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

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

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

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

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

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

2.1. The population: structure and distribution. The population structure describes the restrictions upon how members of the population can interact with each other, including through the different places each individual can and cannot visit. This paper focuses on a Markov movement model, and in the type of examples that we consider all places are visitable by all individuals. The structure here will reduce to simply considering the distribution of the population individuals at any given time, and so we shall find it convenient to talk about distribution in place of structure. In a population of N individuals who can move around M places, 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 $\mathbf{m}_{<t}$.
π_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).
$f_{n,t}$	≥ 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.
$w_{i,j,t}$	≥ 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.
$u_{i,j,t}$	≥ 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.
α_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	≥ 0	Payoff to I_n .
λ	$\in [0, \min(R_n))$	Movement cost.
T	$\in \mathbb{Z}^+$	Exploration time.
$C_\alpha (D_\alpha)$		Cooperator (defector) with staying propensity α .
$\gamma (\delta)$	$\in [0, 1]$	Nash equilibrium staying propensity of cooperator (defector).

TABLE 1. Notation used in the paper.

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

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

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

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

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

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

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

The population distribution probability function (PDPF) $\pi_t(\mathbf{m})$ gives the probability that the population distribution is $\mathbf{m}$ after t time steps regardless of the population distribution history. It can be expressed using the transition probabilities as

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

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

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

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

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

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

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

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

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

The individual transition probability function is then defined as follows

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

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

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

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

$$123 \quad P_n(m_{n,<t}) = p_{n,t-1}(m_{n,t-1}|m_{n,<t-1}) \cdots p_{n,1}(m_{n,1}|m_{n,0})\pi_0(m_{n,0}). \quad (11)$$

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

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

130 and therefore the PDPF can simply be written

$$131 \quad \pi_t(\mathbf{m}) = p(\mathbf{m}). \quad (13)$$

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

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

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

$$141 \quad \bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t})p_t(\mathbf{m}|\mathbf{m}_{<t})P(\mathbf{m}_{<t}). \quad (15)$$

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

$$146 \quad F_{n,t} = \frac{1}{t} \sum_{k=1}^t \bar{f}_{n,k}. \quad (16)$$

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

151 When there is fully independent movement, the mean fitness change simplifies
 152 to

$$153 \quad \bar{f}_{n,t} = \sum_{\mathbf{m}} \sum_{\mathbf{m}_{<t}} f_{n,t}(\mathbf{m}|\mathbf{m}_{<t})p(\mathbf{m})P(\mathbf{m}_{<t}). \quad (17)$$

155 In [9] it is assumed that the fitness contribution of individual I_n only depends upon
 156 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	$\mathbf{r}_{ij} = \frac{w_{ij}F_i}{\sum_{n,k} w_{nk}F_n}$	LD	$\mathbf{r}_{ij} = \frac{w_{ij}F_j^{-1}}{\sum_{n,k} w_{nk}F_k^{-1}}$

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 $\mathbf{r}_{ij} = b_i d_{ij}$, for DBD and DBB dynamics $\mathbf{r}_{ij} = d_j b_{ij}$.

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

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

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

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

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

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

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

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

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

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

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

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

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

For the fully independent movement model, the mean replacement weight contribution is defined as follows

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

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

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

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

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

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

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

with boundary conditions

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

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

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

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

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

for the mean change in fitness we have

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

and for the mean replacement weight change we have

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

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

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

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

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

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

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

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

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

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

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 α_n of individual I_n and the attractiveness of remaining in group $\mathcal{G}_n(\mathbf{m}_{t-1})$. The
 293 staying propensity α_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 β_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 β_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 β_C and β_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

being defined using the following step function

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4. Results. In this section the effect of the model parameters on the fixation probability are investigated. In particular, we investigate how the model parameters affect *assortment*, which is the mechanism that allows cooperation to evolve as shown in [22]. There is positive assortment between cooperators if they are more likely to interact with other cooperators than defectors. In our model, this occurs due to an increase (decrease) in the time it takes for defectors (cooperators) to find cooperators. According to [20] the time to find cooperators should depend upon the density of the population and an individual's movement speed. In their model, N individuals pair up with one another to form a coalition such that the probability of a pair forming is exponentially distributed with rate μ , which is a function of N and the population density. The time to find cooperators in their model is essentially determined by the rate μ . We have one-to-one correspondence between individuals and places and therefore the density remains constant; on the other hand, since we consider a complete graph, the movement speed is high as individuals can directly get from one place to another. Therefore, the time it takes to find cooperators is mostly determined by the staying propensity of the individuals, however, this relationship is not so straightforward as it is not globally controlled and the individuals may have different staying propensities (which are subject to the evolutionary process). This means that some individuals may find cooperators faster than others. The parameters used in the simulations are summarised in Table 3.

