Evolutionary dynamics in set structured populations

Corina E. Tarnita^a, Tibor Antal^a, Hisashi Ohtsuki^b, and Martin A. Nowak^{a,1}

^aProgram for Evolutionary Dynamics, Department of Mathematics, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138; and ^bDepartment of Value and Decision Science, Tokyo Institute of Technology, Tokyo 152-8552, Japan

Communicated by Robert May, University of Oxford, Oxford, United Kingdom, April 2, 2009 (received for review February 8, 2009)

Evolutionary dynamics are strongly affected by population structure. The outcome of an evolutionary process in a well-mixed population can be very different from that in a structured population. We introduce a powerful method to study dynamical population structure: evolutionary set theory. The individuals of a population are distributed over sets. Individuals interact with others who are in the same set. Any 2 individuals can have several sets in common. Some sets can be empty, whereas others have many members. Interactions occur in terms of an evolutionary game. The payoff of the game is interpreted as fitness. Both the strategy and the set memberships change under evolutionary updating. Therefore, the population structure itself is a consequence of evolutionary dynamics. We construct a general mathematical approach for studying any evolutionary game in set structured populations. As a particular example, we study the evolution of cooperation and derive precise conditions for cooperators to be selected over defectors.

cooperation | game | social behavior | stochastic dynamics

Human society is organized into sets. We participate in activities or belong to institutions where we meet and interact with other people. Each person belongs to several sets. Such sets can be defined, for example, by working for a particular company, living in a specific location, going to certain restaurants, or holding memberships at clubs. There can be sets within sets. For example, the students of the same university have different majors, take different classes, and compete in different sports. These set memberships determine the structure of human society: they specify who meets whom, and they define the frequency and context of meetings between individuals.

We take a keen interest in the activities of other people and contemplate whether their success is correlated with belonging to particular sets. It is therefore natural to assume that we do not only imitate the behavior of successful individuals, but also try to adopt their set memberships. Therefore, the cultural evolutionary dynamics of human society, which are based on imitation and learning, should include updating of strategic behavior and of set memberships. In the same way as successful strategies spawn imitators, successful sets attract more members. If we allow set associations to change, then the structure of the population itself is not static, but a consequence of evolutionary dynamics.

There have been many attempts to study the effect of population structure on evolutionary and ecological dynamics. These approaches include spatial models in ecology (1–8), viscous populations (9), spatial games (10–15), and games on graphs (16–19).

We see “evolutionary set theory” as a powerful method to study evolutionary dynamics in structured populations in the context where the population structure itself is a consequence of the evolutionary process. Our primary objective is to provide a model for the cultural evolutionary dynamics of human society, but our framework is applicable to genetic evolution of animal populations. For animals, sets can denote living at certain locations or foraging at particular places. Any one individual can belong to several sets. Offspring might inherit the set memberships of their parents. Our model could also be useful for studying dispersal behavior of animals (20, 21).

Let us consider a population of N individuals distributed over M sets (Fig. 1). Individuals interact with others who belong to the same set. If 2 individuals have several sets in common, they interact several times. Interactions lead to payoff from an evolutionary game.

The payoff of the game is interpreted as fitness (22–26). We can consider any evolutionary game, but at first we study the evolution of cooperation. There are 2 strategies: cooperators, C , and defectors, D . Cooperators pay a cost, c , for the other person to receive a benefit, b . Defectors pay no cost and provide no benefit. The resulting payoff matrix represents a simplified Prisoner’s Dilemma. The crucial parameter is the benefit-to-cost ratio, b/c . In a well-mixed population, where any 2 individuals interact with equal likelihood, cooperators would be outcompeted by defectors. The key question is whether dynamics on sets can induce a population structure that allows evolution of cooperation.

Individuals update stochastically in discrete time steps. Payoff determines fitness. Successful individuals are more likely to be imitated by others. An imitator picks another individual at random, but proportional to payoff, and adopts his strategy and set associations. Thus, both the strategy and the set memberships are subject to evolutionary updating. Evolutionary set theory is a dynamical graph theory: who interacts with whom changes during the evolutionary process (Fig. 2). For mathematical convenience we consider evolutionary game dynamics in a Wright–Fisher process with constant population size (27). A frequency-dependent Moran process (28) or a pairwise comparison process (29), which is more realistic for imitation dynamics among humans, give very similar results, but some aspects of the calculations become more complicated.

The inheritance of the set memberships occurs with mutation rate v : with probability $1 - v$, the imitator adopts the parental set memberships, but with probability v a random sample of new sets is chosen. Strategies are inherited subject to a mutation rate, u . Therefore, we have 2 types of mutation rates: a set mutation rate, v , and a strategy mutation rate, u . In the context of cultural evolution, our mutation rates can also be seen as “exploration rates”: occasionally, we explore new strategies and new sets.

