

# A dynamical model of two-level selection

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## ABSTRACT

**Question:** How do continuous-time evolutionary trajectories of two-level selection behave?

**Approach:** Construct and solve a dynamical model of two-level selection capable of predicting evolutionary trajectories and equilibrium configurations.

**Mathematical methods:** Evolutionary birth–death processes, simulation, large population asymptotics, numerical solutions of hyperbolic PDEs.

**Key assumptions:** Environment composed of distinct groups of individuals. Individuals' birth and death rates are differentiable functions of the state of the environment. Groups' fissioning and extinction rates are integrable functions of the state of the environment.

**Main results:** A continuous-time, discrete-state, stochastic model of two-level selection that can be simulated exactly. A continuous-time, continuous-state, deterministic (PDE) model of two-level selection that can be solved numerically. A mathematical connection between the stochastic and deterministic models. Equilibrium configurations of the environment in models of the evolution of cooperation by two-level selection often consist of complicated mixtures of groups of varying sizes, ages, and levels of cooperation.

*Keywords:* evolution of cooperation, evolutionary birth–death process, evolutionary dynamics, group selection, MLS1, MLS2, multi-level selection, social evolution.

## 1. INTRODUCTION

There is a large and rapidly growing literature on the evolution of cooperation, and related topics that involve evolving populations of socially interacting individuals. Theoretical work, mathematical models, and empirical work have combined to paint a complicated (and sometimes contentious) picture of how the processes might work (e.g. Darwin, 1871; Hamilton, 1964, 1975; Maynard Smith, 1964; Williams, 1966; Dawkins, 1976; Queller, 1992; Goodnight, 1997, 2005; Frank, 1998; Maynard Smith and Szathmary, 1998; Sober and Wilson, 1998; Keller, 1999; Michod, 1999; Boyd and Richerson, 2002; Trivers, 2002; Gintis, 2003; Bowles and Gintis, 2004, 2009; Traulsen *et al.*, 2005, 2008; Bowles, 2006; Buss, 2006; Gardner and West, 2006; Lehmann and Keller, 2006; Nowak, 2006; Okasha, 2006; Traulsen and Nowak, 2006; Lehmann *et al.*, 2007; West *et al.*, 2007a, 2007b, 2008; Wilson and Wilson, 2007; Gardner and Grafen, 2008; Goodnight *et al.*, 2008; Fletcher and Doebeli, 2009).

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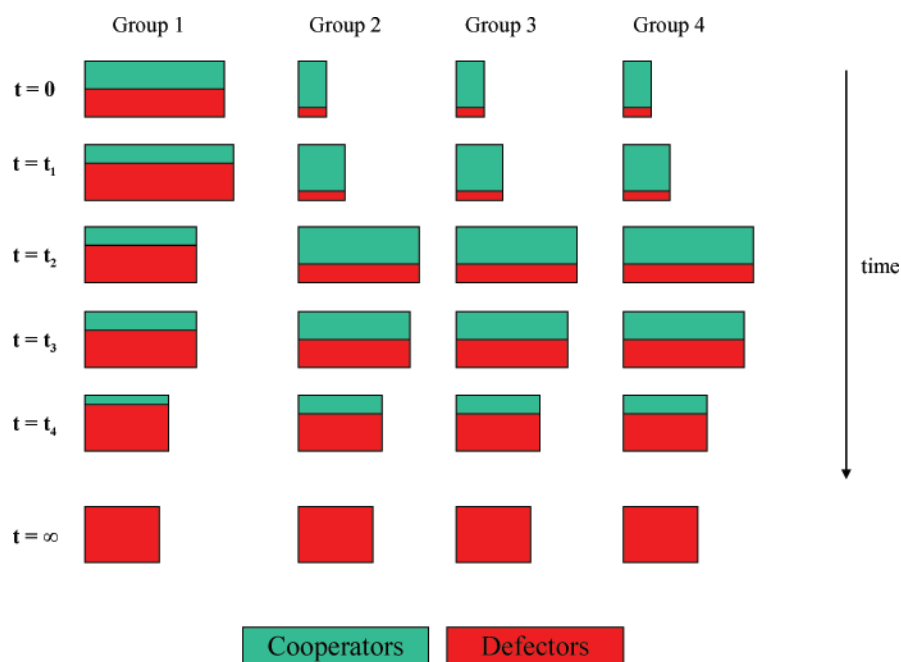
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Although evolution is a process of continuous change, many of the mathematical models proposed for multi-level selection, group selection, and other theories of the evolution of cooperation, do not attempt to fully address time dynamics. In general, to find the evolutionary trajectories and equilibrium configurations of a model of an evolutionary process, it is necessary to have a dynamical (time-dependent) solution of the model from which it is possible to calculate the state of the environment as it changes over time, from its initial conditions, indefinitely into the future.

The present work is probably best described as the construction of a fully dynamical model of group selection featuring births and deaths of individuals within the groups, and births and deaths of groups within the environment. It is the author's view that the process of group selection necessarily involves births and deaths of groups, not just individuals, so that group 'fitness' in a model of group selection is not simply a function of the reproductive success (fitness) of the individuals within the group. For example, the fitness of a group may depend (in part) on how it does against other groups in the environment at a particular group-level game. In general, group-level skill at this group-level game has little or nothing to do with the current reproductive rates of the members of the group. The process of group selection involves the interplay of individual-level births and deaths, and group-level births and deaths. Group growth (or contraction) is due to individual-level births and deaths within the group. However, the population dynamics at the group level (how the number of groups in the environment and the types of groups present in the environment change in time) are determined by group fissioning (when a group breaks apart into two or more pieces, forming new groups) and group extinction (when the last individual in a group dies, or when all the individuals in a group die simultaneously). It is shown here that if certain structural conditions on a model of group selection are satisfied (in particular, distinct groups and asexual group fissioning), the dynamics of the two-level process are amenable to exact mathematical analysis. The present work therefore contributes to the literature on group selection and the evolution of cooperation by explicitly including the interplay of individual-level events (births and deaths) and group-level events (fissioning and extinction) in a model, and formulating the model so that time-dependent solutions and equilibrium configurations of the model environment can be calculated.

To illustrate the interesting and complicated dynamics that can occur in a two-level evolutionary process, and the consequent advantages of a fully dynamical model, consider the following thought experiment. At time  $t=0$ , an environment contains several small groups of (mostly) Cooperators, and one large group consisting of about half Cooperators and half Defectors. Individuals play Prisoner's Dilemma within their groups, so Cooperators are at a significant disadvantage relative to Defectors in the big group. The big group makes up most of the total population in the environment, so the average Cooperator initially is at a disadvantage relative to the average Defector. Cooperation therefore initially decreases relative to defection in the environment. However, since the small groups of Cooperators start out far below the equilibrium size for a successful group, they will grow quickly (nearly exponentially) at first, while retaining most of their Cooperator majorities. [Assume that there is clonal reproduction within each group. Birth rates are proportional to individual fitness, and death rates within each group are proportional to the size of the group, e.g. an 'evolutionary birth-death process' (Simon, 2008).] If there are enough small groups, then at some point in time, cooperation will begin to increase in the environment relative to defection, and cooperation might even gain a majority status in the environment.



**Fig. 1.** Population dynamics for non-interacting, non-fissioning, immortal groups based on the thought experiment in Section 1. In each group the fraction of Defectors always increases. However, since the small groups (groups 2, 3, 4) grow quickly at first, it is the Cooperators that increase fastest at the start. As time goes by, the rate of growth of groups 2, 3, and 4 slows down and Defectors begin to dominate. Eventually, the Cooperators vanish.

But, as time goes by, defection increases within each group due to differing birth rates. If the original groups stay intact (do not fission), each of them will eventually be taken over by Defectors. Defection therefore will eventually begin to increase relative to cooperation, and cooperation will ultimately go extinct. The population dynamics just described are illustrated in Fig. 1.

If there are no group-level events (i.e. if groups are immortal and do not interact), the extinction of cooperation in the environment is inevitable in this thought experiment. But suppose that groups occasionally fission into two or more pieces when they reach or exceed a certain size. Group fissioning necessarily has a random component, so (by chance) some fissioned pieces will be more cooperative than the parent group (i.e. a larger fraction of Cooperators). The new groups with a higher fraction of Cooperators grow faster and can support a larger population of individuals. Such groups are less likely to succumb to group extinction, and are more likely than their less cooperative ‘sibling’ groups to successfully fission in the future. Evolution at the group level can therefore occur. As time goes by, the result may be an equilibrium in the environment, consisting of groups of varying sizes, ages, and levels of cooperation. The two-level population dynamics just described in this thought experiment are illustrated in Fig. 2.

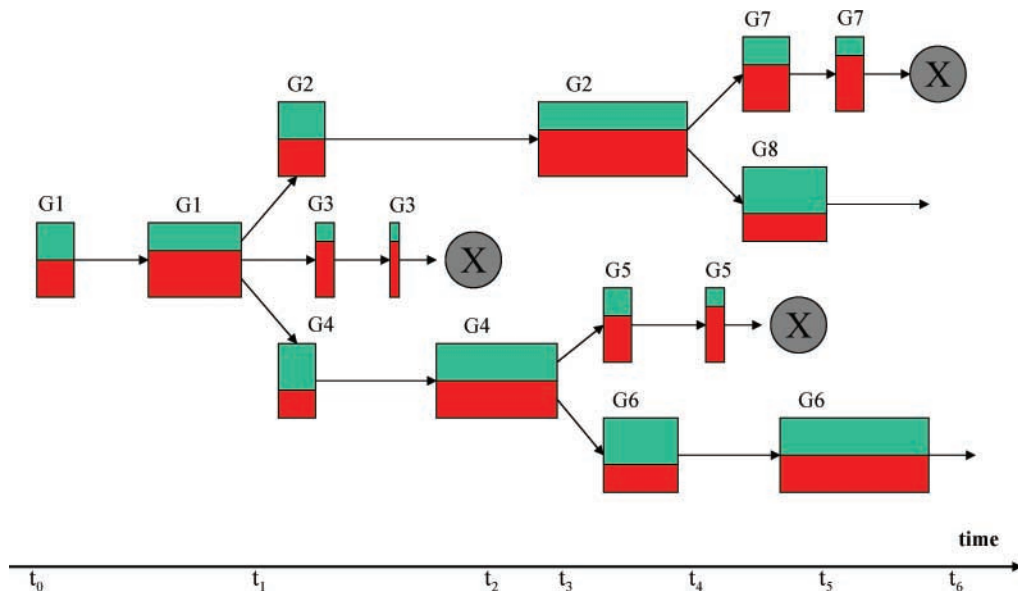
In this paper, a dynamical model of two-level selection is proposed that can be used to study the kinds of evolutionary dynamics just described in the thought experiment, and other similar two-level evolutionary processes. In this paper, I:

- propose a continuous-time, discrete-state, stochastic model of an environment evolving under two-level selection that can be analysed by simulation;
- derive a continuous-time, continuous-state, deterministic (PDE) model of two-level selection from the stochastic model that can be solved numerically; and
- demonstrate that several interesting and important examples of two-level selection can be well modelled within the proposed framework.

The proposed models feature individual-level events (births, deaths, and migration) and group-level events (fissioning and extinction). The proposed models can therefore be used to study MLS1 and/or MLS2 (Damuth and Heisler, 1988; Okasha, 2006) depending on the objective of the study. If the primary objective is to study the evolution of cooperation by group selection, then the model is of type MLS1, since it is individual-level traits that are of interest. In contrast, in a model of species selection, the traits of interest are often at the group level, so the model is MLS2. Sometimes the line between MLS1 and MLS2 is not so clear, so the model has elements of both. In the next section, we will see that the proposed modelling technique is reasonably flexible, so a wide range of two-level evolutionary phenomena can be studied within the same mathematical framework.

## 2. THE SCOPE OF THE PRESENT METHODOLOGY

To fully analyse a dynamical model of two-level selection, whether it is stochastic or deterministic, the model must have a relatively simple and exploitable mathematical



**Fig. 2.** A group-level 'family tree' starting from a single group G1, based on the thought experiment in Section 1. At time  $t_1$ , group G1 fissions into three pieces, G2, G3, and G4. G3 is small and very uncooperative, and soon dies of extinction. G4 grows and fissions into G5 and G6. G5 shrinks and dies, but G6 prospers. At time  $t_5$ , there are three groups, G6, G7, and G8, which are a bit more cooperative on average than G1 was at  $t_0$ .

structure. Not all models of two-level selection have the appropriate mathematical structure to allow a complete dynamical analysis. However, the following modelling assumptions lead to a sufficiently exploitable mathematical structure so that an exact dynamical analysis is possible.

- (A1) The environment contains distinct groups of distinct individuals.
- (A2) The migration of individuals from group to group (if any) is random (i.e. individuals act independently).
- (A3) The population dynamics of the individuals within a group depends on its present state and (possibly) the present states of the other groups in the environment.
- (A4) Groups occasionally fission into two or more pieces that become new groups on their own [e.g. ‘asexual’ group fissioning (Okasha, 2006)].
- (A5) All groups eventually die (of extinction) if they do not fission first.
- (A6) Group-level variables, such as fissioning rates, extinction rates, etc., are functions of the present states of the groups in the environment.

