



City Research Online

City St George's, University of London

Citation: Broom, M. & Rychtar, J. (2012). A general framework for analysing multiplayer games in networks using territorial interactions as a case study. *Journal of Theoretical Biology*, 302, pp. 70-80. doi: 10.1016/j.jtbi.2012.02.025

This is the unspecified version of the paper.

This version of the publication may differ from the final published version. To cite this item please consult the publisher's version.

Permanent repository link: <https://city-ref-test.eprints-hosting.org/id/eprint/1318/>

Link to published version: <https://doi.org/10.1016/j.jtbi.2012.02.025>

Copyright and Reuse: Copyright and Moral Rights remain with the author(s) and/or copyright holders. Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge, unless otherwise indicated, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way. For full details of reuse please refer to [City Research Online policy](#).

A general framework for analyzing multiplayer games in networks using territorial interactions as a case study

Mark Broom^{a,*}, Jan Rychtář^b

^a*Centre for Mathematical Science, City University London, Northampton Square,
London, EC1V 0HB, UK*

^b*Department of Mathematics and Statistics, The University of North Carolina at
Greensboro, Greensboro, NC 27402, USA*

Abstract

Recently, models of evolution have begun to incorporate structured populations, including spatial structure, through the modelling of evolutionary processes on graphs (evolutionary graph theory). One limitation of this otherwise quite general framework is that interactions are restricted to pairwise ones, through the edges connecting pairs of individuals. Yet many animal interactions can involve many players, and theoretical models also describe such multi-player interactions. We shall discuss a more general modelling framework of interactions of structured populations with the focus on competition between territorial animals, where each animal or animal group has a “home range” which overlaps with a number of others, and interactions between various group sizes are possible. Depending upon the behaviour concerned we can embed the results of different evolutionary games within our structure, as occurs for pairwise games such as the Prisoner’s Dilemma

*Corresponding author.

Email addresses: `mark.broom@city.ac.uk` (Mark Broom), `rychtar@uncg.edu` (Jan Rychtář)

or the Hawk-Dove game on graphs. We discuss some examples together with some important differences between this approach and evolutionary graph theory.

Keywords: structured populations, evolution, game theory, territory

1. Introduction

1.1. Modelling structured populations

Recently, models of evolution have begun to incorporate structured populations using evolutionary graph theory [1, 2]. These models embed standard games such as the Prisoner’s Dilemma, or the Hawk-Dove game within a graph structure [3, 4, 5]. One limitation of this otherwise quite general framework is that interactions are restricted to pairwise ones, through the graph edges despite the fact that animal interactions can involve many players. Thus the models may be appropriate for some special situations, such as territorial animals with non-overlapping territories, but not the fluid situations with multiple overlaps that we describe below. The same applies to the related concept of cellular automata see e.g. [6, 7, 8].

In this paper we discuss a more general framework of interactions of structured populations focusing on competition between territorial animals. We can embed the results of different evolutionary games within our structure, as occurs for pairwise games on graphs. Graph models have three elements: graph, game and dynamics. We can use the dynamics (almost) unchanged, see the discussion in Section 6, once we have evaluated the fitnesses of the individuals using the underlying game and structure. However, a more general mode of interaction is needed, as well as the possibility of involving

21 multi-player games. Our method in general allows for this extra flexibility.

22 1.2. *Animal groups and territoriality*

23 Animals of many species live alone or in distinct groups on a (reasonably)
24 well-defined territory, and they forage for food almost exclusively within that
25 territory. Similarly, it may be that the males of the species occupy territories
26 for the purposes of mating. In either case, territories will often be defended
27 against rivals and so interactions occur at the boundaries of territories. In
28 this scenario, we can think of non-overlapping areas with interaction only at
29 the borders.

30 However, it is often the case that the area that an animal or animal group
31 uses for foraging is not in fact exclusive to itself, but can overlap considerably
32 with the territories of others. In this case the more general term *home range*
33 [9] is used for the area that an individual or group utilises. Thus there will
34 be parts of the environment that are utilised by two or more individuals or
35 groups and there can be interactions between these groups when they meet.
36 Such interactions may occur just when the groups meet, or a meeting and
37 competition may be caused by the presence of major items of food. We note
38 that even when territories are non-overlapping, intrusion into the territory
39 of others can still cause these types of interaction.

40 A good example of this phenomenon occurs in the case of the African
41 wild dog. Woodroffe [10], [11] describe aspects of the territorial behaviour
42 of wild dogs. The size of home ranges varies considerably from site to site,
43 ranging from 500 square kilometres up to over 1500 square kilometres. In fact
44 these areas vary in size throughout the year as well; for instance packs use
45 much smaller areas when they are feeding pups at a den. Across different

46 sites, with such large home ranges, a common feature is significant home
47 range overlap, where there can be interactions between different dog packs.
48 Ginsberg & Macdonald [12] measured a home range overlap from 50% to
49 80%. The size of the regions of interaction can vary throughout the year,
50 and the environment and the likelihood of interactions are thus very fluid.

51 Other examples of animals using overlapping home ranges include chee-
52 taks [13], roadrunners [14], caracara [15], woodchuck [16], chimpanzees [17]
53 and lynx [18]. In some cases many groups can interact at significant food
54 sources, and often food loss to neighbours can be considerable [19].

55 *1.3. Outline of the paper*

56 In the following sections we shall outline the model framework in its
57 full generality before focusing on some example population structures which
58 illustrate how the model may be applied. The first of these applications
59 considers a simple model of animal interactions where territories are distinct.
60 For example, we shall see in Figure 2 in Section 3.1 two alternative ways to
61 view the model; the natural way involving real space, and a more general
62 graphical representation. We repeat this process with the other examples as
63 well. We then consider an example involving a particular evolutionary game,
64 and come to some conclusions about the influence of the population structure
65 on the outcome of the game. This is followed by a discussion of our results,
66 and ideas for how to develop this work.

67 2. The model framework

68 2.1. The population and its distribution

69 We consider a population of N individuals $I_1, \dots, I_N$ who can move be-
 70 tween and potentially interact at M distinct places $P_1, \dots, P_M$. Let $\mathbf{X}(t) =$
 71 $(X_{n,m}(t))$ be a binary $N \times M$ matrix representing the presence of individual
 72 I_n at place P_m ; i.e.

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

73 The n^{th} row of $\mathbf{X}$, $(X_{n,o})$ represents individual I_n and the m^{th} column of $\mathbf{X}$,
 74 $(X_{o,m})$ represents place P_m . As a whole, $\mathbf{X}(t)$ represents the distribution of
 75 the population over the whole habitat (all of the places) at time t . We use
 76 a matrix representation instead of a single vector with N elements (where
 77 the n^{th} value would be the position of I_n) in order to talk more easily about
 78 probability distributions of the position of I_n .

79 In general the probability of $\mathbf{X}(t)$ taking any particular value $\mathbf{x} = (x_{n,m})$
 80 may depend upon the entire history of the system $\mathbf{x}_{<t} = (\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_{t-1})$.
 81 We write this conditional distribution as

$$P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = P(\mathbf{X}(t) = \mathbf{x} | \mathbf{X}(1) = \mathbf{x}_1, \dots, \mathbf{X}(t-1) = \mathbf{x}_{t-1}). \quad (2)$$

82 Individuals have to be at some place, and since they cannot be at two places
 83 at the same time (places are distinct), at any time every row of $\mathbf{X}$ contains
 84 exactly one 1, and there is a unique distribution of the population over the
 85 places. This gives the following

$$\sum_{\mathbf{x}} P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = 1 \quad \forall t, \mathbf{x}_{<t}. \quad (3)$$

Let $p_{n,m,t}(\mathbf{x}_{<t}) = P(X_{n,m}(t) = 1)(\mathbf{x}_{<t})$ denote the probability of individual I_n being in place P_m at time t given the history of the system $\mathbf{x}_{<t}$. For any given individual, we thus have

$$\sum_m p_{n,m,t}(\mathbf{x}_{<t}) = 1 \quad \forall n, t, \mathbf{x}_{<t}. \quad (4)$$

It may be that not all individuals can go to all places, and that each individual I_n has a subset of the overall set of places $\mathcal{P}_n$ available to it. A *home range* or *territory* of individual I_n is defined by

$$\mathcal{P}_n = \{P_m; p_{n,m,t}(\mathbf{x}_{<t}) > 0 \text{ for some } t \text{ and some history } \mathbf{x}_{<t}\} \quad (5)$$

i.e. is the set of places that I_n has a non-zero probability of visiting at some point.

In our general framework the whole population follows a single random process, which can depend upon its entire history. This would be very complex, and perhaps not very realistic, and there are a number of simplifications that we can make based upon different types of independence, some of which we discuss in Appendix A. We consider two important concepts only here.

It may be that a given population distribution is independent of the history of the process so that

$$P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = P(\mathbf{X}(t) = \mathbf{x}). \quad (6)$$

In this case we call the model *history-independent*.

