

## EVOLVING MULTIPLAYER NETWORKS: MODELLING THE EVOLUTION OF COOPERATION IN A MOBILE POPULATION

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ABSTRACT. We consider a finite population of individuals that can move through a structured environment using our previously developed flexible evolutionary framework. In the current paper the behaviour of the individuals follows a Markov movement model where decisions about whether they should stay or leave depends upon the group of individuals they are with at present. The interaction between individuals is modelled using a public goods game. We demonstrate that cooperation can evolve when there is a cost associated with movement. Combining the movement cost with a larger population size has a positive effect on the evolution of cooperation. Moreover, increasing the exploration time, which is the amount of time an individual is allowed to explore its environment, also has a positive effect. Unusually, we find that the evolutionary dynamics used does not have a significant effect on these results.

1 **1. Introduction.** Evolutionary game theory has proved to be an effective method  
2 of modelling the evolution of populations. The original models focused on well-  
3 mixed infinite populations [36, 35], with games such as the Hawk-Dove game [34] and  
4 the sex ratio game [26] being used. With further development, these models can be  
5 considered within well-mixed finite populations [39, Chapters 6-9] ([37, 38] provided  
6 important results for finite populations without game theoretical methods).

7 The seminal work of [31] (see also [5, 10, 53, 32], and [3, 49] for reviews) in which  
8 evolutionary graph theory was developed, allowed the modelling of structured finite  
9 populations within a given framework. It also provided important results in the  
10 fixed fitness case [31, 33, 45]. However, this approach is limited by the fact that it  
11 is suited to modelling pairwise interactions, whereas in real populations, there are  
12 interactions between multiple individuals [50, 19], and there are many examples of  
13 multiplayer games used in the literature [44, 8, 14, 24]. In [41] it was shown that  
14 evolutionary graph theory can be used in conjunction with a different ‘interaction’  
15 graph to model more complex behaviours but there is no obvious link between the  
16 two graphs, that is, one graph has not been derived from the other nor is there some

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17 clear connection, for instance both being derived from some common population-  
18 derived factors.

19 We should also mention that structured populations have been considered in  
20 an evolutionary context in different ways, see for example [51]. This includes is-  
21 land models, where populations evolve in isolated communities with a low rate of  
22 migration between them, as in [18]. Community-structured populations were con-  
23 sidered in [54], where interactions occur at multiple levels, with members of the  
24 same community interacting more commonly than those in different communities.

25 A more general framework that can be used is that of [11] where it is possible  
26 to consider multiplayer interactions in groups of any size, depending upon various  
27 factors like the population's history, whilst keeping the beneficial aspects of evolu-  
28 tionary graph theory. More recently this framework has been used to model different  
29 kinds of multiplayer behaviour [13, 9, 12]. In this paper, we extend this work to  
30 consider a population of mobile individuals, focusing on a specific multiplayer game,  
31 a public goods game [6, 7, 25, 55].

32 When using the evolutionary graph theory approach [30, 52, 29, 46, 58], individ-  
33 uals group with their neighbours within a fixed population structure. One potential  
34 problem with this is that individuals could spend more time with some of their  
35 neighbours, less with others and some time alone. The framework of [11] solves this  
36 problem as shown in [13, 9] using a simple model where individuals are confined  
37 to their neighbourhood but are still allowed to form groups of different sizes. The  
38 framework, though, is capable of handling much more complex movement behaviour  
39 [1, 2, 21] where individuals make a choice of where to move given the information  
40 they have at hand. In this paper we apply the framework for the first time to one  
41 such model where the movement of individuals follows the Markov property.

42 The paper is structured as follows: in Section 2 the model framework is described  
43 in general, with examples of each concept being given to motivate how it can be  
44 applied, in Section 3 the framework is applied to create a Markov movement model,  
45 in Section 4 we describe the results of the Markov movement model, and Section 5  
46 is a general discussion.

47 **2. The framework of [11].** This section presents the framework of [11] for mod-  
48 elling the evolution of a population in a which the movement of individuals follows a  
49 discrete-time stochastic process. In particular we update the terminology from the  
50 original paper somewhat, and the methodology described here will be applicable to  
51 a wide variety of scenarios, although we focus on a Markov movement model (and  
52 indeed a specific one only) in the current paper. The framework can be broken  
53 down into three components that each describe a certain aspect of the population:  
54 structure, fitness, and evolutionary dynamics.

55 **2.1. The population: structure and distribution.** The population structure  
56 describes the restrictions upon how members of the population can interact with  
57 each other, including through the different places each individual can and cannot  
58 visit. This paper focuses on a Markov movement model, and in the type of examples  
59 that we consider all places are visitable by all individuals. The structure here will  
60 reduce to simply considering the distribution of the population individuals at any  
61 given time, and so we shall find it convenient to talk about distribution in place  
62 of structure. In a population of  $N$  individuals who can move around  $M$  places,  
63 the population distribution at time  $t$  is given in [11] by an  $N \times M$  binary matrix

**Table of Notation**

<i>Notation</i>	<i>Definition</i>	<i>Description</i>
$N$	$\in \mathbb{Z}^+$	Population size.
$M$	$\in \mathbb{Z}^+$	Number of places.
$I_n$		Individual $n$ .
$P_m$		Place $m$ .
$m_{n,t}$	$\in \{1, \dots, M\}$	Place where $I_n$ is at time $t$ .
$\mathbf{m}_t$	$= [m_{n,t}]_{n=1}^N$	Population distribution at time $t$ .
$\mathbf{m}_{<t}$	$= (\mathbf{m}_{t-1}, \dots, \mathbf{m}_0)$	Population distribution history.
$p_t(\mathbf{m} \mathbf{m}_{<t})$	$\in [0, 1]$	Probability population has distribution $\mathbf{m}$ at time $t$ given history $\mathbf{m}_{<t}$ .
$\pi_t$	$\in [0, 1]$	Population distribution probability function (PDPF).
$P(\mathbf{m}_{<t})$	$\in [0, 1]$	Probability that population has history $\mathbf{m}_{<t}$ .
$\pi_{n,t}$	$\in [0, 1]$	Individual distribution probability function (IDPF).
$f_{n,t}$	$\geq 0$	Fitness contribution of $I_n$ at time $t$ .
$F_{n,t}$	$> 0$	Fitness of $I_n$ at time $t$ .
$\mathcal{G}_n$	$\subset \{1, 2, \dots, N\}$	<i>Direct group</i> : group that $I_n$ is in.
$w_{i,j,t}$	$\geq 0$	Replacement weight that $I_i$ replaces $I_j$ at time $t$ .
$\mathbf{W}_t$	$= [w_{i,j,t}]_{i,j=1, \dots, N}$	Weighted adjacency matrix of evolutionary graph.
$u_{i,j,t}$	$\geq 0$	Replacement weight contribution that $I_i$ assigns to $I_j$ at time $t$ .
$A, B$		Two types of individuals in population.
$\mathcal{S}$	$\subset \{1, 2, \dots, N\}$	Population state, $n \in \mathcal{S}$ if $I_n$ has type $A$ .
$\mathcal{N}$	$= \{1, 2, \dots, N\}$	State consisting of all type $A$ individuals.
$P_{\mathcal{S}\mathcal{S}'}$	$\in [0, 1]$	Probability of transitioning from $\mathcal{S}$ to $\mathcal{S}'$ .
$\rho_{\mathcal{S}}^A$	$\in [0, 1]$	Fixation probability of type $A$ when initial state is $\mathcal{S}$ .
$\mathbf{r}_{ij}$	$\in [0, 1]$	Probability that $I_i$ replaces $I_j$ .
$h_n$	$\in [0, 1]$	Probability that $I_n$ stays.
$\alpha_n$	$\in [0, 1]$	<i>Staying propensity</i> : probability that individual $I_n$ stays when alone.
$C (D)$		Cooperator and defector interactive strategy.
$\beta_C (\beta_D)$	$\in \mathbb{R}$	Benefit of being with cooperator (defector).
$S$	$\in (0, 1)$	Sensitivity shown to group members.
$v$	$> 0$	Reward as a multiple of background fitness.
$c$	$\in [0, 1)$	Cost as a multiple of background fitness.
$R_n$	$\geq 0$	Payoff to $I_n$ .
$\lambda$	$\in [0, \min(R_n))$	Movement cost.
$T$	$\in \mathbb{Z}^+$	Exploration time.
$C_\alpha (D_\alpha)$		Cooperator (defector) with staying propensity $\alpha$ .
$\gamma (\delta)$	$\in [0, 1]$	Nash equilibrium staying propensity of cooperator (defector).

TABLE 1. Notation used in the paper.

64 denoted  $\mathbf{X}_t = (X_{n,m}^{(t)})$  and defined

$$65 \quad X_{n,m}^{(t)} = \begin{cases} 1 & \text{if } I_n \text{ is in } P_m \text{ at time } t, \\ 0 & \text{otherwise.} \end{cases} \quad (1)$$

66

67 To consider the Markov movement models that are the subject of the current paper,  
 68 it is convenient to use an alternative matrix representation of the population dis-  
 69 tribution. Here the population distribution at time  $t$  will be denoted by the matrix  
 70  $\mathbf{M}_t = [M_{n,t}]_{n=1,\dots,N}$ , where  $M_{n,t} = m$  if individual  $I_n$  is in place  $P_m$  at time  $t$ .

71 The framework assumes that the movement of individuals is probabilistic such  
 72 that there is dependence upon time and the current and past movements of in-  
 73 dividuals in the population. In particular, the transition probability function de-  
 74 noted  $p_t(\mathbf{m}|\mathbf{m}_{<t})$  gives the probability that the movement of individuals at time  
 75  $t$  results in a population distribution  $\mathbf{m}$  given the population distribution history  
 76  $\mathbf{m}_{<t} = (\mathbf{m}_{t-1}, \dots, \mathbf{m}_1, \mathbf{m}_0)$ . The transition probability function is defined as follows

$$77 \quad p_t(\mathbf{m}|\mathbf{m}_{<t}) = \mathbb{P}(\mathbf{M}_t = \mathbf{m} | \mathbf{M}_{t-1} = \mathbf{m}_{t-1}, \dots, \mathbf{M}_0 = \mathbf{m}_0) \quad (2)$$

79 whose exact form will depend upon the model being used but will always satisfy

$$80 \quad 1 = \sum_{\mathbf{m}} p_t(\mathbf{m}|\mathbf{m}_{<t}) \quad \forall t, \mathbf{m}_{<t}. \quad (3)$$

81 The population distribution probability function (PDPF)  $\pi_t(\mathbf{m})$  gives the prob-  
 82 ability that the population distribution is  $\mathbf{m}$  after  $t$  time steps regardless of the  
 83 population distribution history. It can be expressed using the transition probabili-  
 84 ties as

$$86 \quad \pi_t(\mathbf{m}) = \mathbb{P}(\mathbf{M}_t = \mathbf{m}) = \sum_{\mathbf{m}_{<t}} p_t(\mathbf{m}|\mathbf{m}_{<t}) P(\mathbf{m}_{<t}) \quad (4)$$

87 where  $P(\mathbf{m}_{<t})$  denotes the historical PDPF that gives the probability that the  
 88 population distribution history is  $\mathbf{m}_{<t}$  and is written as

$$90 \quad \begin{aligned} P(\mathbf{m}_{<t}) &= \mathbb{P}(\mathbf{M}_0 = \mathbf{m}_0, \mathbf{M}_1 = \mathbf{m}_1, \dots, \mathbf{M}_{t-1} = \mathbf{m}_{t-1}) \\ 92 \quad &= p_{t-1}(\mathbf{m}_{t-1}|\mathbf{m}_{<t-1}) \cdots p_1(\mathbf{m}_1|\mathbf{m}_0) \pi_0(\mathbf{m}_0) \end{aligned} \quad (5)$$

93 where the probability of the initial population distribution,  $\pi_0(\mathbf{m}_0)$ , is assumed to  
 94 be known.

