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# Evolutionary dynamics and the evolution of multiplayer cooperation in a subdivided population

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## Abstract

The classical models of evolution have been developed to incorporate structured populations using evolutionary graph theory and, more recently, a new framework has been developed to allow for more flexible population structures which potentially change through time and can accommodate multiplayer games with variable group sizes. In this paper we extend this work in three key ways. Firstly by developing a complete set of evolutionary dynamics (BDB, BDD, DBD, DBB, LB and LD) so that the range of dynamic processes used in classical evolutionary graph theory can be applied. Secondly, by building upon previous models to allow for a general subpopulation structure, where all subpopulation members have a common movement distribution. Subpopulations can have varying levels of stability, represented by the proportion of interactions occurring between subpopulation members; in our representation of the population all subpopulation members are represented by a single vertex. In conjunction with this we extend the important concept of temperature (the temperature of a vertex is the sum of all the weights coming into that vertex; generally, the higher the temperature, the higher the rate of turnover of individuals at a vertex). Finally, we have used these new developments to consider the evolution of cooperation in a class of populations which possess this subpopulation structure using a multiplayer public goods game. We show that cooperation can evolve providing that subpopulations are sufficiently stable, with the smaller the subpopulations the easier it is for cooperation to evolve. We introduce a new concept of temperature, namely “subgroup temperature”, which can be used to explain our results.

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## 1. Introduction

2 Evolutionary game theory has proved to be a very successful way of mod-  
3 elling the evolution of, and behaviour within, populations. The classical models

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4 mainly focused on well-mixed populations playing two player games [31, 30], or  
5 alternatively playing games against the entire population [30]. Simple models  
6 such as the Hawk-Dove game [29] and the sex ratio game [20] have been used  
7 to explain important biological phenomena.

8 These models were developed to consider finite populations explicitly [34,  
9 Chapters 6-9] (although see [32, 33] for important earlier non-game theoretic  
10 work) and structured populations using the now widespread methodology of  
11 evolutionary graph theory originated in [26] (see also [3, 9, 52, 27], and [1, 44]  
12 for reviews). Such population structures can have a profound effect on the result  
13 of the evolutionary process even when individuals have a fixed fitness [26, 28, 40].  
14 Further, even for a given structure, the rules of the evolutionary dynamics have  
15 a significant effect on the evolution of the population.

16 Previous work has investigated a number of important questions, the most  
17 widely considered being how cooperation can evolve. The evolution of cooper-  
18 ation, where individuals make sacrifices to help others, can seem paradoxical  
19 within the context of natural selection, especially amongst unrelated individu-  
20 als. There are a number of ways that mathematical modelling has demonstrated  
21 that cooperation can occur [35]; one key way is through the presence of popula-  
22 tion structure, which can mean that cooperative individuals are more likely to  
23 interact with other cooperators, which makes them resistant to exploitation by  
24 defectors [36, 42]. In particular, this is true for structures where individuals are  
25 heterogeneous [43] allowing hubs or clusters of cooperators to form. The dynam-  
26 ics that one uses are also important; for example [36] showed that death-birth or  
27 birth-death dynamics with selection on the second event promotes cooperation  
28 but not when selection happens in the first event.

29 One limitation of evolutionary graph theory is that it naturally lends itself  
30 to pairwise games, whereas real populations can often involve the simultaneous  
31 interaction of many individuals [45, 15]. Multiplayer games, whilst more com-  
32 mon in economic modelling [21, 6], have become used in increasing frequency  
33 within evolutionary games starting with [38, 7] (see also [14, 18]) and it is im-  
34 portant to incorporate these too into the modelling of structured populations.  
35 A multiplayer public goods game [4, 5, 19, 54], (and this type of game is central  
36 to our paper too, see Section 2.4) has been used in evolutionary graph theory  
37 [25, 51, 24, 41, 56], but this typically involves forming an individual and all of  
38 its neighbours into a group and allowing them to play a game. Although this is  
39 convenient, it is not really natural because there is no mechanism for deciding  
40 how individuals spend their time, and so how they share that time with others,  
41 either singly or in groups.

42 More recently a general framework has been developed [10, 13, 8, 11] which  
43 considers the interaction of populations in a more flexible way, where groups of  
44 any size can form, with different propensity potentially depending upon a num-  
45 ber of factors, including the history of the process. Crucially, the key elements  
46 of evolutionary graph theory of population structure, game and evolutionary  
47 dynamics occur for this new framework too; this makes it capable of analysing  
48 different spatial structures whilst providing the flexibility for different multi-  
49 player interactions. Prior to the current paper, the actual applications of the

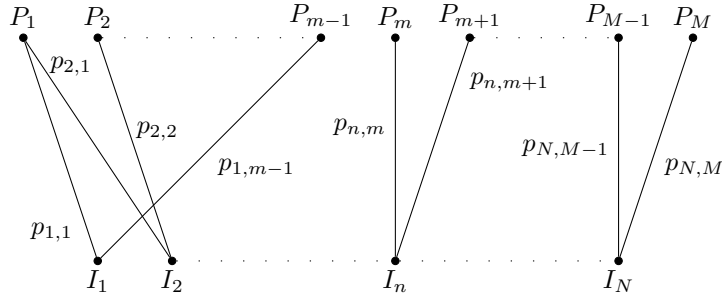


Figure 1: The fully independent model from [10]. There are  $N$  individuals who are distributed over  $M$  places such that  $I_n$  visits place  $P_m$  with probability  $p_{nm}$ . Individuals interact with one another when they meet, for example,  $I_1$  and  $I_2$  can interact with one another when they meet in  $P_1$ .

50 above framework have been limited. In particular only a single evolutionary  
 51 dynamics (the BDB dynamics from the current paper) has been used, and only  
 52 relatively simple populations, which resembled those in evolutionary graph theory  
 53 (the population consisting of individuals each resident at a unique graph  
 54 vertex) have been considered.

55 In this paper we further develop the general theory of the framework origi-  
 56 nated in [10]. We first show how to represent subpopulations using a reduced  
 57 graphical representation within our structure, which will then allow us to po-  
 58 tentially consider larger populations with a richer structure than previously. We  
 59 then demonstrate how to apply a standard set of evolutionary dynamics to con-  
 60 sider a range of evolutionary processes. This is vital since, as mentioned above,  
 61 dynamics can have a big effect on the outcome of evolution within other models,  
 62 including evolutionary graph theory, and as we will see, this is certainly also  
 63 true for our work. Finally we use these new tools to consider the evolution of  
 64 cooperation using a multiplayer public goods game [51, 48, 49, 4] and show that  
 65 cooperation can occur when both the structure and evolutionary dynamics act  
 66 together in favour of the cooperators.

67 The paper is structured as follows: in Section 2 the model framework is  
 68 described, including how to incorporate subpopulations. In Section 3 a standard  
 69 set of evolutionary dynamics to be used with our model are defined. In Section  
 70 4 we introduce and discuss the important concepts of fixation probability and  
 71 temperature. In Section 5 we study the evolution of cooperation in our model  
 72 with subpopulations. Section 6 is then a general discussion.

## 73 2. A framework for modelling evolution in structured populations

74 A framework for modelling the movement of individuals was presented in  
 75 [10]. This is a very general and flexible methodology, the details of which are  
 76 not necessary for the current paper. Below we describe the fully independent  
 77 version of this framework in which individuals move independently of each other

**Table of Notation**

<i>Notation</i>	<i>Definition</i>	<i>Description</i>
$N$	$\in \mathbb{Z}^+ \setminus \{0\}$	Population size.
$M$	$\in \mathbb{Z}^+ \setminus \{0\}$	Number of places.
$I_n$		Individual $n$ .
$P_m$		Place $m$ .
$\mathcal{G}$	$\subset \{1, 2, \dots, N\}$	Group of individuals.
$p_{nm}$	$\in [0, 1]$	Probability that $I_n$ is in $P_m$ .
$\chi(m, \mathcal{G})$	$\in [0, 1]$	Probability of group $\mathcal{G}$ forming in place $P_m$ .
$F_n$	$\in (0, \infty)$	Fitness of individual $I_n$ .
$R_{n,m,\mathcal{G}}$	$\in [0, \infty)$	Payoff to $I_n$ in $\mathcal{G}$ present in $P_m$ .
$h$	$\in (0, \infty)$	Home fidelity.
$d$	$\in \mathbb{Z}^+ \setminus \{0\}$	Number of neighbours.
$r, v$	$\in (0, \infty)$	Background fitness, reward.
$C, D$		Cooperator, Defector.
$R_{c,d}^C$	$\in [0, \infty)$	Payoff to cooperator in a group (including itself) of $c$ cooperators and $d$ defectors.
$R_{n,G}$	$\in [0, \infty)$	Payoff to $I_n$ in group $G$ .
$\mathcal{S}$	$= \{n : I_n \text{ is cooperator} \}$	State of the population.
$\mathcal{N}$	$= \{1, 2, \dots, N\}$	State in which all individuals are cooperators.
$P_{\mathcal{S}\mathcal{S}'}$	$\in [0, 1]$	State transition probability.
$\rho_{\mathcal{S}}^C$	$\in [0, 1]$	Probability of fixating in $\mathcal{N}$ when initial state is $\mathcal{S}$ .
$\rho^C$	$\in [0, 1]$	Mean fixation probability of a cooperator.
$\mathbf{W} = (w_{ij})$	$w_{ij} \in (0, \infty)$	Weighted adjacency matrix that represents an evolutionary graph.
$v_n$		Vertex $n$ of an evolutionary graph.
$b_i$	$\in [0, 1]$	Probability $I_i$ is selected for birth.
$d_{ij}$	$\in [0, 1]$	Probability $I_i$ replaces $I_j$ given $I_i$ is selected for birth.
$d_i$	$\in [0, 1]$	Probability $I_i$ is selected for death.
$b_{ij}$	$\in [0, 1]$	Probability $I_i$ replaces $I_j$ given $I_j$ is selected for death.
$\mathbf{r}_{ij}$	$\in [0, 1]$	Probability $I_i$ replaces $I_j$ .
$T_i^+$	$= \sum_j w_{ij}$	Out temperature of $I_i$ .
$T_i^-$	$= \sum_j w_{ji}$	In temperature of $I_j$ .
$\mathcal{Q}_m$	$\subset \{1, 2, \dots, N\}$	Subpopulation of individuals.
$T_{\mathcal{Q}_m}$	$= \sum_{i \in \mathcal{N} \setminus \mathcal{Q}_m} \sum_{j \in \mathcal{Q}_m} w_{ij}$	Strict subpopulation temperature.