If the process satisfies

$$p_{n,m,t}(\mathbf{x}_{<t}) = p_{n,m} \quad \forall n, m, t, \mathbf{x}_{<t} \quad (7)$$

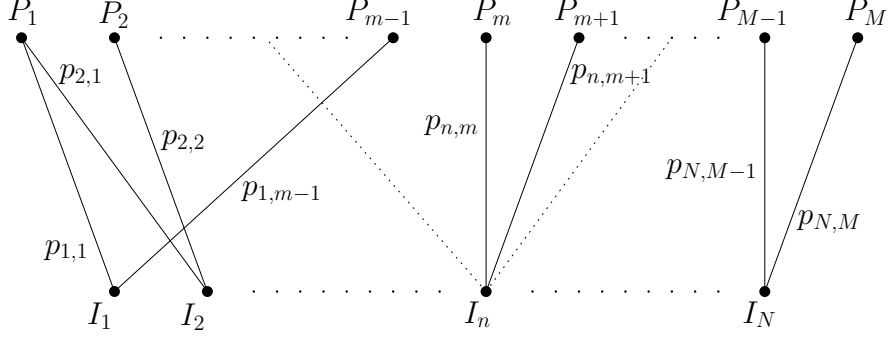


Figure 1: Representing an independent model as a bipartite graph where the weight between the vertex representing individual I_n and place P_m is $p_{n,m}$.

we simply call the model *independent* and can think of it in terms of a bi-
partite graph as in Figure 1. In Appendix A we discuss some intermediate
cases between history independence and (full) independence.

2.2. Fitnesses

To model the evolution of a population, we must evaluate the fitnesses
of the individuals. In general the fitness of each individual depends upon
which place(s) it visits, which other individuals also visit the same place,
and possibly even which individuals visit which other places (e.g. if others
deplete resources which it might wish to use later). In general the reward for
individual I_n at time t given the current distribution of individuals $\mathbf{X}(t) = \mathbf{x}$
and the historical distributions $\mathbf{x}_{<t}$ will be denoted by $R(n, \mathbf{x}, t, \mathbf{x}_{<t})$.

The reward to an individual will in general be a weighted combination
of contributions from a succession of time points. Here we shall consider
cases where only the current distribution affects the reward. In such a case
the history can be ignored, and as we are only evaluating the fitness at
a snapshot in time, the time index is not strictly necessary either, and so

119 the reward to I_n thus becomes $R(n, \mathbf{x})$. Note that if fitness did directly
 120 depend on time, and not just through how time affected the distribution
 121 of individuals, and we had to evaluate fitness at different time points e.g.
 122 to update the population composition through evolutionary dynamics, then
 123 the explicit inclusion of time would still be necessary. We also note that
 124 for homogeneous history independent processes this is entirely equivalent to
 125 more general reward functions, since in this case $R(n, \mathbf{x}, t, \mathbf{x}_{<t}) \equiv R(n, \mathbf{x})$.

126 Perhaps the most natural reward function, and the one that we will gen-
 127 erally use, is the *mean reward*, which we label R_n where

$$R_n = \sum_{\mathbf{x}} P(\mathbf{X} = \mathbf{x}) R(n, \mathbf{x}). \quad (8)$$

128 If $x_{n,m} = 1$, then individual I_n is at place P_m in the group G of individuals

129

$$G = \{I_j; x_{j,m} = 1\}. \quad (9)$$

130 Let $P(X_{o,m} = \chi_G)(\mathbf{x}_{<t})$ be the probability of group G meeting at place P_m
 131 at time t , given the history $\mathbf{x}_{<t}$. Assuming our model is row-independent i.e.
 132 players move independently of each other (see Appendix A), we obtain

$$P(X_{o,m} = \chi_G)(\mathbf{x}_{<t}) = \prod_{j \in G} p_{j,m,t}(\mathbf{x}_{<t}) \prod_{j \notin G} (1 - p_{j,m,t}(\mathbf{x}_{<t})). \quad (10)$$

133 For the independent model, this becomes

$$P(X_{o,m} = \chi_G) = \prod_{j \in G} p_{j,m} \prod_{j \notin G} (1 - p_{j,m}). \quad (11)$$

134 Often the reward to an individual will only depend upon the place that
 135 it occupies and the group of individuals at that place. We label such payoffs

136 as *direct group interaction payoffs*, and in such cases

$$R(n, \mathbf{x}) = R(n, m, \chi_G) \quad (12)$$

137 where $R(n, m, \chi_G)$ is the reward to I_n at place P_m occupied by group G and
 138 then

$$R_n = \sum_{m=1}^M \sum_G P(X_{\circ, m} = \chi_G)(\mathbf{x}_{<t}) R(n, m, \chi_G). \quad (13)$$

139 3. Example models

140 3.1. Territorial interaction model

141 Here we introduce a general model of interactions within a population
 142 with overlapping territories, and illustrate it with a simple example. Consider
 143 the scenario in Figure 2a) where there are three individuals I_1, I_2, I_3 and
 144 each one of them can move freely within a territory in the shape of a square.
 145 The individuals' territories overlap, creating six distinct places $P_1, \dots, P_6$.
 146 Assuming the territories are relatively small and that individuals roam freely
 147 and randomly, we may assume that at any given time, the probability of an
 148 individual being at a place within its own territory is proportional to the
 149 area of the place. We thus get an independent model with

$$(p_{n,m}) = \begin{pmatrix} \frac{1}{2} & \frac{1}{4} & \frac{1}{4} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & \frac{1}{4} & 0 & \frac{1}{4} & \frac{1}{4} \end{pmatrix}. \quad (14)$$

150 We get, for example, that all of the individuals can be together only at place
 151 P_3 and, by (11), that happens with probability $p_{1,3}p_{2,3}p_{3,3} = \frac{1}{64}$. Also, a
 152 group $G = \{I_1, I_3\}$ can meet either on P_2 or P_3 and we get,

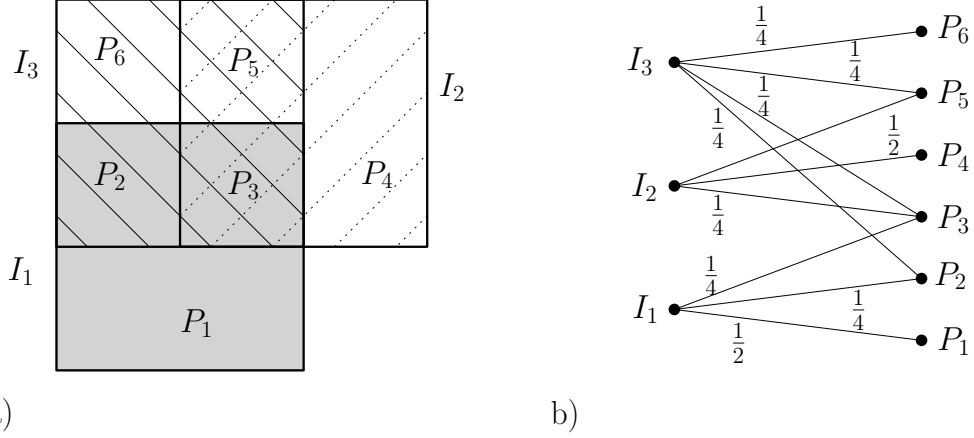


Figure 2: Territorial interaction model. a) The territory of individual I_1 is the square in grey, the territory of I_2 is the square encompassed by the dotted lines, the territory of I_3 is the square encompassed by full lines; b) is the corresponding graphical representation as a general independent model.

$$P(X_{o,2} = \chi_G) = p_{1,2}p_{3,2} = \frac{1}{16}, \quad (15)$$

$$P(X_{o,3} = \chi_G) = p_{1,3}p_{3,3}(1 - p_{2,3}) = \frac{3}{64}. \quad (16)$$

3.2. The boundary interaction model

We similarly introduce a general model of interactions within a population with non-overlapping territories, and illustrate it with a simple example. Consider the scenario in Figure 3a) where there are four individuals I_1, I_2, I_3, I_4 and each one of them can move freely within an area in the shape of a regular hexagon; guarding the boundaries of their own area. An interaction between individuals can thus occur only at the boundaries and assuming the presence of an individual at a particular boundary segment is proportional to the length of the segment relative to the total length of the

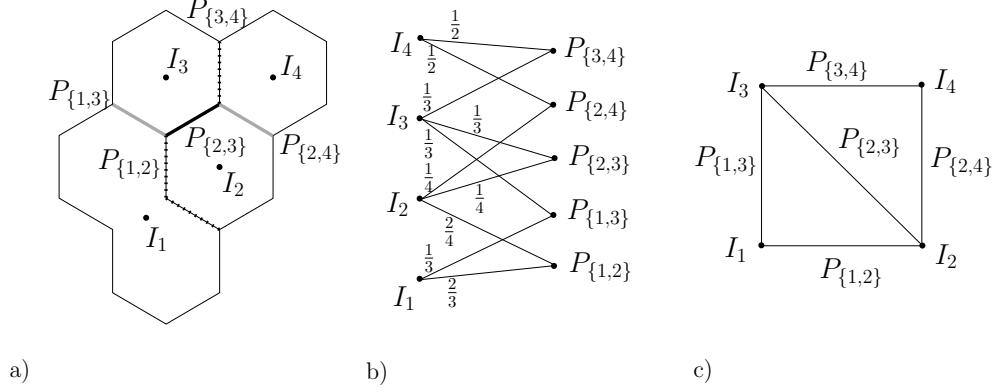


Figure 3: The boundary interaction model. a) Individuals are guarding their areas; b) is the corresponding graphical representation as a general independent model; c) is an alternative visualization as pairwise interactions on graphs.