It may be possible to relax some of these assumptions without compromising the nice mathematical structure too much. For example, certain simple kinds of non-asexual (‘sexual’) group fissioning, where fissioned pieces from one group can join other fissioned pieces or groups, may be mathematically tractable. It may also be possible to analyse certain spatial dynamical models. Examples of two-level selection in the real world that (approximately) satisfy (A1)–(A6) include the evolution of virulence, social insect colonies, social mammal groups, hunter-gatherer tribes, and species selection.

For an example of the kind of two-level evolutionary phenomenon that satisfies (A1)–(A6), imagine an idealized tribe of hunter-gatherers in an environment containing other tribes of hunter-gatherers. In this example, early humans are the individuals, and their tribes are the groups. In our idealized model, individuals are either Cooperators or Defectors. Cooperators are more likely to engage in altruistic behaviour than Defectors. The Cooperators and Defectors within a given tribe may play a form of Prisoner’s Dilemma against each other, or perhaps some sort of public goods game.

New tribes are born when an existing tribe breaks up into two or more independent pieces. This split of the original tribe is an example of group fissioning. If a new tribe survives long enough, it will grow and perhaps undergo fissioning itself. Individual humans may occasionally migrate from one tribe to another one, but the tribes remain unambiguous biological structures. New tribes are always born of the fissioning of an existing tribe. When a tribe undergoes fissioning, the pieces obviously cannot be precisely like the original, although they may be similar in important ways. For example, the ratios of the numbers of Cooperators and Defectors within the parent and offspring tribes will be correlated. This observation strongly suggests that there is the sort of reproductive variability (at the tribal level) that is necessary for an evolutionary process.

Tribes compete for limited resources in the environment, so the environment cannot support an unlimited number of them. Interactions between tribes can be thought of as some sort of game, with relative winners and losers. For example, tribes may occasionally attempt to scare other tribes away from their hunting grounds, so tribes must have a strategy for retaining their hunting grounds and/or obtaining new hunting grounds. The result may resemble a game like Chicken. The tribes that do best in the environment, because they are internally cooperative and/or because they play the game (e.g. Chicken) well against other

tribes, are more likely to grow and fission successful new tribes. Tribes that cannot compete die of extinction, or fission into pieces that cannot survive long on their own. All tribes eventually die or fission.

Now, if each tribe had an unambiguous ‘genotype’ that did not change during its lifetime, and if tribes fissioned new tribes with genotypes similar to but not exactly like their own, then the tribes in the environment, thought of as organisms at the next higher level of organization, would constitute a textbook example of a population expected to undergo standard Darwinian change. However, the picture is not that simple. Unlike the individual humans, the tribes do change genetically during their lifetimes. Distinct tribes can persist for many generations of the humans that make them up, so it is possible for selective forces within a tribe to change its genetic make-up over time. For example, within the tribes, the Defectors do not share in as much of the hard and dangerous work as the Cooperators, so they are at a selective advantage within their tribes. Over time, Defectors will increase in numbers within each tribe, changing its genetic make-up. Furthermore, as the Defectors prosper, the basic nature of the tribe is changed, as it descends into internal chaos. Eventually, it becomes one of the weak tribes that cannot compete in the environment, and fissions apart or dies of extinction.

Cooperative tribes typically live longer and fission more successfully than non-cooperative tribes, so they are at a selective advantage (as tribes) in the environment; but Defectors have a selective advantage over Cooperators within each tribe, so tribes typically become less cooperative over time. If cooperative tribes have time to fission new cooperative tribes before they die or descend into chaos, cooperation may evolve in the environment by selection at the tribal level. If defection at the individual level is too much of an advantage over cooperation, then even if a cooperative tribe somehow did emerge, it (and its descendant tribes) would almost surely revert back to defection. When they are of similar magnitudes, the opposing evolutionary forces at the individual and tribal levels may reach an equilibrium of some sort, where the environment consists of tribes of varying sizes, ages, and levels of cooperation.

Of course, there are examples of multi-level evolutionary processes that do not fit well into the framework of (A1)–(A6). In particular, if groups are not distinct from each other, (A1) is violated and the mathematical structure that is exploited here is lost. For example, if the relevant groups in a model are made up of the individuals within a fixed distance of an object, like a tree, then the groups may overlap. Similarly, if groups of individuals are defined by kinship levels (e.g. first cousins), then the groups may overlap as well (see Okasha, 2006, section 2.1). However, examples where groups do not overlap are quite common, like the hunter-gatherer tribes just described. As another example, in a model of the evolution of virulence, groups of parasites reside in different hosts, so they are distinct. Furthermore, since the groups of parasites occasionally fission (e.g. when some or all of the parasites disperse from a host), and since every group eventually dies (e.g. when the host dies), the evolution of virulence can be nicely modelled within the framework developed here.

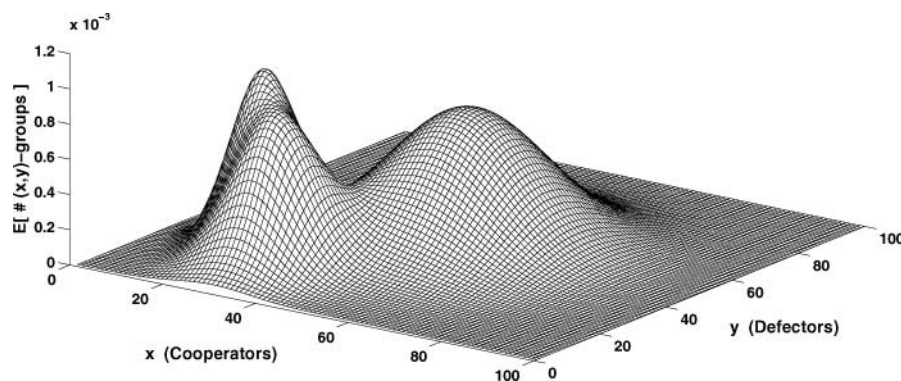
### 3. GROUP FISSIONING

In nature, groups may persist for many generations of the individuals within them, but all groups are mortal, and eventually cease to exist as cohesive units. Thus, if the environment is to contain a thriving population of groups, then groups must occasionally give rise to new groups in some way. Group birth and death mechanisms must be an integral part of any

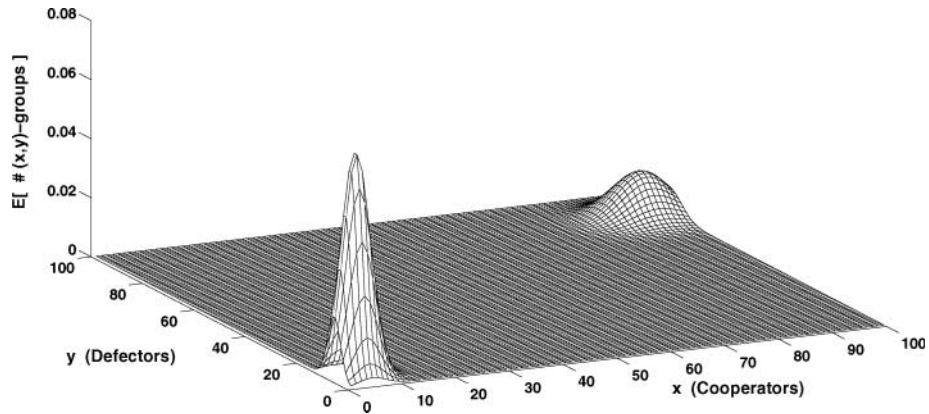
model of two-level selection. Every physically realizable group reproduction mechanism must involve the break-up of a pre-existing group, since new groups cannot ‘appear out of thin air’. Okasha (2006, section 2.2) describes four ‘modes of collective reproduction’. He distinguishes between ‘fissioning’, where a group splits into two pieces, and ‘propagule emission’, or the complete dispersal of the individuals. He also distinguishes between asexual and sexual collective reproduction. In asexual reproduction, each new group is a piece of exactly one parent group. Other sorts of group reproduction are sexual. In this paper, we will not distinguish between different types of asexual group reproduction because the mathematics is the same in each case. All of them will be referred to as (asexual) group fissioning.

From a modelling perspective, the simplest kind of group birth mechanism that could occur in nature is asexual group fissioning. When fissioned pieces from one group join fissioned pieces from other groups to form a new group, or if fissioned pieces join pre-existing groups, then the group fissioning is sexual, and the model is typically more difficult to solve. Empirical work (Wade, 1977, 1980; Goodnight, 1997) has demonstrated that cooperation can establish itself in artificial environments containing groups that undergo asexual group fissioning. The only kind of group reproduction that is fully analysed in this paper is asexual group fissioning. An attempt to extend the results of the present paper to sexual group reproduction will be left for future work.

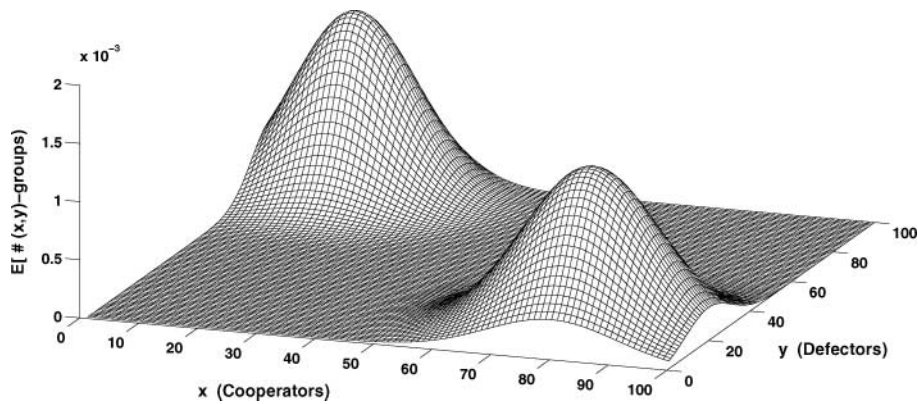
The nature of an asexual fissioning process is specified by a ‘fissioning density’, like the ones shown in Figs. 3–5. The precise statistical nature of the fissioning process can have a large effect on the resulting two-level evolution. For example, if groups fission into a small number of roughly similar-sized pieces, like hunter-gatherer tribes might (e.g. Fig. 3), the resulting evolutionary dynamics are likely to be quite different from what would result from a dispersal of small pieces from a group that remains largely intact (e.g. Fig. 4). One can also imagine examples where the fissioning might be roughly along the Cooperator/Defector divide (e.g. Fig. 5), or any number of other possibilities. The statistical properties of an asexual fissioning event are encoded in the fissioning density. The fissioning density specifies



**Fig. 3.** Fissioning density. A fissioning density at  $(x, y)$  is interpreted as the expected number of  $(x, y)$ -groups that result from the fissioning of a parent group. The density in the figure corresponds to a split of a large group into two or three pieces, where one of the pieces has between 40 and 70 Cooperators and Defectors, and the other pieces are smaller with about 20 or 30 Cooperators and Defectors. The total number of Cooperators and Defectors in the pieces cannot be larger than the parent group.



**Fig. 4.** Fissioning density. The density in the figure corresponds to a dispersal of a number of very small pieces from the original group with about 100 Cooperators and 100 Defectors. There is a small bulge near (100, 100) corresponding to the remains of the original group. The larger bulge near (0, 0) corresponds to the numerous small groups that are dispersed. The total number of Cooperators and Defectors in the pieces cannot be larger than the original group.



**Fig. 5.** Fissioning density. The density in the figure corresponds to a split of a group with about 100 Cooperators and 100 Defectors along the Cooperator/Defector divide. The result is two groups, one with about 100 Cooperators and very few Defectors, and the other with about 100 Defectors and very few Cooperators.

the expected number of offspring groups of each possible size and configuration. The mathematical properties of fissioning densities will be described in more detail in Sections 6 and 7.

Among groups of large organisms in nature (e.g. social animals), asexual group fissioning is a common method of group reproduction. It is observed (approximately) in social insects (Holldobler and Wilson, 2008; Seppa *et al.*, 2008), in (human) early village societies (Bandy, 2004), as well as in chimpanzees (Goodall, 2006), whales (Mann *et al.*, 2000), and other mammal species.

Group fissioning occurs in groups of parasites when an infected host expels some of the parasites. In this case, the majority of the group typically remains in the host, while a small fraction of the group disperses into the environment (e.g. Fig. 4). The dispersed parasites

can infect other hosts individually or in small groups. Some or all of them might die before finding a new host. If the likely fate of the dispersed parasites is to either perish or infect one or more previously uninfected hosts, then the fissioning is asexual. If the dispersed parasites often enter previously infected hosts, then the group fissioning is sexual. From a modelling perspective, if the population of potential hosts is large and mostly healthy, then the fissioning would be approximately asexual. In an epidemic, where a large fraction of the potential hosts are infected, the fissioning would typically be sexual.

#### 4. THE UNDERLYING MODEL OF TWO-LEVEL SELECTION

The underlying model of two-level selection, which has discrete-stochastic and continuous-deterministic versions, will be described in words in this section. To keep things as simple as possible, for as long as possible, the underlying model will be described for the case of two individual types, generically referred to as Cooperators and Defectors. The state of a group is specified by  $(x, y)$ , the number of Cooperators and Defectors in the group, respectively. In this model, the term ‘fitness’ will be used in a somewhat unusual way. It measures ‘well-being’, and only affects reproductive success indirectly. In the underlying model, reproductive success for an individual is a function of its birth rate and death rate, while reproductive success for a group is a function of its fissioning rate and extinction rate. These various rates, in turn, are functions of fitness and other factors, as will be explained below. Except in equilibrium, the birth and death rates for the Cooperators and Defectors in a given group will not remain equal, so the populations of Cooperators and Defectors in each group, as well as their sum (the total population), change in time. Likewise, the group-level events, fissioning and extinction, occur at rates that change in time as the environment changes, so that the number of groups in the environment, and the statistical distribution of the states of those groups, change in time until an equilibrium is reached.

