SCIENTIFIC REPORTS

OPEN

SUBJECT AREAS:
POPULATION DYNAMICS
COMPLEX NETWORKS

Received
5 March 2014

Accepted
2 May 2014

Published
22 May 2014

Correspondence and requests for materials should be addressed to J.L. (jhlu@iss.ac.cn)

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

Shaolin Tan[1,2] & Jinhu Lü[2]

[1]College of Electrical and Information Engineering, Hunan University, Changsha 410082, China, [2]LSC, Institute of Systems Science, Academy of Mathematics and Systems Science, Chinese Academy of Sciences, Beijing 100190, China.

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[1,2]. It has been widely applied to explore the emergence of cooperation and strategy selection in real-world systems[3–8]. 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[9,10]. The population structure, which is usually represented by complex networks[11–14], 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 r invades a population of N-1 residents with fitness 1. 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[15–17]. For $r = 1$, the invasion process is determined by random drift. In this case, the fixation probability of mutant is $1/N$. For $r \neq 1$, the invasion process relies on the joint action of random drift and selection. In this case, if the population is well-mixed, then the fixation probability is $\frac{1-1/r}{1-1/r^N}$,which is regarded as a result of the balance between random drift and selection[18–20].

Several recent studies have indicates that the population structure can break the balance between random drift and selection[1,21–25]. Some kinds of networks, called selection amplifiers, amplify the selection effect on population evolution. Examples of selection amplifiers include the star graph and the funnel[1]. However, some kinds of networks, called selection suppressors, suppress the selection effect on population evolution. The above finding evokes an increasing interest in analysis of the network structural effect on evolutionary dynamics[26–33]. In 2014, the work by *Maciejewski* clarified how node degree affects the fixation probability of a neutral mutant. It was shown that the fixation probability of a node is proportional and inverse proportional to the node degree for death-birth and birth-death processes, respectively[2]. 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[34].

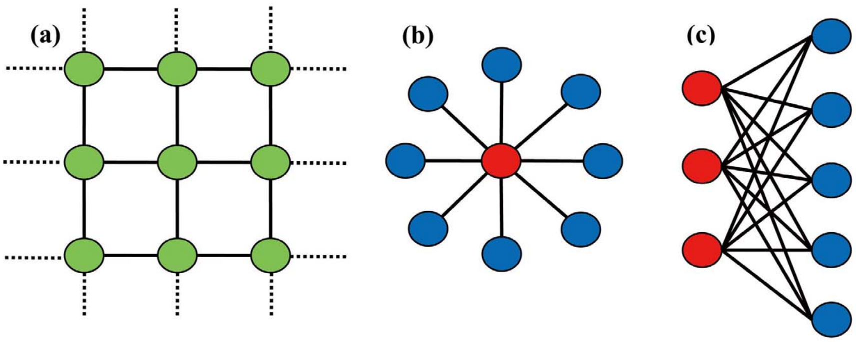

Figure 1 | Illustration of temperature distribution in (a): regular graph, (b): star graph, and (c): complete bipartite graph. In each graph, nodes with relative high temperature, low temperature and averaged temperature are colored in red, blue and cyan, respectively.

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[35]. 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, ..., d_N. The temperature of node i is defined by $T_i = \sum_{k\in N(i)} {}^{1}/_{d_k}$, where $N(i)$ denotes the neighbor set of node i[1]. For connected networks, $d_k \geq 1$ holds for all nodes $k = 1, 2, ..., N$. 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

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

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[1,22]. 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.*[34], 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 $H_d(G) = \frac{1}{N}\sum_{i=1}^{N}\left(d_i - \bar{d}\right)^2$, 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 ρ_1 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 ρ_1 for evolutionary dynamics on complex networks. However, the networks in Fig. 2 contradict this