162 guarded boundary, we get that the interactions can only be pairwise with
 163 the corresponding $p_{n,m}$ given below. We get

$$(p_{n,\{i,j\}}) = \begin{pmatrix} \frac{2}{3} & \frac{1}{3} & 0 & 0 & 0 \\ \frac{2}{4} & 0 & \frac{1}{4} & \frac{1}{4} & 0 \\ 0 & \frac{1}{3} & \frac{1}{3} & 0 & \frac{1}{3} \\ 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{pmatrix}. \quad (17)$$

164 In general, we consider a graph with $I_1, \dots, I_N$ as individuals on vertices,
 165 and places as edges, as shown on Figure 3c). Any place can contain at most
 166 two individuals and there are $M = N(N - 1)/2$ places, some of which may
 167 be empty with probability 1, if the edge does not exist on the graph. We
 168 write $P_{\{n,n'\}}$ for a place at the edge between individuals I_n and $I_{n'}$.

169 In Appendix B we discuss the reward function for the boundary inter-
 170 action model, and discuss some potentially important consequences for the
 171 evaluation of reward functions for evolutionary games on graphs.

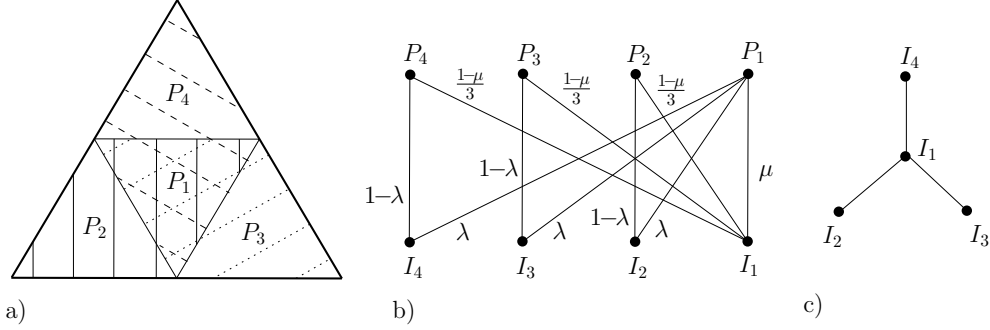


Figure 4: The territorial raider model. a) Individual I_n lives in place P_n but can raid neighbouring places. The territory of I_1 is the whole triangle and the home place is the central smaller triangle. The territory of I_2 is the rhombus encompassed by full lines, the territory of I_3 the rhombus encompassed by dotted lines and the territory of I_4 the rhombus encompassed by dashed lines; b) is the corresponding graphical representation as a general independent model; c) is an alternative visualization as some multi-player interactions on a graph.

172 3.3. The territorial raider model

173 Now, consider a special case of the territorial interaction model. As-
 174 sume that there are N individuals $I_1, \dots, I_N$ each living in their own place
 175 $P_1, \dots, P_N$. The individuals can also move to one of the places neighbouring
 176 theirs. Such a situation with $N = 4$ is shown in Figure 4a).

177 This can be modelled by a graph (V, E) , where the vertices represent both
 178 the individuals as well as the places of interactions. We again let $\mathbf{A}$ be the
 179 adjacency matrix of the graph. An individual can stay at its own place or it
 180 can move and raid one of the neighbouring places. For example, consider a
 181 star graph with node I_1 in the centre, and $N - 1$ leaf nodes $I_2, \dots, I_N$ (see
 182 Figure 4c).

183 Suppose that for each individual on a leaf, the probability that they go to

184 the centre is λ , and so the probability that they stay on a leaf is $1 - \lambda$, and
 185 that the probability that the individual from the centre stays in the centre
 186 is μ , it going to each leaf with equal probability $(1 - \mu)/(N - 1)$ otherwise.

187 We get

$$(p_{n,m}) = \begin{pmatrix} \mu & \frac{1-\mu}{N-1} & \frac{1-\mu}{N-1} & \cdots & \frac{1-\mu}{N-1} \\ \lambda & 1-\lambda & 0 & \cdots & 0 \\ \lambda & 0 & 1-\lambda & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \lambda & 0 & 0 & \cdots & 1-\lambda \end{pmatrix}. \quad (18)$$

188 An individual from the leaf can be in the following groups:

- 189 • alone (either on the leaf or in the centre),
- 190 • with the centre individual only (either on the leaf or in the centre),
- 191 • with the centre individual and k others (in the centre); there are $\binom{N-2}{k}$
 192 such distinct groups,
- 193 • without the centre individual but with k others (in the centre); there
 194 are $\binom{N-2}{k}$ such distinct groups.

The respective probabilities of seeing such a group are as follows:

$$P(G = \{I_n\}) = \lambda(1 - \mu)(1 - \lambda)^{N-2} + \left(1 - \frac{1 - \mu}{N - 1}\right)(1 - \lambda), \quad (19)$$

$$P(G = \{I_1, I_n\}) = \lambda\mu(1 - \lambda)^{N-2} + \frac{1 - \mu}{N - 1}(1 - \lambda), \quad (20)$$

$$P(G = \{I_1, I_n\} \cup \{k > 0 \text{ others}\}) = \binom{N-2}{k} \lambda\mu(1 - \lambda)^{N-2-k} \lambda^k, \quad (21)$$

$$P(G = \{I_n\} \cup \{k > 0 \text{ others from the leaves}\}) = \binom{N-2}{k} \lambda(1 - \mu)(1 - \lambda)^{N-2-k} \lambda^k. \quad (22)$$

195 An individual from the centre can be in the following groups:

- 196 • alone (either in the centre or on one of the leaves),
- 197 • with one other individual, either in the centre or on one of the leaves;
- 198 there are $N - 1$ distinct pairs for each of these two possibilities,
- 199 • with $k > 1$ others (in the centre); there are $\binom{N-1}{k}$ such distinct groups.

The prospective probabilities thus become

$$P(G = \{I_1\}) = \mu(1 - \lambda)^{N-1} + (1 - \mu)\lambda, \quad (23)$$

$$P(G = \{I_1\} \cup \{\text{one other}\}) = (N - 1) \left(\mu(1 - \lambda)^{N-2}\lambda + \frac{1 - \mu}{N - 1}(1 - \lambda) \right), \quad (24)$$

$$P(G = \{I_1\} \cup \{k > 1 \text{ others}\}) = \binom{N - 1}{k} \mu(1 - \lambda)^{N-1-k} \lambda^k. \quad (25)$$

200 If $E(n)$ denotes the mean size of the group where I_n is, we get from above
 201 that

$$E(n) = \begin{cases} 2 - \lambda - \mu + \lambda\mu N, & \text{for the centre individual; } (n = 1) \\ 1 + \lambda\mu + (N - 2)\lambda^2 + \frac{(1-\lambda)(1-\mu)}{N-1}, & \text{for a leaf individual; } (n > 1). \end{cases} \quad (26)$$

202 For fixed λ and μ and any $2 \leq n \leq N$, we get that the ratio $E(n)/E(1)$ tends
 203 to λ/μ in the limit $N \rightarrow \infty$. When $\lambda = 1/2$ and $\mu = 1/N$, we get

$$\frac{E(n)}{E(1)} = \frac{N^2 + 2N + 4}{4(2N - 1)} \approx \frac{N}{8}, \quad \text{for large } N. \quad (27)$$

204 Numerical values for a specific example are shown in Table 1.

	$i = 1$	$i = 2$	$i = 3$	$i = 4$	$i = 5$	$E[G]$
Focal from leaf	0.45	0.2625	0.1875	0.0875	0.0125	1.95
Focal from centre	0.4125	0.45	0.075	0.05	0.0125	1.8
Average	0.4425	0.3	0.165	0.08	0.0125	1.92

Table 1: Numerical values of $P(|G| = i)$ and expected group size $E[|G|]$ on the star for $N = 5, \lambda = 1/2$ and $\mu = 1/5$. The randomly selected individual has probability of $1/5$ of being in the centre which gives the values for the average individual.

205 4. The role of strategy and example games

206 In general, we would often find the distribution of groups as above, then
207 play the game within each possible group. Thus if we can define the payoffs
208 in any given mixture of individuals, we can find the payoffs in the overall
209 game. This is the scenario in our first example. It is possible also that how
210 individuals move between places is a strategic decision, and we explore this
211 possibility in our second example.