Apart from an individual's interactive strategy and staying propensity, all other parameters are considered to be fixed. Each individual inherits these two characteristics from its parent, and different interactive strategies or staying propensities are introduced into the population through mutations. Staying propensities can take any value $0.01m$ for $m = 1, \dots, 99$; this means that no individual moves all the 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
λ	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.

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

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

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

A defector mutant is of the type D_{δ_M} where the staying propensity δ_M satisfies

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

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

A cooperator mutant is of the type C_{γ_M} where the staying propensity γ_M satisfies

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

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

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

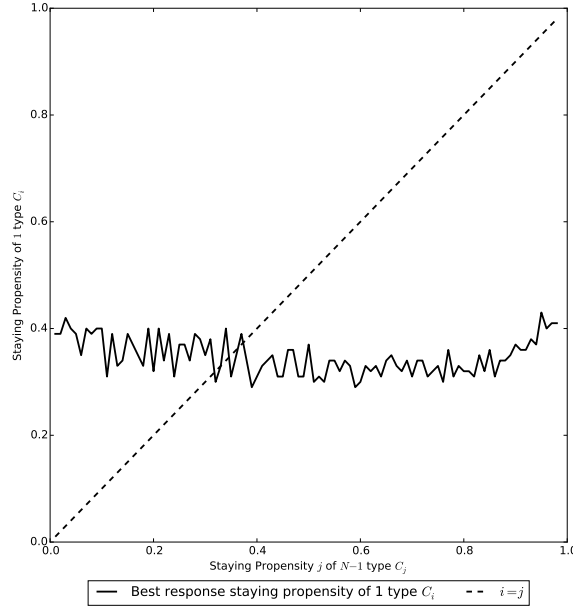


FIGURE 1. This plot shows the best response staying propensities for 1 type C_i individual playing against $N - 1$ type C_j individuals. Parameter set 1 is used with $\lambda = 0.2$ and $i, j \in \{0.01, 0.02, \dots, 0.99\}$. The intersection point of the plots gives the unique strategy which is a best response to itself, i.e. the unique cooperator resident Nash equilibrium staying propensity γ_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.

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

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

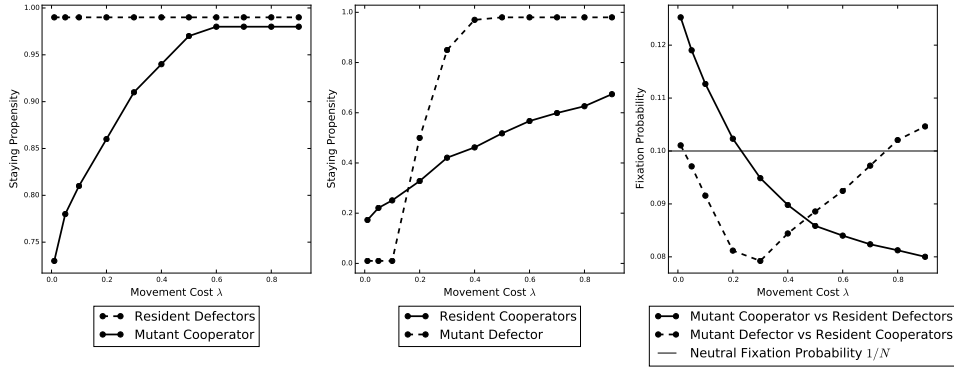


FIGURE 2. These plots show the effect of movement cost on the evolution of cooperation using parameter set 1. The left (centre) plot shows the staying propensities $\delta_R = 0.99$ (γ_R) for resident defectors (cooperators) and γ_M (δ_M) for a mutant cooperator (defector) used to invade the resident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

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

In Figure 3 reducing the exploration time T from 10 to 5 steps decreases the coalition time which adversely affects the cooperators. One of the key differences 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.

