correlation between $R_{\text{C}}$ and $Q$ was found ($R = 0.35$, Supplementary Fig. S9b). Similarly, a recent social network model\(^{36}\) (Fig. 4; SN) yielded integrative weight organization with a positive correlation between $R_{\text{C}}$ and $Q$. In the social network model, as well as in our study, moderate correlations were also found between $R_{\text{C}}$ and $M$, further supporting the idea that local rules shape global network properties to some extent. On the other hand, the negative or weak correlation between $R_{\text{C}}$ and $M$ after the initial phase of last-step learning (Supplementary Fig. S8a) and social network growth (Supplementary Fig. S8b), and the demonstration of integrative weighting models that produce negative $M$ (Supplementary Fig. S8c), further exemplifies the non-trivial relationship between $R_{\text{C}}$ and $M$. It seems from the networks analysed in the present study that the local integrative property is a necessary, but not sufficient, condition for obtaining highly robust networks.

Our learning model demonstrates another benefit of integrative weight organization in that clustered neighbourhoods do not necessarily stall traffic or trap information flow, which supports efficient communication across the network. Integrative networks are established on the basis of activation history if adjustments are limited to the recent history, for example the last step of the propagation, which tags and removes information trapping. This ‘learning at the last step’ paradigm is similar to temporal difference reinforcement learning, a widely used learning algorithm in artificial intelligence which links sensory input to a desired action outcome\(^{29}\). In neuroscience, it bears great similarity to reward-mediated learning, in which the last step in a sequence of actions taken, that is, the nodes activated, is rewarded given the desired outcome\(^{40}\). Importantly, this learning rule does not require specific global information about the network despite dynamically reconfiguring the network as a function of recent activity.

The predominance of integrative weight organization in natural, complex networks seems to reflect a general local weighting principle that results in networks which maintain robust functionality and efficient communication while adapting their weights to changing environments.

**Methods**

**Link clustering analysis.** As the correlation $R_{\text{C}}$ between $w$ and $C_{\text{i}}$ is a linear measure, we also studied the trend of link clustering with respect to weight rank. Links ordered by their weight rank were block-averaged to obtain $\langle C_{\text{orig}}(i) \rangle$ for the $n_{\text{th}}$ block, $i = 1, \ldots, 10$. We similarly obtain $\langle C_{\text{DSPR}}(i) \rangle$ from degree sequence preserving randomized (DSPR; ref. 41) controls, which show no trend, and subtract this constant offset to obtain the average excess link clustering for each block, $\langle \Delta C_{\text{DSPR}}(i) \rangle = \langle C_{\text{DSPR}}(i) \rangle - \langle C_{\text{orig}}(i) \rangle$. Here, $C_{\text{DSPR}}$ is the link clustering coefficient of the DSPR controls that corrects for the overlap contributed by the node degree distribution alone.

**Pruning analysis.** We studied network topology as a function of the fraction $f$ of the weakest (bottom-pruning) or strongest (top-pruning) links removed. Thus, weights in our pruning analysis mainly serve as labels for link ordering, allowing for easier comparisons between different weighted networks, as any monotonic transformation of the weights does not affect our pruning results. The order of removal for links with identical weights was randomized.

We define the excess clustering as $\Delta C = C - C_{\text{DSPR}}$, where $C$ and $C_{\text{DSPR}}$ are the average node clustering coefficients of the network and its randomized control, respectively. It corrects for the trivial appearance of clustering in finite-size networks and converges to $C$ for very large, sparse networks. Many networks maintained high and approximately constant $\Delta C$ for a particular pruning direction, which we defined as robust excess clustering (REC) and quantified using the inverse of the coefficient of variation of the $\Delta C(j)$ measured across ten values of $j = [0, 0.1, \ldots, 0.9]$. To reduce large variations in the measure when the standard deviation (s.d.) is extremely small, we used a transformation which confines this measure to the range $-1$ to $1$:

$$M_{\text{REC}} = 2\arctan(\langle \Delta C(j) \rangle / \text{s.d.}(\Delta C(j))) / \pi$$

We calculated $M_{\text{REC}}$ for bottom-pruning ($M_{\text{Bottom}}$) and top-pruning ($M_{\text{Top}}$) profiles, $\Delta C(f)$, and use their difference $M$ to quantify the asymmetry in invariance $M = M_{\text{Bottom}} - M_{\text{Top}}$. $M$ is positive for networks that are more robust to bottom-pruning and negative for networks that are more robust to top-pruning.

