A computational model of task allocation in social insects – ecology and interactions alone can drive specialisation

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May 7, 2018

Abstract

Social insect colonies are capable of allocating their workforce in a decentralised fashion; addressing a variety of tasks and responding effectively to changes in the environment. This process is fundamental to their ecological success, but the mechanisms behind it remain poorly understood. While most models focus on internal and individual factors, empirical evidence highlights the importance of ecology and social interactions. To address this gap we propose a game theoretical model of task allocation. Individuals are characterised by a trait that determines how they split their energy between the two prototypical tasks of foraging and regulation. A viable colony needs to learn to adequately split their energy between the two tasks. We study two different social processes: individuals can learn to play this game by relying exclusively on their own experience, or by relying on the experiences of others via social learning. A computational model allows for direct manipulation of individual interactions and ecology. We find that social organisation can be completely determined by the ecology alone: irrespective of interaction details, weakly specialised colonies in which all individuals tend to both tasks emerge when foraging is cheap; harsher environments, on the other hand, lead to strongly specialised colonies in which each individual fully engages in a single tasks. We compare the outcomes of self-organised task allocation with optimal group performance. Counter to intuition, strongly specialised colonies perform suboptimally, whereas the group performance of weakly specialised colonies is closer to optimal. Differences in social interactions are salient when the colony deals with dynamic environments. Colonies whose individuals rely on their own experience are better able to deal with change. Our computational model is aligned with

mathematical predictions in tractable limits. We believe this different kind of model is useful in framing relevant and important empirical questions.

Introduction

Social insects are among the ecologically most successful life forms. They live in elaborately organised colonies, capable of managing a complex network of simultaneous tasks; from scouting and foraging to colony defence, nest building, thermoregulation, and brood care. Their ecological success is in part due to the colony's ability to efficiently allocate its workforce to these different tasks, responding to frequent changes in external conditions and internal requirements [9, 29, 33, 47, 32, 10, 14, 17, 21, 24, 42, 45, 52]. The resulting "division of labour" (DOL) emerges from the task choices of individual workers without any central coordination or control. Deciphering the individual-based rules behind task selection is thus at the heart of understanding how colonies can achieve their collective plasticity in task allocation.

Task allocation in social insects has received a significant amount of attention [2]. The majority of research has focused on the influence of internal factors such as genetics [46], morphology [47] and hormones [51]. Comparatively, little attention has been given to the underlying mechanisms of social interactions and their role in regulating task allocation. This is in part because the dominant analysis framework does not provide a direct link between interactions among individuals and environmental conditions. Investigating the mechanistic roles of these factors has recently been proposed as the foundation to a more comprehensive understanding of DOL [24].

Mathematical and computational models have played an important role in this discussion – see [3, 14] for comprehensive reviews. Among these, response threshold models are arguably the most established [39, 35]. In these, individuals are are assumed to have an internal task-related response threshold, and they are more likely to respond to a task stimulus, the more it exceeds their threshold [4, 57, 48, 37, 26, 27, 13]. This simple idea has been implemented in many different forms, but regardless of the modelling details interactions among individuals are always indirect. They only take place through stigmergy: individual actions change the task-related stimulus (for example, nest temperature for a task of thermoregulation) and the modified stimulus can in turn influence the task readiness of other individuals. Direct interactions do not feature in the models. This is in contrast to the empirical literature, which suggests that social

context is a significant determinant of task engagement [11, 25, 28].

In addition the idea of stimulus intensity does not capture enough information to account for complex ecological factors. The cost required to tackle a task as well as the reward obtained from performing it can vary widely depending on environmental conditions. How costly and successful a foraging task is can depend on factors such as ambient temperature, abundance of food sources and presence of predators, which in turn affects the individuals' decisions about task engagement. In other words, response threshold models do not provide a link to empirically established environmental factors.

To overcome these limitations we propose a new modelling framework, based on game theory. It directly incorporates social interactions and environmental conditions as the main factors. Although game theory is a well-established toolbox for the study of interdependent decision-making and has been very successfully applied to many other aspects of sociality in biology [34, 44, 15, 6], it has gone virtually unnoticed in the study of task allocation. An exception is [61], which investigates DOL in co-viruses. However, this study addresses evolutionary timescales rather than behavioural change in an individual's lifetime.