In the underlying model, the fissioning rate of a given group depends only on the state of the group. Typically, larger groups are more likely to fission, but the rate could also depend on the level of cooperation of the group. The extinction rate of a group depends on its state, and on its (group-level) fitness. The fitness of a group is a sum of two pieces. The external fitness of a group is calculated from its state and the states of the other groups in the environment via game payoffs. The group-level game, and the set of possible strategies for that game, is chosen by the modeller. For example, our model of hunter-gatherer tribes in Section 10 has groups playing a form of ‘Chicken’ against each other, where larger and more cooperative groups have an advantage over smaller and less cooperative groups. The external fitness of a group is calculated as its expected payoff in a game played against a randomly chosen opponent group from the environment. The internal fitness of a group is a function of the state of the group (chosen by the modeller) and nothing else. It is a measure of the internal well-being of the group, and will normally be higher for more cooperative groups.

The birth and death rates of the individuals in a given group are functions of their (individual-level) fitness. The fitness of an individual is calculated as the expected payoff in a game chosen by the modeller (e.g. Prisoner’s Dilemma) played against a randomly chosen opponent from its group. Thus, all the Cooperators in a given group have the same fitness, and all the Defectors have the same fitness; but the fitness levels of Cooperators and Defectors in different groups will typically be different. The fitness levels within a group change in time as the populations of Cooperators and Defectors within the group change.

The group-level game and the individual-level game in the underlying model are unrelated, so that, for example, the individuals may play Prisoner's Dilemma within their groups, while the groups play Chicken against each other.

The underlying model assumes that groups have finite lifetimes that can terminate in two ways. The first is extinction, which means that all the individuals within a group die simultaneously. The other method is (asexual) fissioning, which means that a group comes apart and partitions itself into two or more distinct pieces; each piece becomes a new group, while the old group ceases to exist as a group. Some of the pieces may die (of extinction) immediately, so that not all the original group survives the fissioning process. Extinction can be thought of as the outcome of a fissioning process where none of the group survives, but in this paper extinction and fissioning are treated as two different events. In the present model, a group that undergoes fissioning ceases to exist as a group, while the fissioned pieces live on. One could also identify the original group as one of the pieces of the fissioning, in which case the original group still exists, but this appears to cause an unnecessary complication in the mathematical notation, so we will not formulate the model this way.

In the underlying model, individuals have finite lifetimes, and do not change their type during their lifetimes. During its lifetime, an individual may spawn (asexually) new individuals, which then become part of the same group. Mutations are possible, and make up some fraction of the births. If there are only Cooperators and Defectors, then mutant Cooperators are Defectors, and vice versa. The birth rates of the individuals in a group are based on fitness, and fitness is based on game payoffs within the group. The strategy that an individual uses in games against other individuals in its group is specified by its type. The death rate of an individual in a group depends on its fitness and the size of the group. The resulting stochastic process describing the population dynamics of Cooperators and Defectors within a group is an example of an evolutionary birth–death process, which will be described in the next section.

The underlying model also allows for migration of individuals from one group to another. From the perspective of a given group, an individual that emigrates is a death and an immigrant is a birth, so that the total birth and death rates of Cooperators and Defectors in a group depend on the state of the group and the state of the other groups in the environment. The assumption here is that Cooperators and Defectors leave their groups at (possibly different) rates that depend on the current state of the group. When an individual leaves a group, it will either join another group or die. Migrating Cooperators and Defectors choose another group to join at random, and are accepted into that group with probability  $\eta \leq 1$ . If a migrating individual is not accepted into the group it chooses, it is assumed to die. More sophisticated models of migration may be mathematically tractable, but we will not pursue them here.

In the underlying model, populations of individuals within groups are modelled as evolutionary birth–death processes, so a small group has the potential to grow into a larger group. This point is crucial, since without the possibility of group growth, fissioning would eventually reduce the environment to nothing but isolated individuals. Groups often die by extinction or undergo fissioning long before the individuals within them reach any kind of population equilibrium. Thus, the environment may contain very few groups in an equilibrium configuration. In general, the environment may reach an equilibrium consisting of groups of various sizes, ages, and configurations. In other words, an equilibrium environment is not an environment full of equilibrium groups. Determining the equilibrium

configuration for the environment (if there is one), and the population dynamics that lead to the equilibrium, is the goal of the modelling analysis.

The full model of two-level selection developed here is therefore composed of four submodels:

- (M1) A model of individual population dynamics within groups (involving  $k \geq 2$  types of individuals). If there is no migration, the within-group population dynamics can be formulated as statistically independent evolutionary birth–death processes (Section 5), with rates depending on (individual-level) game payoffs. Migration makes the model more complicated, but it can still be analysed exactly (e.g. Sections 6 and 7).
- (M2) A model of group-level fitness based on internal (within-group) and external (inter-group) fitness functions. Internal group fitness depends only on the group state, while external group fitness depends on the state of the environment and the outcomes of group-level game payoffs.
- (M3) A model specifying how and when group fissioning and extinction occur. In the stochastic model, the timing of the fissioning and extinction events follows statistically independent non-stationary Poisson processes (Karlin and Taylor, 1975, ch. 4). The fissioning and extinction rates depend on group size, composition, and fitness. The statistical properties of the fissioning event (e.g. the number of pieces and their compositions) are specified by a fissioning density (Sections 6 and 7).
- (M4) A model of individual migration patterns (between groups). The timing of migration events in the stochastic model follows statistically independent non-stationary Poisson processes, with rates for individuals depending on their group’s size and composition.

There are many possible variations of (M1)–(M4), so the scope of the full model is fairly broad. In every case, the state of a group is a complete description of the group, so the environment at time  $t$  is completely characterized by a function specifying how many groups in each state there are.

## 5. EVOLUTIONARY BIRTH–DEATH PROCESSES

The term ‘evolutionary birth–death process’ was coined by Simon (2008), and defined there in a way that is slightly more general than is needed in the present work. [The diffusion terms in equation (11) in Simon (2008) are set to zero here.] The evolutionary birth–death process described here will contain only the generality needed for the underlying model described in Section 4.

Suppose that there are  $k$  types of individuals in a population. An evolutionary birth–death process is a single-level evolutionary process, so the population can be thought of as a single group. (The full two-level stochastic population model described in Section 6 is an evolving collection of semi-autonomous evolutionary birth–death processes; one corresponding to each group.)

Let  $n_t(i)$  be the number of type  $i$  individuals in the population at time  $t$ , and let  $N_t = \sum_{i=1}^k n_t(i)$  be the total population at time  $t$ . Let  $F_t(i)$  be the fitness of type  $i$  individuals at time  $t$ . Typically,  $F_t(i)$  is defined to be the average payoff type  $i$  individuals get from playing a certain game (e.g. Prisoner’s Dilemma or a public goods game) against randomly chosen opponent(s) from the population, but in theory, fitness can be virtually any function

of the state of the environment. Each individual in the population is mortal, and may (or may not) spawn new individuals during its lifetime. The birth (spawning) and death rates of a type  $i$  individual at time  $t$ , denoted  $\beta_t(i)$  and  $\delta_t(i)$  respectively, are usually functions of  $F_t(i)$ ,  $N_t$ , and perhaps other time-dependent quantities. Mutation can be modelled by assuming that when a type  $i$  individual spawns, the result is a type  $j$  individual with probability  $\mu_{ij}$ . [The ‘rates’ just mentioned are stochastic rates, i.e. if a particular type  $i$  individual is observed during a time interval  $[t, t + dt]$ , then the probability it spawns during the interval is  $\beta_t(i) dt + o(dt)$  and the probability it dies during the interval is  $\delta_t(i) dt + o(dt)$ , where  $o(u)$  is a function satisfying  $\lim_{u \rightarrow 0} o(u)/u = 0$ . Roughly speaking, when  $u$  is small,  $o(u)$  is negligible. See Karlin and Taylor (1975, ch. 4).]

As a simple and illustrative example of an evolutionary birth–death process, suppose birth rates are equal to fitness and death rates are proportional to the total population, i.e.

$$\beta_t(i) = F_t(i) \quad \text{and} \quad \delta_t(i) = cN_t, \quad i = 1, 2, \dots, k \quad (1)$$

We can define  $F_t(i)$  to be the average payoff in a game against a random opponent, i.e.

$$F_t(i) = N_t^{-1} \sum_{j=1}^k n_t(j) G_{ij},$$

where  $G_{ij}$  is the payoff to  $i$  in a game against  $j$ . The total rate that individuals in the population are spawning at time  $t$  is

$$\beta_t^* = \sum_{i=1}^k n_t(i) \beta_t(i) = \bar{\beta}_t N_t,$$

where  $\bar{\beta}_t$  is the average per-individual birth rate at time  $t$ , and the total death rate in the population is

$$\delta_t^* = \sum_{i=1}^k n_t(i) \delta_t(i) = cN_t^2.$$

Thus,

$$E(N(t + dt) - N(t)) = (\bar{\beta}_t - cN(t))N(t)dt + o(dt),$$

so at time  $t$  the total population moves towards the value

$$\bar{N}_t = \bar{\beta}_t / c. \quad (2)$$

Since  $\bar{\beta}_t$  is stochastic,  $\bar{N}_t$  varies in time, so it is not an equilibrium in the usual sense. If fitness levels are bounded (as they usually are), then  $\bar{N}_t$  is likewise bounded. (Strictly speaking, the evolutionary birth–death process just described has no *steady state*, since the entire population will eventually go extinct with probability 1. However, if  $\bar{N}$  is large enough, the expected time to extinction is astronomically large.) Since

$$E(n_i(t + dt) - n_i(t)) = \left( \sum_{j=1}^k n_j(t) \beta_j(t) \mu_{ji} - \delta_i(t) n_i(t) \right) dt + o(dt),$$

it is reasonable to expect that the stochastic trajectories,  $n_t(i)$ ,  $i = 1, 2, \dots, k$  will resemble the deterministic trajectories,  $z_i(t)$ ,  $i = 1, 2, \dots, k$ , which obey the system of ordinary differential equations,

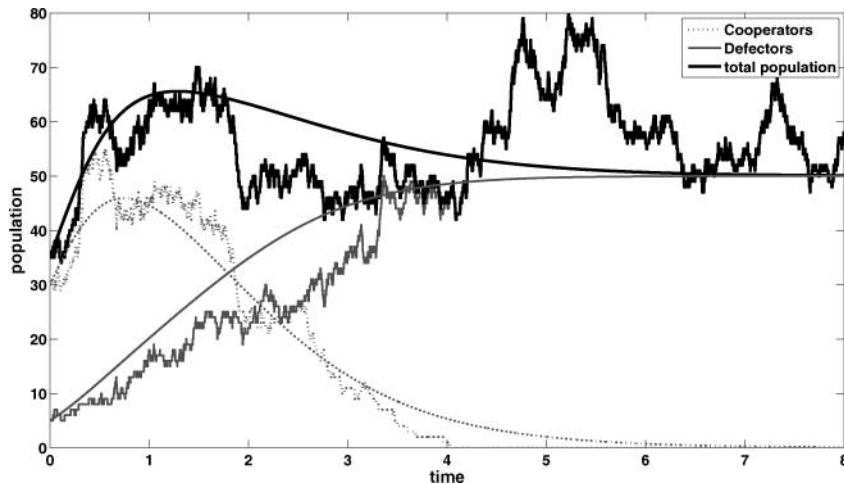
$$z'_i(t) = \sum_{j=1}^k \beta_j(t) \mu_{ji} z_j(t) - \delta_i(t) z_i(t). \tag{3}$$

Figures 6 and 7 illustrate the similarity between the stochastic and deterministic population models, and further suggest that as the population increases the similarity increases. Figures 6 and 7, and other numerical experiments by the author, strongly support the conjecture that a properly scaled sequence of evolutionary birth–death processes converges to a deterministic path specified by a system of ordinary differential equations like (3). The logic behind the derivation of the PDE in Section 7 from the stochastic equations in Section 6 is based on this observation.