95 *2.1.1. An individual movement model.* In this model it is assumed that individuals  
 96 move independently of each other. The PDPF can then be defined as follows

$$97 \quad \pi_t(\mathbf{m}) = \prod_n \pi_{n,t}(m_n) \quad (6)$$

98 where  $\pi_{n,t}(m_n)$  denotes the individual distribution probability function (IDPF) that  
 99 gives the probability of individual  $I_n$  being present in place  $P_{m_n}$  at time  $t$  indepen-  
 100 dently of the history of the process. The expression for  $\pi_{n,t}(m_n)$  will depend upon  
 101 whether the movement of  $I_n$  is dependent upon the whole population distribution  
 102 history or just its own individual history.

104 *Dependence on the population distribution history.* When the movement of individ-  
 105 ual  $I_n$  depends upon the distribution history of the whole population, the individual  
 106 transition probability function  $p_{n,t}(m_n|\mathbf{m}_{<t})$  gives the probability that  $I_n$  moves to  
 107 place  $m_n$  at time  $t$  given the population history  $\mathbf{m}_{<t}$  and is given as follows

$$108 \quad p_t(m_n|\mathbf{m}_{<t}) = \mathbb{P}(M_{n,t} = m_n | \mathbf{M}_{t-1} = \mathbf{m}_{t-1}, \dots, \mathbf{M}_0 = \mathbf{m}_0). \quad (7)$$

110 The individual transition probability function is then defined as follows

$$111 \quad \pi_{n,t}(m_n) = \sum_{\mathbf{m}_{<t}} p_{n,t}(m_n|\mathbf{m}_{<t}) P(\mathbf{m}_{<t}). \quad (8)$$

113 *Dependence on the individual distribution history.* When the movement of individ-  
 114 ual  $I_n$  depends only upon its own distribution history  $m_{n,<t} = (m_{n,t-1}, \dots, m_{n,0})$ ,  
 115 independent from the history of the other individuals, then the individual transition  
 116 probability function is given as follows

$$117 \quad p_t(m_n | m_{n,<t}) = \mathbb{P}(M_{n,t} = m_n | M_{n,t-1} = m_{n,t-1}, \dots, M_{n,0} = m_{n,0}). \quad (9)$$

119 The IDPF is then given by

$$120 \quad \pi_{n,t}(m_n) = \sum_{m_{n,<t}} p_{n,t}(m_n | m_{n,<t}) P_n(m_{n,<t}) \quad (10)$$

121 where  $P_n(m_{n,<t})$  denotes the individual history distribution as follows

$$122 \quad P_n(m_{n,<t}) = p_{n,t-1}(m_{n,t-1} | m_{n,<t-1}) \cdots p_{n,1}(m_{n,1} | m_{n,0}) \pi_0(m_{n,0}). \quad (11)$$

123  
 125 2.1.2. *The fully independent movement model.* In this model individuals move in-  
 126 dependently of each other, history and time. In this case, the individual transition  
 127 function is denoted  $p_n(m)$  and we have that

$$128 \quad \pi_{n,t}(m_n) = p_n(m_n) \overbrace{\sum_{m_{n,<t}} P_n(m_{n,<t})}^1 = p_n(m_n) \quad (12)$$

129 and therefore the PDPF can simply be written

$$130 \quad \pi_t(\mathbf{m}) = p(\mathbf{m}). \quad (13)$$

131  
 133 2.2. **Fitness.** In the framework the contribution to an individual's fitness depends  
 134 upon the time  $t$ , the current population distribution  $\mathbf{m}$  and historical population  
 135 distributions  $\mathbf{m}_{<t}$ . The fitness contribution of  $I_n$  is denoted

$$136 \quad f_{n,t}(\mathbf{m} | \mathbf{m}_{<t}) \quad (14)$$

137 where the exact form will depend upon the assumptions about the factors that  
 138 contribute to an individual's fitness. The mean fitness contribution at time  $t$  is  
 139 then as follows

$$140 \quad \bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m} | \mathbf{m}_{<t}) p_t(\mathbf{m} | \mathbf{m}_{<t}) P(\mathbf{m}_{<t}). \quad (15)$$

141 We assume that the fitness of an individual at time  $t$  is given by averaging the  
 142 mean fitness contribution across all time periods up to and including  $t$ . The fitness  
 143 function is then defined as follows

$$144 \quad F_{n,t} = \frac{1}{t} \sum_{k=1}^t \bar{f}_{n,k}. \quad (16)$$

145 Note that there are other definitions of the fitness function that one can use instead  
 146 of the one given here, for example, one could use a weighted average of the mean  
 147 fitness contribution instead.

148 When there is fully independent movement, the mean fitness change simplifies  
 149 to

$$150 \quad \bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m} | \mathbf{m}_{<t}) p(\mathbf{m}) P(\mathbf{m}_{<t}). \quad (17)$$

151 In [9] it is assumed that the fitness contribution of individual  $I_n$  only depends upon  
 152 those individuals that it can directly interact with. The *direct group* (or simply the

### 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 weights and fitnesses as in [45]. In each case, B (D) is appended to the name of the dynamics if selection happens in the birth (death) event. For BDB and BDD dynamics  $\tau_{ij} = b_i d_{ij}$ , for DBD and DBB dynamics  $\tau_{ij} = d_j b_{ij}$ .

157 *group*) of individual  $I_n$ , denoted  $\mathcal{G}_n(\mathbf{m})$ , is the set of individuals that are present  
 158 with it in the same place for population distribution  $\mathbf{m}$  and is defined as follows

$$159 \quad \mathcal{G}_n(\mathbf{m}) = \{i : m_i = m_n\}. \quad (18)$$

161 We then denote the fitness contribution as  $f_n(\mathcal{G}_n(\mathbf{m}))$ . In this case, the mean fitness  
 162 change is constant over time and therefore the fitness is equal to the mean fitness  
 163 contribution, that is

$$164 \quad F_n = \bar{f}_n = \sum_{\mathbf{m}} f_n(\mathcal{G}_n(\mathbf{m}))p(\mathbf{m}). \quad (19)$$

166 **2.3. Evolutionary Dynamics.** In the framework it is assumed that there is one  
 167 birth and death per replacement event. A replacement event at time  $t$  is governed  
 168 by an evolutionary graph defined using an  $N \times N$  weighted adjacency matrix  $\mathbf{W}_t =$   
 169  $[w_{i,j,t}]_{i,j=1,\dots,N}$  where the replacement weight  $w_{i,j,t}$  gives the weight of the edge  
 170 from node  $i$  to node  $j$  in the evolutionary graph that represent individuals  $I_i$  and  
 171  $I_j$  respectively.

172 The contribution to a replacement weight depends upon the time  $t$ , the current  
 173 population distribution  $\mathbf{m}$  and the historical population distributions  $\mathbf{m}_{<t}$ . The  
 174 replacement weight contribution that individual  $I_i$  assigns individual  $I_j$  is denoted  
 175 by

$$176 \quad u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t}). \quad (20)$$

178 The exact form will depend upon the assumptions made about the replacement  
 179 weight contributions. The mean replacement weight contribution is given as follows

$$180 \quad \bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t})p_t(\mathbf{m}|\mathbf{m}_{<t})P(\mathbf{m}_{<t}). \quad (21)$$

182 In this paper, we choose the replacement weight at time  $t$  as the mean replacement  
 183 weight contribution at time  $t$  as in [21] that is

$$184 \quad w_{i,j,t} = \bar{u}_{i,j,t} \quad (22)$$

186 but, as for the fitness function, there are other definitions that one can use.

187 The probability that the offspring of individual  $I_i$  replaces individual  $I_j$ , denoted  
 188  $\tau_{ij}$ , is defined using the replacement weights and fitnesses as in [45]. The different  
 189 definitions of the replacement probabilities are summarised in Table 2.

190 For the fully independent movement model, the mean replacement weight con-  
 191 tribution is defined as follows

$$192 \quad \bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m} < t} u_{i,j,t}(\mathbf{m}, \mathbf{m} < t) p(\mathbf{m}) P(\mathbf{m} < t). \quad (23)$$

193  
 194 In [9], the replacement weight contribution is independent of time and history, and  
 195 depends only upon direct groups. This implies that the mean replacement weight  
 196 is invariant over time and is as follows

$$197 \quad w_{i,j} = \bar{u}_{i,j} = \sum_{\mathbf{m}} u_{i,j}(\mathcal{G}_n(\mathbf{m})) p(\mathbf{m}). \quad (24)$$

198  
 199 **2.4. The evolutionary Markov chain.** The evolution of the population can now  
 200 be described in terms of a Markov chain. We will assume that there are only two  
 201 types of individuals in the population, which we label  $A$  and  $B$ . Furthermore, each  
 202 type is made up of made up of two different characteristics, and we will say more  
 203 about this in the following sections. A state of the population gives its composition  
 204 in terms of type  $A$  and  $B$  individuals. We use  $\mathcal{S}$  to denote a state of the population  
 205 such that  $n \in \mathcal{S}$  if  $I_n$  is of type  $A$ . There are a total of  $2^N$  different states where  
 206  $\mathcal{N}(\emptyset)$  is the state consisting of all type  $A$  ( $B$ ) individuals. The state transition  
 207 probabilities are described using the dynamics as follows

$$208 \quad P_{\mathcal{S}\mathcal{S}'} = \begin{cases} \sum_{i \in \mathcal{S}} \mathbf{r}_{ij} & \mathcal{S}' = \mathcal{S} \cup \{j\}, \\ \sum_{i \notin \mathcal{S}} \mathbf{r}_{ij} & \mathcal{S}' = \mathcal{S} \setminus \{j\}, \\ \sum_{\substack{i,j \in \mathcal{S} \\ i,j \notin \mathcal{S}}} \mathbf{r}_{ij} & \mathcal{S}' = \mathcal{S}, \\ 0 & \text{otherwise.} \end{cases} \quad (25)$$

209  
 210 Given that the state of the population is given by  $\mathcal{S}$ , type  $A$  ( $B$ ) is said to fixate  
 211 from that state when all type  $B$  ( $A$ ) individuals have been replaced and we reach  
 212 state  $\mathcal{N}(\emptyset)$ . Once a certain type has fixated no more changes can take place and the  
 213 population remains in this state. The probability of type  $A$  individuals given by  $\mathcal{S}$   
 214 fixating in a population where the type  $B$  individuals are given by  $\mathcal{N} \setminus \mathcal{S}$  is denoted  
 215  $\rho_{\mathcal{S}}^A$  (and we denote the equivalent fixation probability for type  $B$  individuals by  $\rho_{\mathcal{S}}^B$ ).  
 216 This probability is found by solving the following equation

$$217 \quad \rho_{\mathcal{S}}^A = \sum_{\mathcal{S}'} P_{\mathcal{S}\mathcal{S}'} \rho_{\mathcal{S}'}^A \quad (26)$$

218  
 219 with boundary conditions

$$220 \quad \rho_{\emptyset}^A = 0 \quad \text{and} \quad \rho_{\mathcal{N}}^A = 1. \quad (27)$$

222 For type  $B$  individuals we can use the fact that  $\rho_{\mathcal{S}}^B = 1 - \rho_{\mathcal{S}}^A$ .

223 We shall consider a population where a population is all of a single type, but  
 224 where a single population member is selected uniformly at random to be replaced  
 225 by one of the opposite type. We are thus interested in calculating the fixation  
 226 probability where state  $\mathcal{S}$  consists of only one individual (all but one individual).  
 227 There are  $N$  initial states from which the fixation probability can be calculated,  
 228 and we take an arithmetic mean of these fixation probabilities, which we denote  
 229 as  $\rho^A$  ( $\rho^B$ ). Alternatively, one could weight the fixation probability of a mutant  
 230 using the likelihood of that mutant appearing [4]. Sometimes this is an important  
 231 distinction, but in the examples considered in the current paper the differences are  
 232 small, and so we have stuck with the traditional, simpler, version.

