Evolutionary Graphs on Two Levels

Pu-yan Nie [1] [2] [3]

Abstract Evolutionary graphs were initially proposed by Lieberman et al. and evolutionary dynamics on two levels are recently introduced by Traulsen et al. We now introduce a new type of evolutionary dynamics, evolutionary graphs on two levels, and the fixation probability is analyzed. Some interesting results, evolutionary graphs on two levels are more stable than single level evolutionary graphs, are obtained in this paper.

Key words: Evolutionary graph, two-level, fixation probability, game theory

AMS Subject Classification(2000): 05C20, 62P99

1 Introduction

Evolutionary graphs (EGs) were recently introduced by Lieberman et al. [3] to explain some biological phenomena. Evolutionary graph theory (EGT) is an approach to implementing evolutionary dynamic where the individuals in a population are arranged on a graph. EG provides a general account of how population structure affects evolutionary dynamic [3]. There exist various papers on dynamic, see in [1, 2, 8, 9, 6, 7] and the references mentioned therein. In particular, evolutionary dynamics were analyzed in [2, 8, 9].

In [3], several kinds of evolutionary graphs, including isothermal structure, star structure and directed cycles, were introduced and analyzed, respectively. In isothermal graphs, the fixation probability $\rho(r, N)$ of all N vertexes is equal to

$$\rho(r, N) = \frac{1 - \frac{1}{r}}{1 - \frac{1}{r^N}}, \tag{1.1}$$

where r is the fitness of a new mutant and the fitness of others are 1, and N is the population size. For the K-star structure (see in [3]), the fixation probability is

$$\rho_K(r, N) = \frac{1 - \frac{1}{r^K}}{1 - \frac{1}{r^{KN}}}. \tag{1.2}$$

[1] College of Economics and Trade, Hunan University, Changsha,410079,P.R.China.

[2] Department of Mathematics, Jinan University, Guangzhou, 510632, P.R.China

[3] This work is partially supported by National Natural Science Foundation of China (No. 10501019), and the Scientific Research Foundation for Returned Overseas Chinese Scholars, State Education Ministry.

For the directed cycles, four cases, positive-symmetric, negative-symmetric, positive-anti-symmetric and negative-anti-symmetric, were all considered in [3].

Star structure EGs are reconsidered in this paper. For the star structure evolutionary graphs [3], it is always assumed that there just exists a center. In many practical problems, there exists multiple centers and the centers are related to each other. Furthermore, in [10], evolutionary dynamics on two levels were introduced and analyzed. We now introduce the selection and the Moran process in brief.

Multi-level selection arises whenever reproducing units form aggregates that also produce. For example, cells form multi-cellular organization, animals form social groups [10]. Multi-level selection is related to kin selection, spatial selection and to the long standing debate on group selection, see in [10] and the attached references. There exists a debate about group selection [12], which brought on a denial of group selection in 1960s and 1970s. Wade [11] did some experiments with the red four beetle, which provides a theoretical explanation for the efficiency of group selection. More experiments further confirmed the effitiveness of group selection. Furthermore, group selections were employed in the context of the origin of life [4]. Group selection is also related to parasite evolution. A parasite evolution can be modelled as a two level problems. In this paper, the model is based on group selection because the parasites can be modelled as a group selection. Group selection can favor the cooperation of parasites in a host.

Selection dynamic in a finite population is described by Moran process [5]. When there are two groups, an individual is randomly selected for reproduction with a probability that is proportional to its fitness. The offspring replaces a randomly chosen individual and the total population remains constant, see more detail introduction in [10] and the references mentioned therein. The results about Moran process are also employed in this paper and many results directly resort to that in [10] and [3].

All these motivate us to consider the star structure EGs on two levels. We further point out that the EGs on two levels in this paper are different from that in [10]. For the evolutionary dynamics on two levels in [10], the mutants are divided into several parts with the same number of individuals. While in the EGs on two levels of this paper, two sub-groups constitute a group and the two sub-groups lie in two hierarchies. Assume that there exists no difference for the individuals in the same group. We now consider these cases and analyze them.

This paper is organized as follows: In Section 2, EGs on two levels are introduced, which are a theoretic extension of the EGs in [3] and the fixation probability is analyzed. Some remarks are given in the final section.

2 The Problems and The Properties

In many practical situations, such as some organizations in strict hierarchy, some populations and so on, the following EGs with star structure on two levels can be induced. We formally introduce them as follows. In this EG, all vertexes are divided into two parts. One set including some nodes lying in the upper level consists in an EG. The other set is also an EG. To simplify the problem, we assume that the upper level has the special structure, such as isothermal structure, or cycle structure. The vertexes in the lower level and any vertex in the upper level induce an EG with star structure (See Figure 1 for the detail). We just consider the special case that EG on the upper level has the isothermal structure in this paper. We also note that the relation between upper and lower level nodes is the same as the leaders and the followers in hierarchy within an organization, because the EG is also an organization which resorted to graph technique.