Table 1: Notation used in the paper.

78 and independently of the population's history (any past movements). Important  
79 terms used in the current paper are given in Table 1.

80 *2.1. The fully independent model*

81 The population is made up of  $N$  individuals  $I_1, \dots, I_N$  who can move around  
 82  $M$  places  $P_1, \dots, P_M$ . The probability of individual  $I_n$  being at place  $P_m$  is  
 83 denoted by  $p_{nm}$ ; see Figure 1 for a visual representation using a bi-partite  
 84 graph. When individuals move around they form groups. Let  $\mathcal{G}$  denote any  
 85 group of individuals, then the probability  $\chi(m, \mathcal{G})$  that group  $\mathcal{G}$  forms in place  
 86  $P_m$  is given by

$$87 \quad \chi(m, \mathcal{G}) = \prod_{i \in \mathcal{G}} p_{im} \prod_{j \notin \mathcal{G}} (1 - p_{jm}). \quad (2.1)$$

89 We can show from equation (2.1) that

$$90 \quad 1 = \sum_m \sum_{\substack{\mathcal{G} \\ n \in \mathcal{G}}} \chi(m, \mathcal{G}) \quad \forall n. \quad (2.2)$$

92 This follows intuitively from the fact that individual  $I_n$  has to be present in some  
 93 place  $P_m$  in some group  $\mathcal{G}$  at any given time. The mean size of an individual's  
 94 group (see also [13]) is given by

$$95 \quad \bar{G} = \sum_m \sum_{\mathcal{G}} \frac{\chi(m, \mathcal{G}) |\mathcal{G}|^2}{\sum_m \sum_{\mathcal{G}} \chi(m, \mathcal{G}) |\mathcal{G}|} = \sum_m \sum_{\mathcal{G}} \frac{\chi(m, \mathcal{G}) |\mathcal{G}|^2}{N} \quad (2.3)$$

97 where the simplification of the denominator follows from equation (2.2).

98 When a group of individuals is formed they will then interact with one  
 99 another. In particular, individual  $I_n$  will receive a payoff that depends upon  
 100 the group  $\mathcal{G}$  it is present in and the place  $P_m$  occupied by this group. This  
 101 is denoted as  $R_{n,m,\mathcal{G}}$  and was referred to in [10] as a *direct group interaction*  
 102 *payoff* because individual  $I_n$  only interacts with other individuals with whom it  
 103 is directly present with ([10] allowed for a more general class of payoff but this  
 104 is the only type we will consider, and hence will just refer to it as the payoff).  
 105 Individual  $I_n$ 's fitness is then calculated by averaging its payoffs over all possible  
 106 groups and places that these groups can form as follows:

$$107 \quad F_n = \sum_m \sum_{\substack{\mathcal{G} \\ n \in \mathcal{G}}} \chi(m, \mathcal{G}) R_{n,m,\mathcal{G}}. \quad (2.4)$$

108 A version of the fully independent model called the territorial raider model  
 109 was introduced in [10] and further developed in [8]. A generalization of this  
 110 model forms the basis of much of the work in this paper, although we note that  
 111 Section 3 in particular is more general.

112 *2.2. The territorial raider model*

113 In the territorial raider model, each individual  $I_n$  has its own place  $P_n$  with  
 114 no unoccupied places and, therefore, there is a one-to-one correspondence be-  
 115 tween individuals and places. A graph is used to represent the structure of the

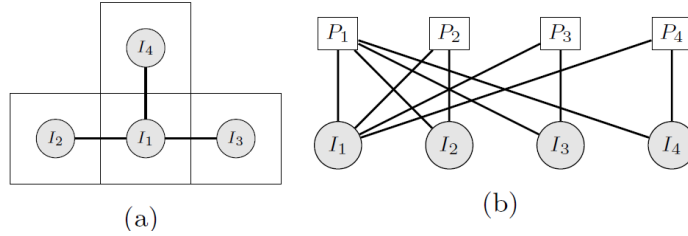


Figure 2: The territorial raider model of [10, 8]. (a) Population structure represented using a graph where vertices represent individuals and places. Individual  $I_n$  lives in place  $P_n$  and can visit any neighbouring places. For example, the home place of  $I_1$  is place  $P_1$  but it can visit places  $P_2, P_3$  and  $P_4$ . (b) An alternative visualization on a bi-partite graph where individuals and places are clearly separated.

116 population where each vertex represents an individual and its corresponding  
 117 home such that two connected individuals can raid each others home places  
 118 (see Figure 2). The probability of raiding another’s home place is governed by  
 119 a common movement parameter called home fidelity,  $h$ , that measures an in-  
 120 dividuals’ preference for their home place. In particular, an individual with  $d$   
 121 neighbours would stay on their home place with probability  $h/(h + d)$  or raid  
 122 any one of its neighbours’ home places with an equal probability of  $1/(h + d)$   
 123 (see Figure 2).

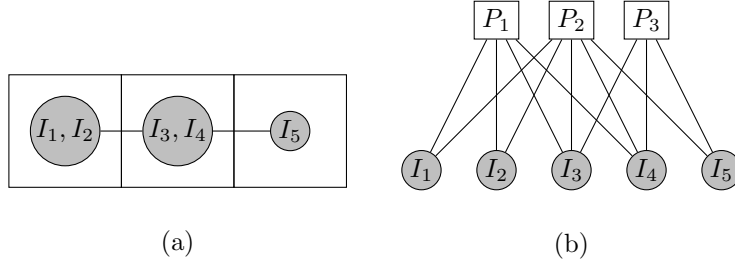


Figure 3: The generalized territorial raider model. (a) Individuals that are members of subpopulation  $Q_m$  live in place  $P_m$  but can visit neighbouring places. The territory of subpopulation  $\{I_1, I_2\}$  consists of places  $P_1$  and  $P_2$ , the territory of subpopulation  $\{I_3, I_4\}$  consists of places  $P_1, P_2$  and  $P_3$ , the territory of subpopulation  $\{I_5\}$  consists of  $P_2$  and  $P_3$ . (b) An alternative visualization as multiplayer interactions on a bi-partite graph where individuals and places are clearly separated.

124 *2.3. The generalized territorial raider model*

125 In this section we generalise the territorial raider model to include subpopu-  
 126 lations, based upon their movement distributions. We will see that individuals  
 127 within a given subpopulation are more likely to interact with each other than  
 128 with members of other subpopulations, and this will affect the success of their  
 129 strategies.

130 Consider the fully independent model. We define a subpopulation of individ-  
 131 uals as a division of individuals from the main population that is *well-mixed* [10],  
 132 which simply means that all of these individuals have an identical distribution  
 133 over the places. In particular, for a subpopulation  $\mathcal{Q}$  we have that  $p_{im} = p_{jm}$   
 134  $\forall i, j \in \mathcal{Q}$  and  $m = 1, \dots, M$ . This can be visualised in terms of a bipartite  
 135 graph as in Figure 1 where the  $I$ -vertices are now occupied by subpopulations  
 136 rather than individuals. This subpopulation structure is thus a special case of  
 137 the fully independent model.

138 For simplicity we will assume that individuals move as they do in the terri-  
 139 torial raider model; thus our model is a generalization of the territorial raider  
 140 model. A population of  $N$  individuals is divided into  $M$  non-overlapping sub-  
 141 populations  $\mathcal{Q}_1, \dots, \mathcal{Q}_M$  where  $|\mathcal{Q}_m| \geq 0$  such that  $N = \sum_m |\mathcal{Q}_m|$ . We will  
 142 assume that individuals in subpopulation  $\mathcal{Q}_m$  treat place  $P_m$  as their home  
 143 place, so that there is a one-to-one correspondence between subpopulations and  
 144 places. However, because we allow subpopulations to be empty, we can have  
 145 places in which no individuals reside. As before, the movement probabilities of  
 146 the individuals is governed by the home fidelity  $h$ . In particular, a subpopula-  
 147 tion  $\mathcal{Q}_m$  that can visit  $d$  neighbouring places will stay in home place  $P_m$  with  
 148 probability  $h/(h+d)$  or move to one of its neighbouring places with probability  
 149  $1/(h+d)$ . Note that when there is one individual in each subpopulation, that  
 150 is  $|\mathcal{Q}_m| = 1 \forall m$ , we recover the territorial raider model in Section 2.2. This  
 151 information can be visually represented in two different ways as shown in Fig-  
 152 ure 3, which includes a graph whose vertices represent both subpopulations and  
 153 places. This generalized territorial raider model will be the basis of our detailed  
 154 investigation of the evolution of cooperation in Section 5.

#### 155 2.4. A multiplayer public goods game

156 A multiplayer Hawk-Dove game [46] and a public goods game were con-  
 157 sidered in [8], though there are other games that can be considered like the  
 158 multiplayer stag hunt game [37].