We study the mutation-selection balance of cooperators versus defectors in a population of size N distributed over M sets. In the [supporting information \(SI\) Appendix](#), we show that cooperators are more abundant than defectors (for weak selection and large population size) if $b/c > (z - h)/(g - h)$. The term z is the average number of sets 2 randomly chosen individuals have in common. For g we pick 2 random, distinct, individuals in each state; whether they have the same strategy, we add their number of sets to the average, otherwise we add 0; g is the average of this average over the stationary distribution. For understanding h we must pick 3 individuals at random: then h is the average number of sets the first 2 individuals have in common

Author contributions: C.E.T., T.A., H.O., and M.A.N. performed research and wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: martin_nowak@harvard.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0903019106/DCSupplemental.

Fig. 1. Evolutionary set theory offers a powerful approach for modeling population structure. The individuals of a population are distributed over sets. Individuals can belong to several sets. Some sets might contain many individuals, whereas others are empty. Individuals interact with others who share the same sets. These interactions lead to payoff from evolutionary games. Both the strategy (= behavior in the game) and the set memberships of individuals are updated proportional to payoff. Sets that contain successful individuals attract more members. In this example, there are 2 strategies (indicated by red and blue). The population size is $n = 10$, and there are $M = 5$ sets.

given that there is a nonzero contribution to the average only if the latter 2 share the same strategy. We prove in the [SI Appendix](#) that for the limit of weak selection these 3 quantities can be calculated from the stationary distribution of the stochastic process under neutral drift. Our calculation uses arguments from perturbation theory and coalescent theory that were first developed for studying games in phenotype space (30).

Analytical calculations are possible if we assume that each individual belongs to K out of the M sets. We obtain exact results for any choice of population size and mutation rates (see [SI Appendix](#)). For large population size N and small strategy mutation rate, u , the critical benefit to cost ratio is given by

Fig. 2. Evolutionary set theory is a dynamical graph theory. The set memberships determine how individuals interact. If 2 individuals have several sets in common, then they interact several times. In this example, there are $N = 5$ individuals over $M = 4$ sets. Each individual belongs to $K = 2$ sets. The broken lines indicate the weighted interaction graph. The graph changes as one individual moves to new sets. The evolutionary updating of strategies and set memberships happens at the same timescale.

Table 1. The minimum benefit-to-cost ratio

K	L	K^*	Minimum b/c
1	1	1	2.17
2	1	2	3.13
2	2	2/9	1.42
3	1	3	4.29
3	2	5/4	2.30
3	3	1/12	1.24
4	1	4	5.80
4	2	64/21	4.35
4	3	19/21	2.09
4	4	1/21	1.18
5	1	5	7.94
5	2	605/126	7.44
5	3	45/14	4.58
5	4	5/6	2.02
5	5	5/126	1.16
6	1, 2	6	11.26
6	3	121/21	10.31
6	4	27/7	5.55
6	5	1	2.17
6	6	1/21	1.18
7	1, 2, 3, 4	7	17.23
7	5	16/3	8.87
7	6	19/12	2.72
7	7	1/12	1.24
8	1, 2, 3, 4, 5, 6	8	31.24
8	7	10/3	4.74
8	8	2/9	1.42
9	1, 2, 3, 4, 5, 6, 7, 8	9	104.7
9	9	1	2.17

Each individual belongs to K sets. Cooperation is triggered if the other person has at least L sets in common. For a fixed total number of sets, $M = 10$, we can vary $K = 1, \dots, 9$ and $L = 1, \dots, K$. The effective number of set memberships, K^* , is given by Eq. 54 in the [SI Appendix](#). For a finite population of $N = 100$, we calculate the minimum benefit-to-cost ratio that is needed for selection to favor cooperators over defectors. For given K , cooperators are favored by larger L , and the smallest b/c ratio is obtained by $L = K$. The global minimum occurs for $L = K = M/2$. Smaller values of K^* imply smaller values of the critical b/c . Note that various symmetries lead to identical K^* values.

$$\frac{b}{c} = \frac{K}{M-K}(\nu+2) + \frac{M}{M-K} \frac{\nu^2+3\nu+3}{\nu(\nu+2)}. \quad [1]$$

Here, we introduced the parameter $\nu = 2Nv$, which denotes an effective set mutation rate scaled with population size: it is twice the expected number of individuals who change their set memberships per evolutionary updating. Eq. 1 describes a U-shaped function of ν . If the set mutation rate is too small, then all individuals belong to the same sets. If the set mutation rate is too large, then the affiliation with individual sets does not persist long enough in time. In both cases, cooperators have difficulties to thrive. But there exists an intermediate optimum set mutation rate which, for $K \ll M$ is given by $\nu_{\text{opt}} = \sqrt{M/K}$. At this optimum value of ν , we find the smallest critical b/c ratio for cooperators to outcompete defectors. If each individual can only belong to a small number of all available sets, $K \ll M$, then the minimum ratio is given by

$$\left(\frac{b}{c}\right)_{\min} = 1 + 2 \sqrt{\frac{K}{M}}. \quad [2]$$

Smaller values of K and larger values of M facilitate the evolution of cooperation. For a given number of sets, M , it is best if individuals belong to $K = 1$ set. Larger values of K make it harder for cooperators to avoid exploitation by defectors. But the

cooperation with group members exists. Our results show that it can be adaptive if certain conditions hold. Our approach can also be used to study the dynamics of tag based cooperation (33–35): some of our sets could be seen as labels that help cooperators to identify each other.