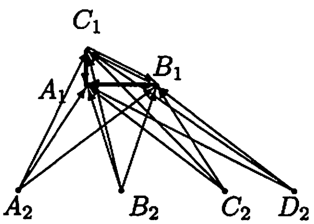

Figure 1 Two-level EG

There exist two types of vertexes in Figure 1. One set includes A_1, B_1 and C_1, which is also an isothermal evolutionary subgraph and is called an upper level EG. The other set includes A_2, B_2, C_2 and D_2, which induces a star structure EG if one vertex in the first set or in the upper level is added, and is named as a lower level EG. This is therefore an EG on two levels where the upper level is isothermal and the lower level is a star structure. Moreover, we always assume that the vertexes in this evolutionary graph act as a whole. Namely, when this organization is invaded by some invader, this invader is defended by the individuals both in lower level and in the upper level, which will simplify the problem.

For the above two levels EG and with 3 vertexes in the upper level and 4 vertexes in the lower level, the fixation probability is denotes as $\phi(r, 3, 5)$ if the fitness of the invader is r and the fitness in this organization is 1. There then exists the following result.

Theorem 1 *For the above EG in Figure 1, the fixation probability is given* *by the following formulation*

$$\begin{aligned}\phi(r,3,5) &= \rho(r,3)\rho_2(r,5)\\ &= \frac{1-\frac{1}{r}}{1-\frac{1}{r^3}}\frac{1-\frac{1}{r^2}}{1-\frac{1}{r^{10}}}\\ &= \frac{r^{10}}{(1+r+r^2)(1+r^2+r^4+r^6+r^8)}.\end{aligned} \tag{2.3}$$

Proof: We consider the fixation probability of some single mutant if a mutant invades from the lower level. Firstly, the mutant has to reach fixation in its subgroup or lower level subgroup, which is an isothermal evolutionary subgraph. This consequently induces $\rho(r,3)$ according to (1.1). The subgroup then has to overwhelm other subgroup or upper level subgroup, which is a 2-star structure EGs, and $\rho_2(r,5)$ is immediately obtained according to (1.2). The fixation probability is hence $\phi(r,3,5) = \rho(r,3)\rho_2(r,5)$. The latter part of (2.3) can be immediately obtained with simple calculation.

The same result as the above can be immediately obtained if a mutant invades from the upper level. The result is consequently obtained through simple calculation and the proof is complete. □

We further point out that the fixation probability may change if the structure of the EG is modified, which is obvious according to Theorem 1. Moreover, in the above result, the mutant seems to invade this organization (or EG) from upper level. The result are identical no matter the organization is attacked from the lower level or the upper level because we assume that all the individuals in this organization equally defend the invaders.

The above result can be easily extended to more general situation with m nodes in the upper level and n vertexes in the lower level. The proof is similar to that in Theorem 1 and the detail proof is omitted.

Theorem 2 *For EG on two levels with m nodes in the upper level and n nodes in the lower level, we obtain that the fixation probability $\phi(r,m,n)$ is*

$$\begin{aligned}\phi(r,m,n) &= \rho(r,m)\rho_2(r,n+1)\\ &= \frac{1-\frac{1}{r}}{1-\frac{1}{r^m}}\frac{1-\frac{1}{r^2}}{1-\frac{1}{r^{2(n+1)}}}\\ &= \frac{r^{2n+m-1}}{(1+r+r^2+\cdots+r^{m-1})(1+r^2+r^4+r^6+\cdots+r^{2n})}.\end{aligned} \tag{2.4}$$

For (1.1), we have $\rho(r,m+n) = \frac{1-\frac{1}{r}}{1-\frac{1}{r^{m+n}}}$, the probability that a single mutant reaches fixation in a large, unstructured population of size $m+n$. We aim to compare the fixation probability of an unstructured population with that of a two-level population. We also have the following conclusion about the above model