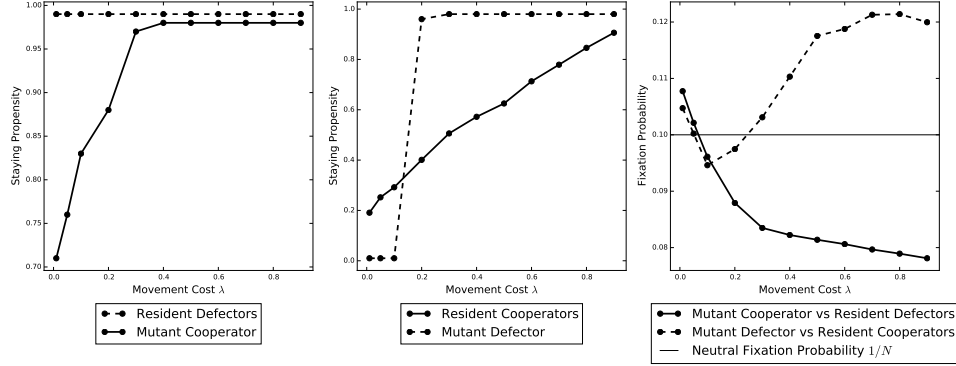


FIGURE 3. Plots created using parameter set 2. The exploration time T has been decreased from 10 to 5.

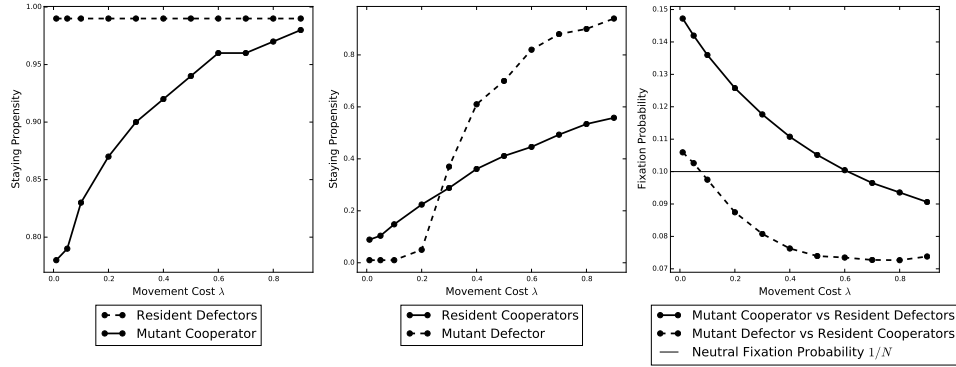


FIGURE 4. Plots created using parameter set 3. The exploration time T has been increased from 10 to 25.

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

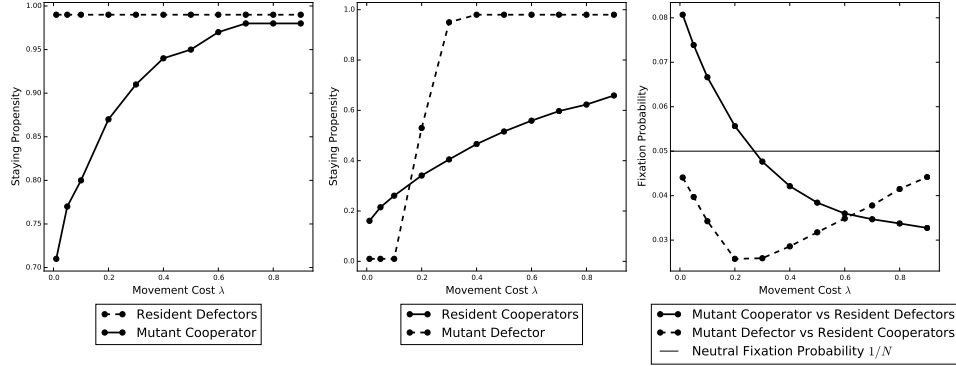


FIGURE 5. Plots created using parameter set 4. The population size has been increased from 10 to 20.