233 **3. The Markov movement model.** In the previous models [9] considered in  
 234 this framework, the movement of individuals is limited to their neighbourhood and  
 235 exogenously controlled by the *home fidelity* parameter that measures how likely  
 236 the individual is to remain in their home. A natural extension to this is to allow  
 237 individual distributions to vary with time. A logical first step is to consider a Markov  
 238 model, which is based on the assumption that history dependence is Markov, that is,  
 239 the current population distribution is only dependent upon the previous population  
 240 distribution. The concept of a Markov movement model within the framework was  
 241 introduced in [11], but was only discussed in general terms. In this paper we fully  
 242 develop it and apply it to example populations for the first time. The definitions  
 243 we have given before would then change as follows; for the PDPF we have

$$244 \quad \pi_t(\mathbf{m}) = \sum_{\mathbf{m}_{<t}} p_t(\mathbf{m}|\mathbf{m}_{t-1})P(\mathbf{m}_{<t}), \quad (28)$$

246 for the mean change in fitness we have

$$247 \quad \bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t})p_t(\mathbf{m}|\mathbf{m}_{t-1})P(\mathbf{m}_{<t}) \quad (29)$$

249 and for the mean replacement weight change we have

$$250 \quad \bar{u}_{i,j,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} u_{i,j,t}(\mathbf{m}|\mathbf{m}_{<t})p_t(\mathbf{m}|\mathbf{m}_{t-1})P(\mathbf{m}_{<t}). \quad (30)$$

252 **3.1. Movement with dependence only upon individual history.** In this  
 253 model it is assumed that an individual would move independently of the other in-  
 254 dividuals in the population but its current position is dependent upon its previous  
 255 position. The IDPF is then given as follows

$$256 \quad \pi_{n,t}(m) = \sum_{m_{n,<t}} p_{n,t}(m|m_{n,t-1})P(m_{n,<t}). \quad (31)$$

258 This expression can be rewritten using the  $M \times M$  probability matrix  $\mathbf{p}_{n,t} =$   
 259  $[p_{n,t}(m_n|m_{n,t-1})]$  for  $m_n, m_{n,t-1} = 1, \dots, M$  as follows

$$260 \quad \boldsymbol{\pi}_{n,t} = \boldsymbol{\pi}_{n,0} \prod_{k=1}^t \mathbf{p}_{n,k} \quad (32)$$

262 where  $\boldsymbol{\pi}_{n,t} = [\pi_{n,t}(m)]_{m=1,\dots,M}$ . Furthermore, if we assume that there is time  
 263 homogeneity, that is  $\mathbf{p}_{n,t} = \mathbf{p}_n$  for all  $t$ , then this simplifies to

$$264 \quad \boldsymbol{\pi}_{n,t} = \boldsymbol{\pi}_{n,0} \mathbf{p}_n^t. \quad (33)$$

266 In this case, assuming that  $\mathbf{p}_n$  is irreducible and aperiodic for all  $n$ , then as  $t \rightarrow \infty$   
 267 the IDPF  $\boldsymbol{\pi}_{n,\infty}$  is stationary for all  $n$ . Essentially, our model is then equivalent to  
 268 the fully independent movement model. We do not consider this case further here,  
 269 but rather refer the reader to [9] for a detailed discussion of this kind of model.

270 **3.2. Individual movement with dependence on population history.** In this  
 271 model individuals move to a new position independently of each other but dependent  
 272 upon the current distribution of the whole population. The IDPF is then as follows

$$273 \quad \pi_{n,t}(m) = \sum_{\mathbf{m}_{<t}} p_{n,t}(m|\mathbf{m}_{t-1})P(\mathbf{m}_{<t}). \quad (34)$$

274



275 In this paper we construct a model of this type that is made up of the following  
 276 four components: population structure, movement strategy, game and evolutionary  
 277 dynamics.

278 3.2.1. *The population structure.* The population is assumed to be of size  $N$  where  
 279 each individuals has a home that they can return to. The structure is described by  
 280 a graph such that each node represents a place. We consider the complete graph  
 281 structure where all places are connected to each other. We assume that every place  
 282 is home to precisely one individual.

283 3.2.2. *Individual movement.* We assume that the individual transition probabilities  
 284 are time homogeneous but dependent upon the previous group and previous position  
 285 of the individuals, that is

$$286 \quad p_{n,t}(m|m_{n,t-1}, \mathcal{G}_n(\mathbf{m}_{t-1})) = \begin{cases} h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) & m = m_{n,t-1} \\ \frac{1-h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))}{N-1} & m \neq m_{n,t-1} \end{cases} \quad (35)$$

288 where  $h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))$  denotes the staying probability of individual  $I_n$  and  $N - 1$  is  
 289 the number of neighbouring places that an individual can move to in a complete  
 290 graph.

291 The staying probability  $h_n(\mathcal{G}_n(\mathbf{m}_{t-1}))$  will depend upon the *staying propensity*  
 292  $\alpha_n$  of individual  $I_n$  and the attractiveness of remaining in group  $\mathcal{G}_n(\mathbf{m}_{t-1})$ . The  
 293 staying propensity  $\alpha_n$  measures the likelihood that individual  $I_n$  will stay where  
 294 it is, in particular,  $h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \alpha_n$  when  $I_n$  is alone ( $\mathcal{G}_n(\mathbf{m}_{t-1}) = \{n\}$ ). The  
 295 staying propensity is assumed to be one of the characteristics that makes up the type  
 296 of an individual. However, when present in a group ( $|\mathcal{G}_n(\mathbf{m}_{t-1})| > 1$ ), individual  
 297  $I_n$  would take into account the benefit of remaining in that group. The benefit  
 298  $\beta_i$  of group member  $I_i$  to others depends upon its *interactive strategy*, the second  
 299 characteristic that makes up the type of an individual. We will assume that there  
 300 are two interactive strategies, cooperate ( $C$ ) and defect ( $D$ ). The benefit function,  
 301  $\beta_i$  is then defined as follows

$$302 \quad \beta_i = \begin{cases} \beta_C & \text{if } I_i \text{ cooperator,} \\ \beta_D & \text{if } I_i \text{ defector} \end{cases} \quad (36)$$

304 where  $\beta_C$  and  $\beta_D$  are the *benefits* of being with a cooperator and defector, respec-  
 305 tively. The benefit of group  $\mathcal{G}_n(\mathbf{m}_{t-1})$  to individual  $I_n$  is then defined as follows

$$306 \quad \beta_{\mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}} = \sum_{i \in \mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}} \beta_i. \quad (37)$$

308 Finally, combining the effects of the staying propensity and the group benefit, in  
 309 the rest of the paper the staying probability is expressed as the following sigmoid  
 310 function

$$311 \quad h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \frac{\alpha_n}{\alpha_n + (1 - \alpha_n)S^{\beta_{\mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}}}} \quad (38)$$

313 where  $0 < S < 1$  is the sensitivity shown to group members. So, for example,  $S \rightarrow 0$   
 314 implies that  $I_n$  shows great sensitivity and would move away immediately if remain-  
 315 ing in group  $\mathcal{G}_n(\mathbf{m}_{t-1})$  is unattractive, which is the case when  $\beta_{\mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}} < 0$ .  
 316 An alternative way of representing the  $S \rightarrow 0$  limit involves the staying probability

317 being defined using the following step function

$$318 \quad h_n(\mathcal{G}_n(\mathbf{m}_{t-1})) = \begin{cases} 0 & |\mathcal{G}_n(\mathbf{m}_{t-1})| > 1 \text{ and } \beta_{\mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}} < 0, \\ \alpha_n & |\mathcal{G}_n(\mathbf{m}_{t-1})| = 1, \\ 1 & |\mathcal{G}_n(\mathbf{m}_{t-1})| > 1 \text{ and } \beta_{\mathcal{G}_n(\mathbf{m}_{t-1}) \setminus \{n\}} \geq 0. \end{cases} \quad (39)$$

319 For example, if we set  $\alpha_n = 0 \forall n$ ,  $\beta_C = 0$  and  $\beta_D < 0$  then the attractiveness  
320 of a group is completely determined by the presence or absence of defectors. An  
321 individual would therefore leave with probability 1 if a defector is present in the  
322 group. This was referred to as the ‘walk away’ strategy in [1].

323 In our model we select an *exploration time*  $T$ , which is the number of steps an  
324 individual takes moving around the region before returning to its home place. Thus  
325 the larger  $T$ , the more time cooperators have to find other cooperators, but also  
326 the more time there is for them to be found by defectors.  
327

328 **3.2.3. Fitness.** We assume that the change in fitness of an individual depends upon  
329 direct group interactions and whether a movement has been made.

330 For these group interactions we will consider a public goods game in which the  
331 payoffs are determined by the interactive strategies, cooperate and defect, that we  
332 introduced earlier. Each individual receives a base reward of 1 regardless of their  
333 strategy. A cooperator always pays a cost  $0 \leq c < 1$  so that every individual that  
334 it can directly interact with (excluding itself) receives an equal share of a reward  
335  $v > 0$ . The cost cannot exceed 1 in order to prevent the fitness contribution from  
336 going negative (this is done for convenience of calculation; it is important that total  
337 fitness is not negative, and we could deal with large costs if necessary by truncating  
338 the resulting total fitness at 0). A defector does not pay a cost but receives a share  
339 of the reward from cooperators present in the group. Note that the base reward has  
340 been normalised to 1 and the reward  $v$  and cost  $c$  are multiples of the base reward.  
341 The direct group interaction payoff functions are then defined as follows

$$342 \quad R_{n,t}(\mathcal{G}_n(\mathbf{m}_t)) = \begin{cases} 1 + \frac{|\mathcal{G}_n(\mathbf{m}_t)|_C - 1}{|\mathcal{G}_n(\mathbf{m}_t)| - 1} v - c & I_n \text{ cooperator and } |\mathcal{G}_n(\mathbf{m}_t)| > 1, \\ 1 - c & I_n \text{ cooperator and } |\mathcal{G}_n(\mathbf{m}_t)| = 1, \\ 1 + \frac{|\mathcal{G}_n(\mathbf{m}_t)|_C}{|\mathcal{G}_n(\mathbf{m}_t)| - 1} v & I_n \text{ defector and } |\mathcal{G}_n(\mathbf{m}_t)| > 1, \\ 1 & I_n \text{ defector and } |\mathcal{G}_n(\mathbf{m}_t)| = 1 \end{cases} \quad (40)$$

343 where  $|\mathcal{G}|_C$  is the number of cooperators in group  $\mathcal{G}$ . Note the cooperators still pay  
344 a cost when they are alone.  
345

346 An individual will pay a cost of  $\lambda$  for every movement that it makes. The  
347 movement cost is chosen so that it does not exceed the direct group interaction  
348 payoff an individual receives (for the same reasons as for the cooperative cost  $c$ ,  
349 and large movement costs could be similarly accommodated if necessary), that is  
350  $0 \leq \lambda < \min(R_{n,t}(\mathcal{G}_n(\mathbf{m}_t)))$ . The fitness contribution is then given by

$$351 \quad f_{n,t}(m, \mathcal{G}_n(\mathbf{m}_t) | m_{t-1}) = \begin{cases} R_{n,t}(\mathcal{G}_n(\mathbf{m}_t)) - \lambda & m_t \neq m_{t-1}, \\ R_{n,t}(\mathcal{G}_n(\mathbf{m}_t)) & m_t = m_{t-1}. \end{cases} \quad (41)$$

352 It is clear that these fitness contributions vary with time, as the first move from  
353 the home place follows the distribution for a lone individual, and then movement  
354 depends upon the groups formed. For instance in a population entirely composed of  
355 cooperators, individuals would almost cease to move when they had found another  
356 cooperator, so the level of movement would decrease (and the fitness contributions  
357 would increase) with time, until the exploration time  $T$  is reached.  
358

359 3.2.4. *Evolutionary dynamics.* We assume that the replacement weight contribu-  
 360 tion will only depend upon the direct group. As in [9], the replacement weight  
 361 contribution will depend upon the amount of time spent with each individual. In  
 362 particular, it is assumed that an individual spends an equal amount of time with  
 363 each individual in the group excluding itself. However, if the individual is alone,  
 364 then it effectively allocates all the time to itself. The replacement weight contribu-  
 365 tion function is then defined as follows

$$366 \quad u_{i,j,t}(\mathcal{G}_i(\mathbf{m}_t)) = \begin{cases} 1/|\mathcal{G}_i(\mathbf{m}_t) \setminus \{i\}| & i \neq j \text{ and } j \in \mathcal{G}_i(\mathbf{m}_t), \\ 0 & i \neq j \text{ and } j \notin \mathcal{G}_i(\mathbf{m}_t), \\ 1 & i = j \text{ and } |\mathcal{G}_i(\mathbf{m}_t)| = 1, \\ 0 & i = j \text{ and } |\mathcal{G}_i(\mathbf{m}_t)| > 1. \end{cases} \quad (42)$$

367  
 368 We note that combining equations (24) and (42), we have that  $w_{i,j} = w_{j,i}$  and  
 369  $w_{i,i} = 1 - \sum_{j \neq i} w_{i,j}$ , which implies that our selected weights have the *isothermal*  
 370 property (see [31]).