159 In this paper we focus only on the multiplayer public goods game based on  
 160 the game defined by [51], where an individual's payoff is an average of two player  
 161 public goods games (just a version of the standard prisoner's dilemma) played  
 162 with each of its group mates. Players can either cooperate ( $C$ ) or defect ( $D$ ).  
 163 A cooperator always pays a cost 1 so that the other player receives a reward  
 164  $v$  and a defector pays no cost but only receives a reward when present with a  
 165 cooperator. Note that the cost is set to 1 because scaling all the payoffs by  
 166 some other cost value does not affect the outcome of the game and, therefore,  
 167 the reward  $v$  is a multiple of the cost. The payoff matrix is thus given by

$$\begin{array}{c|cc} & C & D \\ \hline C & v-1 & -1 \\ D & v & 0 \end{array} \quad (2.5)$$

170 In [51] and most models involving public goods games, individuals are never  
 171 alone, and so what happens in the case they are alone is not considered. How-  
 172 ever, in our case it is possible for an individual to be alone, for example, an



173 individual could remain on its home place and not be raided. As in [8], we will  
 174 assume that a lone cooperator still pays a cost but does not receive a reward  
 175 and lone defectors receive nothing. There are other ways that we can allocate  
 176 rewards to lone individuals; for example, in [22] there is a specific strategy, the  
 177 loner strategy, where cooperators choose to be alone and not pay a cost. Our  
 178 choice seems a natural generalisation of the prisoners dilemma model [51], where  
 179 individuals pay a cost but do not benefit from their own contributions. We note  
 180 that our version makes cooperation harder to evolve than the alternatives. Thus  
 181 if cooperators thrive in a population using our model, this can be thought of as  
 182 strong support for the evolution of cooperation.

183 In the multiplayer public goods game, the payoffs to cooperators and defec-  
 184 tors playing within a group of  $c$  cooperators and  $d$  defectors (including them-  
 185 selves) is then respectively given by

$$186 \quad R_{c,d}^C = \begin{cases} r - 1, & c = 1 \\ r - 1 + \frac{c-1}{c+d-1}v, & c > 1 \end{cases} \quad \text{and} \quad R_{c,d}^D = \begin{cases} r, & c = 0 \\ r + \frac{c}{c+d-1}v, & c > 0 \end{cases} \quad (2.6)$$

188 where  $r$  is a background payoff, which is also a multiple of the cost, that every  
 189 individual receives, representing the contribution from activities that are not  
 190 related to the games. Generally, the effect of selection is weaker the larger  
 191 the value of  $r$  (for example, see [12], Chapter 2). The payoff is then given by  
 192  $R_{n,m,\mathcal{G}} \equiv R_{c,d}^C$  ( $\equiv R_{c,d}^D$ ) when  $I_n$  is a cooperator (defector) and  $|\mathcal{G}| = c+d$ , which  
 193 can then be substituted into Equation 2.4 to find the individual's fitness. Note  
 194 that here the payoffs do not depend upon the place occupied by the individuals,  
 195 that is,  $R_{n,m,\mathcal{G}} \equiv R_{n,\mathcal{G}}$ .

### 196 3. Evolutionary dynamics

197 In this section we revisit the standard dynamics of evolutionary graph theory,  
 198 before demonstrating how we can adapt each of them to our framework. For  
 199 the current work there will actually only be two distinct dynamics, but for more  
 200 general cases each will be distinct, and so it is important to consider them all.  
 201 We start by recalling the dynamics from evolutionary graph theory.

#### 202 3.1. Evolutionary dynamics in evolutionary graph theory

203 An evolutionary graph [26, 40] is a graph represented by a weighted adja-  
 204 cency matrix  $\mathbf{W} = (w_{ij})$  where  $w_{ij} \in [0, \infty)$  is referred to as the replacement  
 205 weight. Each vertex  $v_n$  of the evolutionary graph is occupied by one individual  
 206 and if  $w_{ij} > 0$  then the individual on  $v_i$  can place a copy of itself in  $v_j$  by  
 207 replacing the individual there. It is assumed that the weights are chosen so that  
 208 the evolutionary graph is strongly connected, which means that there is a route  
 209 of finite length between any pair of vertices  $v_i$  and  $v_j$ . The weighted adjacency  
 210 matrix  $\mathbf{W}$  is therefore said to define the replacement structure.

211 Assuming that there is only one replacement per update event, there are  
 212 several different ways to calculate the probability of a replacement event  $\mathbf{r}_{ij}$

## Dynamics

BDB	$b_i = \frac{F_i}{\sum_n F_n}, d_{ij} = \frac{w_{ij}}{\sum_n w_{in}}$	BDD	$b_i = \frac{1}{N}, d_{ij} = \frac{w_{ij}F_j^{-1}}{\sum_n w_{in}F_n^{-1}}$
DBD	$d_j = \frac{F_j^{-1}}{\sum_n F_n^{-1}}, b_{ij} = \frac{w_{ij}}{\sum_n w_{nj}}$	DBB	$d_j = \frac{1}{N}, b_{ij} = \frac{w_{ij}F_i}{\sum_n w_{nj}F_n}$
LB	$\tau_{ij} = \frac{w_{ij}F_i}{\sum_{n,k} w_{nk}F_n}$	LD	$\tau_{ij} = \frac{w_{ij}F_j^{-1}}{\sum_{n,k} w_{nk}F_k^{-1}}$

Table 2: Dynamics defined using the replacement weight as in [40]. In each case, B (D) is appended to the name of the dynamics if selection happens in the birth (death) event.

213 where a copy of the individual on  $v_i$  replaces the individual on  $v_j$ . In particular,  
 214 we can broadly classify these in terms of the order in which  $v_i$  and  $v_j$  are  
 215 picked. For birth-death dynamics (BD) the birth event happens first where the  
 216 individual on  $v_i$  is chosen for birth with probability  $b_i$ . The individual on  $v_j$   
 217 is then chosen for death conditional on the individual on  $v_i$  giving birth with  
 218 probability  $d_{ij}$ , thus  $\tau_{ij} = b_i d_{ij}$ . For death-birth dynamics (DB) the death event  
 219 happens first where the individual on  $v_j$  is chosen for death with probability  
 220  $d_i$ . The individual on  $v_i$  is then chosen for birth conditional on the death of  
 221 individual on  $v_j$  with probability  $b_{ij}$ , thus  $\tau_{ij} = d_i b_{ij}$ . For link dynamics (L)  
 222 both birth and death events happen simultaneously and therefore  $\tau_{ij}$  cannot be  
 223 decomposed.

224 For each of these dynamics, natural selection can influence the birth (‘B’ appen-  
 225 ded to name) or death (‘D’ appended to name) event. We use the definitions  
 226 of [28] who extensively studied a set of each of these dynamics. In terms of the  
 227 exact formulae of the transition probabilities, we use those of [40] as summarised  
 228 in Table 2. In these definitions, the dynamics are a function of the replacement  
 229 structure  $\mathbf{W}$  and the fitnesses of the individuals such that the individual on  
 230 vertex  $v_n$  has fitness  $F_n$ .

### 3.2. Evolutionary dynamics in our framework

232 In [8] a birth-death dynamics was defined to be used with the territorial  
 233 raider model. In this section we shall develop a consistent set of dynamics  
 234 for our framework. In particular, we will show that we can adapt the above  
 235 dynamics widely used in evolutionary graph theory.

236 To consider the evolution of the population it is useful to think of the in-  
 237 dividuals in the population in an abstract way. In particular, individuals in  
 238 the population change through time and, therefore, it is better to think of  $I_i$   
 239 as a position that an individual can occupy. These positions are referred to  
 240 as  $I$ -vertices in [8] and have a particular relationship to the places, although  
 241 as the population evolves the actual individual, and in particular the type of  
 242 individual, occupying the position may change. We will generally simply refer  
 243 to these  $I$ -vertices as “individuals” but make the distinction where necessary.

244 This leads to a natural way to create evolutionary dynamics for our frame-  
 245 work; namely, by mapping each individual  $I_i$  to vertex  $v_i$ , we can incorporate  
 246 the replacement weights of different interaction methods straight into the for-  
 247 mulae from Table 2. All that remains is to choose the replacement weights  
 248 appropriately.

249 The replacement weights used here are based on the assumption that an  
 250 offspring of individual  $I_i$  is likely to replace another individual  $I_j$  proportional  
 251 to the time  $I_i$  and  $I_j$  spend together. The offspring of  $I_i$  can also replace  $I_i$   
 252 itself and it does this proportional to the time  $I_i$  spends alone. Therefore, when  
 253  $i \neq j$ , the probability that  $I_i$  and  $I_j$  meet is given by summing  $\chi(m, \mathcal{G})$  over all  
 254  $m$  such that  $i, j \in \mathcal{G}$ . When they meet, we assume that  $I_i$  will spend an equal  
 255 amount of time with each other individual in group  $\mathcal{G}$  and, therefore, weight  
 256  $\chi(m, \mathcal{G})$  with  $1/(|\mathcal{G}| - 1)$  since there are  $|\mathcal{G}| - 1$  other individuals (an alternative  
 257 weighting could be  $1/|\mathcal{G}|$  that allows interaction within groups larger than one  
 258 to contribute to the probability of  $I_i$ 's offspring replacing itself). Note that this  
 259 is consistent with the payoffs from our public goods game, where each pairwise  
 260 payoff equally contributes to the total payoff an individual receives. On the  
 261 other hand, when  $i = j$ , we sum  $\chi(m, \mathcal{G})$  over all  $m$  such that  $\mathcal{G} = \{i\}$ . Here  
 262 there is no need to weight  $\chi(m, \mathcal{G})$  because  $I_i$  is alone.

263 The replacement weights are therefore calculated as follows

$$264 \quad w_{ij} = \begin{cases} \sum_m \sum_{i, j \in \mathcal{G}} \frac{\chi(m, \mathcal{G})}{|\mathcal{G}| - 1} & i \neq j, \\ \sum_m \chi(m, \{i\}) & i = j. \end{cases} \quad (3.1)$$

265

266 Thus we have a new set of evolutionary dynamics which can be applied to  
 267 our framework in a wide variety of situations (including those that we consider  
 268 later in this paper). Note that the dynamics used in [8] is the BDB dynamics  
 269 defined from the above process.

270 By our definition  $\mathbf{W}$  is symmetric, that is  $w_{ij} = w_{ji} \forall i, j$ , because the  
 271 probability of  $I_i$  meeting  $I_j$  within any given group is clearly the same as that  
 272 of  $I_j$  meeting  $I_i$ . We also have that  $\mathbf{W}$  is doubly stochastic, that is  $1 = \sum_j w_{ij} =$   
 273  $\sum_i w_{ij}$  for all  $i, j$ , because  $w_{ij}$  is the proportion of time  $I_i$  spends with  $I_j$  (with  
 274  $w_{ii}$  the proportion of time it spends alone), and it is always in precisely one of  
 275 these  $N$  categories. In this case,  $\mathbf{W}$  is referred to as being *isothermal* [26, 40].