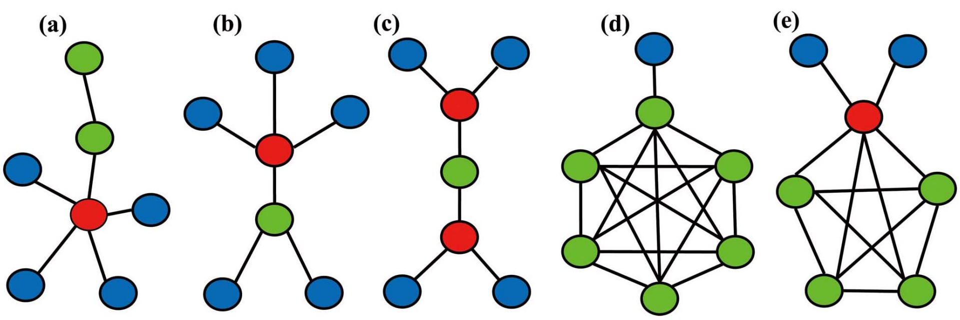

Figure 2 | Some specific networks[34]. On these networks, the fixation probability of a random mutant cannot be evaluated by degree heterogeneity, however, it can be revealed by heat heterogeneity. The color of each node is a symbol of its temperature. Red nodes are relatively "hot", blue nodes are relatively "cold", and the temperature of cyan nodes falls in between.

Table 1 | The fixation probability of a random mutant ρ_1, degree heterogeneity $H_d(G)$, and heat heterogeneity $H_t(G)$ of the specific networks in Fig. 2[24]

Graph label	ρ_1(BD)	ρ_1(DB)	$H_d(G)$	$H_t(G)$
a	0.424	0.209	1.918	2.157
b	0.409	0.224	1.347	1.369
c	0.398	0.248	0.776	0.913
d	0.374	0.258	2.816	0.774
e	0.352	0.285	2.244	0.243

observation[34]. 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.*[36]. 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

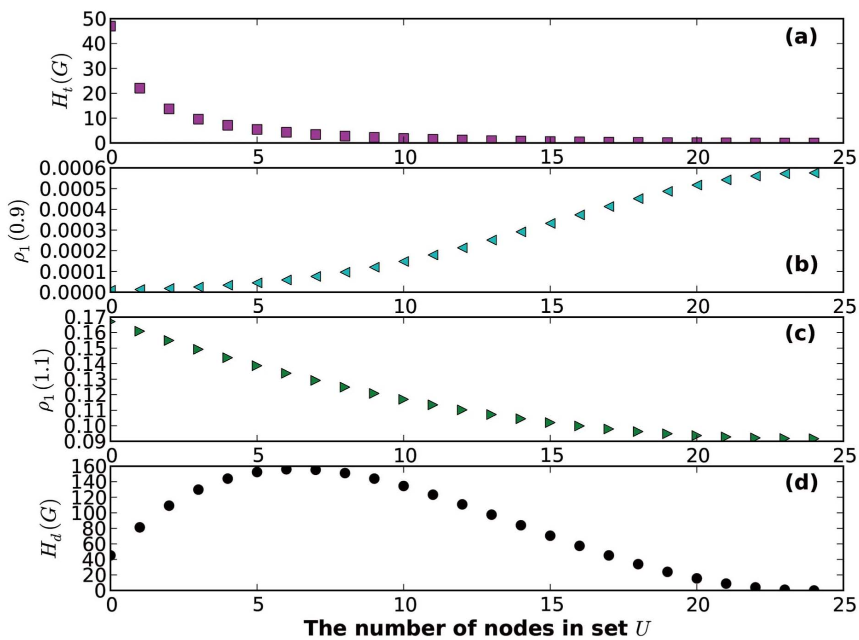

Figure 3 | Correlation between the heterogeneity and fixation probability for the birth-death process on a class of complete bipartite graphs. (a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 0.9; (c) the fixation probability of a random mutant with fitness 1.1; (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.