371 3.2.5. *Simulating the evolutionary Markov chain.* The approach used in this paper  
 372 to calculate the fixation probability is a semi-analytic one where the fitnesses of  
 373 individuals are found by simulation, and these results are then used to evolve the  
 374 population using the evolutionary Markov chain, which results in a more accurate  
 375 solution than simulating the whole process (the movement process is too complex  
 376 to allow for a fully analytic solution).

377 Individuals start on their home place and then undergo an exploration phase of  
 378  $T$  time steps as described in Section 3.2.2. To calculate the fitness, the individuals  
 379 move  $T$  times such that their fitness contribution is calculated for each of these  
 380 movements; the total of these  $T$  fitness contributions gives their fitness for one  
 381 simulation. The position of the individuals is then reset, that is, they return to  
 382 their home place before the next simulation is run. Their average fitness for 10,000  
 383 simulations is used in the evolutionary Markov chain.

384 To calculate the replacement weights, individuals start on their home place and  
 385 move only one time to determine their replacement weight. This represents indi-  
 386 viduals returning to their home place to reproduce, with individuals being replaced  
 387 according to the corresponding local connections. This counts as one simulation  
 388 and, before the next simulation is run, we reset the position of the individuals so  
 389 they all start in their home place. The replacement weights are calculated exactly  
 390 because they comprise of only one movement. This involves calculating the prob-  
 391 ability that an individual is alone, which gives the self-replacement weight. The  
 392 other replacement weights are simply 1 minus the self-replacement weight divided  
 393 by  $N - 1$  because the probability of replacing the other individuals is the same for  
 394 a complete graph.

395 The fitnesses and the replacement weights are all that is required to construct  
 396 the transition probabilities of the evolutionary Markov chain. The transition prob-  
 397 abilities are substituted into the formula of [28] to give the fixation probability of  $i$   
 398 type  $A$  mutants in a population of  $N - i$  type  $B$  residents as follows

$$399 \quad \rho_i^A = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^j \frac{P_k^-}{P_k^+}}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^j \frac{P_k^-}{P_k^+}} \quad (43)$$

400

401 where  $P_k^-$  ( $P_k^+$ ) is the backward (forward) transition probability for a state with  
 402  $k$  type  $A$  individuals. Note that the weights  $w_{ij}$  and the fitnesses from Section  
 403 3.2.3 depend upon the composition of the population, so at successive steps of the  
 404 evolutionary Markov chain the transition probabilities will in general be different.

405 We also note that this formula can easily be modified to find the fixation proba-  
 406 bility of type  $B$  individuals. What exactly makes a type  $A$  or  $B$  individual would  
 407 depend upon its interactive strategy and staying propensity. For example, we could  
 408 have that  $A = C_{0.1}$  and  $B = D_{0.5}$ , which means that type  $A$  is a cooperator with  
 409 a staying propensity of 0.1 and type  $B$  is a defector with staying propensity 0.5,  
 410 or we could have  $A = C_{0.1}$  and  $B = C_{0.2}$  so both types have the same behavioural  
 411 strategy but different staying propensities. However, the important thing to note is  
 412 that, at any one time, there are only two unique types  $A$  and  $B$  in the population.

413 The advantage of such an approach is that we can relatively quickly calculate the  
 414 fixation probability starting from any state. The saving comes from the fact that  
 415 we do not simulate the entire process, which would take much longer because the  
 416 number of steps to reach fixation could be high. However, this approach necessarily  
 417 requires that we have a population in which individuals can differ only in terms  
 418 of their type. To ensure that this is the case, we consider a complete structure  
 419 with  $N$  places such that each individual has their own home place. We note that the  
 420 advantage of efficient algorithmic processes over simulations was demonstrated in  
 421 [48], but also that it was shown in [27] that for frequency-dependent selection this  
 422 approach will not work for arbitrary spatial populations.

423 **4. Results.** In this section the effect of the model parameters on the fixation prob-  
 424 ability are investigated. In particular, we investigate how the model parameters af-  
 425 fect *assortment*, which is the mechanism that allows cooperation to evolve as shown  
 426 in [22]. There is positive assortment between cooperators if they are more likely  
 427 to interact with other cooperators than defectors. In our model, this occurs due  
 428 to an increase (decrease) in the time it takes for defectors (cooperators) to find co-  
 429 operators. According to [20] the time to find cooperators should depend upon the  
 430 density of the population and an individual's movement speed. In their model,  $N$   
 431 individuals pair up with one another to form a coalition such that the probability of  
 432 a pair forming is exponentially distributed with rate  $\mu$ , which is a function of  $N$  and  
 433 the population density. The time to find cooperators in their model is essentially  
 434 determined by the rate  $\mu$ . We have one-to-one correspondence between individuals  
 435 and places and therefore the density remains constant; on the other hand, since we  
 436 consider a complete graph, the movement speed is high as individuals can directly  
 437 get from one place to another. Therefore, the time it takes to find cooperators is  
 438 mostly determined by the staying propensity of the individuals, however, this rela-  
 439 tionship is not so straightforward as it is not globally controlled and the individuals  
 440 may have different staying propensities (which are subject to the evolutionary pro-  
 441 cess). This means that some individuals may find cooperators faster than others.  
 442 The parameters used in the simulations are summarised in Table 3.

443 Apart from an individual's interactive strategy and staying propensity, all other  
 444 parameters are considered to be fixed. Each individual inherits these two charac-  
 445 teristics from its parent, and different interactive strategies or staying propensities  
 446 are introduced into the population through mutations. Staying propensities can  
 447 take any value  $0.01m$  for  $m = 1, \dots, 99$ ; this means that no individual moves all the  
 448 time or never, and so makes some adjustment to their behaviour depending upon

Parameter Set	1	2	3	4	5	6
$N$	10	10	10	20	10	10
$T$	10	5	25	10	10	10
$\lambda$	Variable	Variable	Variable	Variable	0.20	0.20
$c$	0.04	0.04	0.04	0.04	0.04	0.09
$v$	0.40	0.40	0.40	0.4	Variable	Variable

TABLE 3. Parameters used for the simulations. The other parameters are fixed such that we have a complete structure with each individual having its own home,  $\beta_C = 1$ ,  $\beta_D = -1$ ,  $S = 0.03$  and the dynamics used are BDB.

449 the group they are in. In particular we have  $\max(\alpha) = 0.99$ ; some movement is a  
450 necessary requirement otherwise the replacement weights would be zero and there  
451 would be no evolution within the population. In a real world setting, a minimum  
452 movement requirement can be explained by, for example, foraging behaviour where  
453 an individual searches its environment to find food and therefore needs to move in  
454 order to survive.

455 The mutations of these characteristics are sufficiently infrequent that the popu-  
456 lation is assumed to consist of a maximum of two types; resident and mutant, whose  
457 competition will result in fixation of one of the types before a new mutant appears.  
458 We consider two different scenarios to account for the different mutation rates of  
459 each characteristic.

460 **4.1. Scenario A: Interactive strategy mutations are rare.** As previously  
461 stated, it is assumed that fixation happens much faster than new mutations arise.  
462 A mutation can result in a change of the interactive strategy and/ or the staying  
463 propensity. In this scenario, the mutation rate of an individual's interactive strat-  
464 egy is much slower than the rate of mutations that involve their staying propensity.  
465 Since it is much more likely that the staying propensity mutates than the inter-  
466 active strategy does, once one of the interactive strategies (cooperate or defect) is  
467 removed from the population, it will be a long time before a new mutant involving  
468 this strategy appears. During this time, there will be a sequence of contests among  
469 individuals with the same interactive strategy but different staying propensities and  
470 the population will eventually evolve to the point where all individuals have the  
471 same interactive strategy and are using a (strict) Nash equilibrium staying propen-  
472 sity (a strict Nash equilibrium propensity is one where the fixation probability is  
473 maximised and changing the staying propensity is disadvantageous). Eventually, a  
474 mutant with a different interactive strategy and staying propensity will appear, and  
475 the quantity of interest at this point is the fixation probability of this mutant type.  
476 We assume that the staying propensity of the mutant can be different from the  
477 Nash equilibrium staying propensity of the resident population it is invading. The  
478 resident population will therefore be stable if it can resist invasion from a mutant  
479 using any staying propensity. Rather than considering any arbitrary mutant, the  
480 focus will be on the mutant most likely to invade, i.e. one maximising its fixation  
481 probability.

482 Cooperator residents are of the type  $C_{\gamma_R}$  where their Nash equilibrium staying  
483 propensity  $\gamma_R$  is the staying propensity where  $a = b$  in the set

$$484 \quad \left\{ (a, b) : \rho_1^{C_a, C_b} = \max \left( \rho_1^{C_c, C_b} : c \in (0, 1) \right) \text{ and } b \in (0, 1) \right\}.$$

486 In this set we identify all the points  $(a, b)$  where  $a$  is the best response staying  
487 propensity of 1 individual of type  $C_a$  when playing against  $N - 1$  individual of type  
488  $C_b$ , who are using some arbitrary staying propensity  $b$ . Therefore, at the point  
489 where  $a = b$ ,  $C_a$  is a best response to itself, i.e. a Nash equilibrium.

490 A defector mutant is of the type  $D_{\delta_M}$  where the staying propensity  $\delta_M$  satisfies

$$491 \quad \rho_1^{D_{\delta_M}, C_{\gamma_R}} = \max \left( \rho_1^{D_c, C_{\gamma_R}} : c \in (0, 1) \right).$$

493 Defector residents are of the type  $D_{0.99}$  (i.e. in the equivalent terminology to the  
494 above  $\delta_R = 0.99$ ) where their Nash equilibrium staying propensity is  $\max(\alpha) = 0.99$   
495 whenever the movement cost is greater than 0 because the only way for them to  
496 maximize their fixation probability is by moving as little as possible.

497 A cooperator mutant is of the type  $C_{\gamma_M}$  where the staying propensity  $\gamma_M$  satisfies

$$498 \quad \rho_1^{C_{\gamma_M}, D_{0.99}} = \max \left( \rho_1^{C_c, D_{0.99}} : c \in (0, 1) \right).$$

500 The Nash equilibrium staying propensity of the resident cooperators  $\gamma_R$  is cal-  
501 culated as follows. We consider  $N - 1$  residents of the type  $C_b$  and calculate the  
502 fixation probability of 1 individual of the type  $C_a$  for all values of  $a$  in the range  
503  $[\max(0.01, b - 0.09), \min(b + 0.09, 0.99)]$ , and the  $a$  that gives the highest fixation  
504 probability is picked. Note that using a wider range of values for  $a$  gives the same  
505 result so this range is used for efficiency. The  $N - 1$  residents then use the staying  
506 propensity  $a$  that was picked and this process is repeated several times. After around  
507 20 repetitions, the staying propensity that gives the maximum fixation probability  
508 remains the same, that is, we can see that is a (strict) Nash equilibrium because  
509 it is a best response to itself and any other strategy will be disadvantageous. We  
510 therefore set  $\gamma_R$  to the value of  $a$  we get after 20 repetitions.