276 We note that the results above hold because of the particular weights  $w_{ij}$  that  
 277 we have chosen. Although these are natural, they are not the only possibility.  
 278 In particular we could have alternative weights where  $w_{ij}$  and  $w_{ji}$  are not in  
 279 general equal and/or where  $\mathbf{W}$  is not isothermal.

## 280 4. Fixation probability and the temperature

### 281 4.1. The fixation probability

282 The (mean) *fixation probability*  $\rho^C$  ( $\rho^D$ ) is the probability that the offspring  
 283 of a randomly placed mutant cooperator (defector) eventually replaces the entire

284 population. This can be uniformly at random as in [26]; alternatively, one can  
 285 use the *mutant appearance distribution* as described in [2]. [8] used a version of  
 286 this where they weighted the fixation probabilities using the mean temperature.  
 287 For this current work we use the arithmetic mean, as the difference between  
 288 these two approaches is negligible here, with the arithmetic mean being greater  
 289 than or equal to the weighted mean [2]. For more details on how the fixation  
 290 probability is calculated, see the Appendix.

291 As in [50], we will use the neutral fixation probability  $1/N$  as a benchmark  
 292 when comparing cooperators and defectors using their fixation probabilities. In  
 293 particular, [50] say that *selection opposes D replacing C* when  $\rho_C < 1/N$  and  
 294 *selection favours C replacing D* when  $1/N < \rho_C$ . It is said that type  $C$  evolves  
 295 if both these conditions hold, i.e. if

$$296 \rho_D < 1/N < \rho_C. \quad (4.1)$$

#### 298 4.2. Concepts of temperature

299 In [26] the *in temperature* (or just the *temperature*) of a vertex of an evo-  
 300 lutionary graph was introduced to measure how likely an individual occupying  
 301 a particular vertex is to be replaced by another individual's offspring. [28]  
 302 extended this definition and introduced the *out temperature* of a vertex of an  
 303 evolutionary graph to measure how likely the offspring of the individual occupy-  
 304 ing that vertex will replace another individual. These definitions of the in and  
 305 out temperatures of individual  $I_n$  for an evolutionary graph  $\mathbf{W}$  are respectively  
 306 defined as follows

$$307 T_n^- = \sum_i w_{in} \quad \text{and} \quad T_n^+ = \sum_i w_{ni}. \quad (4.2)$$

309 In general, the in and out temperatures can be different. However, in our  
 310 case,  $\mathbf{W}$  is doubly stochastic and symmetric and, therefore, the in and out  
 311 temperatures are identical. We therefore work with the definition of only in  
 312 temperature and simply refer to it as the temperature.

313 An alternative version of the definition of temperature (used in [8]) is the  
 314 *strict* temperature that measures how often an individual is likely to be replaced  
 315 by other individuals excluding itself. Since  $\mathbf{W}$  is doubly stochastic, the strict  
 316 temperature of individual  $I_n$  for an evolutionary graph  $\mathbf{W}$  is given by

$$317 T_n = \sum_{i \neq n} w_{in} = 1 - w_{nn}. \quad (4.3)$$

319 The definition of strict temperature can be extended to subpopulations to  
 320 give the strict subpopulation temperature. This measures how likely an in-  
 321 dividual in subpopulation  $\mathcal{Q}_m$  is to be replaced by an individual in another  
 322 subpopulation. Clearly all individuals in a subpopulation have the same tem-  
 323 perature (for any of our temperature definitions), since they all have the same  
 324 movement distribution. The strict subpopulation temperature is calculated by

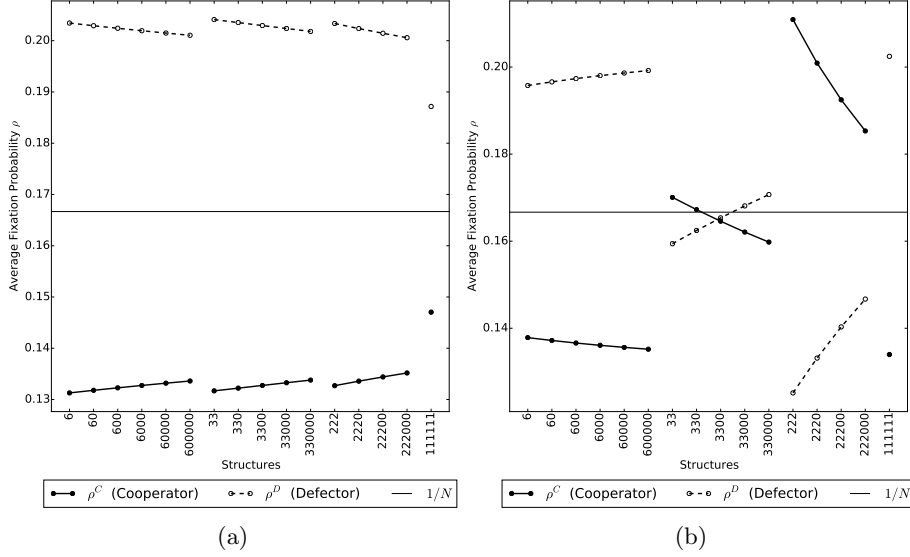


Figure 4: Comparing average fixation probability for different complete structures where figure (a) uses DBD dynamics and figure (b) uses DBB dynamics. Each number indicates a subpopulation of a certain density. For example 60 is a complete structure with 2 subpopulations of size 6 and 0 respectively; 2220 has three subpopulations of size 2 and one of size 0. In each case the public goods game parameters are  $r = 30, v = 10$  and movement parameter is  $h = 30$ . We see that in figure (a) for the DBD dynamics, cooperators perform poorly in all cases. In figure (b), cooperators do better for small groups (greater than one). Increasing the number of empty places is beneficial for defectors.

325 summing all weights  $w_{ij}$  such that  $I_i$  is not part of subpopulation  $\mathcal{Q}_m$  and  $I_j$  is  
 326 part of subpopulation  $\mathcal{Q}_m$  giving

$$327 T_{\mathcal{Q}_m} = \sum_{i \in \mathcal{N} \setminus \mathcal{Q}_m} \sum_{j \in \mathcal{Q}_m} w_{ij}. \quad (4.4)$$

329 This means that if there is only one subpopulation then its strict subpopulation  
 330 temperature is 0 by definition, that is,  $T_{\mathcal{Q}_m} = 0$  if  $\mathcal{Q}_m = \mathcal{N}$ .

331 We note that a strategy introduced in one subpopulation can spread through-  
 332 out the population because  $\mathbf{W}$  is strongly connected. This implies that if there  
 333 is more than one non-empty subpopulation then the strict subpopulation tem-  
 334 perature is non-zero for all non-empty subpopulations, that is,  $T_{\mathcal{Q}_m} > 0$  if  
 335  $|\mathcal{Q}_m| > 0$ . To measure the connectedness of the subpopulations, that is how  
 336 often the different subpopulations interact with one another, we use the mean  
 337 strict subpopulation temperature that is defined as follows

$$338 \langle T_{\mathcal{Q}_m} \rangle = \frac{1}{N} \sum_{m=1}^M |\mathcal{Q}_m| T_{\mathcal{Q}_m}. \quad (4.5)$$

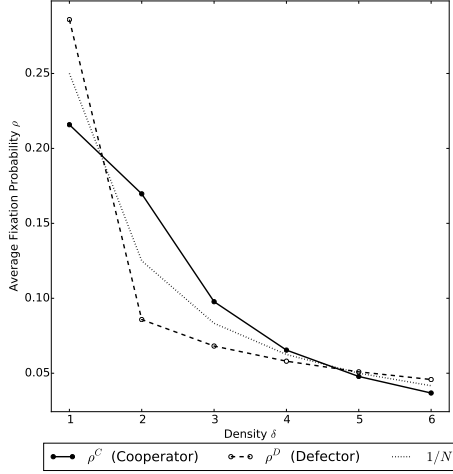


Figure 5: Comparing average fixation probability for different  $\delta$  that is the size (or density) of each subpopulation in a complete graph with 4 subpopulations. The public goods game parameters are set to  $r = 30$ ,  $v = 11$ , the movement parameters are set to  $h = 30$  and dynamics used are DBB. As in Figure 4, cooperators evolve better in small groups (larger than 1), namely groups of size two and three, with a small advantage for groups of size four.

## 340 5. Cooperation in generalized territorial raider models

341 In this section we study the effect that different model parameters have  
 342 on the evolution of cooperation. For models investigating the evolution of co-  
 343 operation using evolutionary graph theory, both the evolution and interaction  
 344 of individuals are dictated by a fixed structure, following games with a fixed  
 345 number of players (almost always two). In our model the replacement struc-  
 346 ture emerges from the interactions between individuals, involving games with a  
 347 varying number of players, and therefore give us a different perspective on the  
 348 evolution of cooperation.

