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

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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

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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

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

1.2. Animal groups and territoriality

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

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

A good example of this phenomenon occurs in the case of the African wild dog. Woodroffe [10], [11] describe aspects of the territorial behaviour of wild dogs. The size of home ranges varies considerably from site to site, ranging from 500 square kilometres up to over 1500 square kilometres. In fact these areas vary in size throughout the year as well; for instance packs use much smaller areas when they are feeding pups at a den. Across different sites, with such large home ranges, a common feature is significant home range overlap, where there can be interactions between different dog packs. Ginsberg & Macdonald [12] measured a home range overlap from 50% to 80%. The size of the regions of interaction can vary throughout the year, and the environment and the likelihood of interactions are thus very fluid.

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

1.3. Outline of the paper

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

2. The model framework

2.1. The population and its distribution

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

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

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

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

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

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

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

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

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

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

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

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

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

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

If the process satisfies

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

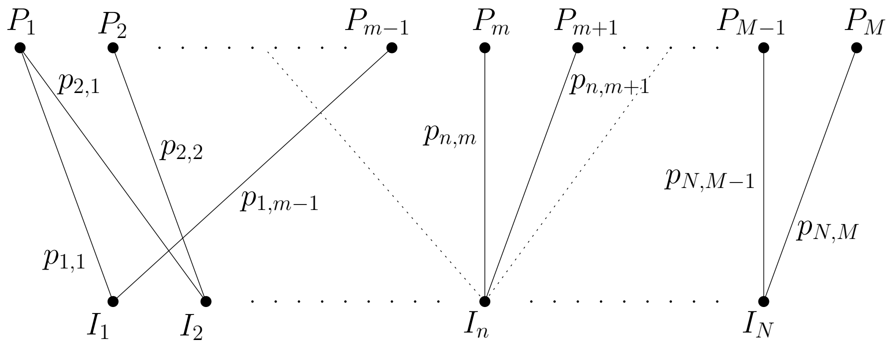


Figure 1: Representing an independent model as a bipartite graph where the weight between the vertex representing individual I_n and place P_m is $p_{n,m}$.

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

Perhaps the most natural reward function, and the one that we will generally use, is the *mean reward*, which we label R_n where

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

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

$$G = \{I_j; x_{j,m} = 1\}. \tag{9}$$

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

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

For the independent model, this becomes

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

Often the reward to an individual will only depend upon the place that it occupies and the group of individuals at that place. We label such payoffs as *direct group interaction payoffs*, and in such cases