We use Evolutionary Game Theory (EGT) [43, 7] to investigate how individual task preferences develop in the lifetime of a colony, and how specialisation emerges as a result of these choices. While EGT was originally conceived to model the evolution of behaviour, it has also been interpreted as "learning game theory" to explore behavioural change in ecological timescales [34, 60].

We model task allocation as a simple game. Individuals choose how to divide their energy between different tasks. Task performance results in rewards that can be shared between colony members or go directly to the individual. Rewards are modulated by collective levels of investment into the tasks as well as by environmental factors. Groups of individuals repeatedly engage in collective task execution and modify their strategies based on the rewards they receive individually or collectively. This framework is aligned with empirical evidence identifying social interactions and ecology as key factors [18, 49, 50, 36, 25, 28, 11]. This modelling framework provides a large degree of flexibility via simulations, while also allowing for mathematical predictions based on game theory [31].

The proposed formal model of task allocation directly addresses the influence of environmental factors and social interactions. Our model shows that ecological conditions are a crucial determinant for the emergence of different forms of specialisation. We also find that specialisation can emerge from interactions

between individuals alone, under a large range of environmental conditions. Contrary to intuition, we find that specialisation does not always result in colony efficiency. Our theoretical results thus point towards promising new directions for empirical work that can bring us a step closer to understanding how social insects achieve their outstanding ecological success.

Models and methods

A task-allocation game

Any colony needs to balance its workforce allocation between different tasks in response to the conditions of the environment. As there is no centralised control mechanism, this allocation can only emerge from the task engagement decisions that individuals make. From the perspective of the individual, task engagement can be driven by the costs and benefits of the task as they accrue to the individual and by the task choices of other individuals. This suggests game theory as an appropriate framework to investigate task allocation mechanisms. More specifically, shared benefits and individual costs place our scenario squarely into the context of public goods games [55, 1].

We assume a large group of workers in a colony, who need to balance two prototypical tasks with different characteristics. Costs and benefits for each task vary under different ecological conditions. The benefits of task execution are shared by the whole colony, whereas costs accrue to individual workers. The payoff to a single individual equals the shared benefits generated by the task performance of the whole colony minus the individual cost of performing the tasks. Payoffs can be thought of as primarily metabolic or energetic in nature.

We use EGT to investigate how individuals modify and adjust their task choice behaviour based on simple rules that take only individual experience and social information into account. Importantly, unlike in classical game theory, there is no underlying assumption of rationality for the individuals and the processes are not driven by striving for collective efficiency or optimality. Only individual behaviour enters explicitly into the model, and colony-level task allocation patterns arise as an emergent property.

In our model individuals can choose between two tasks: a regulatory task T (for thermo-regulation) and a maximising task F (for foraging). T represents a homeostatic task: colonies need to maintain nest and brood temperature within certain bounds, for which a certain amount of collective effort is required. Allo-

cating too little collective effort to this task can lead to regulation failure, and allocating too much effort does not improve the homeostasis and may in fact lead to subopptimal regulation, such as overcooling. Thus, group benefit for T as a function of group effort is a strictly concave function: the maximum benefit is obtained at an intermediate level of group effort. On the other hand, foraging is a maximising task; i.e., the benefit from F is monotonically increasing in collective effort devoted to foraging: the more food is collected, the better.

Individual task preferences are determined by an inherent response trait [16, 38, 23]. The response trait of an individual i is modelled as a continuous value $0 \leq x_i \leq 1$, which represents the fraction of effort that individual i invests into task T. Conversely, worker i will invest $1 - x_i$ effort into Task F. Thus, the state of the colony at any time is given by a vector $(x_i)_{i=1...N}$. We assume that workers interactions are restricted to groups of size n, where $n < N$. This captures physical and spatial constraints. For example, a fanning worker will cool brood only locally, not in every location of the brood chamber. Likewise, social interactions can only take place when workers are in proximity and are thus limited to smaller groups at any point of time.

Individual payoffs depend on x_i, as well as on the collective effort invested by all workers in the group $X = \{x_j | j = 1, 2, ..., n\}$. More specifically, worker i receives payoff

$$\Pi_i(X) = \frac{1}{n} B(X) - C(x_i) \tag{1}$$

where $B(X)$ is the total benefit for the group, and $C(x_i)$ is the cost for worker i. This reflects that benefits arising from both tasks are shared, whereas costs are born individually.