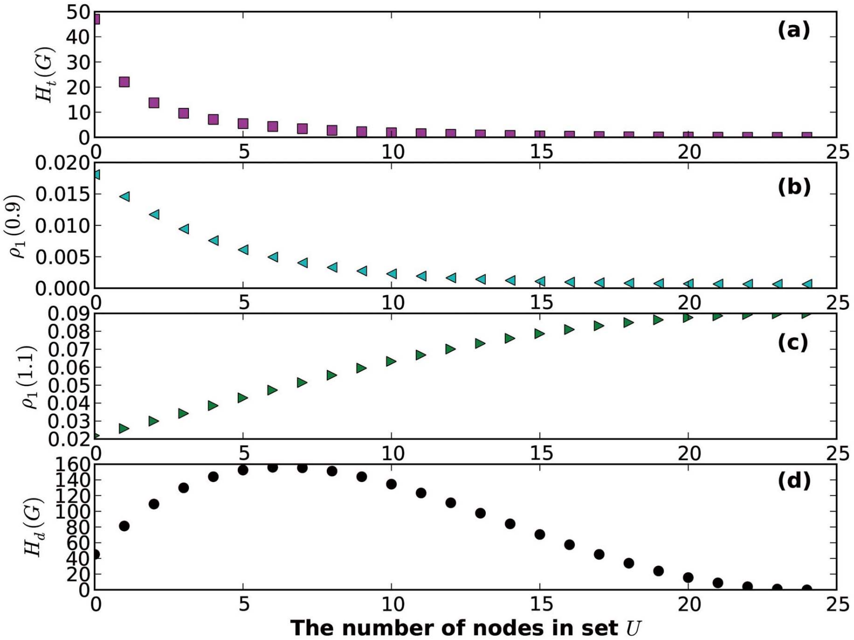

Figure 4 | Correlation between the heterogeneity and fixation probability for the death-birth process on a class of complete bipartite graphs. (a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 0.9; (c) the fixation probability of a random mutant with fitness 1.1; (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 ρ_1 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, and 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

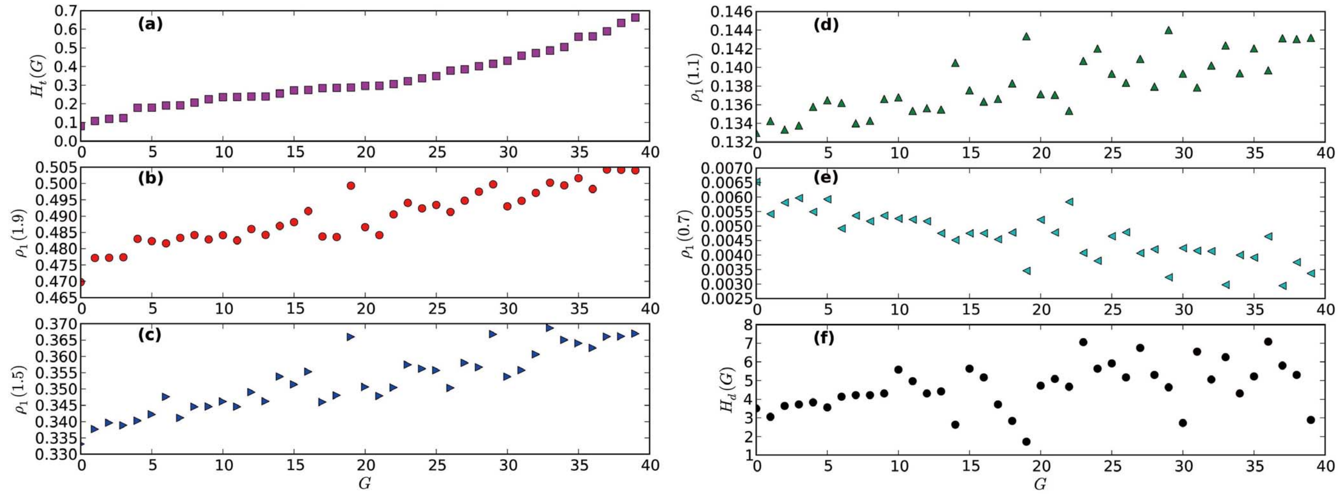

Figure 5 | Correlation between the heterogeneity and fixation probability for the birth-death process on general undirected networks. (a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 1.9; (c) the fixation of a random mutant with fitness 1.5; (d) the fixation probability 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 networks are almost uniformly randomly sampled from the undirected connected graph set with 12 nodes. Here the network index is ordered according to increasing its heat heterogeneity. The rank order correlations of the fixation probability with heat heterogeneity are −0.84, 0.83, 0.91, 0.94 for $r = 0.7$, 1.1, 1.5, 1.9, respectively; while with degree heterogeneity, they are only −0.37, 0.34, 0.45, 0.48 for $r = 0.7$, 1.1, 1.5, 1.9, respectively.