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

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

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

3. Example models

3.1. Territorial interaction model

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

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

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

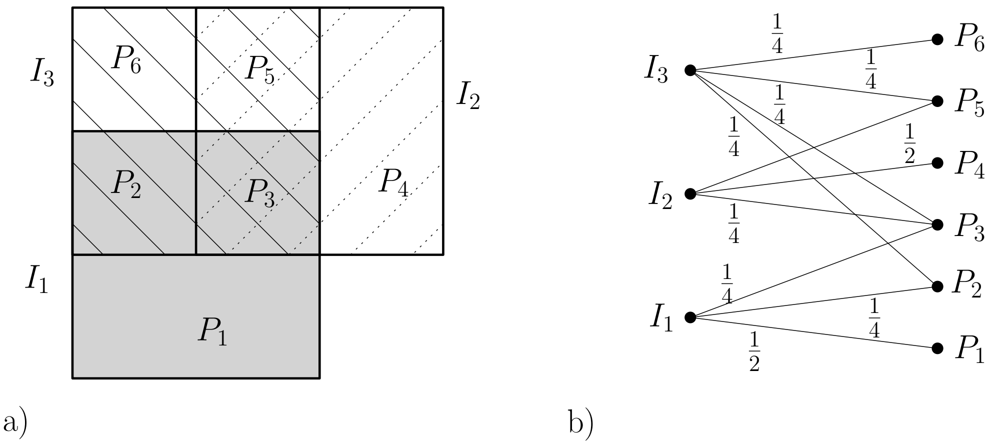


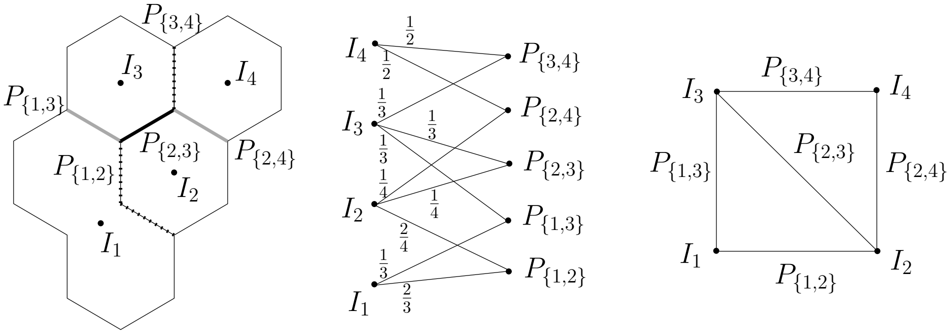
Figure 2: Territorial interaction model. a) The territory of individual I_1 is the square in grey, the territory of I_2 is the square encompassed by the dotted lines, the territory of I_3 is the square encompassed by full lines; b) is the corresponding graphical representation as a general independent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

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

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

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



a) b) c)

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.

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

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

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

In Appendix B we discuss the reward function for the boundary interaction model, and discuss some potentially important consequences for the evaluation of reward functions for evolutionary games on graphs.

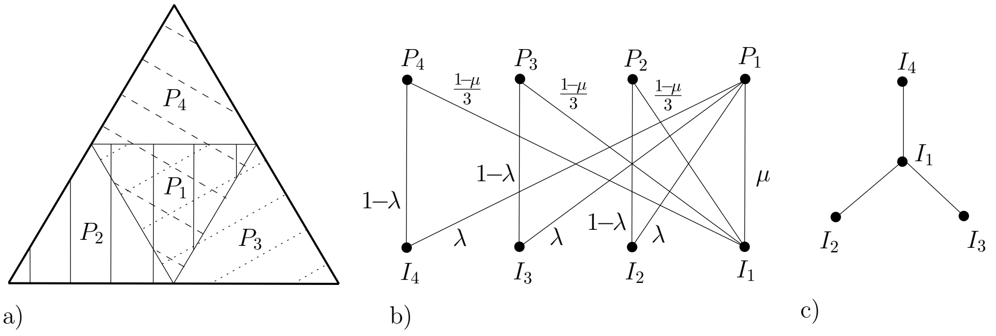


Figure 4: The territorial raider model. a) Individual I_n lives in place P_n but can raid neighbouring places. The territory of I_1 is the whole triangle and the home place is the central smaller triangle. The territory of I_2 is the rhombus encompassed by full lines, the territory of I_3 the rhombus 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.

3.3. The territorial raider model

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

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

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

We get

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

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

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

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

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

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

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

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

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

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

The prospective probabilities thus become

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

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

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

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

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

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

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

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.

4. The role of strategy and example games

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

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

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

$$R^D_{d,h} = \begin{cases} 0; & \text{if } h > 0 \\ \frac{V}{d+1}; & \text{if } h = 0 \end{cases} \tag{28}$$

$$R^H_{d,h} = \frac{V - hC}{h+1}. \tag{29}$$

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

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

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

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

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

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

Let us now consider this game on the star with $N = 5, \lambda = 1/2$ and $\mu = 1/5, V = 1$ and $C = 2$ as described in Table 1. In particular we shall assume a large population consisting of many identical star structures, with mixing over time. We seek the Evolutionarily Stable Strategy (ESS) value of α where the payoff $E_H(\alpha)$ for playing Hawk is the same as the payoff $E_D(\alpha)$ for playing Dove. It should be noted that we have assumed that individuals do not distinguish between whether their home vertex was the centre or a leaf when choosing their strategy; if they did so we would have an asymmetric contest which would be significantly more complicated (there would be two distinct roles here for the star, but in general there could be many roles). We further note that to consider evolution on a finite population fully, we would need to explicitly consider the dynamics of the process, which is outside the scope of this paper. Since, by (31)-(32) and the values in Table 1,

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

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

4.2. The territorial raider model with strategic movement

Consider a territorial raider model, so that a graph $G = (V, E)$ is given, individuals live at places P_m and can either stay in their own place or visit a neighbouring place. Consider a regular graph with every vertex having degree d. Suppose that individuals play a strategy where they stay at their home place with probability $1 - p$ and move to each of the neighbouring places with equal probability p/d. Thus here strategy affects the movement of individuals and the distribution of the population over the places, but it 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.