To quantify the difference in the change of RGG networks and controls were pruned until all links were removed. The area between the random removal curve and the top-pruning and bottom-pruning curves, respectively, was integrated. Positive and negative values indicate cohesiveness less than and greater than random, respectively.

**Analytical results for independent weights.** The pruning of a network in which link weights are independent of topology is equivalent to removing links randomly. On removal of the $t$th link, only the clustering coefficients of the $n_{\text{c}}$ common neighbours of its end nodes (Fig. 1a) are reduced, hence, the average clustering coefficient, $C_{\text{i}}$, changes according to

$$C_{\text{i+1}} = \frac{C_{\text{i}}}{n_{\text{c}}} + \frac{1}{2\alpha (\alpha - 1)} + \frac{(N - n_{\text{c}})}{N} C_{\text{i}}$$

where $\alpha$ is the average degree. In the continuous limit equation (3) becomes

$$\frac{dC}{dt} = -\frac{n_{\text{c}}(t)}{Nz(t)(1-z(t)-1)}$$

Using the relationship $n_{\text{c}}(t) = (z(t)-1)C(t)$ in equation (4), we get

$$\frac{dC}{dt} = -\frac{C}{Nz(t)}$$

One can similarly obtain a differential equation for $z(t)$, of which the solution is

$$z(t) = \frac{z_{0} - t}{N}$$

where $z_{0}$ is the total number of links in the original network. The solution of this equation is

$$C = C_{0}(1-f)$$

where $f = t/z_{0}$ is the fraction of removed links. The excess clustering is a difference of two clustering coefficients, both decaying with the same rate $1-f$, hence

$$\Delta C = \Delta C(1-f)$$

**Local learning rules.** We study the weight organization resulting from dynamical learning which occurs during branching process dynamics\(^{46}\). We simulate a critical branching process on OHO and WN topologies initiated with uniform or random, but narrowly distributed weights (neutral). The weights, $w_{ij}$, are approximately scaled to be interpreted as the critical branching process probabilities of the source node $i$ activating the target node $j$ (ref. 16). Before the next initiation, the scaling factor, which converts link weights into branching process probabilities, is adjusted such that the network dynamics remains critical. After

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each cascade, the network learns by changing link weights in successive time intervals (generations) according to

\[ w_{t+1} = w_t (1 + p_s) \]

\[ p_s = \frac{w_{\text{max}} - w_t}{w_{\text{max}}} \]

where \( p_s \) (ranging from 0.01 to 1%) is a small percentage increase factor and \( w_{\text{max}} \) is the maximum weight allowed (5–500). Importantly, we restrict learning to particular successions (steps) in the following four ways: (1) learning only at a particular step (for example, first, second, …); (2) learning at the last step of every cascade; (3) learning at a particular step, but only if it is also the last step and (4) learning at all steps without restriction. Only with learning restricted to the last steps (cases 2 and 3) does integrative behaviour occur and over a wide range of parameters until all weights eventually saturate to the maximal value \( w_{\text{max}} \). Results are shown before significant weight saturation occurs. We quantify the termination of cascades by the frequency of the appearance of a particular node in the last time interval of a cascade, that is, it was a terminal node. We calculate the fraction, \( f_{\text{TN}} \), of all cascades in which a node was a terminal node and the correlation \( R_{\text{TN}} \), between \( f_{\text{TN}} \) and the clustering coefficient \( C \) across all nodes.

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Author contributions

S.P. did analysis. S.P. and D.P. discussed, commented upon and wrote the manuscript.

Additional information

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