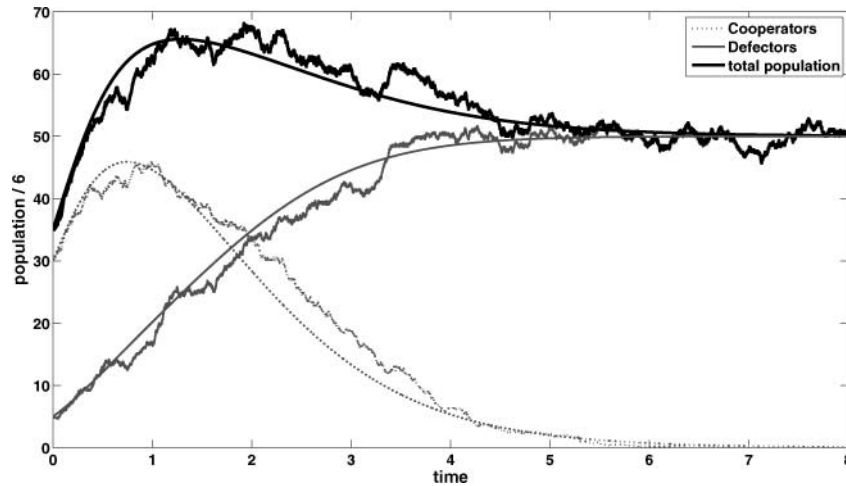
Since an evolutionary birth–death process is a continuous-time Markov chain on a lattice, it is easy (in principle) to simulate. If the process is in state  $n_t = (n_t(1), \dots, n_t(k))$  at time  $t$ , it will move next to state  $n_t + e_i$  with probability  $n_t(i) \beta_i(t) / \lambda_t$  and will move next to state  $n_t - e_i$  with probability  $n_t(i) \delta_i(t) / \lambda_t$ , where  $e_i$  is the  $i$ th unit vector, and

$$\lambda_t = \sum_j n_t(j) (\beta_t(j) + \delta_t(j))$$

is the total rate at which transitions occur at time  $t$ . The elapsed time until the next event is therefore exponentially distributed with mean  $\lambda_t^{-1}$  and independent of the transition that occurs (see Karlin and Taylor, 1975, ch. 4). One can simulate an evolutionary birth–death process by



**Fig. 6.** Evolutionary birth–death process and its deterministic approximation. The example here is based on (1) where the game is a Prisoner’s Dilemma. The death rate parameter is  $c = 0.04$  and the initial population is  $(n_0(c), n_0(d)) = (30, 5)$ . In this example, the stochastic trajectories clearly follow the deterministic trajectories (3), but they deviate significantly at times. The Cooperators begin in the majority and start off increasing at a faster rate than the Defectors, but eventually the Defectors establish themselves and drive the cooperators to extinction at about  $t = 4.0$ .



**Fig. 7.** Evolutionary birth–death process and its deterministic approximation. The example in this figure is the same as that in Fig. 6 except that the death rate parameter is cut by a factor of 6 to  $c = 0.067$ , and the initial population is multiplied by 6 to  $(n_0(c), n_0(d)) = (180, 30)$ . When the resulting trajectories are divided by 6, the deterministic trajectories are the same as in Fig. 6. However, the stochastic trajectories follow the deterministic paths much more closely than in Fig. 6. A scaled sequence of evolutionary birth–death processes, where the death rate of the  $m$ th process is decreased by  $m$ , the initial population is increased by  $m$ , and the resulting population is divided by  $m$ , appears to converge to the deterministic path.

simulating the sequence of transitions that occur. If a transition occurs at time  $t$ , the simulation generates  $2k$  independent exponential random variables  $\{X_1, Y_1, \dots, X_k, Y_k\}$ , where  $X_i$  has mean  $(n_t(i) \beta_i(i))^{-1}$  and  $Y_i$  has mean  $(n_t(i) \delta_i(i))^{-1}$ . The next transition occurs at time  $t + s$  where

$$s = \min \{X_1, Y_1, \dots, X_k, Y_k\},$$

and the identity of the new state is determined by which variable is the minimum (see Karlin and Taylor, 1975, ch. 4).

If  $N_t$  is too big, the simulation will have so many transitions that it will run very inefficiently. It may be possible to design a more sophisticated simulation of an evolutionary birth–death process, but simulations will always be impractical for large enough populations. Fortunately, the associated system of ODEs (3) provides a good approximation to the simulation in exactly the cases when the simulation is inefficient, and (3) is easily solved by standard numerical techniques such as Runge-Kutta.

## 6. FORMULATION OF THE DISCRETE-STATE STOCHASTIC MODEL

At time  $t = 0$ , the environment contains groups with indices  $i \in \{1, 2, \dots, N_0\}$ . Let  $I_t$  be the largest index that has been used up to time  $t$ , so that  $I_0 = N_0$ , and let  $N_t$  be the number of living groups in the environment at time  $t$ . Let  $A_t$  be the set of indices corresponding to the groups that are alive at time  $t$ . Groups die by extinction or by fissioning. When a group dies by extinction, all the individuals in the group die. When a group dies by fissioning, it breaks

into two or more pieces, and each piece becomes a new group. New groups are assigned the smallest indices that have not yet been used. The time that group  $i$  is born is denoted  $\tau_i$  and the time it dies (by extinction or fissioning) is denoted  $T_i$ . Thus, if group  $i$  is born when group  $j$  fissions, then  $\tau_i = T_j$ . The dynamics within each group is handled analogously. Fix a group  $i$ . Let  $(x_t(i), y_t(i))$  be the number of Cooperators and Defectors respectively in group  $i$  at time  $t \in [\tau_i, T_i]$ , i.e.  $(x_t(i), y_t(i))$  is the state of group  $i$  at time  $t$ .

**Definitions:** A group with exactly  $x$  Cooperators and  $y$  Defectors is called an  $(x, y)$ -group. The size of an  $(x, y)$ -group is  $x + y$ . The state of the environment at time  $t$  is denoted  $\Theta_t = \{(x_t(i), y_t(i)) : i \in A_t\}$ .

The spawning rate of a Cooperator in an  $(x, y)$ -group is denoted  $b_c(x, y)$ , so the total spawning rate of the Cooperators in an  $(x, y)$ -group is  $xb_c(x, y)$ . Similarly, the total spawning rate of Defectors in an  $(x, y)$ -group is  $yb_d(x, y)$ . Typically,  $b_c(x, y)$  and  $b_d(x, y)$  are related to fitness, and fitness is a weighted average of the payoffs from the game that Cooperators and Defectors play within their groups, but in theory they can be any functions of the state of the group. The model assumes that Cooperators spawn Cooperators with probability  $\mu_{cc}$ , Defectors spawn Defectors with probability  $\mu_{dd}$ , while  $\mu_{cd} = 1 - \mu_{cc}$  and  $\mu_{dc} = 1 - \mu_{dd}$  are the probabilities of mutations. Thus, the total rate that Cooperators are spawned is  $\mu_{cc}xb_c(x, y) + \mu_{dc}yb_d(x, y)$ , and the total rate that Defectors are spawned is  $\mu_{cd}xb_c(x, y) + \mu_{dd}yb_d(x, y)$ . The death rates for Cooperators and Defectors in an  $(x, y)$ -group are denoted  $d_c(x, y)$  and  $d_d(x, y)$  respectively. Typically, the death rates are assumed to increase as the size of the group increases, and they may also depend on fitness. If there is no migration in the model, all population changes within a given group are due to spawning and death, so the model of intra-group population dynamics does not depend on the state of the rest of the environment.

If migration is possible, the model of population dynamics within group  $i$  is more complicated. At time  $t$ , it depends on the state of the group  $(x_t(i), y_t(i))$  and the state of the environment  $\Theta_t$ . The model of migration has two parts. First, it specifies the rates that Cooperators and Defectors leave their groups. The assumption is that these rates depend on the state of the group only. In other words, there are functions  $\varepsilon_c(x, y)$  and  $\varepsilon_d(x, y)$  that specify the per-individual emigration rates for Cooperators and Defectors from an  $(x, y)$ -group. The second part of the migration model describes what happens to individuals that leave their groups. The model assigns migrating individuals to a group in the environment at random. (More sophisticated models would distinguish between Cooperators and Defectors and the states of the groups in the environment, but no attempt to develop such a model of migration will be made here.) A migrating individual that tries to join a group will be accepted with some probability,  $\eta \leq 1$ . Rejected immigrants are assumed to die.

The rates that Cooperators and Defectors emigrate from an  $(x, y)$ -group are  $x\varepsilon_c(x, y)$  and  $y\varepsilon_d(x, y)$  respectively. Let

$$\varepsilon_c^*(t) = \sum_{i \in A_t} x_t(i)\varepsilon_c(x_t(i), y_t(i)) \quad \text{and} \quad \varepsilon_d^*(t) = \sum_{i \in A_t} y_t(i)\varepsilon_d(x_t(i), y_t(i)) \quad (4)$$

be the total migration rates of Cooperators and Defectors in the environment at time  $t$ . Since migration is random, the immigration rates of Cooperators and Defectors to each group in the environment at time  $t$  are  $\varepsilon_c^*(t)/N_t$  and  $\varepsilon_d^*(t)/N_t$ . Immigrants are

accepted with probability  $\eta$ , so the total birth rate of Cooperators in group  $i$  at time  $t$  due to spawning and immigration is

$$\mu_{cc}x_t(i)b_c(x_t(i)y_t(i)) + \mu_{dc}y_t(i)b_d(x_t(i), y_t(i)) + \eta\varepsilon_c^*(t)/N_t.$$

The total death rate of Cooperators in group  $i$  at time  $t$  due to individual deaths and emigration is

$$x_t(i)d_c(x_t(i), y_t(i)) + x_t(i)\varepsilon_c(x_t(i), y_t(i)).$$

Similarly, the total birth and death rates of Defectors in group  $i$  at time  $t$  are

$$\mu_{cd}x_t(i)b_c(x_t(i), y_t(i)) + \mu_{dd}y_t(i)b_d(x_t(i), y_t(i)) + \eta\varepsilon_d^*(t)/N_t$$

and

$$y_t(i)d_d(x_t(i), y_t(i)) + y_t(i)\varepsilon_d(x_t(i), y_t(i)),$$

respectively.

The fitness of group  $i$  at time  $t$  is denoted  $f_t(i)$ . The fitness of group  $i$  is the sum of its internal fitness and external fitness. Internal fitness depends on the state of the group only, so the internal fitness of an  $(x, y)$ -group is denoted  $f^I(x, y)$ . The external fitness of a group depends on how it fares against other groups in the environment at a certain game. The game that groups play against each other has no relation to the game that individuals play within groups. The strategy that group  $i$  uses at time  $t$  against group  $j$  is a function of their states. The set of allowable strategies used by groups is denoted  $\mathcal{S}$ . Let  $\Psi: \mathcal{S} \times \mathcal{S} \rightarrow \Re$  be the game payoff function for group interactions, and let  $s[(x, y), (u, v)] \in \mathcal{S}$  be the strategy that an  $(x, y)$ -group uses against a  $(u, v)$ -group. The model assumes perfect mixing of group interactions, so external fitness is the average payoff from games against other groups:

$$f_t^E(i) = N_t^{-1} \sum_{j \in \mathcal{A}_t} \hat{\Psi}_t(i, j),$$

where  $\hat{\Psi}_t(i, j)$  is the expected payoff group  $i$  gets against group  $j$  at time  $t$ . The fitness of group  $i$  at time  $t$  is therefore

$$f_t(i) = f^I(x_t(i), y_t(i)) + f_t^E(i).$$

The extinction and fissioning rates for group  $i$  at time  $t$  are denoted  $e_t(i)$  and  $w_t(i)$ , respectively. Typically,  $e_t(i)$  is a function of  $f_t(i)$  and the number of groups (and/or individuals) in the environment, while  $w_t(i)$  depends only on the state of group  $i$ ; but in theory they can be any functions of  $\Theta_t$ .

The last detail in the underlying model is a mathematical description of the fissioning event. For integers  $x$  and  $y$ , let  $\mathcal{P}(x, y)$  be the set of all feasible partitions of  $(x, y)$  under fissioning, and for  $\rho \in \mathcal{P}(x, y)$ , let  $P((x, y), \rho)$  be the probability that partition  $\rho$  occurs when an  $(x, y)$ -group fissions. Then  $P((x, y), \rho)$  is a (discrete) *fissioning density*. The cardinality of  $\mathcal{P}(x, y)$  can be astronomical, so the most complicated models of fissioning are mathematically intractable. Fortunately, in practice a simple model of fissioning will often suffice, such as a random split into two pieces,  $(u, v)$  and  $(x - u, y - v)$  (e.g. Traulsen and Nowak, 2006). In this case, if  $x$  and  $y$  are large enough,  $u$  will be approximately normally distributed with mean  $x/2$  and variance  $x/4$ , and  $v$  will be approximately normally distributed with mean  $y/2$  and variance  $y/4$ . However, when a group of parasites (within a host organism)

undergoes fissioning, usually a small subset leaves, leading to a much different fissioning density (e.g. Fig. 4). One might imagine that some fissioning events in human hunter-gatherer tribes are along the Cooperator/Defector divide. This leads to yet another fissioning density (e.g. Fig. 5). There are many ways to construct fissioning densities. A simple, but relatively flexible class assumes that a group splits into two pieces,  $A$  and  $B$ , where Cooperators join  $A$  with probability  $p$ , and Defectors join  $A$  with probability  $q$ . If  $p = q = 1/2$ , the random split results. If  $p$  and  $q$  are both small (or both big), the result is a small group breaking away from the original group; and if  $p$  is big and  $q$  is small (or vice versa), the result is a split along the Cooperator/Defector divide. These fissioning densities will be derived explicitly in the context of the continuous model below.

If the groups are not too numerous in the environment, and the numbers of individuals in the groups are not too big, it is quite feasible to simulate the stochastic model. However, if there are a large number of groups and/or the groups contain lots of individuals, it is not practical to simulate the stochastic model. In the next section, a continuous and deterministic analog of the stochastic model will be derived. The numerical solution of the resulting PDE can be somewhat time-consuming too, but the numerical complexity does not depend on the size or number of groups in the environment.