511 We hypothesize that there is only one solution to the Nash equilibrium staying  
512 propensity. As seen in Figure 1, the best response staying propensity of one type  
513  $C_a$  against  $N - 1$  type  $C_b$  is relatively flat (the jagged line of the figure being  
514 an approximation to a smooth “real” value, caused by the stochasticity of the  
515 simulations). Intuitively the real solution should be smooth; a small change in the  
516 movement cost would have a small change on the payoff to a focal individual. It is  
517 possible that at some point this would lead to a sudden jump of the best response  
518 strategy as the payoffs from two different values pass. We would expect to see either  
519 a single smooth continuous function for the best response, or a piecewise continuous  
520 collection of distinct parts, and it is the former that we have here. This flatness  
521 means that the best response staying propensity is predominantly determined by  
522 the movement cost  $\lambda$  regardless of what the other players are doing. Therefore,  
523 there is only one intersection point with the line  $a = b$  as shown in Figure 1, which  
524 gives the Nash equilibrium staying propensity  $\gamma_R$  of resident cooperators. A non-  
525 unique solution would occur if there were multiple crossings (or indeed no crossings,  
526 which would need a discontinuity in Figure 1, as described above). We should note  
527 that we have no proof of the uniqueness of the Nash equilibrium staying propensity,  
528 although in all cases considered, the solution to the process described in the previous  
529 paragraph is independent of the starting position.

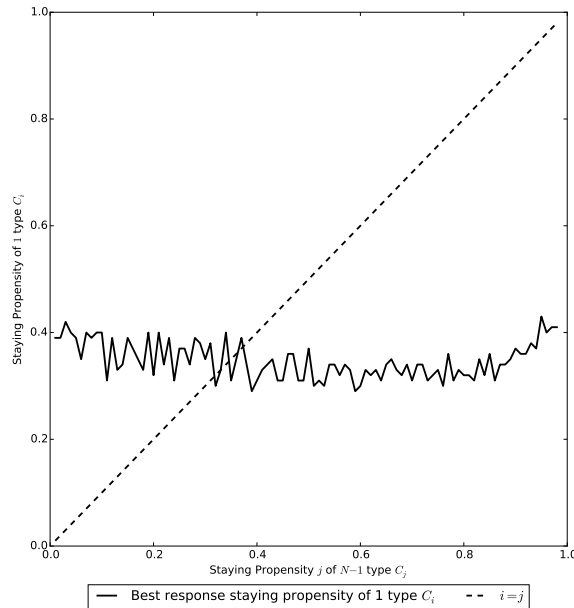


FIGURE 1. This plot shows the best response staying propensities for 1 type  $C_i$  individual playing against  $N - 1$  type  $C_j$  individuals. Parameter set 1 is used with  $\lambda = 0.2$  and  $i, j \in \{0.01, 0.02, \dots, 0.99\}$ . The intersection point of the plots gives the unique strategy which is a best response to itself, i.e. the unique cooperator resident Nash equilibrium staying propensity  $\gamma_R$ , which is somewhere between 0.3 and 0.4. This value is similar to the one obtained using the iterative method (see Figure 2). The values from the current figure are approximate only because of the jagged nature of the lines; these occur because of the very large number of simulations that would be necessary to obtain a smooth version (the figure uses 10000 simulations for each combination). The figure is used to illustrate the uniqueness of the solution only.

530 4.1.1. *The effect of the movement cost.* In Figure 2 the effect of the movement  
 531 cost is shown. In particular, it increases the time it takes to find cooperators by  
 532 increasing the staying propensity, that is,  $\gamma_R, \gamma_M, \delta_M$  are positively correlated with  
 533 movement cost; the (partial) exception is resident defectors, which we know have a  
 534 staying propensity of  $\max(\alpha) = 0.99$  regardless of the movement cost.

535 For very low movement cost, both mutant types have a significantly lower staying  
 536 propensity than the resident population that they are invading. They can therefore  
 537 invade the resident population because they take less time to find cooperators.

538 For higher, but still low, movement costs, whilst mutant cooperators can still  
 539 invade, mutant defectors cannot. Here the resident cooperators are better at pre-  
 540 venting invasion even when  $\delta_M < \gamma_R$  for some values of the movement cost. This  
 541 is because the movement cost impacts the invading mutant defector more adversely  
 542 than the resident cooperators, who on average leave and regroup less often than a  
 543 defector who will be repeatedly deserted by its cooperator groupmates.

544 For intermediate movement costs, neither mutant type can invade. At this point,  
 545 since  $\delta_M > \gamma_R$ , a mutant defector is slower at finding cooperators than the resident  
 546 cooperators and therefore cannot take advantage of them. For a mutant cooperator,  
 547  $\gamma_M$  becomes much larger thereby diminishing their advantage over the resident  
 548 defectors, in particular, not only are they paying a higher movement cost but it  
 549 takes longer to find the other cooperators, which in turn reduces the amount of  
 550 time that they can spend with them.

551 For high movement costs, defecting mutants can invade, but cooperator mutants  
 552 cannot. At this point all types have a large staying propensity and therefore do  
 553 not interact much with one another. However, a mutant defector is helped by the  
 554 fact that the resident cooperators always pay a cooperating cost that they now find  
 555 difficult to recoup because they are moving very little and also paying a very large  
 556 movement cost whenever they do so.

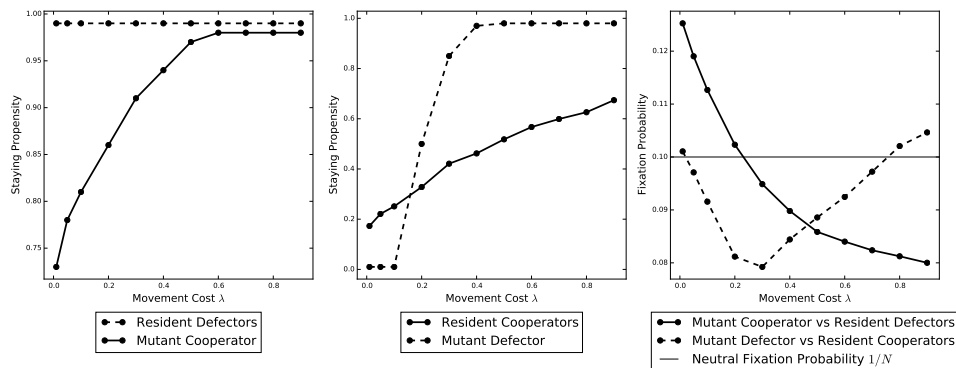


FIGURE 2. These plots show the effect of movement cost on the evolution of cooperation using parameter set 1. The left (centre) plot shows the staying propensities  $\delta_R = 0.99$  ( $\gamma_R$ ) for resident defectors (cooperators) and  $\gamma_M$  ( $\delta_M$ ) for a mutant cooperator (defector) used to invade the resident population. In the right plot, we have the fixation probability of a mutant cooperator  $C_{\gamma_M}$  (defector  $D_{\delta_M}$ ) against  $N - 1$  resident defectors  $D_{0.99}$  (cooperators  $C_{\gamma_R}$ ).

557 4.1.2. *The effect of the exploration time.* The exploration time  $T$  plays an important  
 558 role in the evolution of cooperation. Changing the exploration time has a minimal  
 559 effect on the time it takes to find cooperators because it will not alter the speed of  
 560 movement of the individuals. This is because we are using a complete graph and  
 561 individuals can directly get from one place to any other. However, increasing the  
 562 exploration time has a positive effect on the coalition time, that is, the amount  
 563 of time that cooperators spend cooperating with one another. [20] showed that  
 564 increasing the coalition time helps with the evolution of cooperation. In our model,  
 565 one explanation for this is that the fitness of the individuals, which is the average  
 566 reward over the exploration time, will naturally have a higher value the larger the  
 567 coalition time.

568 In Figure 3 reducing the exploration time  $T$  from 10 to 5 steps decreases the  
 569 coalition time which adversely affects the cooperators. One of the key differences  
 570 is that the resident cooperators now find it much more difficult to prevent invasion



571 from a mutant defector. The shape of the plot for a mutant cooperator is largely  
 572 the same but with a consistently lower fixation probability. In Figure 4 increasing  
 573 the exploration time  $T$  from 10 to 25 steps benefits the cooperators. Not only does  
 574 it help the resident cooperators prevent invasion from a mutant defector but it also  
 575 increases the success of an invading mutant cooperator. This again has to do with  
 576 the increased coalition time that allows the cooperators to increase their fitness.

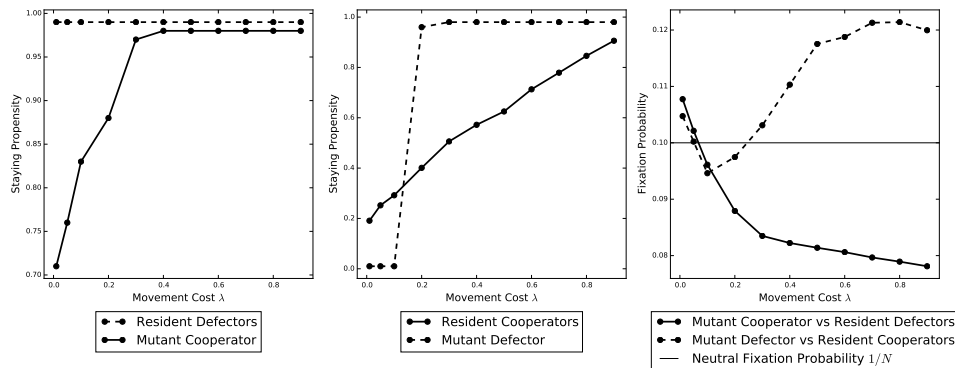


FIGURE 3. Plots created using parameter set 2. The exploration time  $T$  has been decreased from 10 to 5.

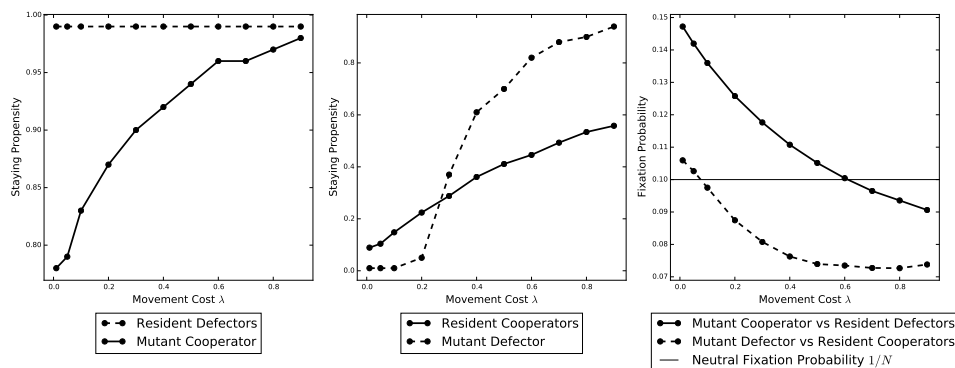


FIGURE 4. Plots created using parameter set 3. The exploration time  $T$  has been increased from 10 to 25.

