Characterizing the effect of population heterogeneity on evolutionary dynamics on complex networks

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Recently, the impact of network structure on evolutionary dynamics has been at the center of attention when studying the evolutionary process of structured populations. This paper aims at finding out the key structural feature of network to capture its impact on evolutionary dynamics. To this end, a novel concept called heat heterogeneity is introduced to characterize the structural heterogeneity of network, and the correlation between heat heterogeneity of structure and outcome of evolutionary dynamics is further investigated on various networks. It is found that the heat heterogeneity mainly determines the impact of network structure on evolutionary dynamics on complex networks. In detail, the heat heterogeneity readjusts the selection effect on evolutionary dynamics. Networks with high heat heterogeneity amplify the selection effect on the birth-death process and suppress the selection effect on the death-birth process. Based on the above results, an effective algorithm is proposed to generate selection adjusters with desired size and average degree.

The evolutionary dynamics on complex networks describes the competition and diffusion of variances in structured biological or social populations. It has been widely applied to explore the emergence of cooperation and strategy selection in real-world systems. An evolutionary dynamic model of structured population generally consists of three basic elements: a behavior set, a behavior updating rule, and an underlying population structure. The individuals each with a certain behavior acquire a corresponding fitness to characterize the competitiveness of the behavior. The population structure, which is usually represented by complex networks, captures the interactions between individuals. Based on the fitness landscape and population structure, the behavior updating rule then determines the evolutionary process of population.

One of the extensively studied evolutionary dynamic models is the invasion process, where a single mutant with fitness invades a population of residents with fitness. The fixation probability, which is the probability that the mutant takes over the whole population, characterizes the extinction, speciation and behavior drift of the invasion process. For , the invasion process is determined by random drift. In this case, the fixation probability of mutant is , which is regarded as a result of the balance between random drift and selection. However, it is still unclear which structural feature mainly determines the impact of networks on evolutionary dynamics. In 2010, Broom et al. observed that the network heterogeneity, defined as the variance of network degree distribution, is positive correlated with the fixation probability. That is, the network heterogeneity amplifies the selection effect. However, some exceptional cases are also reported in the above paper.
In this paper, we initiate a novel concept, called heat heterogeneity, to characterize the network structural heterogeneity. Moreover, we show that the heat heterogeneity mainly determines the impact of network structure on evolutionary dynamics. The networks with high heat heterogeneity amplify the selection effect on the birth-death process and suppress the selection effect on the death-birth process. Moreover, an effective algorithm is also proposed to design selection adjusters (amplifiers or suppressors) with specified number of nodes and edges in this paper.

Results

Model description. Consider the invasion process of a random single mutant into a network of residents. The fitness of mutant and resident is \( r \) and 1, respectively, where \( r > 0 \). The population evolves according to two typical updating rules: the birth-death (BD) and death-birth (DB) updating rules\(^5\). Under the BD updating, at each step, an individual is selected out of the population with a probability proportional to its fitness. And then it reproduces a copy and places the copy into one randomly chosen neighbor of him, while the replaced individual is then eliminated. Under the DB updating, the order of birth and death is reversed. Firstly, a random chosen individual is eliminated, and then with a probability proportional to fitness, a neighbor of the eliminated individual is selected to reproduce an offspring to take over the eliminated node.

Definition of heat heterogeneity. Consider an undirected connected network \( G = (V,E) \) of size \( N \). Denote the degree of each node as \( d_1, d_2, \ldots, d_N \). The temperature of node \( i \) is defined by \( T_i = \sum_{i \in N(i)} 1/d_k \), where \( N(i) \) denotes the neighbor set of node \( i \). For connected networks, \( d_k \geq 1 \) holds for all nodes \( k = 1, 2, \ldots, N \). Hence the above definition is valid for all connected networks.

The heat heterogeneity of a network is defined by the variance of its temperature distribution. In detail, let \( \bar{T} = \frac{1}{N} \sum_{i=1}^{N} T_i \) be the average temperature and \( H_t(G) \) be the heat heterogeneity of network \( G \), then \( H_t(G) \) is defined by

\[
H_t(G) = \frac{1}{N} \sum_{i=1}^{N} (T_i - \bar{T})^2.
\] (1)

The above heat heterogeneity characterizes the structural heterogeneity of a complex network, as illustrated in Fig. 1. For networks with zero heat heterogeneity, the temperature of each node is identical. This kind of networks is called isothermal networks\(^1,2,22\). Regular graphs are typical isothermal networks, as shown in Fig. 1(a). For networks with high heat heterogeneity, there must exist some relative "hot" and "cold" nodes in the network. From the definition of node temperature, the "hot" nodes have many low-degree neighbors, and the "cold" nodes have few but high-degree neighbors. Star networks are representative networks with high heat heterogeneity.