### 349 5.1. The effect of the dynamics

350 As we mentioned in Section 1, for evolutionary graph theory models, coop-  
 351 eration is favoured when using DBB or BDD dynamics, but not DBD or BDB  
 352 dynamics, if the structure allows a cluster of cooperators to form (also see [36]).  
 353 This is consistent with [8] where we studied the effect of the BDB dynamics  
 354 on the public goods game and cooperators generally performed poorly. It was  
 355 shown that defectors dominate regardless of the structure of the population and  
 356 the game parameters. We are now in a position to revisit the public goods  
 357 game with more flexibility both in terms of the dynamics and the structure of  
 358 the population. In terms of the dynamics, the results for BDB and DBD are  
 359 identical (as are those for BDD and DBB), because the replacement structure  
 360  $\mathbf{W}$  is symmetric and doubly stochastic, so whether birth or death occurs first  
 361 (but not whether selection occurs in the first or second position) is irrelevant,  
 362 see Table 2. Furthermore, the LB and LD dynamics are equivalent to the BDB  
 363 and DBD dynamics, respectively, because  $\mathbf{W}$  is isothermal. This can be shown  
 364 for LB dynamics (and similarly for LD dynamics) as follows

$$365 \tau_{ij}^{\text{LB}} = \frac{F_i w_{ij}}{\sum_{n,k} F_n w_{nk}} = \frac{F_i w_{ij}}{\sum_n F_n (\sum_k w_{nk})} = \frac{F_i}{\sum_n F_n} w_{ij} = \tau_{ij}^{\text{BDB}}.$$

367 Thus in what follows, we only mention one dynamics from each pair, in each  
 368 case the DB dynamics.

369 For DBD dynamics, the defectors do better than cooperators regardless of  
 370 the population structure. However, for DBB dynamics, cooperators are favoured  
 371 over defectors for certain population structures. In particular, these structures  
 372 that favour cooperators contain small subpopulations, ideally of two individuals.  
 373 We can see this in Figure 4, where the fixation probability is plotted against  
 374 different complete population structures for the DBD (Figure 4a) and DBB  
 375 (Figure 4b) dynamics (as explained in the caption, for each population, each  
 376 number in its representation corresponds to a subpopulation of that size). For  
 377 example, for the complete structure 222 where there are 3 subpopulations of  
 378 size 2, the cooperators outperform defectors by a large amount.

379 To understand why this is the case, consider a population of two individuals  
 380 where one individual is a cooperator and the other a defector. Within such a  
 381 population, the cooperator will be less fit than the defector. For DBD dynamics,  
 382 the least fit individual is most likely to be chosen for death and the fixation  
 383 probability is proportional to the fitness of the individual. This means that  
 384 a cooperator has a low fixation probability compared to a defector. However,  
 385 when using DBB dynamics, one of the two individuals is randomly chosen for  
 386 death and immediately replaced by the offspring of the other individual. This  
 387 means that regardless of the fitness of the individual, each type will fixate with  
 388 probability  $1/2$ . For sufficiently high home fidelity parameter  $h$ , individuals  
 389 primarily interact with their members of their own subpopulation. Therefore,  
 390 in such a population where there exists a subpopulation of two individuals, a  
 391 cluster of two cooperators is more likely to form when using DBB dynamics.  
 392 This cluster of cooperators has a fitness larger than that of a cluster of defectors,  
 393 provided that  $v > 1$ , thereby establishing a stronghold against defectors. In fact,  
 394 a subpopulation of sufficiently small size (but greater than one) can establish a  
 395 stronghold against defectors as shown in Figure 5. Here the fixation probability  
 396 is plotted against a complete structure with four subpopulations that each have  
 397 size ranging from 1 to 6. Subpopulations of size two are best for cooperation,  
 398 with their advantage over defectors declining as the size of the subpopulation  
 399 increases. Given the parameters used, subpopulations of two to four cooperators  
 400 can successfully resist invasion, but larger subpopulations cannot.

## 401 5.2. *The effect of the temperature*

402 In [8] the strict temperature and mean group size were both shown to be  
 403 strongly correlated with the fixation probability, with the effect of the former  
 404 shown to be stronger. We therefore focus on the temperature, namely the strict  
 405 subpopulation temperature. Note that in [8] there is one-to-one correspondence  
 406 between individuals and places, which implies that the strict temperature and  
 407 strict subpopulation temperature are identical, but this is not the case here.

408 The individual temperature is a measure of how often an individual interacts  
 409 with other individuals including those who are part of the same subpopulation;

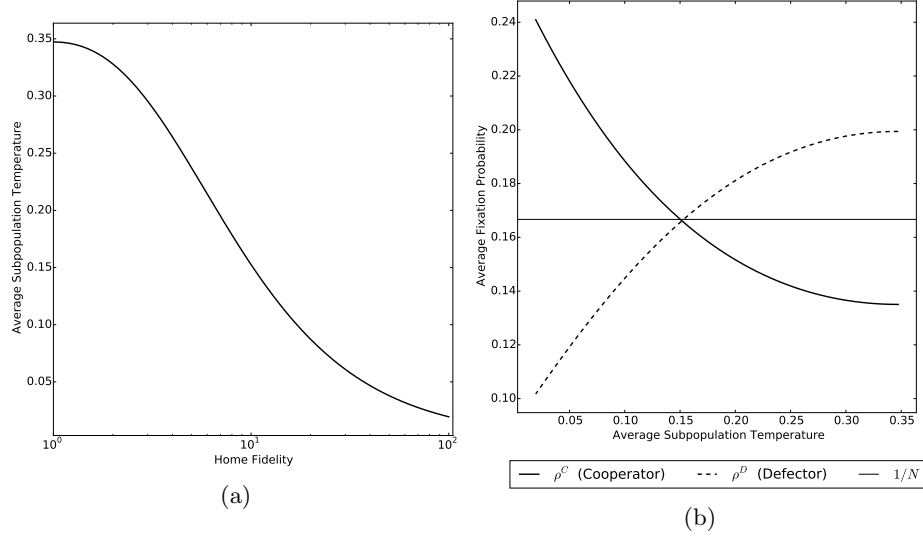


Figure 6: Figure (a) plots the mean subpopulation temperature against the home fidelity  $h$  for a complete population structure with 3 subpopulations of size 2 each. Figure (b) then plots the fixation probabilities against these values of the mean subpopulation temperature where  $r = 30$  and  $v = 10$  for the public goods game, and the dynamics used are DBB. In particular, we notice that the fixation probability of the cooperators is decreasing with the mean subpopulation temperature.

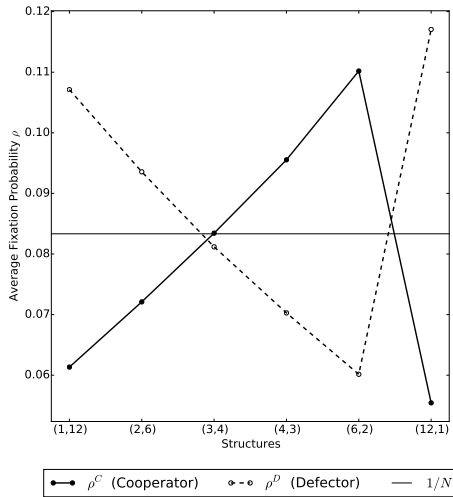


Figure 7: Comparing different population structures for the public goods game with various complete graphs for a population size of 12 where (1,12) means there is 1 subpopulation with 12 individuals, (2,6) means there are 2 subpopulations with 6 individuals and so on. We have set  $r = 30$  and  $v = 10$ , home fidelity  $h = 30$  and the dynamics used is DBB.



410 thus an individual may have a high temperature but that does not mean it is  
411 interacting with individuals from other subpopulations. In particular whenever  
412 individuals are not alone very often, this temperature does not vary so much  
413 between different individuals, and so is not a useful concept when there are non-  
414 trivial subgroups. The strict subpopulation temperature, on the other hand,  
415 considers interactions with individuals only from other subpopulations, and thus  
416 can be very variable. We shall see that this temperature is a good predictor of  
417 important population properties.

418 The mean strict subpopulation temperature decreases when home fidelity  
419 increases as shown in Figure 6a. This is because the individuals are more likely  
420 to remain on their home place than visit another place as home fidelity increases,  
421 therefore reducing interactions with other subpopulations, and in particular the  
422 probability that a member of one subpopulation replaces a member of another  
423 at any given time.

424 In [8] it was shown that for BDB dynamics for structures where each sub-  
425 population is of size one, there was a linear relationship between the strict  
426 (subpopulation) temperature and the fixation probability, with the higher the  
427 temperature, the stronger the effect of selection. We investigated this for DBB  
428 dynamics, and found an opposite linear effect, which is consistent with [28] who  
429 showed that the DBB dynamics suppresses the effect of selection the most for  
430 the complete graph. We note that this relationship only holds for relatively  
431 weak selection, and we can reverse the relationship (and make it non-linear) by  
432 increasing the value of the reward.

433 To promote cooperation we need a structure involving a subpopulation of  
434 size at least two. However, whether these structures promote cooperation or  
435 not also depends upon the base fitness and reward, and so we assume that the  
436 base fitness and reward are sufficiently large for this to be the case, see Section  
437 5.4. In this case, decreasing the temperature by increasing the home fidelity  
438 promotes cooperation. In particular, the relationship between the mean fixa-  
439 tion probability of cooperators and the mean strict subpopulation temperature  
440 is negative and nonlinear as shown in Figure 6b. The nonlinearity arises not  
441 only from the nonlinear payoff function of the public good game, but also from  
442 the fact that there exists a subpopulation that has size at least two. For co-  
443 operators, the mean fixation probability is negatively correlated with the mean  
444 strict subpopulation temperature because the mean strict subpopulation tem-  
445 perature is highest when home fidelity is lowest, i.e. when cooperators cannot  
446 separate themselves from the population and form clusters, consequently defec-  
447 tion evolves. On the other hand, for low mean strict subpopulation temperature,  
448 and so high home fidelity, it is easier to form clusters of cooperators that allows  
449 cooperation to evolve. This kind of behaviour is also evident in Figures 4 and  
450 7.