577 4.1.3. *The effect of population size.* Fixation probability is reduced in general when  
 578 the size of the population increases, as we see when comparing Figures 2 and 5,  
 579 with population sizes of 10 and 20 respectively. The key value to compare fixation  
 580 probabilities against is the neutral fixation probability of  $1/N$ , the horizontal line  
 581 in each of these figures, however. We see that the fixation probability is slightly  
 582 higher for cooperators when compared to this line for the larger population of Figure  
 583 5 (although it is also more sensitive to the movement cost) than for the smaller  
 584 population. The key difference is that a mutant defector has fixation probability  
 585 consistently under the neutral line in Figure 5 and so cannot invade even for very

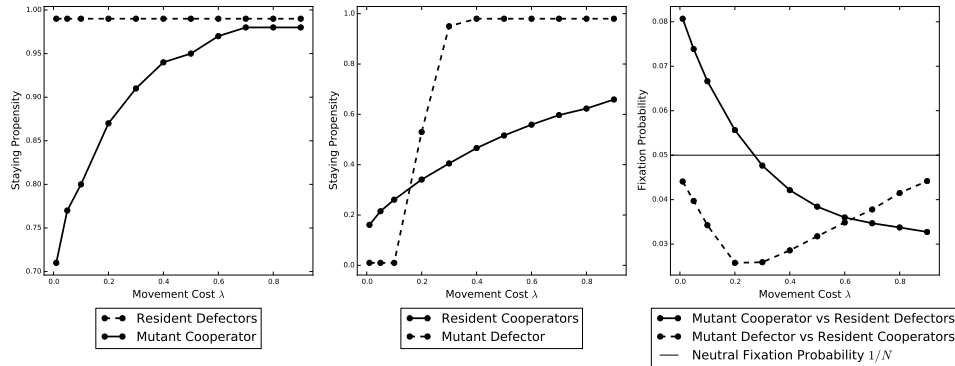


FIGURE 5. Plots created using parameter set 4. The population size has been increased from 10 to 20.

low movement cost in the larger population. Thus larger populations help a little in establishing cooperation, but help a lot in making it stable against defection.

Increasing the population size has a positive impact on the evolution of cooperation because it increases the time it takes to find cooperators. Note that we are assuming that there is a one-to-one correspondence between individuals and places and therefore increasing the number of individuals also increases the number of places. Even though the density remains the same, there would be more places for the individuals to search in order to find cooperators thereby increasing the overall time it takes to find cooperators. In particular, an individual that is currently not in a cooperating group will have to search  $N - 1$  places to find one, therefore, the probability of a defector finding a cooperating group decreases as  $N$  gets larger. This means that cooperators would resist invasion by defectors better, as we have noted above.

4.1.4. *The effect of reward and cost.* The reward to cost ratio  $v/c$  is important because, even if other external factors favour cooperation, cooperation will not evolve if the reward to cost ratio is too low. This is seen in Figure 6 where the cost is set to 0.04 with the reward written as a multiple of the cost. When  $v/c$  is low, a mutant cooperator cannot invade but a mutant defector can. This is simply because the value of  $v/c$  is too low to promote cooperation. Increasing  $v/c$  makes cooperation more viable and, in particular, it allows a mutant cooperator to reduce the time it takes to find cooperators by reducing its staying propensity. It becomes more difficult for a mutant defector to invade because, on average, resident cooperators move less than the mutant defector as they are more in number and the larger  $v/c$  helps them quickly recoup any movement cost they incur whilst evading the mutant defector. This is the case even when  $\delta < \gamma_R$ , that is, a mutant defector takes less time to find cooperators. For comparison with a different value of  $v/c$ , in Figure 7 the cost is set to 0.09. However, there is no fundamental change in what happens and we have a very similar figure to that for  $c = 0.04$ .

4.2. **Scenario B: Interactive strategy mutation is not rare.** In this scenario, the mutation rate of an individual's interactive strategy is not much slower than that of their staying propensity. Since the staying propensity would take a number of mutations to reach the right level for any scenario, any successful strategy will have

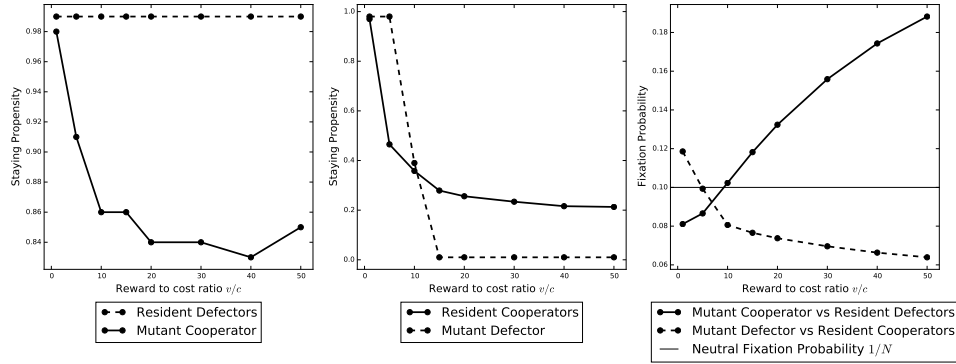


FIGURE 6. Plots have been created using parameter set 5. The plots here are against the reward to cost ratio  $v/c$  such that  $c = 0.04$ .

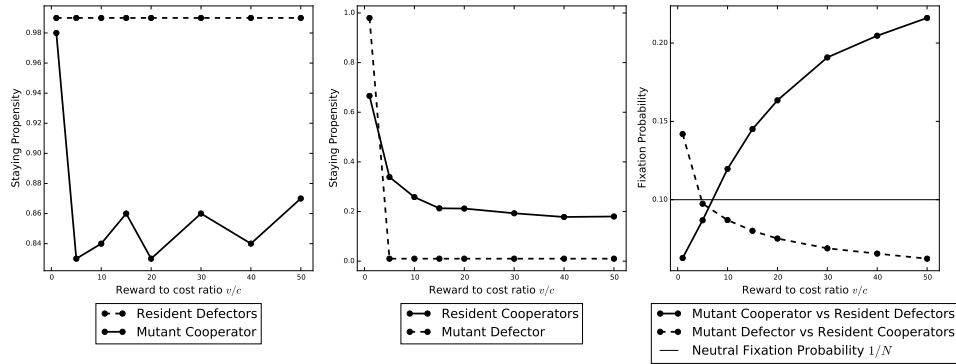


FIGURE 7. Plots have been created using parameter set 6. The plots here are against the reward to cost ratio  $v/c$  such that  $c = 0.09$ .

618 to repeatedly face individuals of both types. The (strict) Nash equilibrium staying  
 619 propensity will then be determined in a mixed population, i.e. there are individuals  
 620 of both types. For simplicity we choose only one mixed state to determine the Nash  
 621 equilibrium staying propensity which is the one where there are  $N/2$  individuals of  
 622 each type. The Nash equilibrium staying propensity for each type is therefore the  
 623 one in which the fixation probability from the mixed state of each type is maximised.

624 Resident and mutant defectors are of the same type  $D_\delta$ . Similarly, resident  
 625 and mutant cooperators are of the same type  $C_\gamma$ . The Nash equilibrium staying  
 626 propensities  $\delta$  and  $\gamma$  are determined by the intersection of the following two sets

$$627 \quad \left\{ (a, b) : \rho_{N/2}^{C_a, D_b} = \max \left( \rho_{N/2}^{C_c, D_b} : c \in (0, 1) \right) \text{ and } b \in (0, 1) \right\},$$

$$628 \quad \left\{ (a, b) : \rho_{N/2}^{D_b, C_a} = \max \left( \rho_{N/2}^{D_c, C_a} : c \in (0, 1) \right) \text{ and } a \in (0, 1) \right\}.$$

629

630 In the first set we are finding the Nash equilibrium staying propensity  $a$  of  $N/2$  type  
 631  $C_a$  playing against  $N/2$  type  $D_b$ , where  $b$  is some arbitrary staying propensity. In  
 632 the second set we are finding the Nash equilibrium staying propensity  $b$  of  $N/2$  type

633  $D_b$  playing against  $N/2$  type  $C_a$ , where  $a$  is some arbitrary staying propensity. The  
 634 point at which these two sets intersect is  $(\gamma, \delta)$ , that is, both types will be using  
 635 their Nash equilibrium staying propensities.

636 To calculate  $\gamma$  and  $\delta$  we use a similar iterative procedure from scenario A. To  
 637 initialise the iterative procedure we arbitrarily choose some staying propensities  $a_0$   
 638 and  $b_0$ , and the iterative step is as follows. We calculate the fixation probability  
 639 of  $N/2$  type  $C_a$  individuals against  $N/2$  type  $D_{b_0}$  for all values of  $a$  in the range  
 640  $[\max(0.01, a_0 - 0.09), \min(a_0 + 0.09, 0.99)]$ . The staying propensity  $a$  that gives the  
 641 maximum fixation probability is picked, which is labelled  $a_1$ . We then calculate the  
 642 fixation probability of  $N/2$  type  $D_b$  individuals against  $N/2$  type  $C_{a_1}$  for all values  
 643 of  $b$  in the range  $[\max(0.01, b_0 - 0.09), \min(b_0 + 0.09, 0.99)]$ . The staying propensity  
 644  $b$  that gives the maximum fixation probability is picked, which is labelled  $b_1$ . Note  
 645 that using a wider ranges for  $a$  and  $b$  gives the same result so these ranges were  
 646 used for efficiency. After around 20 repetitions of the iterative step, the staying  
 647 propensities  $a$  and  $b$  that give the maximum fixation probability remain the same,  
 648 which means that we are at a (strict) Nash equilibrium because any other values  
 649 would be disadvantageous. We therefore set  $\gamma = a_{20}$  and  $\delta = b_{20}$ .

650 We hypothesize that  $\gamma$  and  $\delta$  are unique. For cooperators, their Nash equilibrium  
 651 staying propensity is relatively stable because it is predominantly determined by the  
 652 movement cost regardless of what the defectors are doing. As seen in Figure 8, the  
 653 plot for this is a roughly vertical line. For defectors, their Nash equilibrium staying  
 654 propensity is negatively correlated with the staying propensity of the cooperators  
 655 given that the movement cost is not too large, otherwise it would be  $\max(\alpha)$ . In  
 656 Figure 8, the plot for this slopes downwards as the staying propensity of the coop-  
 657 erators increases. There is therefore only one intersection point of the two curves  
 658 that gives  $\gamma$  and  $\delta$ .

659 4.2.1. *The effect of movement cost.* As in scenario A, the movement cost increases  
 660 the staying propensity of the individuals and, therefore, increases the time it takes  
 661 to find cooperators. As seen in Figure 9, what happens in this case is quite different  
 662 to the situation in scenario A. Here, the mutant cooperator does not benefit from  
 663 the fact that the resident defectors have a very high staying propensity as in scenario  
 664 A. In this case,  $\delta$  changes with the movement cost in a similar way that  $\gamma$  changes.  
 665 Therefore, the key difference here is that a mutant cooperator cannot invade for  
 666 very low movement cost because the resident defectors have a very low staying  
 667 propensity, which means that they take much less time to find cooperators.

668 4.2.2. *The effect of exploration time.* As in scenario A, the cooperators do worse  
 669 when the exploration time is lower; this is shown in Figure 10 where  $T$  is decreased  
 670 from 10 to 5, and in Figure 11 where  $T$  is increased from 10 to 25. The explanation  
 671 is as in scenario A where the coalition time is lower when the exploration time is  
 672 lower and the coalition time increases, since, as we already know, increasing the  
 673 coalition time helps the cooperators do better.

674 4.2.3. *The effect of population size.* Similarly to scenario A, increasing the popu-  
 675 lation size helps cooperators as shown in Figure 12, where  $N$  is increased from 10  
 676 to 20. As before, increasing the population size increases the time it takes to find  
 677 cooperators because there is a one-to-one correspondence between individuals and  
 678 places. Increasing the population size therefore increases the number of places that  
 679 need to be searched to find cooperators. Furthermore, as in scenario A, a mutant  
 680 defector can no longer invade resident cooperators for very small movement cost.