Correlation between heat heterogeneity and fixation probability on some specific graphs. To begin with, consider the evolutionary dynamics on some specific networks proposed by Broom et al.\(^3,4\), as shown in Fig. 2. The heat heterogeneity and degree heterogeneity of each network are listed in Table 1. Here, the degree heterogeneity is defined by \( H_d(G) = \frac{1}{N} \sum_{i=1}^{N} (d_i - \bar{d})^2 \), where \( \bar{d} \) denotes the average degree of a network. Let a random mutant with relative fitness 1.5 invade each network, the corresponding fixation probability \( \rho_f \) of the mutant is computed respectively, as shown in Table 1.

Broom et al. have shown that the degree heterogeneity is a strong indicator of the fixation probability \( \rho_f \) for evolutionary dynamics on complex networks. However, the networks in Fig. 2 contradict this...
observation. In contrary, it can be observed from Table 1 that the fixation probability is completely consistent with the heat heterogeneity on these networks. Indeed, on these networks, the fixation probability is monotone increasing with the heat heterogeneity for the BD process, and it is monotone decreasing with the heat heterogeneity for the DB process. These results partly confirm that the heat heterogeneity mainly determines the structural effect on the fixation probability of a random mutant for evolutionary dynamics on networks.

### Correlation between heat heterogeneity and fixation probability on complete bipartite graphs

The previous example gives a glimpse of the strong correlation between heat heterogeneity and fixation probability of a network. Here, the correlation between heat heterogeneity and fixation probability is further assessed on a class of complete bipartite graphs (see Methods).

For complete bipartite graphs, the fixation probability of mutant can be derived through theoretical analysis for both the BD and DB processes (see the Supplementary Information (SI) for details). With the fixation probability of mutant on each graph, one can investigate the impact of graph structure on evolutionary dynamics. Fig. 3 and Fig. 4 display the correlation between heat heterogeneity and fixation probability of a random mutant for the BD and DB processes, respectively. The underlying network structures are a class of complete bipartite graphs with size $N = 50$.

From Figs. 3 and 4, one has the following observations:

- The heat heterogeneity and fixation probabilities are completely correlated for both the BD and DB processes. It indicates that the heat heterogeneity determines the impact of network structure on evolutionary dynamics for complete bipartite graphs.
- The fixation probability and heat heterogeneity are positively correlated for advantageous mutants ($r = 1.1$) and negatively correlated for disadvantageous mutant ($r = 0.9$) in the BD process. And in DB process, they are positively correlated for disadvantageous mutant and negative correlated for advantageous mutant. Thus, for the BD (DB) process, high heat heterogeneity promotes (inhibits) the fixation of advantageous mutants and inhibits (promotes) the fixation of disadvantageous mutants. That is, the heat heterogeneity amplifies the selection effect on evolutionary dynamics for the BD process and suppresses the selection effect for the DB process.
- The degree heterogeneity and fixation probability are also correlated. However, the correlation is not universal. Heat heterogeneity is better than degree heterogeneity to assess the impact of network structure on evolutionary dynamics.

### Correlation between heat heterogeneity and fixation probability on general networks

We have shown that the heat heterogeneity can capture the structural effect on evolutionary dynamics for some specific networks and complete bipartite graphs. A follow-up question is whether the above principle also holds for general networks. To answer this question, the correlation between heat heterogeneity and fixation probability is further tested on a set of randomly sampled undirected networks.

Suppose that the network size is $N$. The set of randomly sampled undirected networks are generated with the following method. Step one: Assign each node to a random degree from 1 to $N-1$, which returns a degree sequence. Step two: Generate a network according to the above degree sequence by the sequential algorithm proposed by M. Bayati et al.\(^7\). Step three: Repeat the above two steps until enough samples of connected networks have been got. Since the degree sequence is randomly sampled and the sequential algorithm generates almost uniformly random networks with a specified degree

![Figure 3](https://example.com/figure3.png)

**Figure 3** Correlation between the heterogeneity and fixation probability for the birth-death process on a class of complete bipartite graphs.