## 7. THE CONTINUOUS-STATE DETERMINISTIC (PDE) MODEL

In the stochastic model, the number of Cooperators and Defectors in a given group is integer valued. The number of groups in the environment is also integer valued. If the groups are large, the discussion in Section 5 (also Figs. 6 and 7) show that it is very reasonable to approximate the stochastic model  $n_t$  with the deterministic one,  $z_t$ . Similarly, if there are a large number of groups in the environment, it is reasonable to assume that the number of groups in or near a given state  $(x, y) \in \mathfrak{R}_+^2$  can be approximated by a continuous deterministic process. Even if the numbers are relatively small, a continuous approximation can often be justified. In this section, the variables  $x$  and  $y$  are assumed to be continuous, i.e.  $(x, y) \in \mathfrak{R}_+^2$ . The key to the continuous formulation of the two-level selection problem is to define a population density function  $\theta_t(x, y)$ , interpreted as the number of  $(x, y)$ -groups in the environment at time  $t$ . The density  $\theta_t(x, y)$  is analogous to  $\Theta_t$  from the discrete model, and has the same interpretation as the state of the environment.

In the present context, a *continuous model* is a differential equation that specifies how  $\theta_t(x, y)$  changes in time, so  $\theta_t(x, y)$  is assumed to be differentiable in its variables. The benefits of a continuous model over a discrete model come from the clarity of its expression, and also that the full power of mathematical analysis may be brought to bear on the model, as Hofbauer and Sigmund (1998) demonstrate for more traditional population models. Here the population model is specified by a single PDE given by equation (23), which is derived as a continuous deterministic analog of the discrete stochastic model in the previous section. The individual terms in (23) correspond to different aspects of the two-level model. In particular, the partial derivative terms correspond to the within-group population dynamics. This explains (to some extent) how group and individual population dynamics are related in a two-level selection problem.

The continuous model will first be derived for the case of two individual types, Cooperators and Defectors, and then extended to  $k > 2$  types. The numerical complexity in solving the resulting PDE increases rapidly in  $k$ . Many interesting models can be constructed with  $k = 2$  or 3, which is within the practical range. If  $k$  needs to be large,

the only practical way to analyse the model may be to simulate the stochastic model. If there is a continuum of individual types, e.g.  $i \in [0, 1]$ , then there may be some simplifications, but that extension will be left for future work.

In the continuous model, the state of the environment at time  $t$  is completely specified by  $\theta_t(x, y)$ ,  $(x, y) \in \mathfrak{R}_+^2$ , so  $\theta_t(x, y)$ ,  $t \geq 0$  is a complete description of the two-level evolutionary process. Virtually any statistic of interest can be derived easily from  $\theta_t(x, y)$ . For example, the number of groups in the environment at time  $t$  is

$$N_t = \int_0^\infty \int_0^\infty \theta_t(x, y) dy dx, \quad (5)$$

and the total populations of Cooperators and Defectors in the environment at time  $t$  are

$$C_t = \int_0^\infty \int_0^\infty x \theta_t(x, y) dy dx \quad \text{and} \quad D_t = \int_0^\infty \int_0^\infty y \theta_t(x, y) dy dx, \quad (6)$$

respectively. Furthermore, if there is an equilibrium population density in the environment starting from the initial state  $\theta_0(x, y)$ , then it is  $\theta^*(x, y) = \lim_{t \rightarrow \infty} \theta_t(x, y)$ . A method of computing the function  $\theta_t(x, y)$ ,  $(x, y) \in \mathfrak{R}_+^2$ ,  $t > 0$  from the initial condition  $\theta_0(x, y)$ ,  $(x, y) \in \mathfrak{R}_+^2$  is therefore a ‘full dynamical solution’ of the model.

Consider a generic group, and let  $(x_t, y_t)$  be the state of that group at time  $t$ . The continuous model requires a system of (ordinary) differential equations that govern  $(x_t, y_t)$ , of the form

$$\begin{bmatrix} x'_t \\ y'_t \end{bmatrix} = \begin{bmatrix} \gamma_t^c(x_t, y_t) \\ \gamma_t^d(x_t, y_t) \end{bmatrix} \quad (7)$$

where  $\gamma_t^c(x, y)$  and  $\gamma_t^d(x, y)$  are differentiable in  $x$  and  $y$ . The proper choices of these functions are crucial to the two-level model. An evolutionary birth–death process,  $n_t$ , always has a natural approximation by a continuous and deterministic process,  $z_t$ , so if there is no migration between groups,  $\gamma_t^c(x, y)$  and  $\gamma_t^d(x, y)$  reduce to (3).

Borrowing the notation from the previous section, the total birth rate minus the total death rate of Cooperators at time  $t$  in the generic group is

$$\alpha_c(x_t, y_t) = \mu_{cc} x_t b_c(x_t, y_t) + \mu_{dc} y_t b_d(x_t, y_t) - x_t d_c(x_t, y_t), \quad (8)$$

and the total birth rate minus total death rate for Defectors is

$$\alpha_d(x_t, y_t) = \mu_{cd} x_t b_c(x_t, y_t) + \mu_{dd} y_t b_d(x_t, y_t) - y_t d_d(x_t, y_t). \quad (9)$$

If there is no migration, then  $\gamma_t^c(x_t, y_t) = \alpha_c(x_t, y_t)$  and  $\gamma_t^d(x_t, y_t) = \alpha_d(x_t, y_t)$ .

If individuals migrate occasionally from one group to another, then (7) must account for it. Let  $\varepsilon_c(x, y)$  and  $\varepsilon_d(x, y)$  be the (per individual) rates that Cooperators and Defectors emigrate from an  $(x, y)$ -group. The total emigration rates of Cooperators and Defectors in the environment at time  $t$  are therefore

$$\varepsilon_c^*(t) = \int_0^\infty \int_0^\infty x \varepsilon_c(x, y) \theta_t(x, y) dy dx \quad \text{and} \quad \varepsilon_d^*(t) = \int_0^\infty \int_0^\infty y \varepsilon_d(x, y) \theta_t(x, y) dy dx.$$

The model assumes that a migrating individual chooses a group to join at random, and is accepted with probability  $\eta$ . Thus, for each group in the environment at time  $t$ , the immigration rates of Cooperators and Defectors are given by  $\eta \varepsilon_c^*(t)/N_t$  and  $\eta \varepsilon_d^*(t)/N_t$ , respectively. When migration is included in the population dynamics within a given group, equation (7) becomes

$$\begin{bmatrix} x'_t \\ y'_t \end{bmatrix} = \begin{bmatrix} \alpha_c(x_t, y_t) + \eta \varepsilon_c^*(t)/N_t - x_t \varepsilon_c(x_t, y_t) \\ \alpha_d(x_t, y_t) + \eta \varepsilon_d^*(t)/N_t - y_t \varepsilon_d(x_t, y_t) \end{bmatrix}. \tag{10}$$

The first terms on the right-hand side of (10) correspond to internal population dynamics, the second terms correspond to immigration, and the third terms correspond to emigration. More sophisticated migrations models could be developed.

Let  $e_t(x, y)$  be the extinction rate at time  $t$  of  $(x, y)$ -groups in analogy to  $e_t(i)$  from Section 6, and let  $w_t(x, y)$  be the fissioning rate at time  $t$  of  $(x, y)$ -groups in analogy to  $w_t(i)$  from Section 6. Group-level model parameters like  $e_t(x, y)$  and  $w_t(x, y)$  depend on the fitness of  $(x, y)$ -groups. Group fitness is the sum of internal and external fitness. Recall that the internal fitness of an  $(x, y)$ -group,  $f^I(x, y)$ , is only a function of  $x$  and  $y$ , but the external fitness of an  $(x, y)$ -group depends on the precise state of the environment at time  $t$ . The external fitness of an  $(x, y)$ -group at time  $t$  has the form

$$f_t^E(x, y) = N_t^{-1} \int_0^\infty \int_0^\infty \hat{\Psi}((x, y), (u, v)) \theta_t(u, v) dv du, \tag{11}$$

where  $\hat{\Psi}((x, y), (u, v))$  is the expected payoff an  $(x, y)$ -group gets in a match against a  $(u, v)$ -group. Thus,  $f_t^E(x, y)$  is the average payoff an  $(x, y)$ -group gets in a game against a random group from the environment at time  $t$ . The fitness of an  $(x, y)$ -group at time  $t$  is the sum,

$$f_t(x, y) = f^I(x, y) + f_t^E(x, y). \tag{12}$$

When an  $(x, y)$ -group undergoes fissioning, it breaks up into two or more pieces, whose total populations cannot exceed  $(x, y)$ . In the continuous model, fissioning is specified by a fissioning density, defined as follows.

**Definition:** A fissioning density is an integrable function  $h((x, y), (u, v))$ , where  $(x, y) \in \mathfrak{R}_+^2$  and  $0 \leq u \leq x, 0 \leq v \leq y$ , satisfying

$$\int_0^x \int_0^y u h((x, y), (u, v)) du dv \leq x \quad \text{and} \quad \int_0^x \int_0^y v h((x, y), (u, v)) dv du \leq y, \tag{13}$$

for every  $(x, y) \in \mathfrak{R}_+^2$ .

Interpret  $h((x, y), (u, v))$  as the expected number of fissioned pieces of an  $(x, y)$ -group that are approximately  $(u, v)$ -groups. A simple and useful class of fissioning densities can be constructed by assuming  $(x, y)$ -groups fission randomly into two pieces,  $A$  and  $B$ , where Cooperators join  $A$  with probability  $p$ , and Defectors join  $A$  with probability  $q$ . The number of Cooperators in  $A$  is approximately normally distributed with mean  $xp$  and variance  $xp(1 - p)$ . Similarly, the number of Defectors in  $A$  is approximately normally distributed with mean  $yq$  and variance  $yq(1 - q)$ . The fissioning density in this case has approximately the form

$$h((x, y), (u, v)) = h_A((x, y), (u, v)) + h_B((x, y), (u, v)), \tag{14}$$

where

$$h_A((x, y), (u, v)) = \frac{\exp(-(u - px)^2/2xp(1 - p))}{\sqrt{2\pi xp(1 - p)}} \cdot \frac{\exp(-(v - qy)^2/2yq(1 - q))}{\sqrt{2\pi yq(1 - q)}} \tag{15}$$

and

$$h_B((x, y), (u, v)) = \frac{\exp(-(u - (1 - p)x)^2/2xp(1 - p))}{\sqrt{2\pi xp(1 - p)}} \cdot \frac{\exp(-(v - (1 - q)y)^2/2yq(1 - q))}{\sqrt{2\pi yq(1 - q)}}. \quad (16)$$

It is easy to extend (14) to fissioning densities corresponding to three or more pieces (e.g. Fig. 3). Perhaps the simplest fissioning rule is a random split into two pieces ( $p = q = 1/2$  in (14)) used by Traulsen and Nowak (2006) and Bowles (2006). In that case (14), (15), and (16) reduce to

$$h((x, y), (u, v)) \approx \frac{4}{\pi\sqrt{xy}} e^{-2(x-u)^2/x} e^{-2(y-v)^2/y}, \quad 0 \leq u \leq x, 0 \leq v \leq y. \quad (17)$$

If no individuals die during a fissioning event, the constraints (13) are equalities. The fissioning density (14) corresponds to a model where some of the individuals die during fissioning. The lost individuals correspond to the parts of the normal densities that are outside the rectangular domain. The fissioning density can be scaled so that more (or fewer) individuals die during fissioning if the modeller wishes, as long as (13) is satisfied. Violating the constraint means that in total there are more Cooperators and/or Defectors in the fissioned groups than in the original group, which is physically impossible.

### 8. DERIVATION OF THE PDE FROM THE STOCHASTIC MODEL

Let  $R_{(x,y)}$  be a rectangle with one corner at  $(x, y)$  and the opposite corner at  $(x + dx, y + dy)$ , and let  $R_{(x,y)}$ -groups be groups with configurations  $(u, v) \in R_{(x,y)}$ . Consider the change in the number of  $R_{(x,y)}$ -groups between times  $t$  and  $t + dt$ , denoted

$$\Delta(x, y, t) = (\theta_{t+dt}(x, y) - \theta_t(x, y))dxdy + o(dxdydt) = \frac{\partial \theta_t}{\partial t}(x, y)dxdydt + o(dxdydt).$$

The change,  $\Delta(x, y, t)$ , is the result of three factors: group extinction, group fissioning, and the ‘flux’ due to changing populations of individuals within the groups.