212 4.1. A multi-player Hawk-Dove game in the territorial raider model

213 We consider a multi-player game with Hawks and Doves, competing for
214 a single reward. If all individuals in a fighting group are Doves, they split
215 the reward, so each receives the reward divided by the number in the group.
216 If there are any Hawks, all the Doves flee and get 0, all the Hawks fight and
217 one of them receives the reward, and all of the others receive a cost C . Thus
218 if we denote $R_{d,h}^D(R_{d,h}^H)$ as the reward for a Dove (Hawk) in a group with d
219 other Doves and h other Hawks, we get

$$R_{d,h}^D = \begin{cases} 0; & \text{if } h > 0 \\ \frac{V}{d+1}; & \text{if } h = 0 \end{cases} \quad (28)$$

$$R_{d,h}^H = \frac{V - hC}{h + 1}. \quad (29)$$

Thus this situation is an example of direct group interaction payoffs introduced in Section 2.2, since the behaviour of individuals outside the group has no effect on the fitness of group members. We suppose that all individuals play a mixed strategy with probability α of playing Hawk (and so probability $1 - \alpha$ of playing Dove). Thus conditional upon the size of the group being $k + 1$ the number of Hawk groupmates an individual will have follows a Binomial distribution with parameters k and α , so that the probability that an individual will have h Hawk and $d = k - h$ Dove groupmates is given by

$$\binom{k}{h} \alpha^h (1 - \alpha)^{k-h}.$$

220 The expected payoff for Dove (E_D) and for Hawk (E_H) are thus given by

$$E_D(\alpha) = \sum_{d=0}^{N-1} \sum_{h=0}^{N-1-d} P(|G| = d + h + 1) \binom{d+h}{h} \alpha^h (1 - \alpha)^d R_{d,h}^D \quad (30)$$

$$= \sum_{d=0}^{N-1} P(|G| = d + 1) (1 - \alpha)^d \frac{V}{d + 1}, \quad (31)$$

$$E_H(\alpha) = \sum_{d=0}^{N-1} \sum_{h=0}^{N-1-d} P(|G| = d + h + 1) \binom{d+h}{h} \alpha^h (1 - \alpha)^d \frac{V - hC}{h + 1}. \quad (32)$$

221 Let us now consider this game on the star with $N = 5, \lambda = 1/2$ and
 222 $\mu = 1/5, V = 1$ and $C = 2$ as described in Table 1. In particular we shall

223 assume a large population consisting of many identical star structures, with
 224 mixing over time. We seek the Evolutionarily Stable Strategy (ESS) value of
 225 α where the payoff $E_H(\alpha)$ for playing Hawk is the same as the payoff $E_D(\alpha)$
 226 for playing Dove. It should be noted that we have assumed that individuals
 227 do not distinguish between whether their home vertex was the centre or a leaf
 228 when choosing their strategy; if they did so we would have an asymmetric
 229 contest which would be significantly more complicated (there would be two
 230 distinct roles here for the star, but in general there could be many roles). We
 231 further note that to consider evolution on a finite population fully, we would
 232 need to explicitly consider the dynamics of the process, which is outside the
 233 scope of this paper. Since, by (31)-(32) and the values in Table 1,

$$E_H(\alpha) - E_D(\alpha) = 0.33 - 1.05\alpha + 0.35\alpha^2 - 0.0675\alpha^3 + 0.005\alpha^4 \quad (33)$$

234 we get that $\alpha = 0.353$ is the only root of (33) in the allowable interval $[0, 1]$.
 235 Furthermore the derivative of the right-hand side of (33) with respect to α
 236 is negative, so $\alpha = 0.353$ is the unique ESS.

237 4.2. *The territorial raider model with strategic movement*

238 Consider a territorial raider model, so that a graph $G = (V, E)$ is given,
 239 individuals live at places P_m and can either stay in their own place or visit
 240 a neighbouring place. Consider a regular graph with every vertex having
 241 degree d . Suppose that individuals play a strategy where they stay at their
 242 home place with probability $1 - p$ and move to each of the neighbouring
 243 places with equal probability p/d . Thus here strategy affects the movement
 244 of individuals and the distribution of the population over the places, but it
 245 does not affect the payoffs conditional on this distribution. This is the reverse

Symbol	Meaning
B_H	the benefit of foraging at its home place,
B_I	the benefit of foraging at any of its neighbours' place,
L_H	cost per foreign forager at its place when it is at home,
L_I	cost per foreign forager at its place when it is at a neighbouring place,
F_H	cost per fight when at its home place,
F_O	cost of a fight against the owner of a place,
F_I	cost of a fight for each other intruder of the neighbour.

Table 2: Notation for the costs and benefits in the the territorial raider model with strategic movement.

of the previous example, where the strategy affected the payoffs but not the population distribution. It is of course possible for strategies to affect both the population distribution, and the payoffs conditional on this distribution.

Let us assume that all but one individual plays p and find the optimal strategy for our focal individual. We look for values of p such that p is the best choice of our focal individual in a population of p -players. In order to determine the rewards to the individual, we will use a cost-benefit model, $R = B - C$, where benefits come from foraging at a particular place and costs come to an individual in two forms - direct costs from (potential) fights with others trying to forage at the same place and indirect costs from having its home place foraged by others. The notation for this model is summarised in Table 2.

If our individual stays at home, it will get a benefit B_H but will have to fight and the place will be depleted by on average $d \cdot p / d = p$ other individuals.

260 The expected reward will thus be

$$E_{Home} = B_H - p(F_H + L_H). \quad (34)$$

261 If our individual goes to a neighbouring place P_m , it will get the benefit B_I .
 262 There will be on average $(d - 1) \cdot p/d$ other intruders in P_m and the owner
 263 will also be there with probability $(1 - p)$; our focal individual will have to
 264 fight with all of them. There will still be on average $d \cdot p/d = p$ individuals
 265 coming to its home; it will not fight with them but will pay the indirect cost
 266 L_I per individual. Thus, the expected reward when leaving the home place
 267 is

$$E_{Intrude} = B_I - pL_I - p\frac{d-1}{d}F_I - (1-p)F_O. \quad (35)$$

268 We see that this situation is not an example of direct group interaction
 269 payoffs, since the fitnesses of individuals within the group can be affected by
 270 those outside of the group. The difference between the payoffs from staying
 271 or intruding in a population where everybody else intrudes with probability
 272 p is

$$f(p) = E_{Home} - E_{Intrude} \quad (36)$$

$$= (B_H - B_I) + F_O - p[(L_H - L_I) + F_H + (F_O - F_I) + \frac{1}{d}F_I] \quad (37)$$

273 We can now perform the ESS analysis. If

$$0 < f(0) = (B_H - B_I) + F_O \quad (38)$$

274 then staying at home is the best response to everybody staying at home.
 275 Note that typically $F_O > 0$. However, it may still be that $B_H - B_I < 0$

276 because an individual may be careful not to over-harvest its own place, but
 277 may not mind over-harvesting neighbouring places when on them. On the
 278 other hand, if

$$0 > f(1) = (B_H - B_I) - (L_H - L_I) - (F_H - F_I) - \frac{1}{d}F_I \quad (39)$$

279 then always intruding is an ESS. When neither (38) nor (39) holds, then
 280 there is a mixed ESS $p \in (0, 1)$ given by

$$p = \frac{(B_H - B_I) + F_O}{(L_H - L_I) + F_H + (F_O - F_I) + \frac{1}{d}F_I}. \quad (40)$$

281 It is clear that if (38) and (39) do not hold then the numerator and the
 282 denominator of (40) are negative. Conversely if they are both positive then
 283 there is an unstable equilibrium and both (38) and (39) hold so that all
 284 staying at home and all intruding are both pure ESSs.

285 Also, note that whether (39) holds depends on d . The only effect of d
 286 is on the contribution from F_I ; the larger the degree of the graph, the more
 287 likely that other intruders will have to be fought. It is reasonable to assume
 288 that $F_I > 0$, and so the larger d , the less attractive intruding is. It may
 289 thus happen that intruding is an ESS when d is small but it is not an ESS
 290 when d is large (even if the other parameters stay the same), see Figure 5a).
 291 When there is a mixed ESS, from (40), increasing d decreases the probability
 292 of intruding at the ESS, see Figure 5b). Similarly when there are two pure
 293 ESSs the threshold value of the unstable equilibrium increases.