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

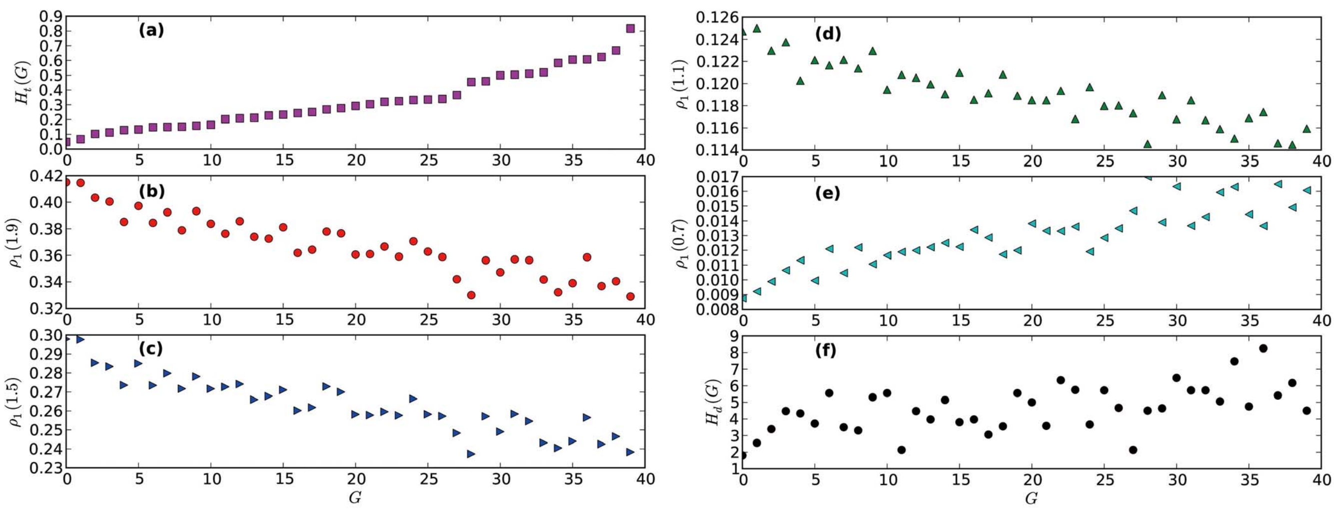

Figure 6 | Correlation between the heterogeneity and fixation probability for the death-birth process on general undirected networks. (a) The heat heterogeneity; (b) the fixation probability of a random mutant with fitness 1.9; (c) the fixation of a random mutant with fitness 1.5; (d) the fixation probability 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.

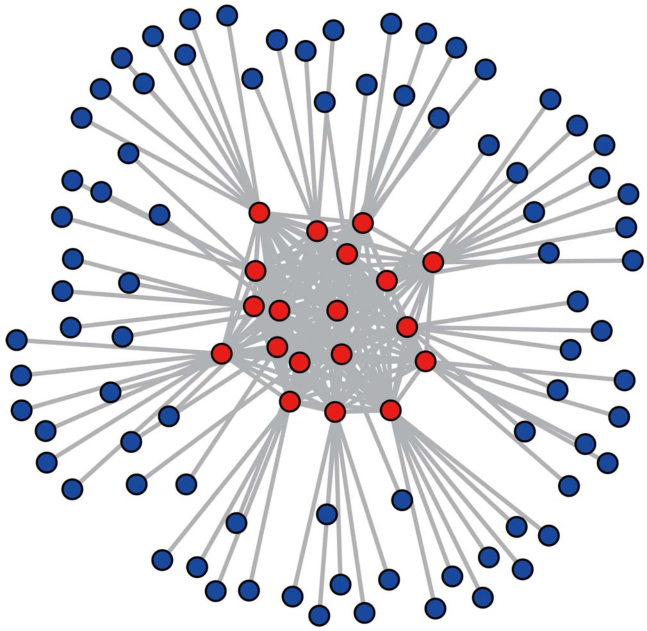

Figure 7 | A typical selection adjuster generated with the proposed algorithm. The size, average degree, and heat heterogeneity of this network is 250, 5, and 8.1, respectively. "Hot" nodes are colored in red and "cold" nodes are in blue.