The simplest factor to analyse is extinction. In the interval  $[t, t + dt]$ , the number of  $R_{(x,y)}$ -groups that die of extinction is

$$\Delta_e(x, y, t) = e_t(x, y)\theta_t(x, y)dxdydt + o(dxdydt). \quad (18)$$

Similarly, the number of  $R_{(x,y)}$ -groups that die of fissioning is  $w_t(x, y)\theta_t(x, y)dxdydt + o(dxdydt)$ , but fissioning is more complicated than extinction because there are also births of  $R_{(x,y)}$ -groups during  $[t, t + dt]$  due to larger groups fissioning. To within  $o(dxdydt)$ , the number of such births is

$$B_t(x, y) = \int_x^\infty \int_y^\infty h((u, v), (x, y))\theta_t(u, v)w_t(u, v)dvdu, \quad (19)$$

where  $h((u, v), (x, y))$  is the fissioning density, e.g. (14). The change in the number of  $R_{(x,y)}$ -groups during  $[t, t + dt]$  due to fissioning is therefore

$$\Delta_f(x, y, t) = (B_t(x, y) - w_t(x, y)\theta_t(x, y))dxdydt + o(dxdydt) \quad (20)$$

From (10) it follows that the instantaneous *rate* that groups cross the left side boundary of  $R_{(x,y)}$  at time  $t$  due to migration and population dynamics within groups is  $\theta_t(x, y)\gamma_t^e(x, y)dy + o(dy)$ . (If this quantity is positive, then more groups are moving left to

right; if it is negative, then more groups are moving right to left.) Similarly, the rate that groups cross the right side boundary of  $R_{(x,y)}$  is  $\theta_t(x + dx, y)\gamma_t^c(x + dx, y)dy + o(dy)$ . The change in the number of  $R_{(x,y)}$ -groups due to changes in the populations of Cooperators within groups in the environment during  $[t, t + dt]$  is therefore

$$\Delta_c(x, y, t) = -\frac{\partial[\theta_t\gamma_t^c]}{\partial x}(x, y)dxdydt + o(dxdydt). \tag{21}$$

Similarly, the change in the number of  $R_{(x,y)}$ -groups due to changes in the populations of Defectors within groups in the environment during  $[t, t + dt]$  is

$$\Delta_d(x, y, t) = -\frac{\partial[\theta_t\gamma_t^d]}{\partial y}(x, y)dxdydt + o(dxdydt). \tag{22}$$

Adding (18), (20), (21), (22), dividing by  $dxdydt$ , and taking a limit yields the PDE model of two-level selection:

$$\frac{\partial\theta_t}{\partial t}(x, y) = B_t(x, y) - (e_t(x, y) + w_t(x, y))\theta_t(x, y) - \frac{\partial[\theta_t\gamma_t^c]}{\partial x}(x, y) - \frac{\partial[\theta_t\gamma_t^d]}{\partial y}(x, y). \tag{23}$$

The dependent variable,  $\theta_t(x, y)$ , is the *state of the environment* at time  $t$ . The first term on the right-hand side of (23) corresponds to births of  $(x, y)$ -groups due to the fissioning of larger groups. The second term corresponds to deaths of  $(x, y)$ -groups due to extinction and fissioning. The partial derivative terms correspond to changes in  $R_{(x,y)}$ -groups due to population dynamics of Cooperators and Defectors within those groups, and migration. In other words, the partial derivative terms correspond to individual-level population dynamics, and the other terms correspond to group-level population dynamics.

### Extension to $k > 2$ individual types

Now that the continuous model has been derived for the case where there are two types of individuals, it requires only a simple change in notation to extend the model to  $k$  types of individuals. Let  $\vec{x}(t) = (x_1(t), x_2(t), \dots, x_k(t))$  be the state of a group at time  $t$ , where  $x_i(t)$  is the population of type  $i$  individuals. A group in state  $\vec{x}$  will be called an  $\vec{x}$ -group. In analogy with (10), the model assumes that population dynamics within groups obey

$$\begin{bmatrix} x_1'(t) \\ x_2'(t) \\ \vdots \\ x_k'(t) \end{bmatrix} = \begin{bmatrix} \gamma_1^1(\vec{x}(t)) \\ \gamma_1^2(\vec{x}(t)) \\ \vdots \\ \gamma_1^k(\vec{x}(t)) \end{bmatrix}, \tag{24}$$

where  $\gamma_i^j(\vec{x}(t)) = \alpha_i(\vec{x}(t)) + \eta\epsilon_i^*(t)/N_t - x_i(t)\epsilon_i(\vec{x}(t))$ . The continuous model is based on an evolutionary birth–death process, so  $\alpha_i(\vec{x})$ ,  $i = 1, 2, \dots, k$  are the differences between the birth and death rates, just as in (8) and (9).

When there are  $k$  individual types, the state of the environment is represented by  $\theta_t(\vec{x})$ ,  $\vec{x} \in \mathfrak{R}_+^k$ . Similarly, the fissioning density has the form  $h(\vec{x}, \vec{u})$ , where  $x \in \mathfrak{R}_+^k$  and  $u_i \leq x_i$ ,  $i = 1, 2, \dots, k$ , so the birth rate of  $\vec{x}$ -groups at time  $t$  due to the fissioning of larger groups is

$$B_t(\vec{x}) = \int_{\vec{u} > \vec{x}} h(\vec{u}, \vec{x})\theta_t(\vec{u})w_t(\vec{u})d\vec{u}. \tag{25}$$

All other functions of  $(x, y)$  in the case  $k=2$  become analogous functions of  $\vec{x}$  in the general case. Finally, equation (23) becomes

$$\frac{\partial \theta_t}{\partial t}(\vec{x}) = B_t(\vec{x}) - (e_t(\vec{x}) + w_t(\vec{x}))\theta_t(\vec{x}) - \sum_{i=1}^k \frac{\partial[\theta_t \gamma_i^t]}{\partial x_i}(\vec{x}). \quad (26)$$

### Practical considerations

An equation like (23) can be solved numerically by iterating the approximation

$$\theta_{t+dt}(x, y) \approx \theta_t(x, y) + \frac{\partial \theta_t}{\partial t}(x, y)dt$$

for  $t=0, dt, 2dt, \dots$ , at the grid points  $x=0, dx, 2dx, \dots$  and  $y=0, dy, 2dy, \dots$ . The numerical procedure therefore estimates the change in the number of  $R_{(x,y)}$ -groups for each grid point during each time step. A little experimenting will reveal a finite region in  $\mathfrak{R}_+^2$  that contains most or all of the population mass, and that region serves as the domain for the approximation.

From (18) and (20) it follows that the change in the number of  $R_{(x,y)}$ -groups between times  $t$  and  $t+dt$  due to the group-level events, extinction and fissioning, is approximately (to within  $o(dydxdt)$ ),

$$\Delta_e(x, y, t) + \Delta_f(x, y, t) = (B_t(x, y) - (e_t(x, y) + w_t(x, y))\theta_t(x, y))dydxdt. \quad (27)$$

Conceptually, it is easy to evaluate (27), although it may be time-consuming since a double integral needs to be evaluated in (19) and (11). A courser grid may be used in some cases to evaluate the integrals to speed up the numerical procedure without sacrificing much accuracy.

Numerical difficulties can arise when approximating the change in the number of  $R_{(x,y)}$ -groups due to internal group population dynamics. If there is no extinction or fissioning, then (23) reduces to

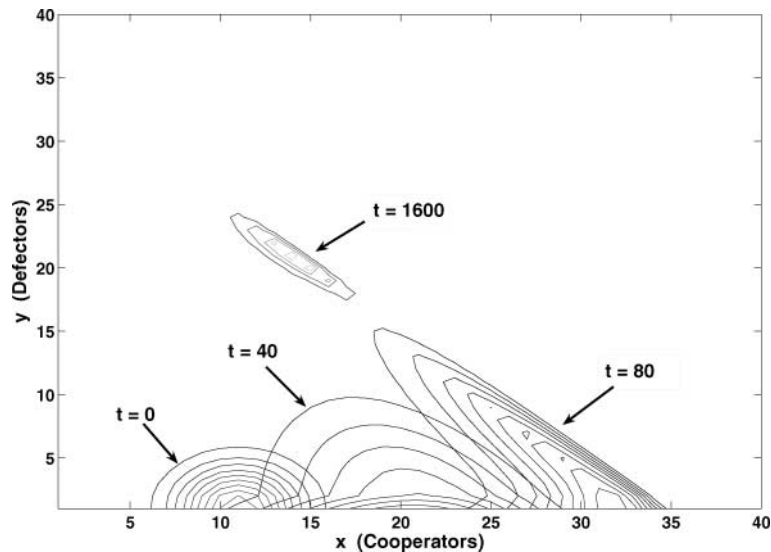
$$\frac{\partial \theta_t}{\partial t}(x, y) + \frac{\partial[\theta_t \gamma_t^c]}{\partial x}(x, y) + \frac{\partial[\theta_t \gamma_t^d]}{\partial y}(x, y) = 0, \quad (28)$$

which is a hyperbolic PDE, also known as a *conservation law*. The density  $\theta_t(x, y)$  changes in time due to internal group population dynamics, but if there is no extinction and fissioning, the total number of groups,  $N_t$  given by (5), is *conserved*. If the partial derivatives with respect to  $x$  and  $y$  in (28) are estimated by simple finite differences,  $N_t$  will gradually change and ruin the numerical solution, unless the grid is extremely fine. One way to avoid this problem is to use a technique called *upwind differencing* (LeVeque, 2007), which has a simple implementation here. Consider what happens to the  $R_{(x,y)}$ -groups in a small time interval of length  $dt$ . If  $dx$  and  $dy$  are small enough, all the groups in  $R_{(x,y)}$  move a little bit in the  $x$  direction and a little bit in the  $y$  direction in (almost) the same amounts. The amount  $R_{(x,y)}$  moves in the  $x$  direction is approximately  $\gamma_t^c(x, y)dt$  and the amount it moves in the  $y$  direction is approximately  $\gamma_t^d(x, y)dt$ . In its new position, the rectangle overlaps  $R_{(x,y)}$ , along with three other neighbouring rectangles (less than three if  $R_{(x,y)}$  is on a boundary). The mass,  $\theta_t(x, y)dx dy$ , associated with  $R_{(x,y)}$  is distributed proportionately among the rectangles it now overlaps. In a properly posed model, there is no flow off the grid, so the result is that

no mass is lost. Let  $\hat{\theta}_t(x, y)$  be the density obtained after upwind differencing at every grid point. Then the change in the number of  $R_{(x,y)}$ -groups due to internal group population dynamics in  $[t, t + dt]$  is approximately  $(\hat{\theta}_t(x, y) - \theta_t(x, y))dydxdt$ . The numerical procedure just described will be used to solve the PDE arising from the model developed in the next section. Figure 8 illustrates the solution of an equation of the form (28) that comes up in the example in the next section.

## 9. A MODEL OF HUNTER-GATHERER TRIBES

A model of an environment containing tribes of hunter-gatherers will now be described, where the tribes consist of ‘Cooperators’ and ‘Defectors’. The terms ‘group’ and ‘tribe’ can therefore be used interchangeably here. The PDE (23) for the model will then be derived and solved numerically. A discrete model of early human groups proposed by Bowles (2006) will serve as a point of comparison. The functions and parameters chosen for the submodels (MI)–(M4) (described in Section 4) in this example were chosen to follow the spirit of Bowles’ model. There are many more details possible in the present modelling framework, so many of the functions and parameters in the present model have no direct analog in



**Fig. 8.** Evolutionary dynamics of  $\theta_t(x, y)$  when there is no extinction and no fissioning, i.e. an environment with immortal groups that do not interact. (The figure is based on the hunter-gatherer example in Section 10.) In this case, the total number of groups remains constant, although the populations within the groups change. In this example, the initial environment consists of small groups of (mostly) Cooperators. After 40 years (2 generations), there has been significant population growth, resulting in much larger groups. The groups are still mostly Cooperators, but Defectors have made gains. By 80 years, population growth within the groups has been slowed down by the increased death rate resulting from the population growth, and the Defectors have started to assert themselves. The total population of a group cannot exceed (approximately) 35 due to the form of the birth and death rate functions (32) and (33). The groups then gradually ‘descend into chaos’, leading to the eventual extinction of the Cooperators. The rate of descent is very slow in this model due to the reproductive levelling (weak selection) assumed.

Bowles' model. In those cases, the choices were made primarily to illustrate the model's flexibility, and not for any sort of anthropological accuracy.

The unit of time in this model will be a year, and it will be assumed that generations are about 20 years. These conventions will help us choose parameters appropriately for the model. Within tribes, individuals play Prisoner's Dilemma against each other. The payoff matrix has the form

$$\begin{array}{c} C \\ D \end{array} \begin{array}{cc} C & D \\ \left[ \begin{array}{cc} b-c & -c \\ b & 0 \end{array} \right], \end{array} \quad (29)$$

where  $b > 0$  is interpreted as the benefit that cooperation brings, and  $c > 0$  is the cost of providing the benefit. If  $c \approx 0$ , there is little advantage in defecting. If  $c > b$ , the game is no longer Prisoner's Dilemma. We will use the values  $b = 0.05$  and  $c = 0.02$ , which are the same values used by Bowles, but the precise values of  $b$  and  $c$  are less crucial here, since birth and death rates depend on other parameters too. The fitness of an individual within a tribe is defined to be its average payoff against an opponent chosen randomly from the same tribe (perfect mixing). Thus, Cooperators in an  $(x, y)$ -group get an average payoff of  $(0.03x - 0.02y)/(x + y)$  and Defectors get  $0.05x/(x + y)$ . The birth rate of an individual is assumed to be exponential in its fitness. There are a few nice advantages to defining birth rates as exponential instead of linear functions of fitness. As Traulsen *et al.* (2008) point out, it allows game payoffs to be positive or negative without leading to negative fecundity and other meaningless outcomes. Furthermore, by adjusting the exponent, the birth rate can be made very sensitive to changes in fitness, or very insensitive, or anything in between. Bowles defines *reproductive levelling* to be a situation where reproductive success is relatively insensitive to small changes in fitness. (This is often referred to as *weak selection*.) Bowles models reproductive levelling by redistributing some fraction of the game payoffs among individuals in the group. There are other ways to accomplish the same effect. Here, the degree of reproductive levelling will be controlled by adjusting  $\ell_1$  in the birth rate formulas,

$$b_c(x, y) = \ell_0 e^{\ell_1(0.03x - 0.02y)/(x+y)} \quad \text{and} \quad b_d(x, y) = \ell_0 e^{\ell_1(0.05x)/(x+y)}. \quad (30)$$

If we choose  $\ell_1 = 1$ , the ratio of the highest possible birth rate to the lowest possible birth rate is  $e^{0.07} \approx 1.095$ , which seems like a fairly level playing field. By choosing  $\ell_1$  smaller, the ratio would be even lower; while raising  $\ell_1$  gives a larger advantage to Defectors. Since an average generation is about 20 years, we assign  $\ell_0 = 0.05$ . The resulting per individual birth rates are approximately in the range 0.98 per generation to 1.05 per generation, which is consistent with the values Bowles suggests. We will assume mutation probabilities of  $\mu_{cd} = \mu_{dc} = 0.01$ .