Ensuring colony fitness requires the performance of both tasks. In the context of our example tasks, poor maintenance of nest temperature can slow down the development of the brood and some brood may not survive if there is a shortage of food intake. Hence, the total benefit is multiplicative in the benefits of each task.

$$B(X) = B_T(X) \cdot B_F(X) \tag{2}$$

where $B_T(X)$, $B_F(X)$ are the benefits of task T and F, respectively.

Costs, on the other hand, are additive:

$$C(x_i) = C_T(x_i) + C_F(x_i) \tag{3}$$

where $C_T(x_i)$, $C_F(x_i)$ are the costs of Task T and F, respectively.

The cost of the regulatory task $C_F(x_i)$ is linear in the effort x_i. Consider cooling fanning in bees: the amount of energy required depends on physiological factors of the individual, but it is proportionate to the length and intensity of the fanning activity (effort). For the maximising task we assume marginally decreasing costs, i.e., $\forall x : \; C'_T(x) > 0$ and $\forall x : \; C''_T(x) < 0$. This reflects efficiency improvement through task experience. A foraging bee may become more efficient at finding high value flowers and thus the marginal investment for an additional unit of food decreases.

To investigate how colonies perform in different environmental conditions we introduce two further parameters b and r that link cost and benefit to the characteristics of the environment (Fig 1). b captures the benefit ratio between F and T. Larger values of b represent abundant ecologies where foraging is cheap relative to regulating, whereas small values of b indicate that foraging is costly compared to regulating. Similarly, r is the cost ratio of T and F: $r < 1$ implies F is more expensive than T per unit effort, and vice versa. Full details are given in Section A, S1 Appendix.

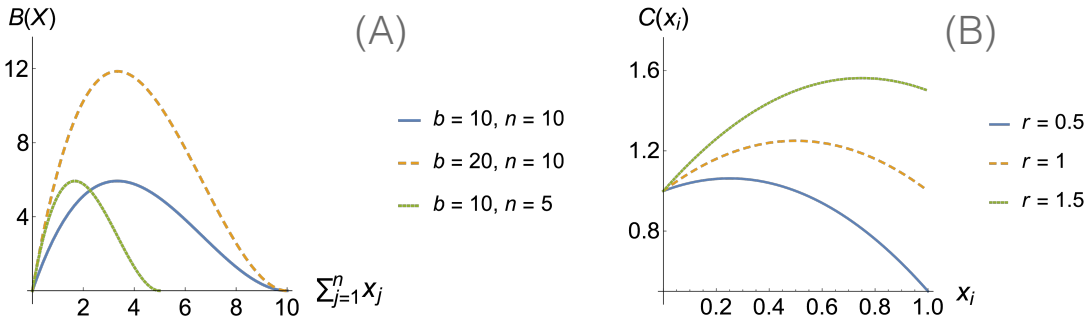


Fig 1. Examples benefit and cost functions. (A): Individual benefit as a function of collective group effort. The benefit reaches a maximal value only if the proportion of group workforce allocated to both tasks is appropriate. **(B)**: Individual cost as a function of her own strategy. For $r < 1$, foraging tends to be more expensive than regulation and the cost is minimised for $x_i = 1$. For $r > 1$, regulation tends to be more expensive than foraging and the cost is minimised for $x_i = 0$. For $r = 1$ both tasks tend to be equally costly.

We now turn to defining how individuals may use their payoffs to adjust their trait values. We consider and simulate two simple update rules that are at two ends of the spectrum of individual information processing: *individual learning* and *social learning*. In individual learning individuals explore small variations of their current strategy and adopt new variants that increase their payoff. With social learning, workers can copy the strategies of other successful workers. We

make no specific assumptions on the proximate mechanisms of social information exchange, and only make the weak assumption that successful strategies are more likely to be adopted by others.

We implement this process in an agent-based model and compare the outcomes to an analytic treatment using adaptive dynamics and Nash equilibria.

The simulations start from a homogeneous population. At each time-step, individuals form random groups of size n, play the game described above, and receive a payoff according to the collective investment in the task and the individual costs. The population then adjusts strategies based on the learning mechanism.

Individual learning

In individual learning, workers assess and improve their strategies by making comparisons between their current and previous task performance [34]. They rely completely on their own experience, without taking into account the experiences of others. More specifically, each individual explores a new strategy with a small probability, and switches to it only if the new variant provides a larger payoff. This is akin to the ideas of reinforcement learning and stochastic hill-climbing.

The dynamics of individual learning at the population level follow Algorithm 1.