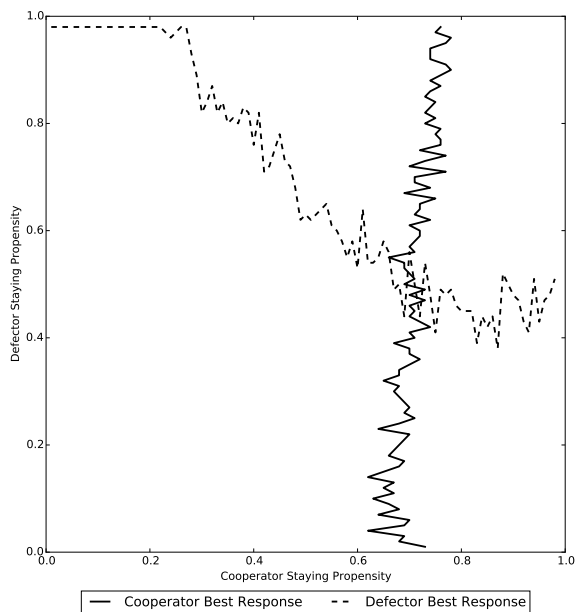


FIGURE 8. This plot shows the best response cooperator staying propensity (solid line, value shown on the x-axis) versus the range of defector staying propensities on the y-axis, and the best response defector staying propensity (dashed line, value shown on the y-axis) versus the range of cooperator staying propensities (on the x-axis) for  $N/2$  cooperators and  $N/2$  defectors. Parameter set 1 is used with  $\lambda = 0.2$  and the staying propensities are chosen from the set  $\{0.01, 0.02, \dots, 0.99\}$ . The best response staying propensities cross at one point only, which is thus the unique Nash equilibrium, where  $\gamma \approx 0.7$  and  $\delta \approx 0.5$ . These values are similar to those obtained using the iterative method described earlier (see Figure 9). As before, the values from the current figure are approximate only because of the jagged nature of the lines; the figure is used to illustrate the uniqueness of the solution only.

681 4.2.4. *The effect of reward and cost.* For a mutant defector, the effect of the reward  
682 to cost ratio  $v/c$  is the same as in scenario A. However, a mutant cooperator does  
683 not do better with increasing  $v/c$ . In this scenario, the fixation probability of a  
684 mutant cooperator peaks, then starts dropping, as  $v/c$  is increased. This is because  
685 the resident defectors have a very low staying propensity, and are therefore faster at  
686 finding cooperators, making it difficult for a mutant cooperator to invade because it  
687 cannot avoid the defectors. This is shown in Figure 13 where  $c = 0.04$ . Increasing  
688 the cost  $c$  though, makes it even more difficult for the cooperators regardless of  $v/c$ .  
689 In Figure 14, a mutant cooperator cannot invade for any  $v/c$ . This is because a  
690 larger  $c$  reduces the cooperators' background fitness by a larger amount, increasing  
691 the handicap that the cooperators already have.

692 4.3. **The effect of other parameters.** The effects of other parameters are not  
693 shown using plots but will be explained in this section.

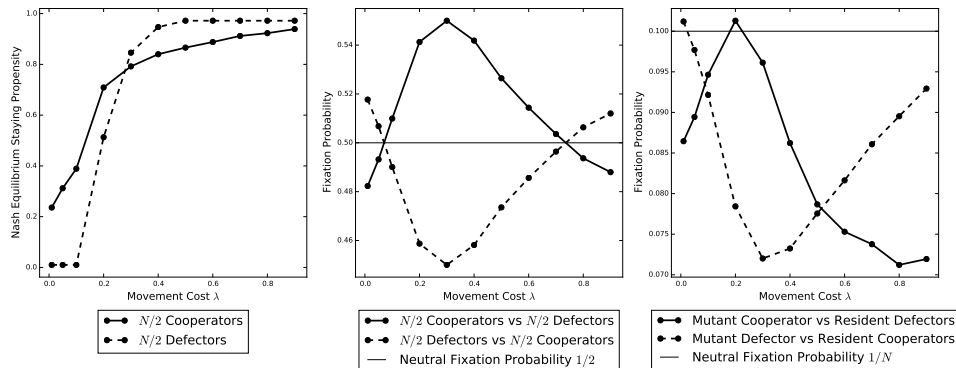


FIGURE 9. These plots show the effect of movement cost  $\lambda$  on the evolution of cooperation and are created using parameter set 1. The plot on the left shows the Nash equilibrium staying propensity  $\gamma$  for cooperators and  $\delta$  for defectors in a mixed population where there are  $N/2$  individuals of each type. The plot in the centre shows the fixation probability of each type from the mixed state with  $N/2$  individuals of each type. The plot on the right shows the fixation probability of a mutant cooperator  $C_\gamma$  (defector  $D_\delta$ ) in a population of  $N - 1$  resident defectors  $D_\delta$  (cooperators  $C_\gamma$ ).

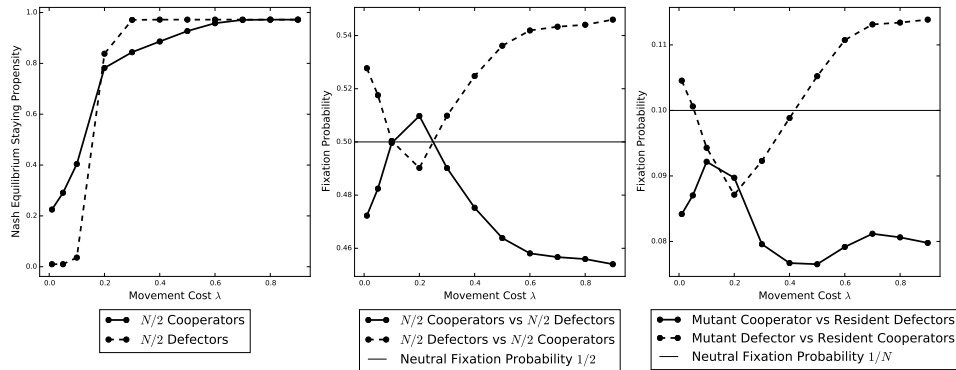


FIGURE 10. Plots created using parameter set 2. Plots are as in Figure 9 with exploration time  $T$  decreased from 10 to 5.

694 Making the individuals more sensitive to their group members by decreasing the  
 695 sensitivity parameter  $S$  improves the chances of cooperation evolving. In equation  
 696 (38), we can see that decreasing  $S$  will increase the size of the denominator if  
 697 the group benefit is negative, thereby increasing the probability that an individual  
 698 moves away from its current position if it is undesirable to stay. Therefore, as  $S \rightarrow 0$   
 699 the more sensitive individuals become, which helps the evolution of cooperation  
 700 because it reduces the exploitation of cooperators (cooperators are now more likely  
 701 to move away if the group they are in becomes undesirable).

702 Another way in which the group member sensitivity can be changed is by choosing  
 703  $\beta_A > 0$  and  $\beta_B < 0$  such that  $\beta_B/\beta_A \rightarrow -\infty$ . As seen in equation (38), this will

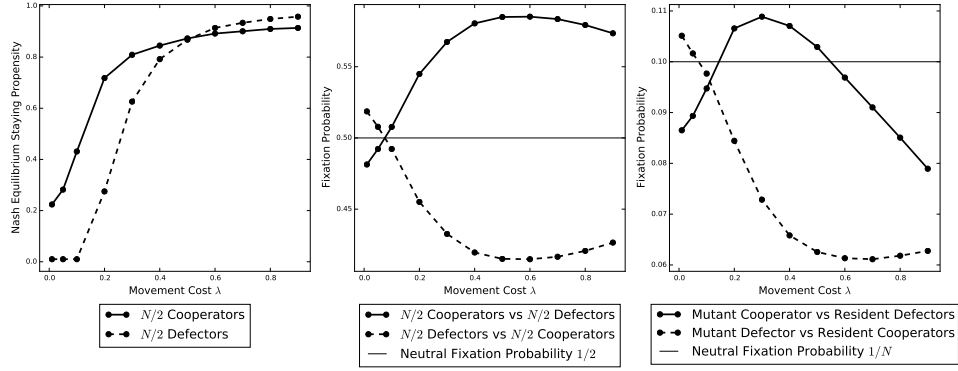


FIGURE 11. Plots created using parameter set 3. Plots are as in Figure 9 with exploration time  $T$  increased from 10 to 25.

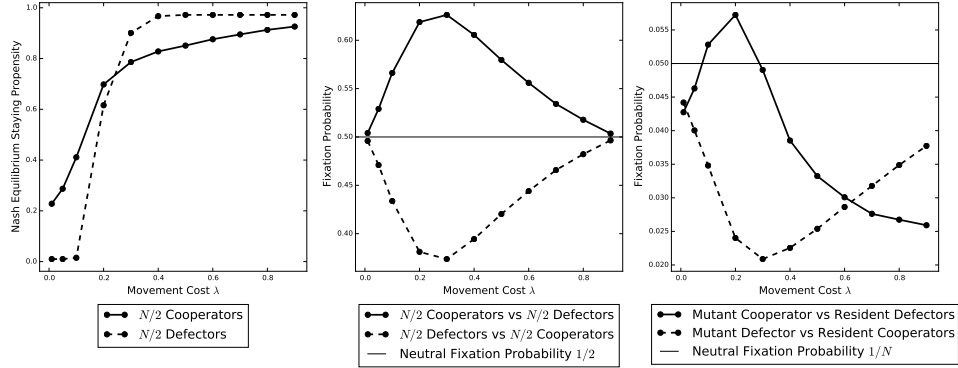


FIGURE 12. Plots created using parameter set 4. Plots are as in Figure 9 with population size  $N$  increased from 10 to 20.

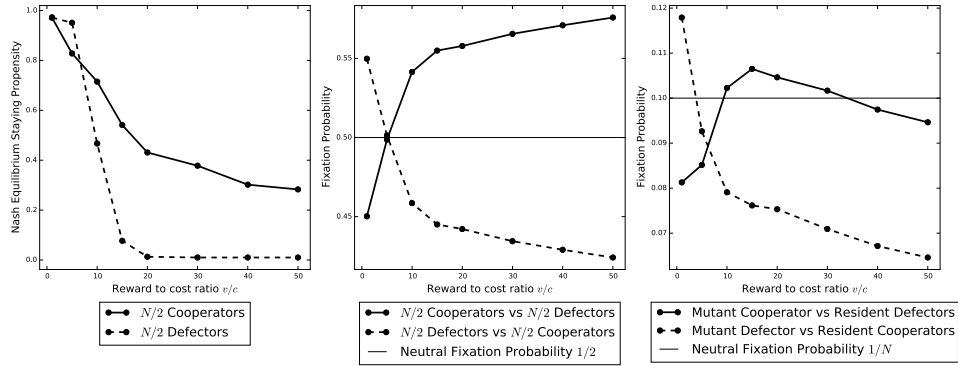


FIGURE 13. Plots created using parameter set 5. Plots are as in Figure 9 but  $\lambda$  is fixed and reward to cost ratio  $v/c$  varied such that  $c = 0.04$ .

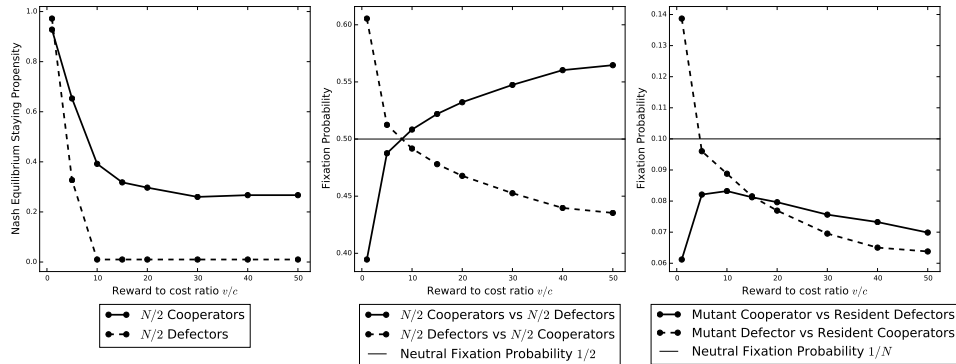


FIGURE 14. Plots created using parameter set 5. Plots are as in Figure 9 but  $\lambda$  is fixed and reward to cost ratio  $v/c$  varied such that  $c = 0.09$ .

704 cause the group benefit to become negative very quickly in the presence of a defector,  
 705 even if there are significantly more cooperators present. Once again, this reduces  
 706 the exploitation of cooperators by defectors, hence, improving the chances that  
 707 cooperation evolves.