The per individual death rates for Cooperators and Defectors in an  $(x, y)$ -group will be assumed to be equal with common value

$$d(x, y) = \frac{1 + d_1(x + y)^2}{d_0^{-1} + (x + y)}, \quad (31)$$

where  $d_0$  and  $d_1$  are positive constants. Thus, for small groups the individual death rate is approximately  $d_0$ , and for big groups the death rate is approximately  $d_1$  times its size. Since the per-individual death rate function increases without bound as  $x + y$  increases, there is a stable population range. Bowles argues that an average hunter-gatherer tribe has about

32 individuals (possibly made up of several smaller ‘bands’). After some experimenting, we set  $d_0 = 0.025$  and  $d_1 = 0.0025$ , which leads to groups of about the right size and individuals with plausible lifetimes. Individuals in established tribes of size 25–35 have average lifetimes of about 20–25 years. Individuals in smaller groups have larger ‘natural lifetimes’ in this model, but often die due to group extinction, so their true average lifetimes are actually shorter. Due to the complexity of the interactions between the pieces of our model, it is difficult to predict beforehand what group sizes and other statistics will emerge from the solution.

We will use a simple model of migration where  $\varepsilon_c^*(t) = 0.002C_t$  and  $\varepsilon_d^*(t) = 0.002D_t$ , where  $C_t$  and  $D_t$  are given by (6), i.e. the per-individual migration rate (4) is  $\varepsilon_c(\cdot, \cdot) = \varepsilon_d(\cdot, \cdot) = 0.002$ . If every immigrant is accepted (i.e.  $\eta = 1$ ), the terms  $\gamma_i^c$  and  $\gamma_i^d$  in (23) have the form

$$\gamma_i^c(x, y) = 0.99x\beta_c(x, y) + 0.01yb_d(x, y) + 0.002C_t/N_t - x(d(x, y) + 0.002), \tag{32}$$

$$\gamma_i^d(x, y) = 0.01x\beta_c(x, y) + 0.99yb_d(x, y) + 0.002D_t/N_t - y(d(x, y) + 0.002), \tag{33}$$

where  $\beta_c(x, y)$ ,  $\beta_d(x, y)$ , and  $d(x, y)$  are given by (30) and (31).

The tribes in the environment play a variant of Chicken against each other. When tribe  $i$  and tribe  $j$  face off, the alternatives to each tribe are Retreat and Attack. The model assumes that the payoffs for Retreat vs. Retreat, Retreat vs. Attack, and Attack vs. Retreat do not depend on the groups involved. Their values will be set to 0,  $-r$ , and  $a$ , respectively. In other words, if both groups Retreat, then neither wins or loses anything. If one group Attacks and the other Retreats, the aggressive group wins  $a$  units and the passive group loses  $r$  units. The key to this game is that the payoffs for Attack vs. Attack depend on the tribes involved. The model assumes that the more cooperators there are in a tribe, the stronger it is in a fight. With that in mind, the payoff to tribe  $i$  in a fight with tribe  $j$  is defined to be  $x_i(i) - x_i(j)$ . (The stronger tribe wins in a fight and the weaker one loses, so the game is really only ‘Chicken’ for the weaker tribe.) The payoff matrix for tribe  $i$  (row) against tribe  $j$  (column) in the group level game is

$$\begin{array}{cc} & \begin{array}{cc} \text{Retreat} & \text{Attack} \end{array} \\ \begin{array}{c} \text{Retreat} \\ \text{Attack} \end{array} & \left[ \begin{array}{cc} 0 & -r \\ a & x_i(i) - x_i(j) \end{array} \right]. \end{array} \tag{34}$$

The orders of magnitude of these payoffs are somewhat arbitrary, since the extinction rate and fissioning rate functions can rescale them. The cost associated with retreat will be set here to  $r = 1$ , so it is always better to win a fight than to retreat, and it is better to retreat than to lose, unless the tribes are almost perfectly matched. We will assume that the attacker wins what the retreator loses, so  $a = 1$  as well. The model assumes that tribe  $i$  uses a mixed strategy against tribe  $j$  that depends on their relative sizes:

$$P(\text{tribe } i \text{ attacks tribe } j) = 1 - e^{-\omega\rho}, \tag{35}$$

where  $\omega \geq 0$  is a constant, and

$$\rho = \frac{x_i(i) + y_i(i)}{x_i(j) + y_i(j)}$$

is the ratio of the group sizes at the time of the encounter, i.e. the larger tribe is more likely to attack than the smaller tribe. Note that  $P(\text{tribe } j \text{ attacks tribe } i) = 1 - e^{-\omega/\rho}$ . We will assign

$\omega = 0.5$ , so a tribe will attack a similar sized tribe with probability  $1 - e^{-1/2} = 0.3935$ , a tribe twice its size with probability  $1 - e^{-1/4} = 0.2212$ , and a tribe half its size with probability  $1 - e^{-1} = 0.6321$ . Large tribes will usually attack small tribes, and the small tribes will usually retreat from them.

In the continuous model, the external fitness of an  $(x, y)$ -group (tribe) is the average payoff it gets from interactions with the other groups in the environment. From (35) it follows that if an  $(x, y)$ -group encounters a  $(u, v)$ -group, then the expected payoff for the  $(x, y)$ -group is

$$\hat{\Psi}((x, y), (u, v)) = (1 - e^{-\rho}) e^{-1/\rho} - e^{-\rho}(1 - e^{-1/\rho}) + (1 - e^{-\rho})(1 - e^{-1/\rho})(x - u),$$

where

$$\rho = \frac{x + y}{u + v}$$

is the ratio of the group sizes. From (11), the external fitness of an  $(x, y)$ -group at time  $t$  is the expected payoff against a random opponent,

$$f_t^E(x, y) = N_t^{-1} \int_0^\infty \int_0^\infty \Psi((x, y), (u, v)) \theta_t(u, v) dv du. \quad (36)$$

The internal fitness of an  $(x, y)$ -group in our model is defined to be

$$f^I(x, y) = x - y, \quad (37)$$

i.e. Cooperators are good and Defectors are bad. The internal fitness and external fitness in our model are roughly of the same order of magnitude, so they are each important in determining the total fitness of a group. The total fitness of an  $(x, y)$ -group at time  $t$  is the sum of (36) and (37),

$$f_t(x, y) = f^I(x, y) + f_t^E(x, y).$$

The extinction rate for  $(x, y)$ -groups ought to depend on how big and/or fit they are, and how crowded the environment is. We will define

$$e_t(x, y) = 0.005 (e^{-0.1f_t(x, y)} + 0.5e^{(C_t + D_t - 1000)/1000} + 4e^{-(x+y)/100}). \quad (38)$$

There are three factors in the extinction rate. The first takes fitness into account: greater fitness means lower extinction rate. The second takes the total population of individuals in the environment into account. If the total population is significantly less than 1000, it has little effect on extinction, but if it is more than 1000, the extinction rate rises quickly. The third term takes the size of the tribe into account. Very small tribes are much more likely to die of extinction. In Bowles' model, 'contests' between tribes are rare and catastrophic for the loser. For a given tribe, he estimates there is about one contest every 6 generations. The average tribe loses half the time, so the average lifetime of an average tribe is about 12 generations or 240 years. The constant terms in (38) were chosen after some initial experiments. It leads to a stable environment with tribe sizes and lifetimes in line with Bowles' estimates. In Bowles' model, tribal reproduction occurs at the same time that tribal conquest occurs. A victorious tribe in a contest spontaneously spawns a copy of itself, occupying the place previously occupied by its opponent. (The number of tribes is held constant.) In the present model, we are not constrained to tie group extinction and

fissioning together like that. We specify an extinction rate function, like (38), a fissioning rate function like

$$w_t(x, y) = 0.02e^{0.01(x + 3y - 50)}, \tag{39}$$

and a fissioning density of the form (14). The idea behind the  $x + 3y - 50$  term in the exponent of (39) is that tribes with lots of Defectors are more likely to fission than an equal sized tribe with lots of Cooperators. The other numerical constants in (39) were chosen after some experimentation. As with most of the parameter choices made here, a wide range of alternatives is available. In keeping with the spirit of Bowles' model, we will assume that fissioning results in a uniform split, i.e.  $p = q = 0.5$  in (14), so

$$B_t(x, y) = \int_x^\infty \int_y^\infty h((u, v), (x, y))\theta_t(x, y)w_t(u, v)dvdu, \tag{40}$$

where  $h((u, v), (x, y))$  is given by (17), and  $w_t(x, y)$  is given by (39).

### Numerical solution of the model

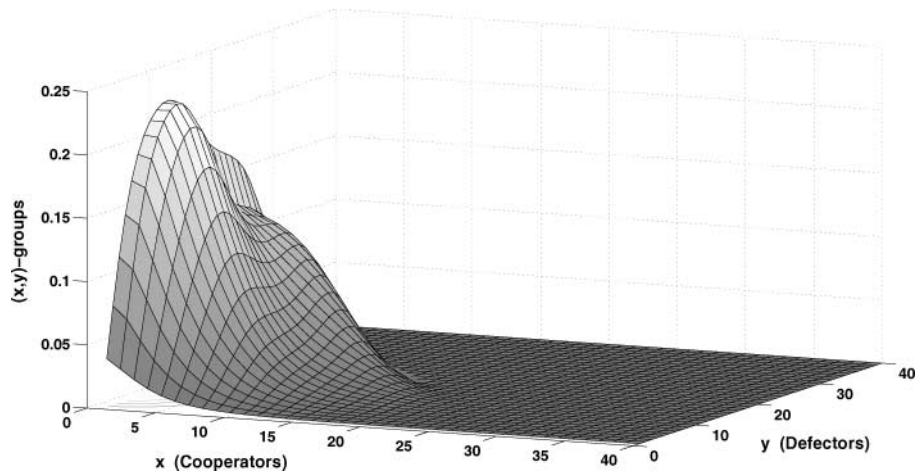
Equation (23) is completely determined by the functions (32), (33), (38), (39), and (40), so all that remains is to solve the PDE numerically. The first step is to find a finite region in  $\mathfrak{R}_+^2$  that always contains the vast majority of the population mass. After some experimenting, it becomes apparent that a tribe cannot grow to have more than about 35 individuals, so the region  $0 \leq x \leq 40$  and  $0 \leq y \leq 40 - x$  suffices as the domain of the approximation. The computational complexity of the numerical procedure is very sensitive to the size of the domain, so choosing the smallest possible domain is important. A uniform grid with  $dy = dx = 0.5$  and a time step of  $dt = 0.1$  was used. This appears to be a fine enough discretization for reasonable accuracy, yet coarse enough so that computer time and memory are not significant issues. Once the numerical procedure is in place, the model can be solved starting from any initial population density function,  $\theta_0(x, y)$ .

It is instructive to see what happens if there is no extinction or fissioning, i.e. if (23) reduces to (28). Figure 8 shows the result when the initial population is made up of small tribes of about 10 (mostly) Cooperators. At first, the tribes grow quickly and retain their Cooperator majorities. Once the tribes reach the equilibrium size of about 35 individuals, the defectors slowly take over and the tribes descend into chaos. Without the group-level events of extinction and fissioning, cooperation cannot survive in the environment, so it slowly goes extinct. (*Slowly*, because of the reproductive levelling in the model.)