Social learning

In social learning, individuals will adopt the strategies of others who are successful. The dynamics of social learning at the population level follow Algorithm 2.

Here, each individual explores a new strategy with a small probability. Individuals are more likely to copy other successful strategies in the population. This is similar to Wright-Fisher process.

Results

Long-term behavioural dynamics

Our results show that colony-level task specialisation can emerge from the interaction dynamics between individuals and their environments alone (see strong specialisation in Fig 2 and Fig 3). Under a certain range of environment conditions, the workforce of colonies initially consisting of individuals with identical strategies split into different groups. In each of these groups, individuals

Algorithm 1 Individual learning

```
t ← 0 (* initialise time *)
∀i : x_i ← 0.5, Π_i ← 0 (* initialise strategy and payoff for individual i *)
while t < t_end do
    m ~ Binomial(N, β)
    uniformly select m individuals into M
    for individual i ∈ M do
        x' ← x_i (* i memorises her previous strategy *)
        x'' ~ N(x_i, γ) (* i innovates to a new strategy *)
        form k games g with i and other n − 1 uniformly selected individuals
        Π' ← (1/k) Σ_{g=1}^{k} ((1/n) B(X_g) − C(x'))
        Π'' ← (1/k) Σ_{g=1}^{k} ((1/n) B(X_g) − C(x''))
        if Π' < Π''_i then
            x_i ← x''
            Π_i ← Π''
        else
            Π_i ← Π'
        end if
    end for
end while
```

Algorithm 2 Algorithm for the model with social learning

```
t ← 0 (* initialise time *)
∀i : x_i ← 0.5 (* initialise strategy for individual i *)
randomly partition individuals into N/n games g_k of size n
while t < t_end do
    for individual i = 1, 2, ..., N do
        Π_i ← (1/n) B(X_k) − C(x_i) (* i ∈ g_k, X_k = {x_j | j ∈ g_k} *)
    end for
    for individual i = 1, 2, ..., N do
        randomly select individual j according to probabilities p_j =
    e^{αΠ_j} / Σ_u e^{αΠ_u}
        x_i ← x_j
    end for
    m ~ Binomial(N, β)
    uniformly select m individuals into M
    for individual i ∈ M do
        x_i ← N(x_i, γ)
    end for
end while
```

specialise into a single task (*strong specialisation*), which is driven by social interactions.

We also find that different environmental conditions (characterised by b and

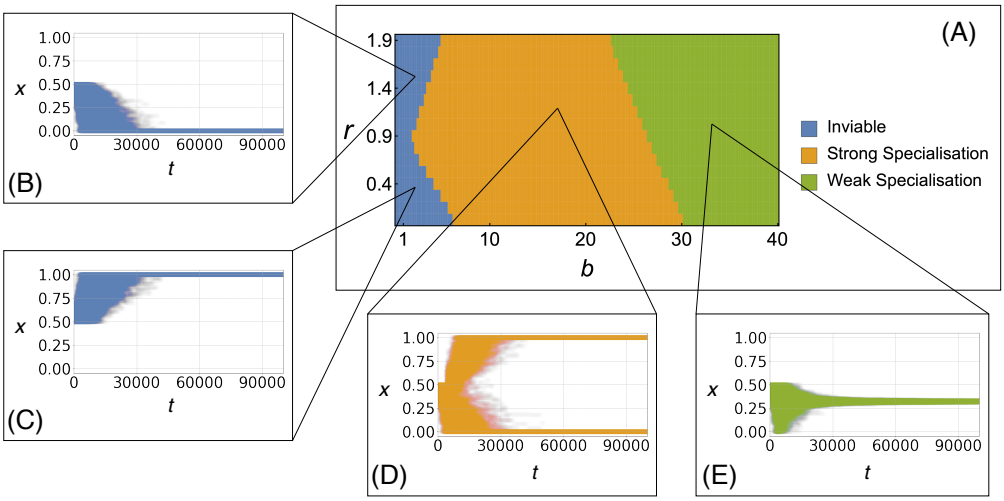


Fig 2. Behavioural patterns for individual learning. (A): The region diagram describes the long-term outcomes of task allocation for the model with individual learning over a range of values for parameters b and r. The inset figures **(B)**, **(C)**, **(D)** and **(E)** show three typical cases of how individual strategies (x) in a colony develop over time (t). A colony is inviable (**(B)** and **(C)**) if the average payoff of individuals is not positive, which means that they fail to coordinate and only respond to a single task. Strong specialisation **(D)** means that the workforce of a colony splits into two different groups each of which focuses exclusively on a single task. Weak specialisation **(E)** means that each individual invests her effort on both tasks. Section D2, S1 Appendix describes the procedure we follow to classify these results from our simulations.