### 451 5.3. *The effect of the number of places*

452 In [8] each individual had their home place and there were no empty places  
453 (non home places) that individuals could visit. In our case, individuals can

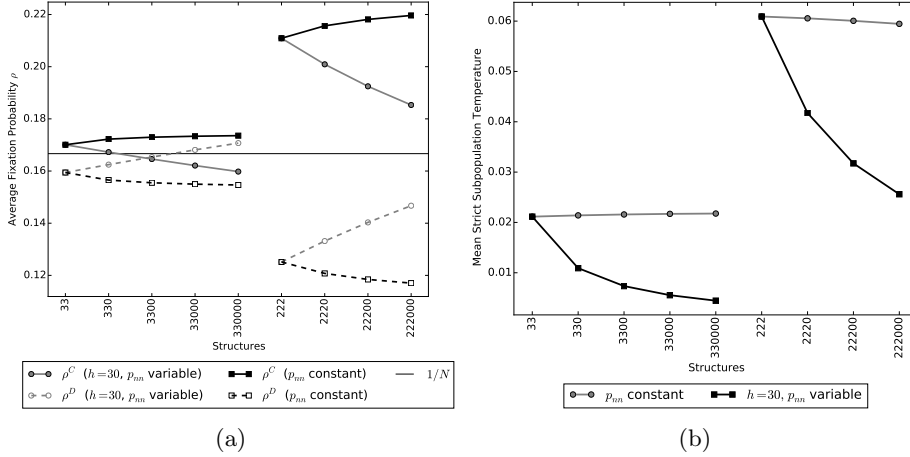


Figure 8: Figure (a) shows the effect of compensating for empty places by increasing the home fidelity such that the probability of staying in their home place,  $p_{nn}$ , remains the same. We start at  $h = 30$  for the 33 and 222 structures. As an empty place is added,  $h$  is increased so that  $p_{nn} = 30/31$  for the 330, ..., 330000 structures and  $p_{nn} = 30/32$  for 2220, ..., 222000 structures. In all cases  $r = 30$  and  $v = 10$ . We can see that after compensating for the above effect, the influence of introducing empty places is both reversed and weakened. Figure (b) shows the mean strict subpopulation temperature dropping off when we compensate for the empty places by increasing the home fidelity such that  $p_{nn}$  remains the same.

454 visit non home places and we therefore investigate what effect this has on the  
 455 evolution of cooperation.

456 As seen in Figure 4, increasing the number of empty places that subpopu-  
 457 lations can visit, whilst keeping all other parameters constant, makes it more  
 458 difficult for cooperation to evolve. In particular, this effect is prominent for  
 459 structures where cooperators were initially doing well. For example, for the  
 460 structure 222 where the cooperators do best, increasing the number of places  
 461 significantly reduces their fixation probability whilst increasing that of the de-  
 462 fectors. Here increasing the number of places acts in the same way as decreasing  
 463 the home fidelity, i.e. as decreasing the amount of time an individual spends in  
 464 its home place with members of its subpopulation. Thus the amount of time  
 465 an individual spends alone or with individuals not from its subpopulation in-  
 466 creases, so that the overall fitness of a cooperative subpopulation will decrease  
 467 (they still pay a cost but do not receive a benefit when alone). In terms of  
 468 the dynamics, spending more time alone would increase the effect of selection  
 469 in DBB dynamics because an individual with higher fitness that is randomly  
 470 chosen for death is more likely to be replaced by its own offspring, which affects  
 471 the cooperators adversely. A cooperative subpopulation will also have lower  
 472 fitness because its members are more likely to interact with individuals from  
 473 other subpopulations, therefore exposing them to defectors. The increased in-  
 474 teraction between individuals will also increase the effect of selection in DBB  
 475 dynamics because an individual with higher fitness that is randomly chosen for

476 death is less likely to be replaced by an individual with lower fitness in the same  
 477 subpopulation.

478 The increase in the number of places can be compensated for by increasing  
 479 the home fidelity, so that individuals stay in their home place with the same  
 480 probability. This has the effect of decreasing the mean strict subpopulation  
 481 temperature as individuals are more likely to spend time with members of their  
 482 subpopulation. This is shown in Figure 8, where we can see that the effect of  
 483 adding empty places is now reversed, although the strength of this reverse effect  
 484 is weak.

#### 485 5.4. The effect of a large home fidelity

486 Consider a well-mixed population of  $M$  subpopulations each containing  $L$   
 487 individuals, so that  $N = ML$ , as described in Section 2.3, where  $h$  is very  
 488 large. Consequently from equation (3.1),  $\chi(m, \mathcal{G})$  is approximately 1 if  $\mathcal{G} = \mathcal{Q}_m$ ,  
 489 and is approximately 0 otherwise. Thus the fitness of an individual can be  
 490 evaluated assuming that we have a group containing precisely all individuals  
 491 from its subpopulation with probability 1. Due to the symmetric nature of our  
 492 population, the weights for any two individuals in the same subpopulation will  
 493 be the same, as will the weights for any two members of different subpopulations.  
 494 Denoting the latter as  $w_O$ , which will be small, we have  $w_{ij} = w_O$  when  $I_i$  and  
 495  $I_j$  are not in the same subpopulation, and  $w_{ij} = w_I \approx [1 - (M-1)Lw_O]/(L-1)$   
 496 otherwise, with the probability of self-replacement negligible.

497 It follows that only replacements within subpopulations will happen, except  
 498 very rarely. Thus we can assume that the battle within any mixed subpopulation  
 499 of cooperator ( $C$ ) and defector ( $D$ ) individuals will be resolved with fixation of  
 500 one type or the other before any new mixed subpopulation appears.

501 We thus consider a two stage process. Firstly, a new mixed group appears.  
 502 This occurs rarely, through the invasion of a cooperator into a defector subpopu-  
 503 lation, or a defector into a cooperator subpopulation. Assuming that there are  
 504 currently  $M_C(M_D = M - M_C)$  cooperator (defector) subpopulations, such a  
 505 transition happens with probability

$$506 \quad p_{CI} = \frac{M_D}{M} \frac{M_C L w_O F_L(C)}{(L-1)w_I F_L(D) + O(w_O)} \quad (5.1)$$

507 of a cooperator into a defector subpopulation, or

$$508 \quad p_{DI} = \frac{M_C}{M} \frac{M_D L w_O F_L(D)}{(L-1)w_I F_L(C) + O(w_O)} \quad (5.2)$$

509 of a defector into a cooperator subpopulation. The terms  $F_L(C)$  and  $F_L(D)$  are  
 510 the fitnesses of cooperator and defector individuals within their own subpopu-  
 511 lations, and are obtained directly from equations (2.4) and (2.6), and the terms  
 512  $O(w_O)$  are of the order of  $w_O$ , and very small. Further denoting  $x = v/[r(L-1)]$   
 513 we obtain that the ratio of the two expressions in equations (5.1) and (5.2), and  
 514 thus the relative frequency that the new invasions happen, is thus

$$515 \quad \frac{p_{CI}}{p_{DI}} \approx \left( \frac{F_L(C)}{F_L(D)} \right)^2 = \left( 1 + \frac{v-1}{r} \right)^2 \approx (1 + (L-1)x)^2 \quad (5.3)$$

516 for large  $v$  and  $r$ .

517 The second process considers fixation within a well-mixed group of size  $L$ .  
 518 Following [23] we obtain the formula

$$519 \quad x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \frac{\delta_k}{\beta_k}}{1 + \sum_{j=1}^{L-1} \prod_{k=1}^j \frac{\delta_k}{\beta_k}}, \quad (5.4)$$

520 for the fixation probability of  $i$  cooperators within a population of size  $L$ . Here  
 521  $\beta_k$  ( $\delta_k$ ) is the probability that the next event is the replacement of a defector  
 522 (cooperator) by a cooperator (defector), when the number of cooperators is  $k$ .  
 523 We have here

$$524 \quad \delta_k = \frac{k(L-k)}{L} \frac{r + \frac{kv}{L-1}}{(L-1)r + ((L-k)k + (k-1)^2) \frac{v}{L-1} - (k-1)}, \quad (5.5)$$

$$525 \quad \beta_k = \frac{k(L-k)}{L} \frac{r + \frac{(k-1)v}{L-1} - 1}{(L-1)r + ((L-k-1)k + k(k-1)) \frac{v}{L-1} - k}. \quad (5.6)$$

527 For sufficiently large  $r$ , we obtain

$$528 \quad \frac{\delta_k}{\beta_k} \approx \frac{1+kx}{1+(k-1)x} f_k(x), \quad (5.7)$$

529 where

$$530 \quad f_k(x) = \frac{L-1+(L-2)kx}{L-1+((L-2)k+1)x} < 1. \quad (5.8)$$

531 The fixation probability of a single cooperator in a group of defectors is given  
 532 by  $\rho_{C,L} = x_1$ , and the fixation probability of a single defector in a group of  
 533 cooperators is  $\rho_{D,L} = 1 - x_{L-1}$ . We thus have

$$534 \quad \frac{\rho_{D,L}}{\rho_{C,L}} = \prod_{k=1}^{L-1} \frac{\delta_k}{\beta_k} = \prod_{k=1}^{L-1} \frac{1+kx}{1+(k-1)x} f_k(x) = (1+(L-1)x) \prod_{k=1}^{L-1} f_k(x). \quad (5.9)$$

536 This implies that

$$537 \quad \frac{p_{CI}}{p_{DI}} > \frac{\rho_{D,L}}{\rho_{C,L}}. \quad (5.10)$$

538 Following our assumptions, the population evolves following a succession of  
 539 invasions of subpopulations either of cooperators by defectors or of defectors by  
 540 cooperators. The probability that the next such event will be the invasion of a  
 541 subpopulation of defectors by a cooperator is simply

$$542 \quad \frac{p_{CI} \rho_{C,L}}{p_{CI} \rho_{C,L} + p_{DI} \rho_{D,L}} = \frac{r_S}{1+r_S}, \quad (5.11)$$

543 where  $r_S = p_{CI} \rho_{C,L} / p_{DI} \rho_{D,L}$  is the *forward bias* [40] of cooperative groups  
 544 within our population. For a cooperator to fixate in the population it must first

545 fixate within its group with probability  $\rho_{C,L}$ , after which, there is a competition  
 546 between groups proceeding precisely as in a Moran process, so that we have

$$547 \quad \rho_C = \rho_{C,L} \frac{1 - 1/r_S}{1 - (1/r_S)^M}, \quad (5.12)$$

548 with the equivalent expression for  $\rho_D$ ,

$$549 \quad \rho_D = \rho_{D,L} \frac{r_S - 1}{r_S^M - 1}. \quad (5.13)$$

550 It is clear from equation (5.10) that  $r_S > 1$ , so that  $\rho_C$  is greater than  $\rho_{C,L}(1 -$   
 551  $1/r_S)$  for any  $M$ . Letting  $M$  become large means that  $1/N = 1/ML$  will be less  
 552 than  $\rho_C$ , but larger than  $\rho_D$ , so that inequality (4.1) holds. This means that  
 553 for sufficiently large  $h, r$  and  $v$ , we have that cooperation evolves for any given  
 554 subpopulation size  $L$ . Thus cooperation can potentially evolve for arbitrarily  
 555 large subpopulations, although as we have seen previously, it is easier for smaller  
 556 subpopulations.