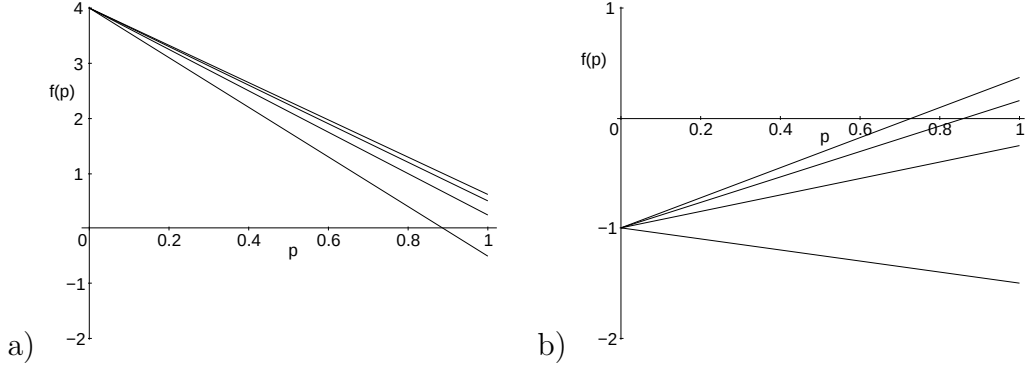


Figure 5: Graphs of $f(p)$ from (37) for varying d . In a), $B_H - B_I = 1, F_O = 3, L_H - L_I = 0, F_H - F_I = 0, F_I = 3$ and $d = 2$ (bottom line), $d = 4, 6$ (middle lines) and $d = 8$ (top line); here $p = 0$ is always ESS, $p = 1$ is ESS only if $d < 3$. In b) $B_H - B_I = -2, F_O = 1, L_H - L_I = -2, F_H - F_I = -1, F_I = 5$ and $d = 2$ (bottom line), $d = 4, 6$ (middle lines) and $d = 8$ (top line); here $p = 0$ is never ESS, $p = 1$ is ESS only if $d \leq 5$ and there is a mixed ESS for $d > 5$.

294 5. Comparing place structures

295 5.1. Fair comparisons

296 We are particularly interested in seeing how (if at all) different place
 297 structures can affect payoffs. Payoffs are usually dependent on the type of
 298 interactions in the population, and this in turn depends on the possible group
 299 sizes. Hence, if the group sizes vary between two given different structures,
 300 we expect the payoffs to vary as well.

301 However, we also want to know whether the structure influences the pay-
 302 offs in some other way as well. We take the approach of comparing a given
 303 place structure with an appropriate well-mixed population. This would then
 304 allow us to compare different place structures with each other through the
 305 medium of their respective well-mixed populations; making it a fair compar-

306 ison not biased by the different group sizes. In this section we shall only con-
 307 sider independent processes, as such comparisons are harder in other cases.
 308 We will call a comparison between a given place model and a well-mixed
 309 population *fair* if the mean group size of the two situations is the same.

310 What do we mean by a well-mixed population? In the game theoretical
 311 literature concerning pairwise games, a well-mixed population is one where
 312 any pair of individuals is equally likely to meet, so that for any given individ-
 313 ual its opponent is equally likely to be any other individual. This idea can
 314 be generalised so that a well-mixed population means one where any group
 315 of size k is equally likely to meet; however this says nothing about the rela-
 316 tive likelihood of groups of size k and $j \neq k$ forming. In the context of our
 317 models, a well mixed population is one where all individuals move following
 318 an identical distribution over the places (i.e. $p_{n_1,m} = p_{n_2,m}$ for all n_1, n_2, m).
 319 These movements need not be independent; for instance in pairwise games
 320 each contest only involves two players, so knowing that a given player is in-
 321 volved necessarily reduces the chance of the involvement of a given second
 322 player (and so such a situation is not row independent according to our defi-
 323 nition from Appendix A). As we are only considering independent processes
 324 here, there is a natural interpretation of well-mixedness in this case; namely
 325 that in addition to all individuals having an identical distribution over the
 326 places, they all move independently of each other.

327 This does not fully specify a unique well-mixed distribution, and to make
 328 fair comparisons it would be convenient to do so. We have already specified
 329 that all individuals are equivalent, and if we extend this to all places being
 330 equivalent also (i.e. $p_{n,m_1} = p_{n,m_2}$) then this gives the required uniqueness.

331 Here we shall say that a population is *completely mixed* if and only if there is
332 a p such that $p_{n,m} = p$ for all n, m . Note that a population of N individuals
333 and M places is completely mixed if and only if $p_{n,m} = 1/M$. Yet, to allow
334 any plausible mean group size associated with any population size, at this
335 point we generalize and allow our parameter p to take any value between 0
336 and 1. This could be achieved in our framework by going beyond the idea
337 of a fixed number of places (e.g. by letting there be M or $M + 1$ available
338 places at any particular time, according to a given probability).

339 Assume a well mixed population with $p_{n,m} = p$ and consider a fixed focal
340 individual (at any place). It is clear that the number of other individuals
341 at the same place as our focal individual follows the binomial distribution
342 with parameters $N - 1$ and p , $\text{Bin}(N - 1, p)$. The mean group size is thus
343 $1 + (N - 1)p$ (including the focal individual).

344 In making comparisons with well-mixed populations, our aim is to match
345 the mean group sizes. The right well-mixed population corresponds to a
346 unique (usually non-integer) number of places, that will not generally be the
347 number of places in the structured game. The appropriate number of places
348 is thus not fixed in advance, and in principle we could define a distribution
349 of the number of places M , ranging from 1 to ∞ , which gives the precise
350 binomial distribution that we have.

351 We discuss the logical consistency of our model with existing concepts of
352 well-mixedness and pairwise contests in Appendix C.

353 5.2. A simple example

354 Consider a star graph of three vertices (equivalent to a line with three
355 vertices), using the territorial raider model, with parameters $\lambda = 1/2$ and

356 $\mu = 1/3$. We will first calculate the group distributions. The probability of
 357 all three individuals being in the same group is

$$P_3 = \frac{1}{3} \times \left(\frac{1}{2}\right)^2 = \frac{1}{12} \quad (41)$$

358 and they can meet only at the centre. Similarly there will be one group of
 359 two and one group of one with probability

$$P_{2,1} = \frac{1}{3} \times \left(\frac{1}{2}\right)^2 (2 + 2 + 1 + 1 + 2) = \frac{8}{12}. \quad (42)$$

360 Finally, there will be three groups of single individuals with probability

$$P_{1,1,1} = \frac{1}{3} \times \left(\frac{1}{2}\right)^2 (1 + 1 + 1) = \frac{3}{12}. \quad (43)$$

361 Hence, the probability of a randomly placed individual ending up in a group
 362 of size 3, 2 and 1 respectively is

$$P_{|G|=3} = \frac{1}{12}, \quad (44)$$

$$P_{|G|=2} = \frac{8}{12} \times \frac{2}{3} = \frac{4}{9}, \quad (45)$$

$$P_{|G|=1} = \frac{8}{12} \times \frac{1}{3} + \frac{3}{12} = \frac{17}{36}. \quad (46)$$

363 The mean group size is thus $29/18$.

364 How do we find a fair comparable completely mixed population for this
 365 case? We need $29/18 = 1 + 2p$ and thus $p = 11/36$. Note that this yields
 366 the probability that the number in the focal group from the corresponding
 367 well-mixed population will be

$$P_{|G|=3}^{cm} = \left(\frac{11}{36}\right)^2, \quad (47)$$

$$P_{|G|=2}^{cm} = 2 \frac{11}{36} \frac{25}{36}, \quad (48)$$

$$P_{|G|=1}^{cm} = \left(\frac{25}{36}\right)^2. \quad (49)$$

368 5.3. A comparison using a multi-player Hawk-Dove game

369 Consider the multi-player Hawk-Dove game. We will compare the ex-
 370 ample on the star introduced in Section 4.1 with the equivalent well-mixed
 371 population. First, we must consider a completely mixed population where
 372 the number of an individual's groupmates follows a $Bin(N-1, p)$ distribu-
 373 tion, and each individual plays a mixed strategy with probability of playing
 374 Hawk α as before.

375 The reward to a Hawk E_H is governed only by the number of Hawks
 376 present (Doves flee, so are equivalent to individuals which do not join the
 377 group). The reward to a Dove can be found by summing over all of the possi-
 378 bilities of other individuals playing Hawk, playing Dove or being absent. This
 379 reward is zero unless there are no Hawks present. Thus, similarly to (31)-(32)
 380 we get

$$E_H = \sum_{h=0}^{N-1} \binom{N-1}{h} (p\alpha)^h (1-p\alpha)^{N-h-1} \frac{V-hC}{h+1} \quad (50)$$

$$= \left(\frac{1 - (1-p\alpha)^N}{Np\alpha} \right) V + C \left(-1 + \frac{1 - (1-p\alpha)^N}{Np\alpha} \right), \quad (51)$$

$$E_D = \sum_{d=0}^{N-1} \binom{N-1}{d} ((1-\alpha)p)^d (1-p)^{N-d-1} \frac{V}{d+1} \quad (52)$$

$$= \left(\frac{(1-\alpha p)^N - (1-p)^N}{N(1-\alpha)p} \right) V. \quad (53)$$

381 Assuming that it is mixed (i.e. not pure Hawk), the unique ESS is obtained
 382 by equating (51) and (53) giving

$$\frac{V}{C} = (1-\alpha) \frac{N\alpha p - 1 + (1-\alpha p)^N}{1 - (1-\alpha p)^N - \alpha(1 - (1-p)^N)}. \quad (54)$$

383 We now go back to the example game on the star with $N = 5, V = 1, C =$
 384 2. As shown in Table 1, the mean group size from the star was 1.92, so that
 385 the fair comparison here equates 1.92 with $1 + (N-1)p$, giving $p = 0.23$.
 386 Inserting these values in (54) we find that the ESS value is $\alpha = 0.394$.