r) can cause variation of task allocation patterns, even in the absence of variation in the underlying individual-based mechanisms. As shown in Fig 2 and Fig 3, strong specialisation tends to emerge in environments with scarce or poor food resources (when b is small). As the quality of food resources in the environment improves (b increases), individuals are less likely to strongly specialise. Individuals may still prefer one task over the other ($x_i \neq \frac{1}{2}$) to balance global demands, but their strategies tend to be consistent across the colony (*weak specialisation*).

From the perspective of abstract modelling, the dynamics of our task-allocation games is similar to the evolution of continuous Snowdrift games [12] and can be analysed based on the framework of adaptive dynamics [19]. A full analytical treatment that confirms our simulation results for individual learning and social learning is given in Section C2, S1 Appendix. The behavioural patterns based on this analysis are illustrated in Fig 4, which are similar to those in Fig2(A)

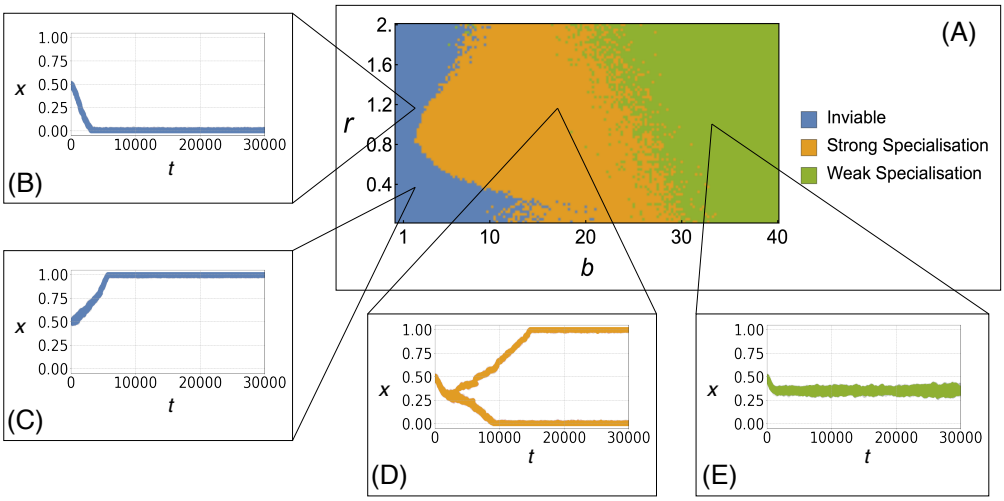


Fig 3. Behavioural patterns for social learning. (A): The region diagram gives the long-term patterns of task allocation of colonies based on the model with social learning in a range of values for parameters b and r. The inset figures **(B)**, **(C)**, **(D)** and **(E)** show three typical cases of how individual strategies (x) in a colony develop over time (t). A colony can be either inviable (**(B)** and **(C)**), strongly specialised **(D)** or weakly specialised **(E)**. Being inviable means that the average payoff of individuals in a colony is not positive and the overall task allocation is out of balance as individuals only respond to a single task. Strong specialisation means that the workforce of a colony splits in two groups each of which specialise in a single task. Weak specialisation means that each individual spends her energy on both tasks. Section D1, S1 Appendix describes the procedure we use to classify the above results from the simulations.

and Fig3(A).

Efficiency analysis

Game-theoretical models provide us a unique opportunity to analyse the efficiency of behaviours. The basis of individuals' decision-making is their payoffs, which can be regarded as their perceived rewards and penalties. Colony optimality is not a driver of the emerging behavioural dynamics. However, we can compare the actual group-level efficiency with what can theoretically be achieved assuming optimal workforce allocation. Here we use the notion of *relative colony performance*, which is the ratio between the average payoff achieved by individuals in a colony and the optimal level that could be achieved (see Section E, S1 Appendix for details).