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

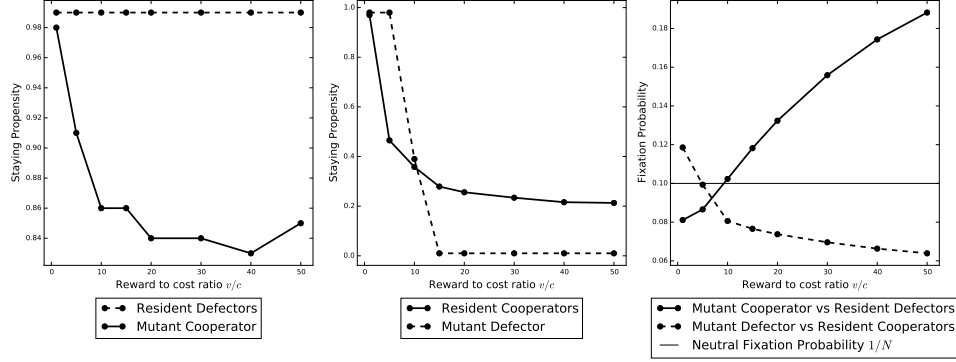


FIGURE 6. Plots have been created using parameter set 5. The plots here are against the reward to cost ratio v/c such that $c = 0.04$.

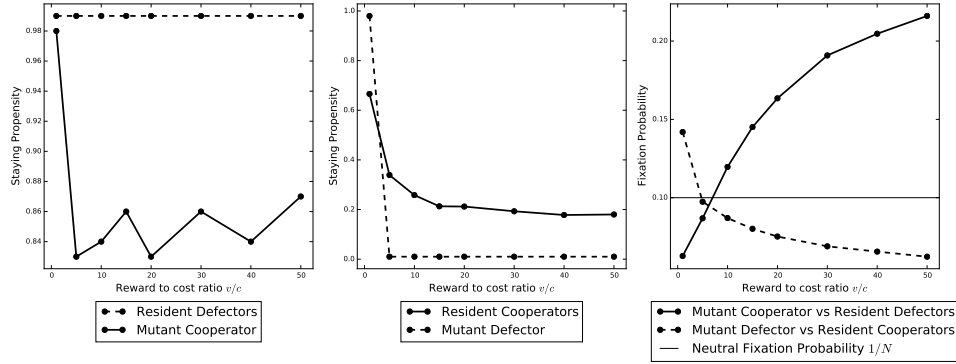


FIGURE 7. Plots have been created using parameter set 6. The plots here are against the reward to cost ratio v/c such that $c = 0.09$.

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

Resident and mutant defectors are of the same type D_δ . Similarly, resident and mutant cooperators are of the same type C_γ . The Nash equilibrium staying propensities δ and γ are determined by the intersection of the following two sets

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

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

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

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

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

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

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

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

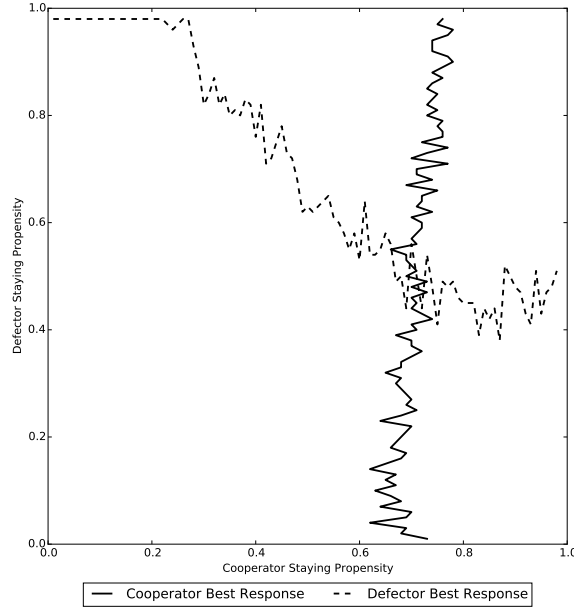


FIGURE 8. This plot shows the best response cooperator staying propensity (solid line, value shown on the x-axis) versus the range of defector staying propensities on the y-axis, and the best response defector staying propensity (dashed line, value shown on the y-axis) versus the range of cooperator 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.