387 Thus the star graph has a lower Hawk proportion than the equivalent
 388 completely mixed population. This is because the graph has a higher prob-
 389 ability of small and large groups, compared to the completely mixed popu-
 390 lation having a higher probability of intermediate groups i.e. the group size
 391 on the star graph is more variable. This is more damaging to Hawks than
 392 Doves as Doves do well when they are alone but do not suffer from being in
 393 large groups, whereas Hawks can pay large costs in large groups.

394 We can illustrate this point about variability by the following. If we set
 395 $p = 1/N$ in the limit as $N \rightarrow \infty$ for our Binomial distribution, we get the

396 limiting Poisson (1) distribution, which has a mean group size of 2 (the focal
397 individual and one other). The payoffs become

$$E_D = \frac{V}{1-\alpha}(e^{-\alpha} - e^{-1}), E_H = \frac{V}{\alpha}(1 - e^{-\alpha}) + C(-1 + \frac{1}{\alpha}(1 - e^{-\alpha})). \quad (55)$$

398 The unique ESS for such a completely mixed population with random group
399 sizes when $V = 1$ and $C = 2$ is 0.364 which is much smaller than the
400 equivalent value of $\alpha = 0.5$ when the group size is fixed at two.

401 6. Discussion

402 In this paper we have developed a new modelling framework to consider
403 the interaction of individuals in a non-homogeneous environment. Individ-
404 uals (or groups) move at successive time points to different “places” where
405 they may interact with no, one or more than one other. Its most natural
406 interpretation, and the one we have focused on here, is that of a spatial rela-
407 tionship between individuals, so that some can go to some places but not to
408 others. Individuals that are closer are then more likely to meet. The main
409 advantages of the new framework are the capability to analyse and com-
410 pare different spatial structures, its flexibility and the potential to consider
411 both overlapping space use and multiplayer interactions just as easily as well-
412 defined boundaries and multiple pairwise interactions. These features can set
413 the framework apart from alternatives, which may be less flexible and overly
414 complex in analysing the influence of spatial structure, multiplayer games
415 and spatial overlap.

416 This framework has some similarities with the concept of evolutionary
417 graph theory, where the relationships between individuals are given by a

418 graph. These individuals interact in a pairwise fashion only, through the
419 edges of the graph (though see [20] which we discuss below). In our framework
420 any number of individuals can theoretically interact, depending upon the
421 nature of the structure involved.

422 Our framework does not include the definition of new games in general,
423 and we incorporate existing game theoretical models into our structure. Since
424 multiple individuals can meet, we can incorporate multiplayer models in
425 such complex structures for the first time. One reason for doing this, as
426 for pairwise games on graphs, is to investigate how a particular population
427 structure may affect the evolutionary process which is governed by particular
428 game theoretical interactions. So just as in evolutionary graph models where
429 researchers investigate the structural effect on the evolution of cooperation
430 in the Prisoner’s Dilemma, we may investigate the evolution of the level of
431 aggressiveness in a multi-player Hawk-Dove game, as we do in Section 5.3.

432 A key influence on the outcome of multiplayer games is the number of
433 players involved. Thus if one structure generates different size groups to
434 another, then this can have a significant effect just through the sizes of the
435 groups generated. Such a group size effect certainly occurs for the multiplayer
436 Hawk-Dove game, for example. This is certainly of interest, but we are also
437 interested in effects caused by structural relationships between the individu-
438 als. To consider this properly, we have defined the idea of “fair comparisons”
439 between different models, which requires the mean group size in each case
440 to be the same. When considering evolutionary games on graphs there is
441 not the same problem, as all games are pairwise. We note, however, that in
442 this case there is the related feature of the degree of a vertex, the number

443 of connections of an individual, and graph models are often compared using
444 different types of graphs with the same average degree.

445 As well as using existing game models, there is also a natural way to
446 develop new game models in the context of our framework; namely to have
447 the strategies of the individuals related to their probability to move to a
448 given place. Thus an animal may decide to go to one place and not another,
449 which will not affect any interactions given that they occur, but will affect
450 the likelihood of any given interaction occurring.

451 When modelling using evolutionary games on graphs, games played with
452 other individuals through the population structure leads to each individual
453 acquiring a fitness, and as we have seen, exactly the same occurs in our
454 framework as well. For evolutionary graph theory, the next step is for the
455 population to evolve following some appropriately defined dynamics. For ex-
456 ample, the invasion process (IP) selects a random individual according to its
457 fitness, and this individual then replaces a randomly chosen neighbour with
458 a copy of itself. We have not considered dynamics in this paper, but we could
459 use very similar dynamics to those used in evolutionary graph theory. For ex-
460 ample, an analogy of the IP would again pick an individual to reproduce with
461 a probability proportional to its fitness, and then groups could be reformed
462 at random, following the original procedure, and a random groupmate then
463 be selected to be replaced. It is clear that the question of dynamics in such
464 processes needs serious consideration. The purpose of the current paper,
465 however, was to introduce a framework for modelling interaction within a
466 population, and so we leave the consideration of dynamics to later work.

467 We should note here that an evolutionarily stable strategy is a static

468 concept suited to large populations, and can be used in our context on the
469 assumption that the population consists of a large number of similar territo-
470 rial structures, with sufficient mixing between them. To consider evolution
471 in finite populations fully, we would need to consider the precise nature of
472 the dynamics. This will be an important priority in the development of our
473 framework, but as we explain earlier, is outside the scope of the current
474 paper.

475 Hinsch and Komdeur [21] consider an interesting model of territorial in-
476 teraction, which relates to the interaction of intruders and defenders in Sec-
477 tion 4.2. In their work, the cost of intrusion resulting from the defence by
478 the territory owner must be severe to prevent significant intrusion and make
479 the defence of a home territory worthwhile. Their direct contests are only
480 between the owner and the intruder (and their model of fights is more so-
481 phisticated than ours, which in this paper is used as an illustrative example
482 rather than a comprehensive model). On the other hand, our model assumes
483 that even two intruders can fight. A difference in the outcomes is that such
484 intruder-intruder contests can make intruding ineffective when the number
485 of neighbours is large without any need of increased defending by the owner
486 (as needed in [21]).

487 Adams [22] discusses a number of studies of territorial behaviour consid-
488 ering the optimisation of territory area and shape. They discuss the spatial
489 organisation of territories [see 23, 24, 25] where individuals must organise
490 themselves within a habitat, where spatial division between individuals is
491 flexible, but there are always territories with well-defined boundaries. Thus
492 our model is more general, in the sense that it considers the possibility of

493 overlapping territories, and indeed this possibility, allowing multiple interac-
494 tions, was a prime reason for developing the framework.

495 van Veelen and Nowak [20] considered a model where individuals occupy
496 the vertices on a circle graph with N vertices, and payoffs are evaluated
497 by games played between all collections of n consecutive individuals on the
498 cycle. Thus in effect there are N possible groups of size n and each form
499 with probability $1/N$. This fits into our framework and is an example of a
500 history-independent, but not row-independent, model with $N - n + 1$ places,
501 where a herd of n move to place 1 and others move singly to places 2 to
502 $N - n + 1$ with no background reward. They analysed multiplayer versions of
503 some classical games of cooperation such as the stag hunt game and public
504 goods games, and found in general that cooperation was harder to achieve
505 the larger the groups involved, but under certain circumstances it was easier
506 to achieve on the circle than in a well-mixed population, which is broadly
507 consistent with results for two-player games, where structure generally helps
508 the evolution of cooperation.

509 As we have stated, an important feature of our framework is its flexi-
510 bility. Nevertheless, in the examples considered in the independent model,
511 the fundamental relationship between individuals and the overall habitat is
512 constant, and truly dynamic aspects of behaviour are absent. Thus if animal
513 interactions or seasonal changes lead to changing the distribution of indi-
514 viduals over a habitat and there are strong temporal correlations for where
515 an individual can move, quite complex dynamical behaviour could occur.
516 This is a significant criticism of evolutionary graph models too. These can
517 be included within more general models, for instance those which are nei-

518 ther history-independent nor row-independent. In its fullest generality our
519 framework would be very complex, and so to model such situations some
520 intermediate level models should be used. We have given a brief indication
521 of some of these in Appendix A.

522 We note that although we have focused on territorial behaviour, our
523 framework relates to many other situations. For example the model of [20]
524 considers the evolution of cooperation on a simple structured population,
525 and as this is a special case of our framework, it is clear that our framework
526 can be valuable in investigating the evolution of cooperative behaviour in
527 general. Another example is the complex interactions within animal social
528 groups, for instance ungulates such as goats or sheep, but especially primate
529 groups. Family and dominance relationships within these groups mean that
530 interactions between some collections of individuals are more likely than oth-
531 ers, and often contests for dominance will feature multiple individuals, often
532 in complex alliances. A discussion of this, and a mathematical model, was
533 developed in [26].