We find that relative colony performance, even for a fixed mode of learning,

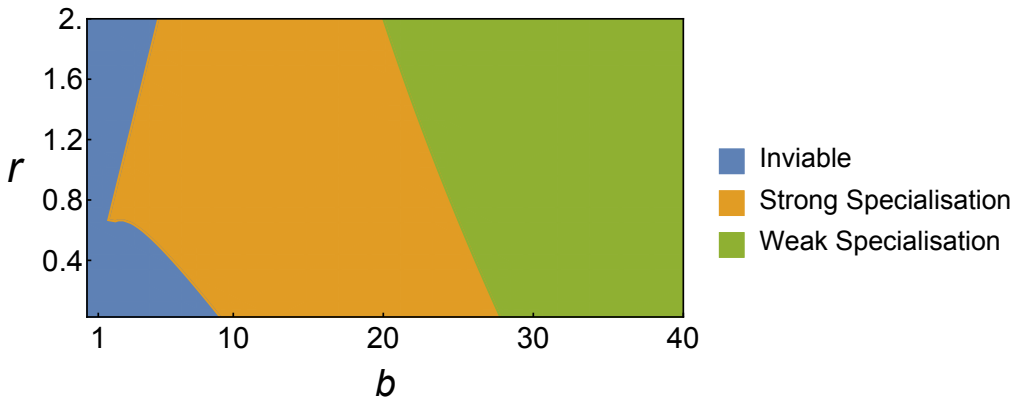


Fig 4. Behavioural patterns predicted by adaptive dynamics. The above diagram describes the patterns of task allocation of colonies based on the mathematical framework of adaptive dynamics in a range of values for parameters b and r (given $n = 10$).

can depend on environmental conditions. In particular, different environmental conditions can result in different specialisation patterns, which in turn leads to different levels of relative colony performance. For both individual learning and social learning (illustrated in Fig 5), colonies with weak specialisation achieve greater efficiency than those with strong specialisation, and their performance tends to be at a high level regardless of environmental conditions.

In addition, learning mechanisms (individual or social) appear to have an effect on colony efficiency. When strong specialisation arises, the relative performance of colonies based on social learning is influenced strongly by r. It tends to degrade when r deviates from 1 (see Fig 5). For individual learning, on the other hand, strong specialisation results in more consistent and overall greater relative colony performance than that for social learning (see Fig 5).

The varying colony efficiency in our results can be linked to the difference between the mean of individual strategies and the Nash equilibrium (see Section C1, S1 Appendix for details). When b is small, strong specialisation tends to emerge in the dynamics based on both individual learning and social learning. In this situation, individuals have the opportunity to only invest their effort into the less-costly task, while still receiving the same shared benefit. This leads to a deviation of individual strategies from the Nash equilibrium and thus lower performance at the colony level, especially in the case of social learning. When b is at a high level, colonies based on either individual learning or social learning tend to show weak specialisation, in which each individual distributes its efforts between both tasks and the average of individual strategies is close to the Nash