708 In all of the plots shown, we have only used BDB dynamics because the effect of a  
 709 change to other dynamics is quite small. The reason for this is that the evolutionary  
 710 graph is always complete, that is, whilst the replacement weights change, all indi-  
 711 viduals can still replace one other. For example, in the case of DBB dynamics, to  
 712 make a significant difference a defector randomly chosen for death should be more  
 713 likely to be replaced with the offspring of a cooperator. However, this is not the  
 714 case here and, in particular, the only way the evolutionary graph can be changed  
 715 is by changing the staying propensity such that increasing the staying propensity  
 716 increases the probability that an individual replaces itself. Therefore, the dynamics  
 717 overall have a small effect. We note that this would not be the case for some other  
 718 underlying structure that was not complete.

719 **4.4. The limiting fixed fitness case.** Our general framework is complex, and  
 720 hence so far there have been few analytical results associated with it. In particular  
 721 payoffs for the games considered, the public goods game as in the current paper and  
 722 the multiplayer Hawk Dove game as in [9], are frequency dependent, and so general  
 723 analytical solutions are hard to find. This is especially true for history-dependent  
 724 models such as the Markov model that we consider in this paper.

725 An alternative, simpler, case is that of fixed fitness, i.e. where payoffs depend  
 726 only upon an individual's type, and not its interactions. This case is considered  
 727 in many of the classical evolutionary graph theory papers, and in particular yields  
 728 some analytical solutions (see for example [31, 10, 53]). We note that this applies  
 729 for the public goods game considered here in the limiting case of either very small  
 730  $v$  or the probability of being alone being close to 1 (i.e.  $|\mathcal{G}_n(\mathbf{m})| = 1$  almost  
 731 always), in which case we approximately have fitnesses of 1 and  $1 - c$  for defectors  
 732 and cooperators, respectively. Here, the interactions only affect the replacement  
 733 probabilities as described in Section 2.3. Below we shall give some new analytical  
 734 results for our framework for this fixed fitness case.



735 The classical fixed fitness models involve a resident population of fitness 1 and  
 736 an invading mutant of fitness  $r$ . The Moran fixation probability is given as

$$\rho_{\mathcal{S}}^A = \begin{cases} \frac{1 - (1/r)^{|\mathcal{S}|}}{1 - (1/r)^N} & r \neq 1, \\ |\mathcal{S}|/N & r = 1, \end{cases} \quad (44)$$

737 where  $\rho_{\mathcal{S}}^A$  denotes the fixation probability of a set of mutants  $\mathcal{S}$  in a completely  
 738 unstructured population (because the population is unstructured, only the number  
 739 of mutants matters). A complete analysis of the conditions under which fixation on  
 740 an evolutionary graph satisfies the Moran probability was carried out in [45] and  
 741 was summarised as Table 2 of that paper.

742 For the weights used in this paper (and commonly elsewhere) the weight matrix  
 743  $\mathbf{W}$  satisfies the isothermal property, as we have noted in Section 3.2.4. The con-  
 744 ditions for the Moran fixation probability to hold were shown in [45] to include all  
 745 isothermal cases for each of the four dynamics BDB, DBD, LB and LD. Thus for  
 746 the fixed fitness case and these selected weights, in our framework every popula-  
 747 tion is equivalent to the well-mixed population for these dynamics. Substituting  
 748 the payoffs we gave above for cooperators and defectors into equation 44, we then  
 749 have the following respective fixation probabilities for  $i$  cooperators (defectors) in  
 750 a population with  $N - i$  defectors (cooperators)

$$\rho_i^C = \frac{1 - (1/(1-c))^i}{1 - (1/(1-c))^N}, \quad (45)$$

$$\rho_i^D = \frac{1 - (1-c)^i}{1 - (1-c)^N}. \quad (46)$$

754 In our results we have used the BDB dynamics, so that in the limiting case of  
 755  $v \rightarrow 0$  we will obtain the fixation probabilities given above. It is easy to see that  
 756 that is indeed the case by substituting  $i = 1$  and  $N = 10$  into equations 45 and 46  
 757 and comparing with the fixation probabilities near the axis in the third subfigure  
 758 of Figures 6 and 13 ( $c = 0.04$ ) and Figures 7 and 14 ( $c = 0.09$ ).

759 This leaves the dynamics BDD and DBB. Only a very special subclass of weight  
 760 matrices, some isothermal and some not, could yield the Moran probability for these  
 761 two dynamics (different for each dynamics). Thus in general these dynamics will  
 762 not yield the Moran probability in the fixed fitness case, although for the structure  
 763 used in this paper this is actually a reasonable approximation.

764 Thus it is clear that, for the weights described in Section 3.2.4, our framework  
 765 affects evolution primarily through how it affects the fitnesses through the interac-  
 766 tion of individuals, and when this effect is removed (as above) significant structural  
 767 effects disappear. We note firstly that we can have different weights that do not  
 768 satisfy the isothermal condition, and so for which these results do not apply; for  
 769 example if self-replacement is replaced by a resampling from the distribution of  
 770 groups when an individual is alone.

771 Secondly, we note that some of the more extreme effects that occur in the fixed fit-  
 772 ness case from evolutionary graph theory come about precisely because the weights  
 773 involved are very uneven, for example relating to the star graph, where there is a  
 774 single central vertex with many neighbours but these vertices only have the central  
 775 vertex as a neighbour. The payoffs are typically calculated using either the average  
 776 or the total of a set of games, one played against each neighbour. Yet if we con-  
 777 sider weights in the way that we think of in the current paper, namely time spent

778 together, there is a problem with this. The central individual can only spend a  
779 small amount of time with each of its many neighbours. What then do these other  
780 individuals do the rest of the time? In the average payoff case they are effectively  
781 able to acquire the same payoff as for the interaction with their single neighbour  
782 (irrespective of what that is), in the total payoff case they gain zero for the rest of  
783 the time. In our framework individuals can gain certain payoffs when alone, and  
784 this would perhaps be logical for classical evolutionary graph theory too.

785 **5. Discussion.** In this paper we have developed the framework of [11], for consid-  
786 ering the evolution of structured populations involving multiplayer interactions, and  
787 in particular created a mode of a mobile population in which the movement of the  
788 individuals is Markov, where the place an individual moves to next depends upon  
789 their current position. In previous models [9], individuals moved independently of  
790 their current position so the model in this paper gives a different perspective on the  
791 movement of individuals. In particular, we looked at the movement of individuals  
792 in relation to the evolution of cooperation. In what follows, we discuss some of the  
793 results of this Markov movement model.

794 In the Markov movement model we considered in detail the version where the  
795 movement of individuals depends upon population history. Here, individuals make a  
796 decision of whether they should stay or leave their current position depending upon  
797 the other individuals present with them in the same place. This movement strategy  
798 is akin to the “walk away” strategy of [1, 2]. However, we note that this is only one  
799 interpretation we can use for the Markov movement model. The framework provides  
800 the tools to construct different kinds of Markov movement behaviour. For example,  
801 in [21], individuals would study all surrounding areas before making a decision about  
802 where to move to next. In terms of the framework, individuals would consider a  
803 larger subset of the current population distribution rather than just the distribution  
804 of individuals that are currently present with each other. Both simple and complex  
805 Markov movement behaviour provide useful insight into the movement behaviour  
806 of individuals but we have opted to start with a simpler behaviour to make it easier  
807 to show how the framework can be applied.

808 For cooperation to evolve, it was shown in [22] that there should be assortment, in  
809 particular there should be a mechanism that allows the cooperators to increase their  
810 preference for interacting with other cooperators. Here, this mechanism is provided  
811 by the Markov movement of the individuals. Our results are in line with [2] who also  
812 modelled the Markov movement of individuals where individuals would stay where  
813 they are if the payoff they received was above some minimum threshold. However,  
814 the structure we have used is substantially different. We have used a complete  
815 graph with one-to-one correspondence between individuals and places instead of a  
816 two-dimensional array. This means that there is a high potential movement speed  
817 as individuals can go directly from one place to another, which is mitigated in our  
818 model with the introduction of a movement cost. A higher staying propensity slows  
819 down an individual because they are more likely to stay where they are. In terms of  
820 choosing the staying propensity an individual should use, we calculated the staying  
821 propensity which maximises their fixation probability. We considered two different  
822 scenarios where the staying propensity of an individual mutates very quickly or  
823 slowly. The key difference between the two scenarios was that a mutant cooperator  
824 can invade a resident population of defectors for very low movement cost if their

825 staying propensity mutates very slowly. We also investigated the effect of changing  
826 the other model parameters.

827 The BDB dynamics used here allows cooperation to evolve even though typically  
828 selection does not favour cooperators with these dynamics [40]. Other dynamics  
829 that favour cooperators showed little improvement over the results we got for BDB  
830 dynamics. This shows that Markov movement is quite effective in allowing coopera-  
831 tion to evolve. Its effectiveness is further backed up by the fact that the structure of  
832 the evolutionary graph is complete, which is known to be detrimental for coopera-  
833 tors [40]. In particular, in a complete evolutionary graph all individuals can replace  
834 each other and, therefore, the individuals with the highest fitness are more likely to  
835 be favoured by selection. This shows that conditional movement makes the choice  
836 of dynamics being used less important.

837 We note that our work effectively involves a coevolution of population strategy  
838 and structure, and that there has been significant research on this over the past ten  
839 years or so, as in for example [42, 43]. In such models the growth and structure  
840 of the graph can be strongly influenced by the game played, as well as previous  
841 interactions of individuals. In this case connections between pairs of individuals  
842 change, and are formed or broken depending upon the types of the individuals,  
843 in a population that evolves with link dynamics happening on a faster timescale  
844 than the evolutionary dynamics. A similar but more general set-centred approach  
845 is considered in [56]. In [23] it is reputation rather than previous interactions that  
846 causes structural changes; in [15] the key factor is prosperity. For an excellent  
847 review of this type of work prior to 2010 see [47] (see also [3] for a more recent but  
848 more general review). As noted by [3], a common feature of a lot of this work is  
849 that cooperative behaviour occurs more readily when cooperators are able to both  
850 group themselves together and exclude defectors to a significant extent, and this is a  
851 feature of our work too. In our case a key difference is the presence of variable-sized  
852 multiplayer interactions, the distribution of which is closely linked to population  
853 structure.

854 Furthermore through our framework, we can see a clear connection between mod-  
855 els with mobile individuals as in the current paper, and those on a fixed structure.  
856 We see an interesting alternative (but which has a similar effect) in [16] and [17],  
857 where individuals are on a lattice and move when their current interactions are  
858 unsatisfactory. In [57] mobility (also on a lattice) is linked to reputation (where  
859 individuals with a higher reputation level than their locality tend to move). These  
860 works demonstrate that an intermediate level of mobility can help cooperation to  
861 evolve, which we have also seen in our different type of structure.

862 In this paper we have made several advances on our previous work. We have  
863 largely completed the development of the framework of [11] and have shown how it  
864 incorporates different aspects of evolutionary game theory thereby making it very  
865 flexible in terms of what can be modelled. We have then applied this to a Markov  
866 movement model, the simplest type of history-dependent model within our frame-  
867 work. In turn we have used this to explore the evolution of cooperative behaviour,  
868 making predictions upon when cooperation can occur, with high exploration time  
869 and low movement cost both helping cooperation; interestingly, the evolutionary  
870 dynamics used is not so important for our chosen model. The example model used  
871 in this paper made use of quite a simplistic territorial structure that allowed the  
872 results to be calculated semi-analytically, that is, only a part of the results were  
873 calculated using a simulation. In future, we would like to model a more complex

874 territorial structure to determine the effect this has on the evolution of coopera-  
 875 tion. As we have seen, the space within which individuals move in has an effect on  
 876 the speed of movement. Indeed, being able to directly move from one location to  
 877 another means that individuals have a very high movement speed. However, hav-  
 878 ing to pass through a number of places before reaching the desired location would  
 879 reduce this movement speed. This again opens up new opportunities for study, for  
 880 example, the effect of common hubs that all individuals regularly pass through on  
 881 the evolution of cooperation.

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