Theorem 3 *If $r \neq 1$, we have the following result:*

$$\phi(r,m,n) < \rho(r,m+n) \tag{2.5}$$

Proof: We show it by comparing $\phi(r, m, n)$ and $\rho(r, m+n)$. Actually, we directly calculate $\phi(r, m, n) - \rho(r, m+n)$ and, for $r \neq 1$, we immediately obtain

$$\begin{aligned}
&\phi(r, m, n) - \rho(r, m+n) \\
&= \frac{1-\frac{1}{r}}{1-\frac{1}{r^m}} \frac{1-\frac{1}{r^2}}{1-\frac{1}{r^{2(n+1)}}} - \frac{1-\frac{1}{r}}{1-\frac{1}{r^{m+n}}} \\
&= \frac{(r-1)(r^2-1)r^{m+2n}}{r(r^m-1)(r^{2n+2}-1)} - \frac{r^{m+n}(r-1)}{r(r^{m+n}-1)} \\
&= \frac{r^{m+n}(r-1)}{r} \frac{r^n(r^2-1)(r^{m+n}-1)-(r^m-1)(r^{2n+2}-1)}{(r^m-1)(r^{2n+2}-1)(r^{m+n}-1)} \\
&= \frac{r^{m+n}(r-1)}{r(r^m-1)(r^{2n+2}-1)(r^{m+n}-1)}[r^n(r^2-1)(r^{m+n}-1)-(r^m-1)(r^{2n+2}-1)] \\
&= \frac{r^{m+n}(r-1)}{r(r^m-1)(r^{2n+2}-1)(r^{m+n}-1)}(r^m + r^{2n+2} + r^n - r^{n+2} - r^{m+2n} - 1) \\
&= \frac{r^{m+n}(r-1)}{r(r^m-1)(r^{2n+2}-1)(r^{m+n}-1)}(r^n-1)(1+r^n-r^m-r^{m+n}) \\
&= \frac{r^{m+n}(r-1)}{r(r^m-1)(r^{2n+2}-1)(r^{m+n}-1)}(r^n-1)(1-r^m)(1+r^n) < 0.
\end{aligned}$$

The result is consequently obtained and the proof is complete. □

This result shows that the EGs on two levels are more stable than those on single level or unstructured EGs. Namely, it is more difficult for a two-level EG to invade by others than for an unstructured EG, which is an interesting result and is highly fit with the practical situations. Furthermore, for all $m > 0$ and $n > 0$, (2.4) always holds. Namely, if the number of individuals is the same for two types of structures, the above inequality holds. If $r = 1$, there is no difference between the mutants and other individuals. We show no interest in these situations.

3 Concluding Remarks

In this paper, EGs on two levels are introduced and the corresponding fixation probability is obtained. EGs have extensive applications in biology field and other fields. Moreover, the models and the corresponding results in Section 2 can be easily extended to multiple levels. About the upper level problems, the similar results can also be immediately obtained for other forms.

Acknowledge Sincere thanks to an anonymous reviewer for his comments which improve the presentation to a great degree.

References

[1] T. Basar and G.J. Olsder, *Dynamic Noncooperative Game Theory.* Academic Press, New York, 1995.

[2] D. Fudenberg and J. Tirole, *Game Theory.* The MIT Press, Cambridge, Massachusetts, London, England, 2003.

[3] E. Lieberman, C. Hauert and M.A. Nowak, Evolutionary dynamics on graphs. *Nature*, Vol. 433(2005), pp. 312-316.

[4] S.J. Maynard and E. Szathmary,*The major transitions in evolution.* W.H. Freeman, Oxford, 1995.

[5] P.A.P. Moran, *The statistical process of evolutionary theory.* Clarendon, Oxford,1962.

[6] P.Y. Nie, Dynamic Stackelberg games under open-loop complete information, *Journal of the Franklin Institute-Engineering and Applied Mathematics* , Vol. 342(2005), pp.737-748.

[7] P.Y. Nie, L.H. Chen and M. Fukushima, Dynamic programming approach for discrete time dynamic feedback Stackelberg games with independent and dependent followers. *European Journal of Operational Research.* Vol. 169(2006), pp.310-328.

[8] M.A. Nowak, A. Sasaki, C.Taylor and C. Fudenberg, Emergence of cooperation and evolutionary stability in finite populations.*Nature*,Vol. 428(2004), pp.646-650.

[9] C. Taylor, D. Fudenberg, A. Sasaki and M.A. Nowak, Evolutionary game dynamics in finite populations. *Bullet of Mathematical Biology*, Vol.66(2004), pp,1621-1644.

[10] A. Traulsen, A.M. Sengupta and M.A. Nowak, Stochastic evolutionary dynamics on two levels. *Journal of Theoretical Biology*, Vol. 235(2005),pp. 393-401.

[11] M.J. Wade, An experimental study of group selection. *Evolution*, 31(1977),pp.134-153.

[12] G.C. Williams, *Adaption and natural selection: A critique of some current evolutionary thought.* Princeton University Press, Princeton, 1966.