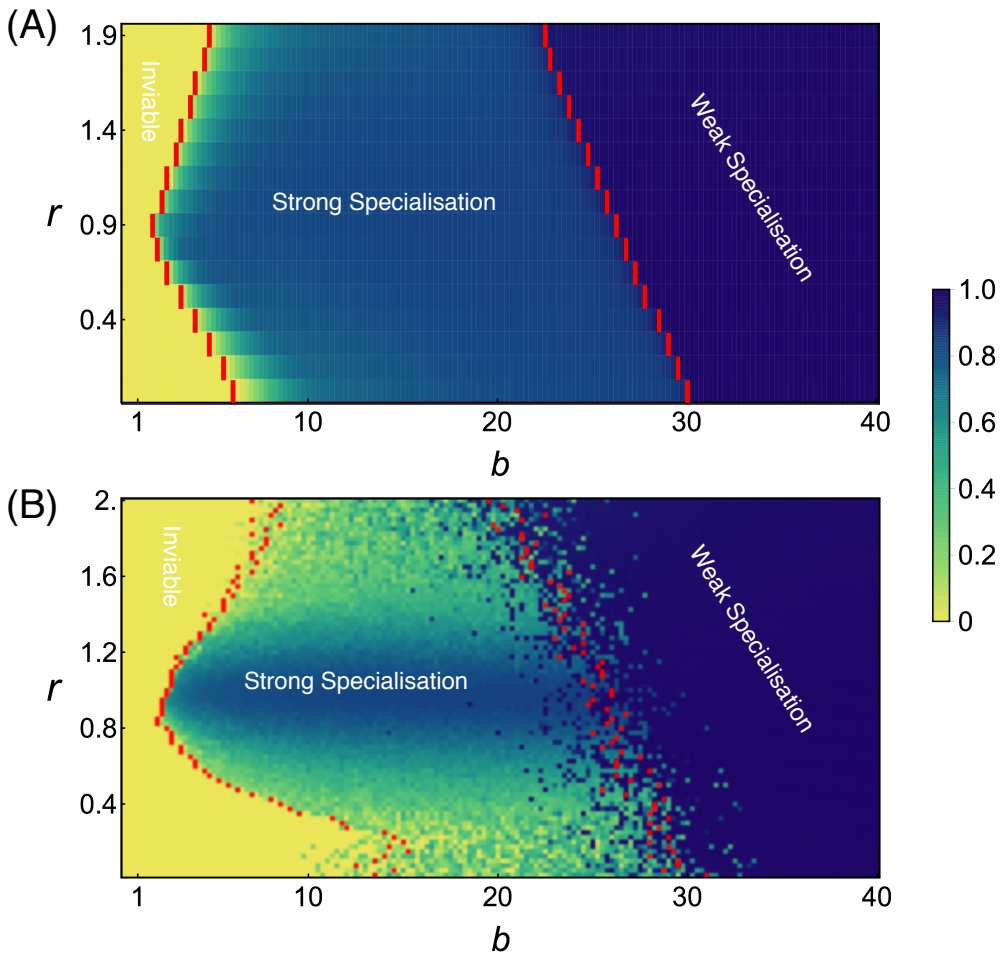


Fig 5. Efficiency achievements for individual learning and social learning. (A): individual learning; **(B)**: social learning. For a particular pair of b and r, the efficiency is quantified as the ratio between the mean of individual payoffs at a long term and the optimal level that can be theoretically achieved under the environmental condition (for details, see Section E, S1 Appendix). We assume that the efficiency range from 0 to 1, followed by the colour scheme in the above figures. For simplicity, we regard the efficiency of inviable colonies as 0. The red lines indicate the boundary between different behavioural patterns based on our simulations (see Fig 2 and Fig 3).

equilibrium. This reduces potential selfishness in task selection and leads to better colony performance.

Dynamic environments

We find that different learning mechanisms can lead to varying behavioural patterns under environmental fluctuations. Our results suggest that individuals in the colonies based on individual learning tend to flexibly adjust their strategies according to the current environmental conditions. As seen in Fig 6, the colony based on individual learning changes from weak specialisation to strong specialisation when foraging becomes less profitable (b decreases), and switches to weak specialisation after the environmental condition is back to the original state. This allows the colony to be near optimal efficiency in spite of the environmental fluctuations.

Surprisingly, for social learning, our results suggest that the colony-level patterns of task allocation do not only depend on the current condition of the environment, but also on the history of these conditions. As illustrated in Fig 6, when b decreases, the colony based on social learning changes from weak specialisation to strong specialisation. However, when the environmental conditions return to the original state, the pattern of task allocation at the colony level does not revert to the original pattern of organisation, and the colony cannot regain its original performance. In other words, suboptimal outcomes arise.

This finding provides evidence that the specifics of learning can have a strong long-lasting effect on the colony performance when the environment fluctuates.

Discussion

We introduce a new modelling framework for task allocation in social insects, based on evolutionary game theory, and use this framework to analyse different behavioural patterns in terms of specialisation. This is motivated by the fact that conventional frameworks do not sufficiently address two aspects that are recognised as crucial to the investigation of task allocation: the role of environmental conditions and the role of social interaction [24]. Specifically, we ask two questions: (1) what are the factors that can determine whether specialisation arises and (2) how do different behavioural patterns relate to the overall colony efficiency.

Two most commonly used types of models in task allocation, response-threshold models [3, 39] and foraging-for-work models [59, 58], share the characteristics that groups of independent individuals are described as acting in parallel. Interaction between these individuals only takes place indirectly through modification of the environment (stigmergy). There is no genuine place for social