The expected reward will thus be

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

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

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

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

$$\begin{aligned} f(p) &= E_{Home} - E_{Intrude} && (36)\\ &= (B_H - B_I) + F_O - p\big[(L_H - L_I) + F_H + (F_O - F_I) + \frac{1}{d}F_I\big] && (37) \end{aligned}$$

We can now perform the ESS analysis. If

$$0 < f(0) = (B_H - B_I) + F_O \tag{38}$$

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

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

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

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

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

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

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

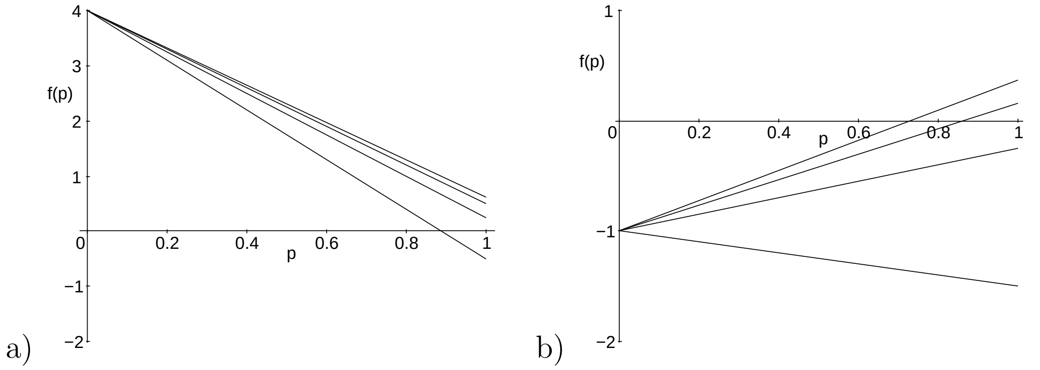


Figure 5: Graphs of $f(p)$ from (37) for varying d. In a), $B_H - B_I = 1, F_O = 3, L_H - L_I = 0, F_H - F_I = 0, F_I = 3$ and $d = 2$ (bottom line), $d = 4, 6$ (middle lines) and $d = 8$ (top line); here $p = 0$ is always ESS, $p = 1$ is ESS only if $d < 3$. In b) $B_H - B_I = -2, F_O = 1, L_H - L_I = -2, F_H - F_I = -1, F_I = 5$ 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 $d > 5$.

5. Comparing place structures

5.1. Fair comparisons

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

However, we also want to know whether the structure influences the payoffs in some other way as well. We take the approach of comparing a given place structure with an appropriate well-mixed population. This would then allow us to compare different place structures with each other through the medium of their respective well-mixed populations; making it a fair comparison not biased by the different group sizes. In this section we shall only consider independent processes, as such comparisons are harder in other cases. We will call a comparison between a given place model and a well-mixed population *fair* if the mean group size of the two situations is the same.

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

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

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

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

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

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

5.2. A simple example

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

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

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

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

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

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

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

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

$$P_{|G|=3} = \frac{1}{12}, \tag{44}$$

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

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

The mean group size is thus 29/18.

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

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

$$P^{cm}_{|G|=2} = 2\frac{11}{36}\frac{25}{36}, \tag{48}$$

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

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

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

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

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

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

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

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

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

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

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

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

We can illustrate this point about variability by the following. If we set $p = 1/N$ in the limit as $N \to \infty$ for our Binomial distribution, we get the limiting Poisson (1) distribution, which has a mean group size of 2 (the focal individual and one other). The payoffs become

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

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

6. Discussion

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

This framework has some similarities with the concept of evolutionary graph theory, where the relationships between individuals are given by a graph. There individuals interact in a pairwise fashion only, through the edges of the graph (though see [20] which we discuss below). In our framework any number of individuals can theoretically interact, depending upon the nature of the structure involved.

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

A key influence on the outcome of multiplayer games is the number of players involved. Thus if one structure generates different size groups to another, then this can have a significant effect just through the sizes of the groups generated. Such a group size effect certainly occurs for the multiplayer Hawk-Dove game, for example. This is certainly of interest, but we are also interested in effects caused by structural relationships between the individuals. To consider this properly, we have defined the idea of "fair comparisons" between different models, which requires the mean group size in each case to be the same. When considering evolutionary games on graphs there is not the same problem, as all games are pairwise. We note, however, that in this case there is the related feature of the degree of a vertex, the number of connections of an individual, and graph models are often compared using different types of graphs with the same average degree.

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

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

We should note here that an evolutionarily stable strategy is a static concept suited to large populations, and can be used in our context on the assumption that the population consists of a large number of similar territorial structures, with sufficient mixing between them. To consider evolution in finite populations fully, we would need to consider the precise nature of the dynamics. This will be an important priority in the development of our framework, but as we explain earlier, is outside the scope of the current paper.