534 It will be of great interest to see how different types of structure affect
535 key evolutionary properties of populations. For example, in Section 5.3 we
536 see that the heterogeneous star graph induces a lower level of aggression than
537 the homogeneous well mixed population in the Hawk-Dove game. The pri-
538 mary cause of this is that the star graph caused more variability in the size
539 of groups which met, and this had the consequence of making the aggressive
540 Hawk strategy less profitable. This leads to the question of whether spatial
541 structure of biological populations is a key factor in the variability of the
542 sizes of groups, and is this variability in turn a key predictor of important

543 within-group behaviour such as the level of aggressiveness or cooperation?
 544 A second example is in the territorial raider model with strategic movement,
 545 where it can be more beneficial to invade other territories than defend your
 546 own when the degree of the graph is sufficiently low. Thus it would be inter-
 547 esting to investigate the preponderance of territory invasion based upon the
 548 number of neighbours (how to allow for such factors as territory size to make
 549 a fair comparison is an interesting question). This paper is only able at this
 550 stage to tentatively raise such questions, as we further develop the frame-
 551 work. An obvious starting point is the consideration of general multi-player
 552 games [27, 28, 29] within our framework. There is enduring interest in the
 553 evolution of cooperation [30, 31, 32] and it will be of considerable interest to
 554 see how different types of our more general structure affect the evolution of
 555 cooperation, in particular when multiplayer games are involved. Other pos-
 556 sibilities include more concrete biological behaviours, for instance we could
 557 consider models of kleptoparasitism [33, 34] or dominance hierarchies [35, 36]
 558 in an explicitly spatial context. The exploration of this framework is clearly
 559 still in its very early stages, and the range of possibilities is considerable.

560 **Acknowledgement**

561 The research was supported by a City University Pump Priming grant to
 562 M. Broom and by the UNCG Regular Faculty Grant to J. Rychtář. We would
 563 also like to thank four anonymous reviewers for their valuable comments and
 564 suggestions.

565 **References**

- 566 [1] E. Lieberman, C. Hauert, M. Nowak, Evolutionary dynamics on graphs,
567 Nature 433 (7023) (2005) 312–316.
- 568 [2] T. Antal, I. Scheuring, Fixation of strategies for an evolutionary game
569 in finite populations, Bulletin of Mathematical Biology 68 (8) (2006)
570 1923–1944.
- 571 [3] H. Ohtsuki, C. Hauert, E. Lieberman, M. Nowak, A simple rule for the
572 evolution of cooperation on graphs, Nature 441 (7092) (2006) 502.
- 573 [4] F. Santos, J. Pacheco, A new route to the evolution of cooperation,
574 Journal of Evolutionary Biology 19 (3) (2006) 726–733.
- 575 [5] C. Hadjichrysanthou, M. Broom, J. Rychtář, Evolutionary games on star
576 graphs under various updating rules, Dynamic Games and Applications
577 1 (3) (2011) 386–407.
- 578 [6] M. Nowak, R. May, Evolutionary games and spatial chaos, Nature
579 359 (6398) (1992) 826–829.
- 580 [7] M. Nowak, R. May, The spatial dilemmas of evolution, International
581 Journal of Bifurcation and Chaos 3 (1993) 35–78.
- 582 [8] G. Ermentrout, L. Edelstein-Keshet, Cellular automata approaches to
583 biological modeling, Journal of Theoretical Biology 160 (1993) 97–133.
- 584 [9] W. Burt, Territoriality and home range concepts as applied to mammals,
585 Journal of Mammalogy 24 (3) (1943) 346–352.

- 586 [10] R. Woodroffe, J. Ginsberg, D. Macdonald, The African wild dog: status
587 survey and conservation action plan, World Conservation Union, 1997.
- 588 [11] R. Woodroffe, J. Ginsberg, Conserving the african wild dog *lycaon pic-*
589 *tus*. i. diagnosing and treating causes of decline, *Oryx* 33 (2) (1999)
590 132–142.
- 591 [12] J. Ginsberg, D. Macdonald, Foxes, wolves, jackals, and dogs: an action
592 plan for the conservation of canids, *Iucn*, 1990.
- 593 [13] L. Marker, A. Dickman, M. Mills, R. Jeo, D. Macdonald, Spatial ecology
594 of cheetahs on north-central namibian farmlands, *Journal of Zoology*
595 274 (3) (2008) 226–238.
- 596 [14] S. Kelley, D. Ransom Jr, J. Butcher, G. Schulz, B. Surber, W. Pinchak,
597 C. Santamaria, L. Hurtado, Home range dynamics, habitat selection,
598 and survival of greater roadrunners, *Journal of Field Ornithology* 82 (2)
599 (2011) 165–174.
- 600 [15] R. Rodríguez-Estrella, L. Rivera-Rodríguez, Kleptoparasitism and other
601 interactions of crested caracara in the cape region, Baja California, mex-
602 ico (cleptoparasitismo y otras interacciones de individuos de *polyborus*
603 *plancus* en la región del cabo, baja california sur, méxico), *Journal of*
604 *Field Ornithology* (1992) 177–180.
- 605 [16] R. Swihart, Home-range attributes and spatial structure of woodchuck
606 populations, *Journal of Mammalogy* 73 (1992) 604–618.
- 607 [17] I. Herbinger, C. Boesch, H. Rothe, Territory characteristics among

- 608 three neighboring chimpanzee communities in the taï national park, côte
609 d’ivoire, *International Journal of Primatology* 22 (2) (2001) 143–167.
- 610 [18] K. Schmidt, W. Jedrzejewski, H. Okarma, Spatial organization and so-
611 cial relations in the eurasian lynx population in bialowieza primeval
612 forest, poland, *Acta Theriologica* 42 (1997) 289–312.
- 613 [19] W. Jetz, C. Carbone, J. Fulford, J. Brown, The scaling of animal space
614 use, *Science* 306 (5694) (2004) 266–268.
- 615 [20] M. van Veelen, M. Nowak, Multi-player games on the cycle, *Journal of*
616 *Theoretical Biology*.
- 617 [21] M. Hinsch, J. Komdeur, Defence, intrusion and the evolutionary stabil-
618 ity of territoriality, *Journal of Theoretical Biology* (2010) 603–613.
- 619 [22] E. Adams, Approaches to the study of territory size and shape, *Annual*
620 *Review of Ecology and Systematics* (2001) 277–303.
- 621 [23] M. Lewis, J. Murray, Modelling territoriality and wolf-deer interactions,
622 *Nature* 366 (6457) (1993) 738–740.
- 623 [24] K. White, M. Lewis, J. Murray, A model for wolf-pack territory for-
624 mation and maintenance, *Journal of Theoretical Biology* 178 (1) (1996)
625 29–43.
- 626 [25] K. White, J. Murray, M. Lewis, Wolf-deer interactions: a mathematical
627 model, *Proceedings of the Royal Society of London. Series B: Biological*
628 *Sciences* 263 (1368) (1996) 299.

- 629 [26] M. Broom, A. Koenig, C. Borries, Variation in dominance hierarchies
630 among group-living animals: modeling stability and the likelihood of
631 coalitions, *Behavioral Ecology* 20 (4) (2009) 844–855.
- 632 [27] M. Broom, C. Cannings, G. Vickers, Multi-player matrix games, *Bulletin*
633 *of Mathematical Biology* 59 (5) (1997) 931–952.
- 634 [28] M. Bukowski, J. Miekisz, Evolutionary and asymptotic stability in sym-
635 metric multi-player games, *International Journal of Game Theory* 33 (1)
636 (2004) 41–54.
- 637 [29] C. Gokhale, A. Traulsen, Evolutionary games in the multiverse, *Proceed-*
638 *ings of the National Academy of Sciences* 107 (12) (2010) 5500–5504.
- 639 [30] R. Axelrod, W. Hamilton, The evolution of cooperation, *Science*
640 211 (4489) (1981) 1390–1396.
- 641 [31] M. Nowak, A. Sasaki, C. Taylor, D. Fudenberg, Emergence of coopera-
642 tion and evolutionary stability in finite populations, *Nature* 428 (6983)
643 (2004) 646–650.
- 644 [32] M. Nowak, *Evolutionary dynamics: exploring the equations of life*, Belk-
645 nap Press, 2006.
- 646 [33] M. Broom, G. Ruxton, Evolutionarily stable stealing: game theory ap-
647 plied to kleptoparasitism, *Behavioral Ecology* 9 (1998) 397–403.
- 648 [34] M. Broom, J. Rychtář, Kleptoparasitic melees: Modelling food stealing
649 featuring contests with multiple individuals, *Bulletin of Mathematical*
650 *Biology* 73 (3) (2011) 683–699.