(a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 0.9; (c) the fixation probability of a random mutant with fitness 1.1; (d) the degree heterogeneity. The rank order correlations of the fixation probability with heat heterogeneity are $-1$ and $1$ for $r = 0.9$ and $r = 1.1$ respectively.
sequence, the generated set of networks are almost uniform samples from the set of undirected connected networks with size $N$.

Fig. 5 shows the correlation between the heat heterogeneity and fixation probability $\rho$, for the BD process on a set of randomly sampled networks. It can be observed that the fixation probability is highly correlated with the heat heterogeneity of networks. In fact, the rank order correlation (see Methods) between the fixation probability and heat heterogeneity is $0.94, 0.91, 0.83, -0.84$ for $r = 1.9, 1.5, 1.1, 0.7$, respectively. Here $r$ is the relative fitness of mutant. The above correlation coefficients greatly outperform those between degree heterogeneity and fixation probability, which are less than 0.5 for all $r$. The results indicate that the heat heterogeneity can still capture the impact of network structure on evolutionary dynamics for the BD process on general undirected networks.

Moreover, Fig. 5 also indicates that the heat heterogeneity amplifies the selection effect for the BD process. Indeed, the fixation probability generally increases with the heat heterogeneity for advantageous mutants ($r = 1.1, 1.5, 1.9$). However, it generally decreases with the heat heterogeneity for disadvantageous mutants ($r = 0.7$). In other words, in networks with high heat heterogeneity, superior mutants are more likely to be preserved, while unfit mutants are more likely to be eliminated. In general, the amplification effect of
a network on selection increases with the heat heterogeneity of the network structure.

In contrary, the heat heterogeneity of network structure suppresses the selection effect for the DB process. For advantageous mutants \((r = 1.1, 1.5\) and \(1.9\)), the fixation probability generally decreases with the heat heterogeneity of networks. However, for disadvantageous mutants \((r = 0.7)\), the fixation probability generally increases with the heat heterogeneity of networks, as shown in Fig. 6. That is, networks with high heat heterogeneity inhibit fixation of advantageous mutants and promote fixation of disadvantageous mutants in the DB process.

For the DB process on general networks, the impact of network structure on evolutionary dynamics is also mainly dominated by the heat heterogeneity. The rank order correlation between fixation probability and heat heterogeneity is \(0.95\), \(-0.96\), \(-0.92\), and \(0.93\) for \(r = 1.9\), \(1.5\), \(1.1\), and \(0.7\), respectively. The above correlation coefficients greatly outperform those between degree heterogeneity and fixation probability, which are less than \(0.71\) for all \(r\).

**Robustness of the strong correlation.** In the above Sections, the strong correlation between the fixation probability and heat heterogeneity has been observed on various undirected connected networks, including some specific networks in Ref. 34, complete bipartite networks, and most importantly, random samples of undirected connected networks. Moreover, it is observed that the strong correlation between the fixation probability and heat heterogeneity is also valid for networks with different order (See Figs. S2 and S3 in Supplementary Information (SI)). Thus, the obtained results are generally robust against different kinds of undirected network structures.

**Discussion**

The above results have shown that the network structure and the fixation probability of a random mutant are strongly correlated for both the BD and DB processes. However, when the mutant’s relative fitness \(r\) approaches 1, a decrease is observed in the rank order correlation between fixation probability and heat heterogeneity (see Fig. 5 and Fig. 6). The reason lies in that random drift dominates the evolutionary dynamics when \(r\) is close to 1, whereas the network structure affects the fixation probability only through readjusting the selection effect. Indeed, for both the neutral BD and DB processes, the fixation probability of a random mutant is \(1/N\) for all kinds of networks with size \(N\) (see the Supplementary Information (SI) for details). That is, the fixation probability of a random mutant is irrelevant to network structure in neutral evolutionary processes.

It has shown that the selection effect on evolutionary dynamics on networks is mainly determined by the heat heterogeneity of networks. This result indicates us an effective algorithm to design selection adjusters with desired average degree \(d\) and size \(N\). The algorithm is as follows. Firstly, generate \(M\) nodes and randomly connect them with \((d/2 - 1)N + M\) edges. Then, add the other \(N-M\) nodes in and link each added node to one of the above \(M\) nodes. Here, \(M\) is set as the smallest integral value larger than \(1.5 + \sqrt{2.25 + N(d - 2)}\) to guarantee the existence of network.