## 557 6. Discussion

558 In [10] a new framework for the flexible modelling of structured populations  
 559 using multiplayer interactions was introduced, see also [8, 13, 11]. This work  
 560 built on classical evolutionary graph theory, but was limited in terms of the  
 561 dynamics used. In this paper we have developed this framework further. Most  
 562 importantly we have developed a full range of dynamics to apply in the frame-  
 563 work, which will allow us to consider many different evolutionary scenarios. In  
 564 particular these can be applied for the fully independent model in general, not  
 565 just the examples considered here, enabling us to use a fuller range of the pos-  
 566 sibilities that our flexible framework allows. Thus this paper can be thought to  
 567 complete the basic development phase of our work.

568 We have then developed the fully independent model to incorporate subpop-  
 569 ulations and in particular consider a generalized version of the territorial raider  
 570 model introduced in [8]. This is beneficial because previously the fully inde-  
 571 pendent model, represented in the bipartite graph in Figure 1, would require  
 572 a vertex for every individual as well as an additional vertex for every available  
 573 place. Now we just need a vertex per subpopulation, potentially allowing a  
 574 small number of very large subpopulations to be considered, which would not  
 575 have been possible previously. Furthermore, generalizing the territorial raider  
 576 model in this allows modelling of more complex movement behaviour as seen  
 577 in, for example, African wild dogs that live in packs [17].

578 This type of structure has been considered in a slightly different context,  
 579 for example, the island- or community-structured populations of [53]. In this  
 580 model interactions occur at multiple levels, interactions between community  
 581 members being more common than those with non-community members where  
 582 interaction occurs at multiple levels. Members of one community first play a  
 583 public goods game and then join the members of another community and play a

584 public goods game such that, at the highest level, the entire population plays a  
585 public goods game. This is in contrast to our case, where individuals only play  
586 a game if they are present in the same place at the same time. They showed  
587 that cooperation can evolve when DBB dynamics are used and selection is weak  
588 within communities, which is consistent with our results.

589 We note that the framework of [8] is capable of modelling far wider be-  
590 haviour than that developed here, in particular it is able to consider dynamic  
591 populations whose distributions continuously change due to their history, and  
592 the interactions that they have. Thus it can incorporate the type of situations  
593 with mobile populations modelled in [55, 47]. In particular, movement can fol-  
594 low a stochastic process in which the individuals move depending upon their  
595 current state as in [16]. In a soon to be recently submitted paper [39] we have  
596 developed a Markov chain version of our model similar to this, and again con-  
597 sider a combination of theoretical developments and the specific application of  
598 the evolution of cooperation.

599 We then applied our new methodology to an example, considering the evolu-  
600 tion of cooperation within a population involving subpopulations. We saw as in  
601 evolutionary graph theory that the choice of dynamics is crucial, and that DBD  
602 (and BDB) dynamics would not allow cooperation to evolve, but that DBB (and  
603 BDD) would, which is consistent with [36]. Further, using the latter dynamics,  
604 the size and the level of isolation of the subpopulations is important, with the  
605 smaller the subpopulations and the greater the isolation, the greater the chance  
606 for cooperation to evolve. Unsurprisingly, the larger the level of reward  $v$ , the  
607 better the cooperators do. In particular, the larger the subpopulations, the  
608 larger the reward  $v$  required for cooperation to evolve; note that this is similar  
609 to the requirement that the benefit-to-cost ratio exceeds the average number of  
610 neighbours an individual has from [36].

611 We see from Figure 6 that our new idea of strict subgroup temperature  
612 is important in explaining the level of cooperation that evolves. Low (high)  
613 temperature helps promote the invasion of cooperators (defectors). In particu-  
614 lar, higher temperatures allow cooperators to cluster more strongly and benefit  
615 more from cooperating with one another. We note that this raises a more gen-  
616 eral question about temperature. Within subpopulation temperature includes  
617 replacement weights between pairs of individuals from different subpopulations,  
618 but excludes weights between pairs from within the same subpopulation. What  
619 if two individuals have very similar, but not identical, movement distributions  
620 (and thus whilst formally not within the same subpopulation, for practical pur-  
621 poses they might as well be)? Under the current definition no distinction is made  
622 between this and two individuals whose distributions are completely different.  
623 We will investigate this question in later work.

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629 **References**

- 630 [1] Allen, B. and Nowak, M. [2014], ‘Games on graphs’, *EMS Surveys in Math-*  
631 *ematical Sciences* **1**(1), 113–151.
- 632 [2] Allen, B. and Tarnita, C. [2014], ‘Measures of success in a class of evolu-  
633 tionary models with fixed population size and structure’, *Journal of Math-*  
634 *ematical Biology* **68**(1-2), 109–143.
- 635 [3] Antal, T. and Scheuring, I. [2006], ‘Fixation of strategies for an evo-  
636 lutionary game in finite populations’, *Bulletin of Mathematical Biology*  
637 **68**(8), 1923–1944.
- 638 [4] Archetti, M. and Scheuring, I. [2011], ‘Coexistence of cooperation and de-  
639 fection in public goods games’, *Evolution* **65**(4), 1140–1148.
- 640 [5] Archetti, M. and Scheuring, I. [2012], ‘Review: Game theory of public  
641 goods in one-shot social dilemmas without assortment’, *Journal of Theo-*  
642 *retical Biology* **299**, 9–20.
- 643 [6] Binmore, K. [1992], *Fun and Games: A Text on Game Theory*, D.C. Heath.
- 644 [7] Broom, M., Cannings, C. and Vickers, G. [1997], ‘Multi-player matrix  
645 games’, *Bulletin of mathematical biology* **59**(5), 931–952.
- 646 [8] Broom, M., Lafaye, C., Pattni, K. and Rychtář, J. [2015], ‘A study of  
647 the dynamics of multi-player games on small networks using territorial  
648 interactions’, *Journal of Mathematical Biology* pp. 1–24.
- 649 [9] Broom, M. and Rychtář, J. [2008], ‘An analysis of the fixation proba-  
650 bility of a mutant on special classes of non-directed graphs’, *Proceedings*  
651 *of the Royal Society A: Mathematical, Physical and Engineering Science*  
652 **464**(2098), 2609–2627.
- 653 [10] Broom, M. and Rychtář, J. [2012], ‘A general framework for analysing  
654 multiplayer games in networks using territorial interactions as a case study’,  
655 *Journal of Theoretical Biology* **302**, 70–80.
- 656 [11] Broom, M. and Rychtář, J. [2016], ‘Ideal cost-free distributions in struc-  
657 tured populations for general payoff functions’, *Dynamic Games and Ap-*  
658 *plications* pp. 1–14.

- 659 [12] Broom, M. and Rychtář, J. [2013], *Game-Theoretical Models in Biology*,  
660 CRC Press, Boca Raton, FL.
- 661 [13] Bruni, M., Broom, M. and Rychtář, J. [2014], ‘Analysing territorial models  
662 on graphs’, *Involve, a Journal of Mathematics* **7**(2), 129–149.
- 663 [14] Bukowski, M. and Miekisz, J. [2004], ‘Evolutionary and asymptotic sta-  
664 bility in symmetric multi-player games’, *International Journal of Game  
665 Theory* **33**(1), 41–54.
- 666 [15] Domenici, P., Batty, R., Similä, T. and Ogam, E. [2000], ‘Killer whales  
667 (orcinus orca) feeding on schooling herring (clupea harengus) using un-  
668 derwater tail-slaps: kinematic analyses of field observations’, *Journal of  
669 Experimental Biology* **203**(2), 283–294.
- 670 [16] Erovenko, I. and Rychtář, J. [2016], ‘The evolution of cooperation in one-  
671 dimensional mobile populations’, *Far East Journal of Applied Mathematics*  
672 *95*(1), 63–88 **95**(1), 63–88.
- 673 [17] Ginsberg, J. and Macdonald, D. [1990], *Foxes, wolves, jackals, and dogs:  
674 an action plan for the conservation of canids*, IUNC, Gland, Switzerland.
- 675 [18] Gokhale, C. and Traulsen, A. [2010], ‘Evolutionary games in the multi-  
676 verse’, *Proceedings of the National Academy of Sciences* **107**(12), 5500–  
677 5504.
- 678 [19] Gokhale, C. and Traulsen, A. [2014], ‘Evolutionary multiplayer games’,  
679 *Dynamic Games and Applications* pp. 1–21.
- 680 [20] Hamilton, W. [1967], ‘Extraordinary sex ratios’, *Science* **156**(3774), 477–  
681 488.
- 682 [21] Harsanyi, J. and Selten, R. [1988], ‘A general theory of equilibrium selection  
683 in games’, *MIT Press Books* **1**.
- 684 [22] Hauert, C., De Monte, S., Hofbauer, J. and Sigmund, K. [2002], ‘Volun-  
685 teering as red queen mechanism for cooperation in public goods games’,  
686 *Science* **296**(5570), 1129–1132.
- 687 [23] Karlin, S. and Taylor, H. [1975], *A First Course in Stochastic Processes*,  
688 London, Academic Press.
- 689 [24] Li, A., Broom, M., Du, J. and Wang, L. [2016], ‘Evolutionary dynamics of  
690 general group interactions in structured populations’, *Physical Review E*  
691 **93**(2), 022407.
- 692 [25] Li, A., Wu, B. and Wang, L. [2014], ‘Cooperation with both synergistic  
693 and local interactions can be worse than each alone’, *Scientific Reports* **4**.
- 694 [26] Lieberman, E., Hauert, C. and Nowak, M. [2005], ‘Evolutionary dynamics  
695 on graphs’, *Nature* **433**(7023), 312–316.