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 $\{K_{m,N-m}|m = 1,2,\ldots,N/2\}$. Here, the constant N denotes the graph size. The heat heterogeneity of graphs in $\{K_{m,N-m}|m = 1,2,\ldots,N/2\}$ can is given by

$$H_t(K_{m,N-m}) = {(N-2m)^2}/{m(N-m)}. \quad (2)$$

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

$$r(x_i) = 1 + \left|j \neq i | x_j > x_i\right| + \frac{1}{2}\left|j \neq i | x_j = x_i\right|, \quad (3)$$

where the notation $|s|$ 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.

1. Lieberman, E., Hauert, C. & Nowak, M. A. Evolutionary dynamics on graphs. *Nature* **433**, 312–316 (2005).
2. Maciejewski, W. Reproductive value in graph-structured populations. *J. Theor. Biol.* **340**, 285–293 (2014).
3. Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390–1396 (1981)
4. Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359**, 826–829 (1992).
5. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1563 (2006).
6. Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505 (2006).
7. Tan, S., Lü, J., Yu, X. & Hill, D. Evolution and maintenance of cooperation via inheritance of neighborhood relationship. *Chin. Sci. Bull.* **58**, 3491–3498 (2013).
8. Tarnita, C. E., Ohtsuki, H., Antal, T., Fu, F. & Nowak, M. A. Strategy selection in structured populations. *J. Theor. Biol.* **259**, 570–581 (2009).
9. Nowak, M. A., Tarnita, C. E. & Antal, T. Evolutionary dynamics in structured populations. Phil. *Trans. R. Soc. B* **365**, 19–30 (2010).
10. May, R. M. Network structure and the biology of populations. *Trends. Ecol. Evol.* **21**, 394–399 (2006).
11. Lü, J. & Chen, G. A time-varying complex dynamical network model and its controlled synchronization criteria. *IEEE Trans. Automat. Contr.* **50**, 841–846 (2005).
12. Lü, J., Yu, X., Chen, G. & Cheng, D. Characterizing the synchronizability of small-world dynamical networks. *IEEE Trans. Circuits Syst. I* **51**, 787–796 (2004).
13. Newman, M. The structure and function of complex networks. *SIAM Rev.* **45**, 167–256 (2003).
14. Wang, P., Lü, J. & Ogorzalek, M. Global relative parameter sensitivities of the feed-forward loops in genetic networks. *Neurocomputing* **78**, 155–165 (2012).
15. Patwa, Z. & Wahl, L. M. The fixation probability of beneficial mutations. *J. Royal Soc. Interface* **5**, 1279–1289 (2008).
16. Volkov, I., Banavar, J. R., Hubbell, S. P. & Maritan A. Neutral theory and relative species abundance in ecology. *Nature* **424**, 1035–1037 (2003).
17. Ewens, W. J. Ed., *Mathematical Population Genetics* (Springer, New York, 2004).
18. Taylor, C., Fudenberg, D., Sasaki, A. & Nowak, M. A. Evolutionary game dynamics in finite populations. *B. Math. Biol.* **66**, 1621–1644 (2004).
19. Traulsen, A., Nowak, M. A. & Pacheco, J. M. Stochastic dynamics of invasion and fixation. *Phys. Rev. E* **74**, 011909 (2006).
20. Moran, P. A. P. *The statistical processes in genetics* (Clarendon Press, Oxford, 1962).
21. Antal, T., Redner, S. & Sood, V. Evolutionary dynamics on degree-heterogeneous graphs. *Phys. Rev. Lett.* **96**, 188104 (2006).
22. Broom, M. & RychtáY, J. An analysis of the fixation probability of a mutant on special class of non-directed graphs. *Proc. R Soc. A* **464**, 2609–2627 (2008).
23. Szabó, G. & Fáth, G. Evolutionary games on graphs. *Phys. Rep.* **446**, 97–216 (2007).
24. Tan, S., Lü, J., Yu, X. & Hill, D. Characterizing the effect of network structure on evolutionary dynamics via a novel measure of structural heterogeneity. Paper presented at *Proceedings of the 25th Chinese Control and Decision Conference,* Guiyang, China. 10.1109/CCDC.2013.6561028. (2013, May 25–27).