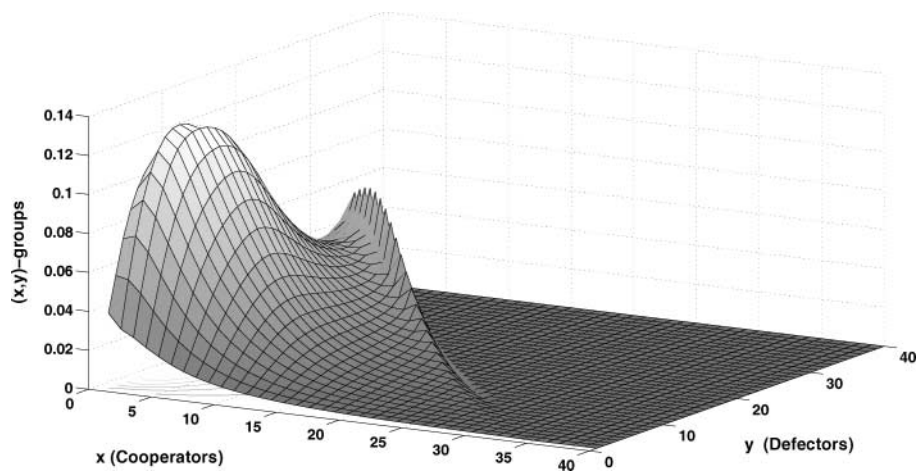
When the group-level events are present, the results are quite different. In the present example, we will assume the environment starts with the initial population density,

$$\theta_0(x, y) = e^{-(x^2 + (y - 10)^2)/20}, \quad (x, y) \in \mathfrak{R}_+^2, \tag{41}$$

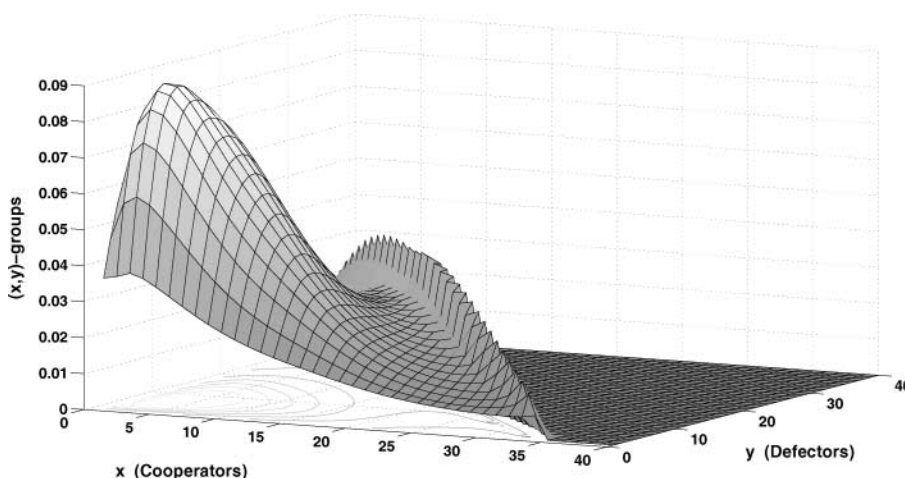
which corresponds to about 35 tribes, each with about 10 Defectors and a small number of Cooperators. Figure 9 shows the population density after 40 years (2 generations). The tribes have grown and there has been a small amount of fissioning, but there have not yet been any qualitative changes in the environment. After 100 years (Fig. 10), the original tribes that have not fissioned or died have reached the population barrier of about 35 individuals, so there are a significant number of large tribes of (mostly) Defectors. In Fig. 10, there are also a small number of tribes with a majority of Cooperators. These tribes are the result of the occasional fissioning of a large (non-cooperative) tribe that (by chance)



**Fig. 9.** The state of the environment,  $\theta_t(x, y)$ , after  $t = 40$  years (2 generations) for the model of tribes of hunter-gatherers from Section 4. The initial state (41) consisted of small tribes of about 10 (mostly) Defectors. The tribes have grown, and Defectors have gained on Cooperators up to this point. Figures 10–12 show the state of the environment after 5 generations, after 15 generations, and after 50 generations.



**Fig. 10.** The state of the environment after 100 years. The original tribes that are still intact have hit the population growth barrier at  $x + y \approx 35$ . These large tribes of (mostly) Defectors have low fitness, and therefore a relatively high extinction rate. A sizeable number of small tribes are also present due to the fissioning of some of the original tribes. These new tribes will grow and replace the large tribes that die or fission. Although the density shows that a large number of the tribes in the environment are small, most individuals, in fact, reside in the large tribes. Due to the occasional fissioned tribe that is (by chance) made up of an unusually high fraction of Cooperators, there are now a small number of tribes with a majority of Cooperators. These are the fittest tribes in the environment, so they are more likely to become large and fission new tribes. The tribes they fission will tend to be more cooperative, so cooperation may gain in the environment.



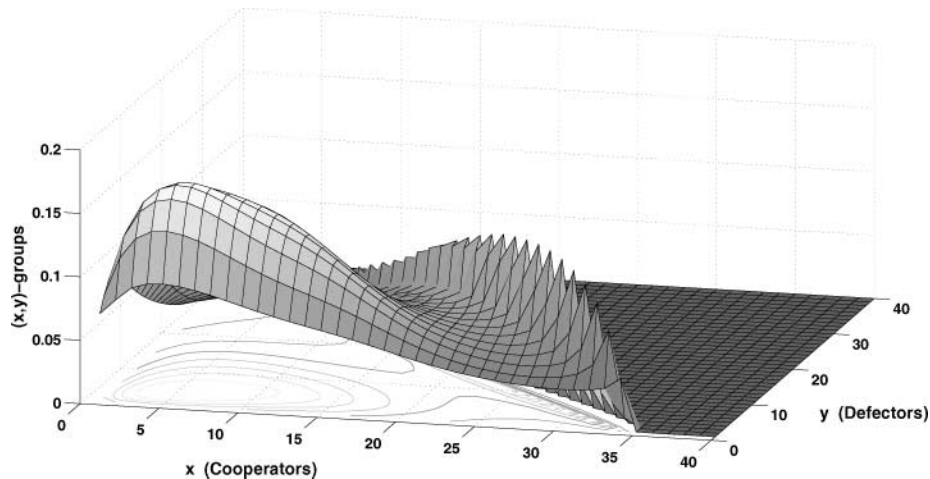
**Fig. 11.** The state of the environment after 300 years. The large tribes of (mostly) Defectors that were present at  $t = 100$  are almost gone, and they have been replaced by large tribes with a more even split of Cooperators and Defectors. There are a significant number of small tribes due to the fissioning of the large tribes, but the majority of individuals reside in the large tribes. There are now a small number of large tribes of (mostly) Cooperators. Cooperation is clearly gaining in the environment.

resulted in a tribe with excess Cooperators, that then started to grow. Figure 11 shows the population density 200 years later. Cooperation is beginning to dominate. The number of large tribes of (mostly) Defectors has dwindled, and now the typical large tribe is made up of about 50% Cooperators. There are a small number of large tribes of (mostly) Cooperators. After 1000 years (50 generations), the environment appears to have reached an equilibrium configuration (Fig. 12), although the population will slowly increase (in the same proportions) for at least another 1000 years (Fig. 13). The equilibrium has a large number of small tribes, and a significant number of large tribes of (mostly) Cooperators. The equilibrium configuration appears to involve a ‘circulation’ of group-types, where

- large tribes of (mostly) Cooperators gradually descend into chaos, but long before they get there, they die of extinction or fission into two pieces;
- the fissioned pieces tend to have a majority of Cooperators too, since the fissioning events usually occur while the tribes still have a majority of Cooperators. However, due to chance, there are a sizeable number of small tribes with a majority of Defectors; small tribes (0–10 individuals) do not grow nearly as quickly as larger tribes (20–30 individuals), so once a tribe starts to grow it takes relatively little time to reach the population barrier. Thus, tribes with 20–30 individuals are comparatively rare in the environment;
- the small tribes of (mostly) Defectors start to grow, but they are significantly less fit than the other tribes in the environment, so they rarely get very big before they die.

The group-size ‘barrier’ along the diagonal  $x + y \approx 35$  in Figs. 10–12 is an artifact of the birth and death rate functions chosen for this model. In fact, the boundary is not exactly linear, but is very close due to the reproductive levelling.

Of course, there are many ways to choose the functions and parameters in the basic model of hunter-gatherer tribes. The reader may wonder how sensitive the evolutionary



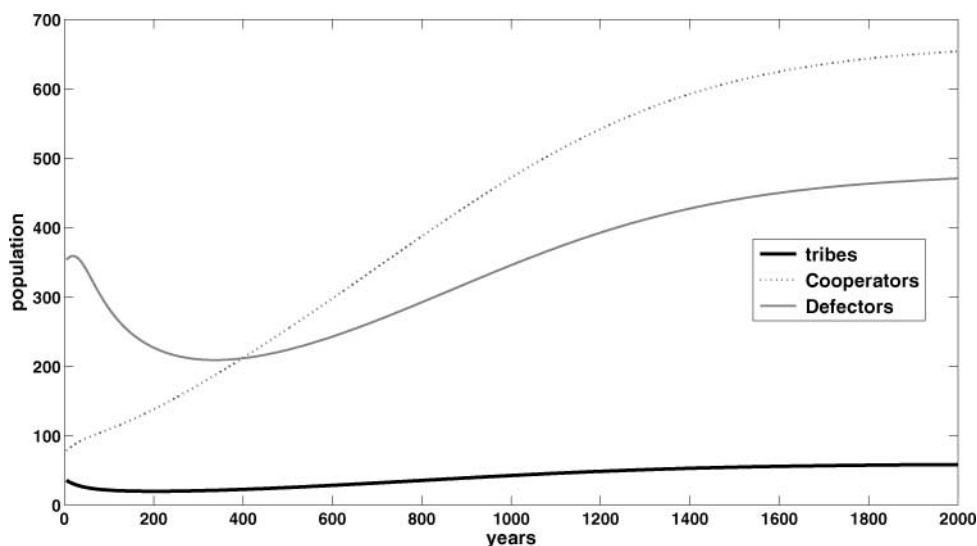
**Fig. 12.** The environment has apparently converged to an equilibrium configuration after about 1000 years (shown here), although the number of tribes will slowly increase for another 1000 years (see Fig. 13). The equilibrium environment contains a large number of tribes of (mostly) Cooperators that contain the majority of the individuals in the environment. The shape of the equilibrium density can be explained as follows: Along the diagonal  $x + y \approx 35$ , the tribes gradually descend into chaos, become less fit, and eventually die of extinction or fission. Large tribes fission smaller tribes, and those smaller tribes occasionally fission even smaller tribes. This accounts for the large number of small tribes. The small tribes are not nearly as fit as their larger neighbours, but (if they live long enough) they grow quickly (Fig. 8), so there are relatively few tribes of size 20–30.

trajectories are to the specifics of the model. Numerical experiments by the author that varied the functions and parameters (extinction rate functions, fissioning rate functions, migration rates, fitness measures, etc.) strongly suggest that the basic form of the equilibrium configuration is fairly robust with respect to the choices made, and to the initial conditions. In particular, the results are very similar when there are no interactions between the tribes (i.e. no group-level games), so cooperation can evolve in these models even when group fitness only depends on the state of the group (internal fitness). The model therefore suggests that in the past, if the hunter-gatherer tribes in an environment were plentiful, and had reached equilibrium in that environment, then the equilibrium probably resembled Fig. 12.

Significant changes in the functional parameters used in the present example can lead to major changes in the equilibrium configuration, however. For example, if the advantage of defection is large enough at the individual level, then cooperation will go extinct (except through occasional mutation). The equilibrium configuration in this case is concentrated near the  $y$ -axis, corresponding to tribes dominated by defectors. If tribes of (mostly) defectors are weak enough, the entire population of hunter-gatherers could go extinct.

## 10. DISCUSSION

It is hoped that the reader comes away from this paper with a better understanding of how cooperation can evolve by two-level selection, and how informative a dynamical model of the phenomenon can be. The dynamical equations of two-level selection constructed here



**Fig. 13.** The number of tribes in the environment, and the total number of Cooperators and Defectors. The extinction rate function (38) is relatively large for small tribes, so a significant number of the original tribes quickly die, especially the tribes with a lot of defectors. The number of tribes decreases from about 35 to a low of about 20 after 40 years. As the remaining tribes grow, their extinction rate decreases and the number of tribes in the environment begins to increase due to fissioning. As the tribes become more cooperative, their fitness increases and their numbers increase even more. Eventually, the number of individuals in the environment gets so large that the extinction rate just balances the fissioning and the population of tribes settles down at about 60. The total population of individuals in the environment settles down at about 1150, so the average size of a tribe is a little less than 20. The average size is a misleading statistic in this model, since the most common tribal configurations are around (5, 5) and (25, 10). The fraction of Cooperators in the environment rises steadily from about 10% at  $t=0$ , reaching about 50% after 400 years, and then gradually increases to about 58%.

can be solved, yielding evolutionary trajectories and equilibrium configurations. The evolutionary trajectories and equilibrium configurations in these sorts of models are often rather complicated (e.g. the thought experiment in Section 1 and the hunter-gatherer example in Section 10), strongly suggesting that a dynamical analysis is necessary to properly understand the phenomenon, and predict its long-term behaviour.

Two models are described in this paper: a stochastic version (continuous-time Markov chain) in Section 6, and a deterministic version (PDE) in Section 7. The two models are related in the sense that the parameters specifying a given stochastic model uniquely specify a corresponding PDE model. The PDE is derived from the stochastic model in Section 8.

From the assumptions (A1)–(A6) in Section 2, it is clear that the kinds of two-level evolutionary processes studied here are a kind of ‘group selection’. Assumption (A1) states that groups are distinct, i.e. at every point in time, every individual alive at that time belongs to exactly one group. The dynamical equations constructed here are therefore not valid for every example of two-level selection. However, in nature there are many examples of two-level selection that (approximately) satisfy (A1)–(A6) (e.g. virulence, insect colonies,

and hunter-gatherer tribes). The modelling analysis developed here can therefore be applied to all of them. Our models of two-level selection are specified by four submodels (M1)–(M4), as described in Section 4. Models of virulence, insect colonies, hunter-gatherer tribes, and other examples of two-level selection will differ from each other in one or more of the submodels. The submodel of individual population dynamics within groups (M1) involves birth and death rates of individuals. Submodel (M3) involves births and deaths of groups (fissioning and extinction). The full model therefore depends on both individual-level and group-level events. Group-level events (fissioning, extinction, group-level games, etc.), which are often present in real biological examples, and which are explicitly accounted for in the present models, are often absent in traditional models of group selection, and the evolution of cooperation.

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