- 696 [27] Maciejewski, W. and Puleo, G. [2014], ‘Environmental evolutionary graph  
697 theory’, *Journal of Theoretical Biology* **360**, 117–128.
- 698 [28] Masuda, N. [2009], ‘Directionality of contact networks suppresses selec-  
699 tion pressure in evolutionary dynamics’, *Journal of Theoretical Biology*  
700 **258**(2), 323–334.
- 701 [29] Maynard Smith, J. [1974], ‘The theory of games and the evolution of animal  
702 conflicts’, *Journal of Theoretical Biology* **47**(1), 209–221.
- 703 [30] Maynard Smith, J. [1982], *Evolution and the Theory of Games*, Cambridge  
704 university press.
- 705 [31] Maynard Smith, J. and Price, G. R. [1973], ‘The logic of animal conflict’,  
706 *Nature* **246**, 15–18.
- 707 [32] Moran, P. [1958], Random processes in genetics, in ‘Mathematical Pro-  
708 ceedings of the Cambridge Philosophical Society’, Vol. 54, Cambridge Univ  
709 Press, pp. 60–71.
- 710 [33] Moran, P. [1962], *The statistical processes of evolutionary theory.*, Claren-  
711 don Press, Oxford.
- 712 [34] Nowak, M. [2006a], *Evolutionary Dynamics, Exploring the Equations of*  
713 *Life*, Harvard University Press, Cambridge, Mass.
- 714 [35] Nowak, M. [2006b], ‘Five rules for the evolution of cooperation’, *Science*  
715 **314**(5805), 1560–1563.
- 716 [36] Ohtsuki, H., Hauert, C., Lieberman, E. and Nowak, M. [2006], ‘A simple  
717 rule for the evolution of cooperation on graphs and social networks’, *Nature*  
718 **441**(7092), 502–505.
- 719 [37] Pacheco, J. M., Santos, F. C., Souza, M. O. and Skyrms, B. [2009],  
720 ‘Evolutionary dynamics of collective action in n-person stag hunt dilem-  
721 mas’, *Proceedings of the Royal Society of London B: Biological Sciences*  
722 **276**(1655), 315–321.
- 723 [38] Palm, G. [1984], ‘Evolutionary stable strategies and game dynamics for  
724 n-person games’, *Journal of Mathematical Biology* **19**(3), 329–334.
- 725 [39] Pattni, K., Broom, M. and Rychtář, J. [2017], ‘Evolving multiplayer net-  
726 works: Modelling the evolution of cooperation in a mobile population’,  
727 *Submitted* .
- 728 [40] Pattni, K., Broom, M., Rychtář, J. and Silvers, L. J. [2015], ‘Evolutionary  
729 graph theory revisited: when is an evolutionary process equivalent to the  
730 moran process?’, *Proceedings of the Royal Society of London A: Mathemat-  
731 ical, Physical and Engineering Sciences* **471**(2182).

- 732 [41] Perc, M., Gómez-Gardeñes, J., Szolnoki, A., Floría, L. M. and Moreno, Y.  
733 [2013], ‘Evolutionary dynamics of group interactions on structured popula-  
734 tions: a review’, *Journal of The Royal Society Interface* **10**(80), 20120997.
- 735 [42] Santos, F. C. and Pacheco, J. M. [2005], ‘Scale-free networks provide a uni-  
736 fying framework for the emergence of cooperation’, *Physical Review Letters*  
737 **95**(9), 098104.
- 738 [43] Santos, F., Santos, M. and Pacheco, J. [2008], ‘Social diversity promotes the  
739 emergence of cooperation in public goods games’, *Nature* **454**(7201), 213–  
740 216.
- 741 [44] Shakarian, P., Roos, P. and Johnson, A. [2012], ‘A review of evolutionary  
742 graph theory with applications to game theory’, *Biosystems* **107**(2), 66–80.
- 743 [45] Similä, T. [1997], ‘Sonar observations of killer whales (*orcinus orca*) feeding  
744 on herring schools’, *Aquatic Mammals* **23**, 119–126.
- 745 [46] Souza, M., Pacheco, J. and Santos, F. [2009], ‘Evolution of cooperation un-  
746 der n-person snowdrift games’, *Journal of Theoretical Biology* **260**(4), 581–  
747 588.
- 748 [47] Suarez, D., Suthaharan, P., Rowell, J. and Rychtář, J. [2015], ‘Evolution  
749 of cooperation in mobile populations’, *Spora-A Journal of Biomathematics*  
750 **1**(1), 2–7.
- 751 [48] Szolnoki, A. and Perc, M. [2010a], ‘Impact of critical mass on the evo-  
752 lution of cooperation in spatial public goods games’, *Physical Review E*  
753 **81**(5), 057101.
- 754 [49] Szolnoki, A. and Perc, M. [2010b], ‘Reward and cooperation in the spatial  
755 public goods game’, *EPL (Europhysics Letters)* **92**(3), 38003.
- 756 [50] Taylor, C., Fudenberg, D., Sasaki, A. and Nowak, M. [2004], ‘Evolutionary  
757 game dynamics in finite populations’, *Bulletin of Mathematical Biology*  
758 **66**(6), 1621–1644.
- 759 [51] van Veelen, M. and Nowak, M. [2012], ‘Multi-player games on the cycle’,  
760 *Journal of Theoretical Biology* **292**, 116–128.
- 761 [52] Voorhees, B. and Murray, A. [2013], ‘Fixation probabilities for simple di-  
762 graphs’, *Proceedings of the Royal Society A: Mathematical, Physical and*  
763 *Engineering Science* **469**(2154).
- 764 [53] Wang, J., Wu, B., Ho, D. and Wang, L. [2011], ‘Evolution of coopera-  
765 tion in multilevel public goods games with community structures’, *EPL*  
766 *(Europhysics Letters)* **93**(5), 58001.
- 767 [54] Wu, B., Traulsen, A. and Gokhale, C. S. [2013], ‘Dynamic properties of  
768 evolutionary multi-player games in finite populations’, *Games* **4**(2), 182–  
769 199.

- 770 [55] Wu, T., Fu, F. and Wang, L. [2011], ‘Moving away from nasty encounters  
771 enhances cooperation in ecological prisoner’s dilemma game’, *PLoS One*  
772 **6**(11), e27669.
- 773 [56] Zhou, L., Li, A. and Wang, L. [2015], ‘Evolution of cooperation on com-  
774 plex networks with synergistic and discounted group interactions’, *EPL*  
775 (*Europhysics Letters*) **110**(6), 60006.

## 776 Appendix A.

777 A state of the population gives the type of each individual in the population.  
778 Let  $\mathcal{S}$  be a state of the population such that  $n \in \mathcal{S}$  if and only if  $I_n$  is a  
779 cooperator. There are then  $2^N$  different states of which  $\mathcal{N}(\emptyset)$  is the state in  
780 which there are all cooperators (defectors). Using any dynamics, the probability  
781 of transitioning from state  $\mathcal{S}$  to  $\mathcal{S}'$  is defined as follows

$$782 P_{\mathcal{S}\mathcal{S}'} = \sum_{i \in \mathcal{S}} \tau_{ij} \text{ for } \mathcal{S}' = \mathcal{S} \cup \{j\}, \text{ or } \sum_{i \notin \mathcal{S}} \tau_{ij} \text{ for } \mathcal{S}' = \mathcal{S} \setminus \{j\}, \text{ or } \sum_{\substack{i,j \in \mathcal{S} \\ i,j \notin \mathcal{S}}} \tau_{ij} \text{ for } \mathcal{S}' = \mathcal{S},$$

783 (A.1)

784 or 0 otherwise.

785 Cooperators (defectors) is said to *fixate* from state  $\mathcal{S}$  in the population when,  
786 starting from state  $\mathcal{S}$ , every defector (cooperator) is replaced by a cooperator  
787 (defector), that is the population reaches state  $\mathcal{N}(\emptyset)$ . At this point no further  
788 changes are possible, since one type is extinct, and so the population remains  
789 in this state. Let  $\rho_{\mathcal{S}}^C$  be the probability that cooperators fixate from any initial  
790 state  $\mathcal{S}$ , then this is obtained by solving the following system of equations

$$791 \rho_{\mathcal{S}}^C = \sum_{\mathcal{S}'} P_{\mathcal{S}\mathcal{S}'} \rho_{\mathcal{S}'}^C \tag{A.2}$$

792

793 with boundary conditions

$$794 \rho_{\emptyset}^C = 0 \quad \text{and} \quad \rho_{\mathcal{N}}^D = 1 \tag{A.3}$$

795

796 where  $P_{\mathcal{S}\mathcal{S}'}$  is the probability of transitioning from state  $\mathcal{S}$  to  $\mathcal{S}'$ . The probability  
797  $\rho_{\mathcal{S}}^D$  that defectors fixate from any initial state  $\mathcal{S}$  is obtained in the same way  
798 with the boundary conditions reversed.

799 The mean fixation probability of cooperators (defectors) is a, potentially,  
800 weighted average of the probabilities  $\rho_{\mathcal{S}}^C$  ( $\rho_{\mathcal{S}}^D$ ), over  $\mathcal{S}$  when there is only one  
801 cooperator (defector) in the population, that is  $|\mathcal{S}| = 1$  ( $|\mathcal{S}| = N - 1$ ). There are  
802 two common weightings used; uniformly weighted (as we use here) or weighted  
803 in proportion to the mutant appearance distribution as defined in [2].

804 The evolution of the population is essentially described by an absorbing  
805 Markov chain. The mean fixation probability is therefore calculated by com-  
806 puting the state transition probabilities that are then used to construct the  
807 state transition matrix of the Markov chain. The state transition matrix is then

808 used to calculate the fixation probability see, for example, [23] for explanation  
809 of how this is done. Note that no simulations were run to calculate the fixation  
810 probability, rather, all the states of the population were explicitly calculated.