25. Santos, F. C., Rodrigues, J. F. & Pacheco, J. M. Graph topology plays a determinant role in the evolution of cooperation. *Proc. R. Soc. B* **273**, 51–55 (2006).
26. Szolnoki, A. & Szabó, G. Cooperation enhanced by inhomogeneous activity of teaching for evolutionary Prisoner's Dilemma games. *EPL* **77**, 30004 (2007).
27. Perc, M. & Wang, Z. Heterogeneous aspirations promote cooperation in the Prisoner's Dilemma game. *Plos ONE* **5**, e15117 (2010).
28. Wang, Z., Szolnoki, A. & Perc, M. If players are sparse social dilemmas are too: Importance of percolation for evolution of cooperation. *Sci. Rep.* **2**, 369 (2012).
29. Perc, M. Does strong heterogeneity promote cooperation by group interactions? *New J. Phys.* **13**, 123027 (2011).
30. Wang, Z., Szolnoki, A. & Perc, M. Percolation threshold determines the optimal population density for public cooperation. *Phys. Rev. E* **85**, 037101 (2012).
31. Wang, Z., Szolnoki, A. & Perc, M. Interdependent network reciprocity in evolutionary games. *Sci. Rep.* **3**, 1183 (2013).
32. Perc, M. & Szolnoki, A. Social diversity and promotion of cooperation in the spatial prisoner's dilemma game. *Phys. Rev. E* **77**, 011904 (2008).
33. Szolnoki, A., Antonioni, A., Tomassini, M. & Perc, M. Binary birth-death dynamics and the expansion of cooperation by means of self-organized growth. *EPL* **105**, 48001 (2014).
34. Broom, M., RychtáY, J. & Stadler, B. Evolutionary dynamics on small-order graphs. *Journal of Interdisciplinary M.* **12**, 129–140 (2009).
35. Ohtsuki, H. & Nowak, M. A. Evolutionary games on cycles. *Proc. R. Soc. B* **273**, 2249–2256 (2006).
36. Bayati, M., Kim, J. H. & Saberi, A. A sequential algorithm for generating random graphs. *Algorithmica* **58**, 860–910 (2010).
37. Centola, D. The spread of behavior in an online social network experiment. *Science* **329**, 1149–1197 (2010).
38. Ziman, J. Ed., *Technological Innovation as An Evolutionary Process* (Cambridge University Press, Cambridge, UK, 2000).
39. Chen, Y., Lü, J. & Lin, Z. Consensus of discrete-time multi-agent systems with transmission nonlinearity. *Automatica* **49**, 1768–1775 (2013).
40. Zhu, J., Lü, J. & Yu, X. Flocking of multi-agent non-holonomic systems with proximity graphs authors. *IEEE Trans. Circuits Syst. I* **60**, 199–210 (2013).
41. Arakji, R. Y. & Lang, K. R. Adoption and diffusion of business practice innovations: An evolutionary analysis. *Int. J. Electron. Comm.* **15**, 145–168 (2010).
42. Barbosa, V. C., Donangelo, R. & Souza, S. R. Early appraisal of the fixation probability in directed networks. *Phys. Rev. E* **82**, 046114 (2006).
43. Masuda, N. & Ohtsuki, H. Evolutionary dynamics and fixation probabilities in directed networks. *New J. Phys.* **11**, 033012 (2009).
44. Tan, S., Lü, J., Chen, G. & Hill, D. *When structure meets function in evolutionary dynamics on complex networks, IEEE Circuits Syst. Mag., in press* (2014).

Acknowledgments

This work was supported by the National Science and Technology Major Project of China under Grant 2014ZX10004-001-014, the 973 Project under Grant 2014CB845302, and the National Natural Science Foundation of China under Grant 61025017.

Author contributions

S. T. and J. L. designed and performed the research as well as wrote the paper.

Additional information

Supplementary information accompanies this paper at http://www.nature.com/scientificreports

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Tan, S. & Lü, J. Characterizing the effect of population heterogeneity on evolutionary dynamics on complex networks. *Sci. Rep.* **4**, 5034; DOI:10.1038/srep05034 (2014).