In our theory, evolutionary updating includes both the strategic behavior and the set associations. Successful strategies leave more offspring, and successful sets attract more members. We derive an exact analytic theory to describe evolutionary dynamics on sets. This theory is in excellent agreement with numerical simulations. We calculate the minimum benefit-to-cost ratio that is needed for selection to favor cooperators over

defectors. The mechanism for the evolution of cooperation (36) that is at work here is similar to spatial selection (10) or graph selection (17). The structure of the population allows cooperators to “cluster” in certain sets. These clusters of cooperators can prevail over defectors. The approach of evolutionary set theory can be applied to any evolutionary game or ecological interaction.

ACKNOWLEDGMENTS. This work was supported by the John Templeton Foundation, the National Science Foundation/National Institutes of Health joint program in mathematical biology (National Institutes of Health Grant R01GM078986), the Japan Society for the Promotion of Science, and J. Epstein.

- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography* (Princeton Univ Press, Princeton, NJ).
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240.
- Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. *Proc Natl Acad Sci USA* 71:2744–2747.
- Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326:388–390.
- Durrett R, Levin SA (1994) Stochastic spatial models: A user's guide to ecological applications. *Philos Trans R Soc London Ser B* 343:329–350.
- Hassell MP, Comins HN, May RM (1994) Species coexistence and self-organizing spatial dynamics. *Nature* 370:290–292.
- Tilman D, Kareiva P, eds (1997) *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (Princeton Univ Press, Princeton, NJ).
- May RM (2006) Network structure and the biology of populations. *Trends Ecol Evol* 21:394–399.
- Hamilton WD (1964) The genetical evolution of social behavior. *J Theor Biol* 7:1–16.
- Nowak MA, May RM (1992) Evolutionary games and spatial chaos. *Nature* 359:826–829.
- Killingback T, Doebeli M (1996) Spatial evolutionary game theory: Hawks and Doves revisited. *Proc R Soc London Ser B* 263:1135–1144.
- Nakamaru M, Matsuda H, Iwasa Y (1997) The evolution of cooperation in a lattice structured population. *J Theor Biol* 184:65–81.
- Szabó G, Tóke C (1998) Evolutionary prisoner's dilemma game on a square lattice. *Phys Rev E* 58:69–73.
- Kerr B, Riley MA, Feldman MW, Bohannan BJ (2002) Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418:171–174.
- Hauert C, Doebeli M (2004) Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* 428:643–646.
- Lieberman E, Hauert C, Nowak MA (2005) Evolutionary dynamics on graphs. *Nature* 433:312–316.
- Ohtsuki H, Hauert C, Lieberman E, Nowak MA (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441:502–505.
- Taylor PD, Day T, Wild G (2007) Evolution of cooperation in a finite homogeneous graph. *Nature* 447:469–472.
- Santos FC, Santos MD, Pacheco JM (2008) Social diversity promotes the emergence of cooperation in public goods games. *Nature* 454:213–216.
- Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature* 269:578–581.
- Taylor PD (1988) An inclusive fitness model for dispersal of offspring. *J Theor Biol* 130:363–378.
- Maynard Smith J (1982) *Evolution and the Theory of Games* (Cambridge Univ Press, Cambridge, UK).
- Colman AM (1995) *Game Theory and Its Applications in the Social and Biological Sciences* (Butterworth-Heinemann, Oxford, UK).
- Hofbauer J, Sigmund K (1998) *Evolutionary Games and Population Dynamics* (Cambridge Univ Press, Cambridge, UK).
- Cressman R (2003) *Evolutionary Dynamics and Extensive Form Games* (MIT Press, Cambridge, MA).
- Nowak MA, Sigmund K (2004) Evolutionary dynamics of biological games. *Science* 303:793–799.
- Imhof LA, Nowak MA (2006) Evolutionary game dynamics in a Wright-Fisher process. *J Math Biol* 52:667–681.
- Nowak MA, A Sasaki, C Taylor, D Fudenberg (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428:646–650.
- Traulsen A, Pacheco JM, Nowak MA (2007) Pairwise comparison and selection temperature in evolutionary game dynamics. *J Theor Biol* 246:522–529.
- Antal T, Ohtsuki H, Wakeley J, Taylor PD, Nowak MA (2008) Evolution of cooperation by phenotypic similarity. *Proc Natl Acad Sci USA*, 10.1073/pnas.0902528106.
- Tajfel H (1982) Social psychology of intergroup relations. *Annu Rev Psychol* 33:1–30.
- Yamagishi T, Jin N, Kiyonari T (1999) Bounded generalized reciprocity. *Adv Group Process* 16:161–197.
- Riolo RL, Cohen MD, Axelrod R (2001) Evolution of cooperation without reciprocity. *Nature* 418:441–443.
- Traulsen A, Claussen JC (2004) Similarity based cooperation and spatial segregation. *Phys Rev E* 70:046128.
- Jansen VA, van Baalen M (2006) Altruism through beard chromodynamics. *Nature* 440:663–666.
- Nowak MA (2006) Five rules for the evolution of cooperation. *Science* 314:1560–1563.