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

Adams [22] discusses a number of studies of territorial behaviour considering the optimisation of territory area and shape. They discuss the spatial organisation of territories [see 23, 24, 25] where individuals must organise themselves within a habitat, where spatial division between individuals is flexible, but there are always territories with well-defined boundaries. Thus our model is more general, in the sense that it considers the possibility of overlapping territories, and indeed this possibility, allowing multiple interactions, was a prime reason for developing the framework.

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

As we have stated, an important feature of our framework is its flexibility. Nevertheless, in the examples considered in the independent model, the fundamental relationship between individuals and the overall habitat is constant, and truly dynamic aspects of behaviour are absent. Thus if animal interactions or seasonal changes lead to changing the distribution of individuals over a habitat and there are strong temporal correlations for where an individual can move, quite complex dynamical behaviour could occur. This is a significant criticism of evolutionary graph models too. These can be included within more general models, for instance those which are neither history-indpendent nor row-independent. In its fullest generality our framework would be very complex, and so to model such situations some intermediate level models should be used. We have given a brief indication of some of these in Appendix A.

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

It will be of great interest to see how different types of structure affect key evolutionary properties of populations. For example, in Section 5.3 we see that the heterogeneous star graph induces a lower level of aggression than the homogeneous well mixed population in the Hawk-Dove game. The primary cause of this is that the star graph caused more variability in the size of groups which met, and this had the consequence of making the aggressive Hawk strategy less profitable. This leads to the question of whether spatial structure of biological populations is a key factor in the variability of the sizes of groups, and is this variability in turn a key predictor of important within-group behaviour such as the level of aggressiveness or cooperation? A second example is in the territorial raider model with strategic movement, where it can be more beneficial to invade other territories than defend your own when the degree of the graph is sufficiently low. Thus it would be interesting to investigate the preponderance of territory invasion based upon the number of neighbours (how to allow for such factors as territory size to make a fair comparison is an interesting question). This paper is only able at this stage to tentatively raise such questions, as we further develop the framework. An obvious starting point is the consideration of general multi-player games [27, 28, 29] within our framework. There is enduring interest in the evolution of cooperation [30, 31, 32] and it will be of considerable interest to see how different types of our more general structure affect the evolution of cooperation, in particular when multiplayer games are involved. Other possibilities include more concrete biological behaviours, for instance we could consider models of kleptoparasitism [33, 34] or dominance hierarchies [35, 36] in an explicitly spatial context. The exploration of this framework is clearly still in its very early stages, and the range of possibilities is considerable.

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Appendix A: Some concepts of independence

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

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

We call a history independent process *homogeneous* if the population distribution is independent of time i.e.

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

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

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

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

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

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

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

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

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

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

If in addition the process is homogeneous then

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

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

Appendix B: General results for the boundary interaction model

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

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

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

$$\begin{aligned} R_n &= \sum_{n'} \frac{A_{n,n'}}{d_n} \text{Reward from going to } P_{\{n,n'\}} && (63) \\ &= \sum_{n'} \frac{A_{n,n'}}{d_n} \left(\frac{1}{d_{n'}} f_{n,\{n,n'\}} + (1 - \frac{1}{d_{n'}}) f_{n,\{n\}} \right) && (64) \\ &= f_{n,\{n\}} + \sum_{n'} A_{n,n'} \frac{1}{d_n} \frac{1}{d_{n'}} \left[f_{n,\{n,n'\}} - f_{n,\{n\}} \right] && (65) \end{aligned}$$

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

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

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

Why should individuals gain rewards only when meeting others, and these rewards be cumulative? Perhaps when individuals meet they swap information, so the more information that is obtained the better for the individual. An alternative reward function is the average reward, where an individual plays all of its neighbours [39, 40], but its reward is the average of the payoffs from these games i.e.

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

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

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

Appendix C: Our framework in the completely mixed limit

Let us consider a population playing pairwise games within a well mixed population, but where groups are formed using our completely mixed population, so each other individual is independently in the same group as our focal individual with probability p (which may or may not correspond to a fixed number of places M, with $p = 1/M$). Thus

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

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

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

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

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

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

$$\begin{aligned} R(n) &= \sum_k p^{k-1}(1-p)^{N-k} \frac{1}{k-1} \binom{N-2}{k-2} \sum_{n' \neq n} R_{(n,n')} & (71) \\ &= \frac{1}{N-1} \sum_{n' \neq n} R_{(n,n')} & (72) \end{aligned}$$

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