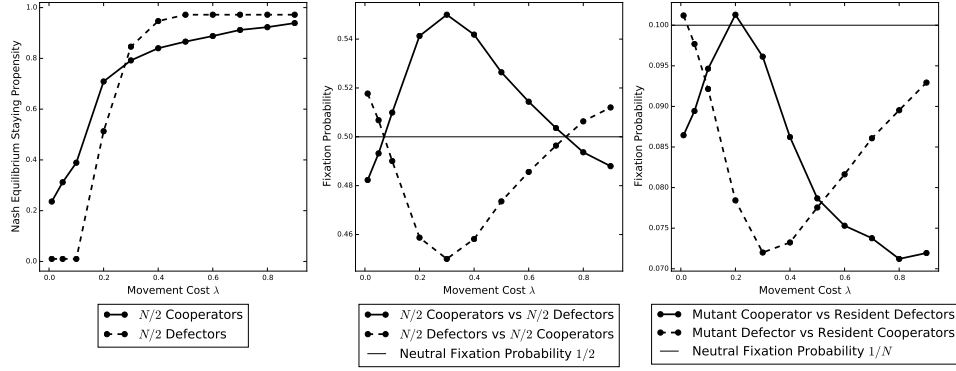


FIGURE 9. These plots show the effect of movement cost λ on the evolution of cooperation and are created using parameter set 1. The plot on the left shows the Nash equilibrium staying propensity γ for cooperators and δ for defectors in a mixed population where there are $N/2$ individuals of each type. 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_γ (defector D_δ) in a population of $N - 1$ resident defectors D_δ (cooperators C_γ).

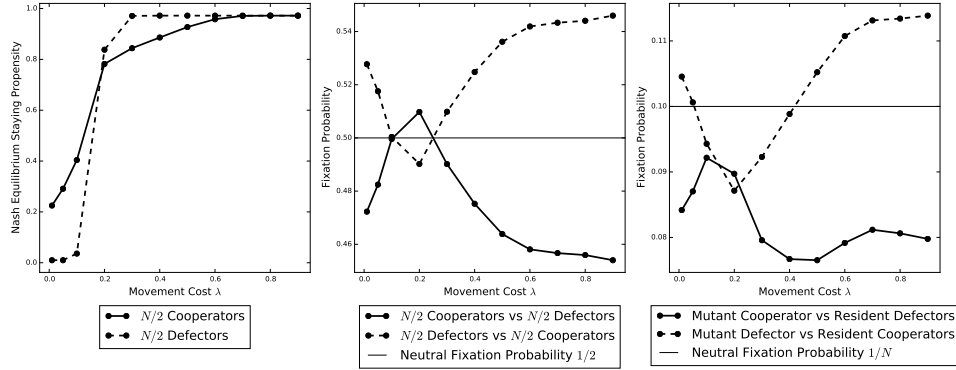


FIGURE 10. Plots created using parameter set 2. Plots are as in Figure 9 with exploration time T decreased from 10 to 5.

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

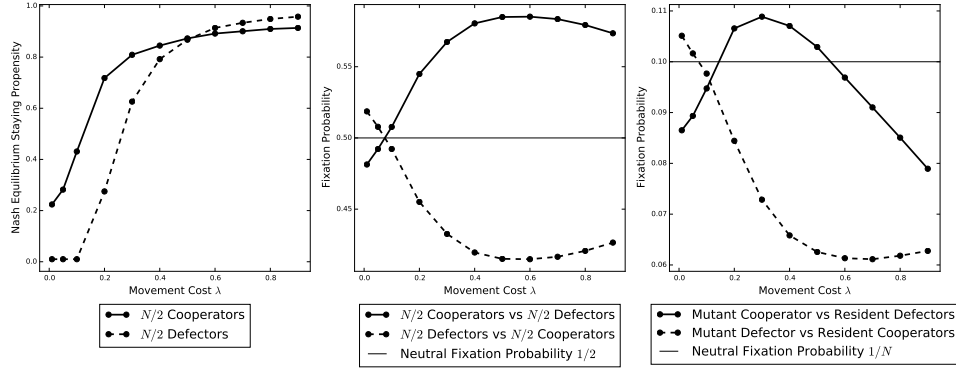


FIGURE 11. Plots created using parameter set 3. Plots are as in Figure 9 with exploration time T increased from 10 to 25.