- 651 [35] M. Mesterton-Gibbons, L. Dugatkin, Toward a theory of dominance
652 hierarchies: effects of assessment, group size, and variation in fighting
653 ability, *Behavioral Ecology* 6 (4) (1995) 416–423.
- 654 [36] M. Broom, C. Cannings, Modelling dominance hierarchy formation as a
655 multi-player game, *Journal of Theoretical Biology* 219 (3) (2002) 397–
656 413.
- 657 [37] A. Szolnoki, M. Perc, Z. Danku, Towards effective payoffs in the pris-
658 oner’s dilemma game on scale-free networks, *Physica A: Statistical Me-
659 chanics and its Applications* 387 (8-9) (2008) 2075–2082.
- 660 [38] B. Voelkl, The “hawk-dove” game and the speed of the evolutionary
661 process in small heterogeneous populations, *Games* 1 (2) (2010) 103–
662 116.
- 663 [39] M. Broom, J. Rychtář, An analysis of the fixation probability of a mu-
664 tant on special classes of non-directed graphs, *Proceedings of the Royal
665 Society A: Mathematical, Physical and Engineering Science* 464 (2098)
666 (2008) 2609–2627.
- 667 [40] M. Broom, C. Hadjichrysanthou, J. Rychtář, Evolutionary games on
668 graphs and the speed of the evolutionary process, *Proceedings of
669 the Royal Society A: Mathematical, Physical and Engineering Science*
670 466 (2117) (2010) 1327–1346.

671 Appendix A: Some concepts of independence

672 As we saw in Section 2.1, a population distribution is history-independent
673 if

$$P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = P(\mathbf{X}(t) = \mathbf{x}). \quad (56)$$

674 We call a history independent process *homogeneous* if the population distri-
675 bution is independent of time i.e.

$$P(\mathbf{X}(s) = \mathbf{x}) = P(\mathbf{X}(t) = \mathbf{x}) \quad \forall s, t \geq 1. \quad (57)$$

676 A given population distribution may not be independent of the history of
677 the process, but may depend only upon the most recent population distribu-
678 tion. In this case we call the model *Markov* and we have

$$P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{<t}) = P(\mathbf{X}(t) = \mathbf{x} | \mathbf{X}(t-1) = \mathbf{x}_{t-1}), \quad (58)$$

679 and we denote this quantity simply as $P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{t-1})$. For a given in-
680 dividual we analogously write $p_{n,m,t}(\mathbf{x}_{t-1})$. Similarly a Markov process is
681 homogeneous if

$$P(\mathbf{X}(s) = \mathbf{x})(\mathbf{x}_{s-1}) = P(\mathbf{X}(t) = \mathbf{x})(\mathbf{x}_{t-1}) \quad \forall s, t \geq 1. \quad (59)$$

682 It is possible that each individual in the population moves independently
683 of what others do *at that time point*, so can only move conditionally on what
684 has happened in the past, then for any m_1, m_2 we have

$$P(X_{n_1, m_1}(t) = 1 \ \& \ X_{n_2, m_2}(t) = 1)(\mathbf{x}_{<t}) = p_{n_1, m_1, t}(\mathbf{x}_{<t}) p_{n_2, m_2, t}(\mathbf{x}_{<t}). \quad (60)$$

685 In this case we call the model *row-independent*. We note that this will not
686 necessarily be the case, for instance if the animals move in groups such as
687 herds, if individuals actively exclude conspecifics or if they follow a strategy
688 of opportunistic intrusion when a conspecific is absent. We also note that the
689 alternative concept of column-independence can never occur, as knowledge of
690 the occupants of one place necessarily gives information about the occupancy
691 of others.

692 If the process is both row independent and history independent then the
693 probability of an individual visiting a place depends only upon the individual,
694 the place and the time so that

$$p_{n,m,t}(\mathbf{x}_{<t}) = p_{n,m,t} \quad \forall n, m, t, \mathbf{x}_{<t}. \quad (61)$$

695 If in addition the process is homogeneous then

$$p_{n,m,t}(\mathbf{x}_{<t}) = p_{n,m} \quad \forall n, m, t, \mathbf{x}_{<t}. \quad (62)$$

696 In this case we simply call the model *independent*, again as discussed in
697 Section 2.1.

698 **Appendix B: General results for the boundary interaction model**

699 In the boundary interaction model of Section 3.2, let $\mathbf{A} = (A_{i,j})$ be the
700 adjacency matrix of the graph, i.e. $A_{i,j} = 1$ if there is an edge between I_i
701 and I_j and $A_{i,j} = 0$ otherwise.

702 Suppose that I_n has degree $d_n = \sum_j A_{n,j}$, so its possible groups are
703 either $\{I_n\}$ (it is alone, which can occur on any boundary of its territory), or
704 $\{I_n, I_{n'}\}$ (two individuals meet on the common boundary of their territories)
705 for each of the d_n individuals $I_{n'}$ such that $A_{n,n'} = 1$.

706 It is possible that an individual is more likely to move to one boundary
707 than another (e.g. if the boundaries vary in size), as is the case in Figure 3.
708 Supposing that this is not the case, and each boundary is visited with equal
709 probability, we get $p_{n,\{n,n'\}} = A_{n,n'}/d_n$. Hence, assuming that the reward for
710 a given individual being alone does not depend upon which boundary of its
711 territory it is at, we obtain

$$R_n = \sum_{n'} \frac{A_{n,n'}}{d_n} \text{Reward from going to } P_{\{n,n'\}} \quad (63)$$

$$= \sum_{n'} \frac{A_{n,n'}}{d_n} \left(\frac{1}{d_{n'}} f_{n,\{n,n'\}} + \left(1 - \frac{1}{d_{n'}}\right) f_{n,\{n\}} \right) \quad (64)$$

$$= f_{n,\{n\}} + \sum_{n'} A_{n,n'} \frac{1}{d_n} \frac{1}{d_{n'}} [f_{n,\{n,n'\}} - f_{n,\{n\}}] \quad (65)$$

712 where $f_{n,\{n\}}$ is the payoff when alone, which can perhaps be regarded as the
713 background fitness and $f_{n,\{n,n'\}}$ is the payoff when being with individual n' .

714 We note here that this reward function is different to those usually used
715 when modelling games on graphs. One common reward function is the total
716 reward [37, 38], where an individual plays a game against each of its neigh-
717 bours and the overall reward is the sum of the payoffs of all of these games.
718 The reward to individual I_n then is given by

$$R_n^t = \sum_{n'} A_{nn'} f_{n,\{n,n'\}}. \quad (66)$$

719 Why should individuals gain rewards only when meeting others, and these
720 rewards be cumulative? Perhaps when individuals meet they swap informa-
721 tion, so the more information that is obtained the better for the individual.
722 An alternative reward function is the average reward, where an individual

723 plays all of its neighbours [39, 40], but its reward is the average of the payoffs
724 from these games i.e.

$$R_n^m = \sum_{n'} \frac{1}{d_n} A_{nn'} f_{n,\{n,n'\}}. \quad (67)$$

725 In this case, perhaps the information obtained takes time to use, and that
726 time is split evenly between all of the pieces of information obtained (e.g.
727 when two bees meet and one communicates the location of flowers to the
728 other). We contend that our version of the fitness function R_n is the more
729 natural fitness function for most situations, and that more attention needs
730 to be paid to the fitness function used for any particular game.

731 We note that for regular graphs, the three fitness functions described
732 above are effectively the same differing only in the addition of an arbitrary
733 constant to all payoffs, but that for irregular graphs there are significant dif-
734 ferences between the three. It is already well known that R_n^t and R_n^m can
735 yield very different results; this is easy to see, since, assuming payoffs are
736 always positive, the better connected vertices will have relatively higher fit-
737 nesses under R_n^t than R_n^m . Similarly if the payoff to being alone is larger than
738 for being in any larger group, for example, which is reasonable in many for-
739 aging situations, individuals on the most connected vertices will have highest
740 fitness under R_n^t but lowest fitness under R_n .

741 **Appendix C: Our framework in the completely mixed limit**

742 Let us consider a population playing pairwise games within a well mixed
743 population, but where groups are formed using our completely mixed pop-
744 ulation, so each other individual is independently in the same group as our

745 focal individual with probability p (which may or may not correspond to a
 746 fixed number of places M , with $p = 1/M$). Thus

$$P(G : \text{where } |G| = k) = p^{k-1}(1-p)^{N-k} \quad k = 1, 2, \dots, N-1. \quad (68)$$

747 As games are simple pairwise ones, these can be played within a group by
 748 picking a random opponent from the group for each individual, or, equiva-
 749 lently, averaging the payoffs gained by playing all the others in a group. This
 750 gives a mean reward to I_n within a group G_i , $|G_i| = k$, of

$$R(n|G_i) = \frac{1}{k-1} \sum_{n' \neq n \in G} R_{(n,n')}. \quad (69)$$

751 Thus an individual's total average fitness using the above formula is

$$\sum_k \sum_{G, |G|=k} p^{k-1}(1-p)^{N-k} \frac{1}{k-1} \sum_{n' \neq n \in G} R_{(n,n')}. \quad (70)$$

752 Each other individual is in precisely $\binom{N-2}{k-2}$ groups of size k that also involve
 753 our focal individual, so (70) becomes

$$R(n) = \sum_k p^{k-1}(1-p)^{N-k} \frac{1}{k-1} \binom{N-2}{k-2} \sum_{n' \neq n} R_{(n,n')} \quad (71)$$

$$= \frac{1}{N-1} \sum_{n' \neq n} R_{(n,n')} \quad (72)$$

754 which is the mean payoff in the well-mixed population for pairwise games.
 755 Thus our framework is consistent with standard results for pairwise games.