Networks generated with the above algorithm possess high heat heterogeneity. In fact, there are \(N-M\) nodes in the network which have only one high-degree neighbor, so the temperature of these nodes is very low. And the other \(M\) nodes connect with a large number of one-degree nodes, thus, their temperature is then very high. Fig. 7 presents a typical generated network by the above algorithm. The temperature distribution of the network is clearly displayed.

Generally, human, economic, and industrial organizations have complicated network structures. Different ideas, behaviors, technological innovations compete and diffuse on these networked organizations\(^{37-41}\). Understanding the effect of network structure on evolutionary dynamics is one of the main goals in studying the evolutionary collective behaviors of networked systems\(^{42-44}\). Through analysis, numerous facts show that the heat heterogeneities of most real-world networks are much larger than those of random networks (refer to Table S1 and Fig. S4). Thus, these real-world network structures have significantly impact on the evolutionary processes of populations.

In this paper, it is shown that the impact of network structure on evolutionary dynamics is mainly determined by the heat heterogeneity of network. In detail, for the BD process, a network with high heat heterogeneity acts as a selection amplifier, favoring spread of advantageous mutants and inhibiting propagation of disadvantageous ones. However, for the DB process, a network of high heat heterogeneity behaves like a selection suppressor, diminishing the

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**Figure 6** Correlation between the heterogeneity and fixation probability for the death-birth process on general undirected networks. (a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 1.9; (c) the fixation of a random mutant with fitness 1.5; (d) the fixation probability of a random mutant with fitness 1.1; (e) the fixation probability of a random mutant with fitness 0.7; (f) the degree heterogeneity. The 40 graphs are almost uniformly randomly sampled from the undirected connected graphs set with 12 nodes. Here the graph index is ordered according to increasing its heat heterogeneity. The rank order correlation of the fixation probability with heat heterogeneity is 0.932 for \(r = 0.7\) and \(-0.916\), \(-0.956\), \(-0.953\) for \(r = 1.1\), \(1.5\), \(1.9\), respectively.
fixation probability of advantageous mutants and increasing that of disadvantageous ones. These results may further help us understand questions such as how a network structure affects the spreading process of innovations and how to design suitable collaboration networks to enhance the spread of favorable innovations and inhibit the propagation of unfit ones.

**Methods**

**Complete bipartite graphs.** A complete bipartite graph \( G = (U + V, E) \) is a bipartite graph such that for any two nodes, \( u \in U \) and \( v \in V \), \( uv \) is an edge in \( G \). Let \( K_{m,n} \) denote a complete bipartite graph \( G = (U + V, E) \), where \( m \) and \( n \) are the number of nodes in set \( U \) and \( V \), respectively. By fixing \( m + n = N \) and varying \( m \) from 1 to \( N/2 \), one gets a class of complete bipartite graphs \( \{ K_{m,N-n} | m = 1, \ldots, N/2 \} \). Here, the constant \( N \) denotes the graph size. The heat heterogeneity of graphs in \( \{ K_{m,N-n} | m = 1, \ldots, N/2 \} \) can be given by

\[
H_t (K_{m,N-n}) = (N-2m)^2 / m(N-m)
\]  

(2)

**Rank order correlation.** The rank order correlation coefficient between two vectors is the Pearson correlation coefficient between the rank vectors of the above two vectors. Given a vector \( x = (x_1, x_2, \ldots, x_n) \), the rank of the \( i \)-th components is

\[
r(x_i) = 1 + \left[ \frac{1}{2} \right] \frac{|x_i - x_{(i)}|}{\max_{j} x_{(j)} - \min_{j} x_{(j)}}
\]  

(3)

where the notation \( x_{(i)} \) denotes the number of elements in set \( s \). The rank order correlation coefficient measures the strength of monotonic association between two vectors. The rank order correlation coefficient can take values from \( +1 \) to \( -1 \), where \( +1 \) (\( -1 \)) indicates a perfect increasing (decreasing) association relationship and zero indicates no association.

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Figure 7 | A typical selection adjuster generated with the proposed algorithm. The size, average degree, and heat heterogeneity of this network is 250, 5, and 8.1, respectively. “Hot” nodes are colored in red and “cold” nodes are in blue.
Author contributions
S. T. and J. L. designed and performed the research as well as wrote the paper.

Additional information
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