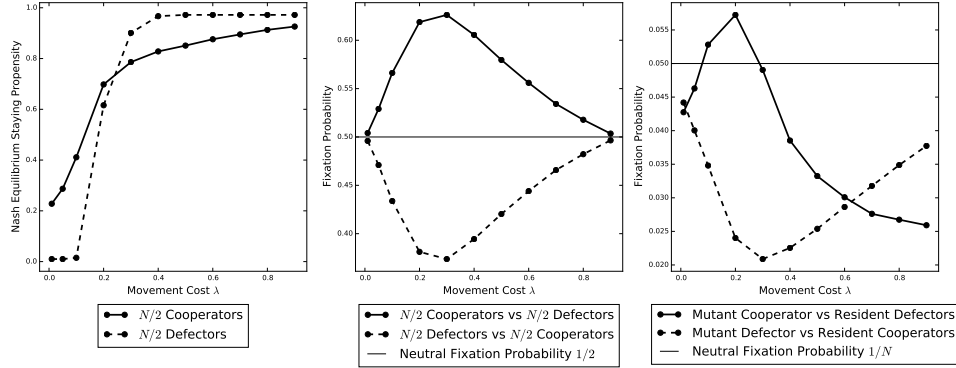


FIGURE 12. Plots created using parameter set 4. Plots are as in Figure 9 with population size N increased from 10 to 20.

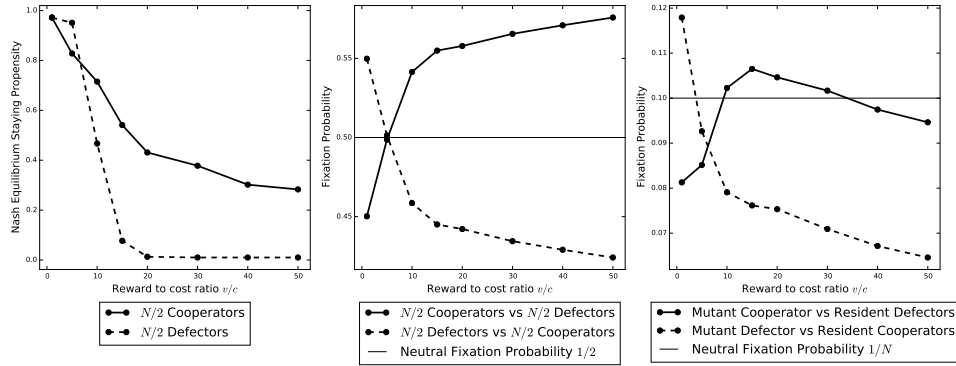


FIGURE 13. Plots created using parameter set 5. Plots are as in Figure 9 but λ is fixed and reward to cost ratio v/c varied such that $c = 0.04$.

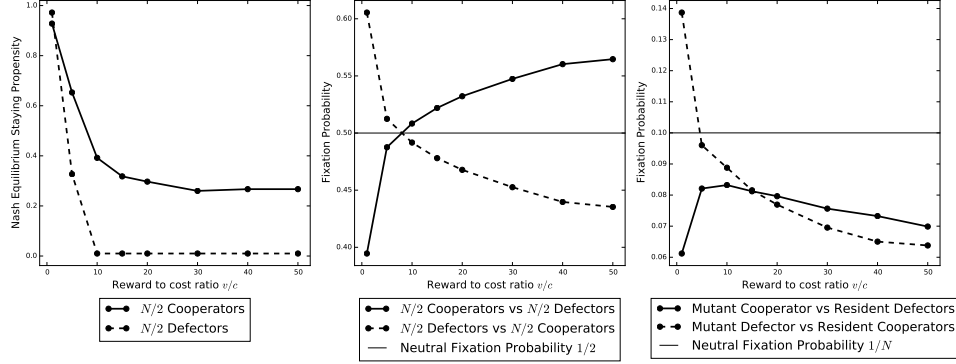


FIGURE 14. Plots created using parameter set 5. Plots are as in Figure 9 but λ is fixed and reward to cost ratio v/c varied such that $c = 0.09$.

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

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

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

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

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

737 where ρ_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

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

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