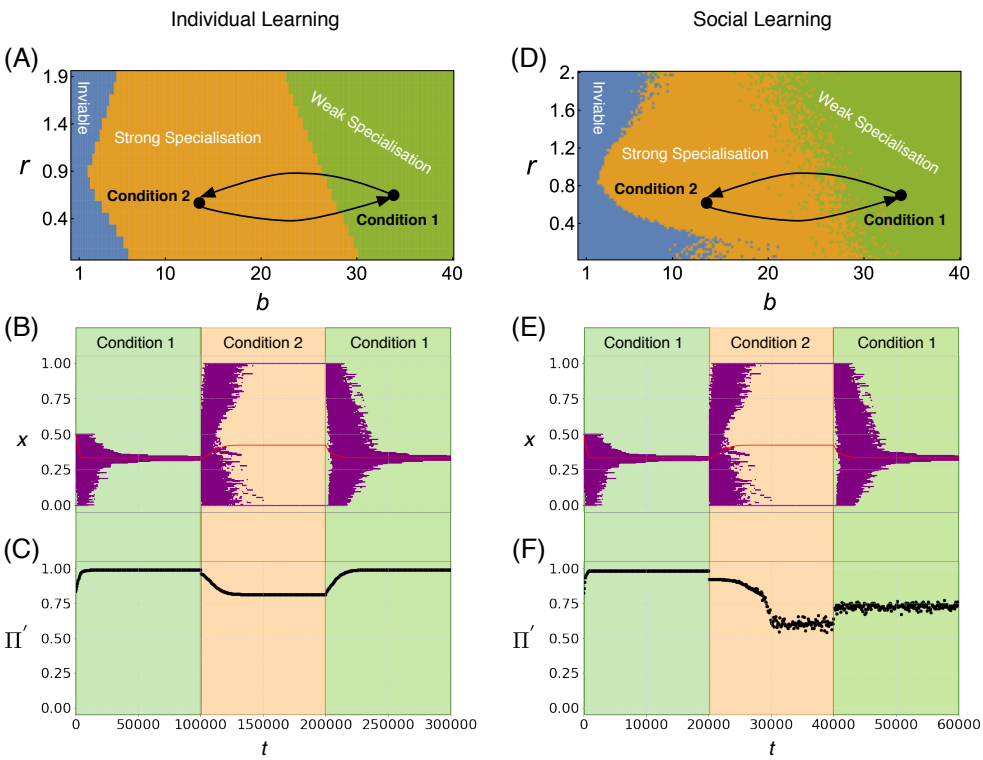


Fig 6. Examples of the models with individual learning and social learning in dynamic environments. For individual learning, the above figures (left column) show **(B)**: the dynamics of individual strategies (x) with the mean (middle red line) and **(C)**: the efficiency (Π') in a colony over time (t) under environmental fluctuations. The environment is set as three stages: (1) Condition 1 ($b = 40$) for $t \in [0, 100000]$; (2) Condition 2 (b is switched to 10) from $t = 100000$ to $t = 200000$; (3) Condition 1 (b is switched back to 40) until the end of simulation ($N = 2000$, $t_{end} = 300000$, $n = 10$, $r = 0.7$, $\beta = 0.001$, $\gamma = 0.1$). Similarly, for social learning, the above figures (right column) give **(E)**: the dynamics of individual strategies with the mean and **(F)**: the efficiency under environmental fluctuations. The environment is also set as three stages: (1) Condition 1 ($b = 40$) for $t \in [0, 20000]$; (2) Condition 2 (b is switched to 10) from $t = 20000$ to $t = 40000$; (3) Condition 1 (b is switched back to 40) until the end of simulation ($N = 2000$, $t_{end} = 60000$, $n = 10$, $r = 0.7$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$). Here **(A)** and **(D)** correspond to the region diagrams in Fig 2 and Fig 3 respectively.

interactions in these models. In contrast, our EGT-based approach integrates social interaction explicitly as a fundamental component.

Furthermore, the EGT framework allows us to easily exchange the underlying mechanisms of learning and compare the effects of such changes. We have exploited this capability to compare the dynamics of social learning with that of

individual learning. It is known that experience-based reinforcement is likely to influence workers' decision-making in task selection [39]. Our model with individual learning predicts that when the resources are less abundant, colonies tend to behave in strong specialisation with different tasks. This is congruent with previous theoretical models of reinforcement of individual experience in task allocation [57]. However, it is interesting to explore whether colony workforce may change into a different form (weak specialisation) if the environmental condition becomes less challenging.

Our analysis reveals similar outcomes in behavioural patterns of task allocation by comparing individual learning and social learning. In our simulations, both types lead to different types of specialisation depending on the environment (or, in broader terms, the ecology). The most striking aspect of this is that the ecology alone can determine which type of specialisation arises, without any changes in the underlying proximate mechanisms of task selection. One of the core interests in the study of task allocation is to investigate the primary sources of variation in workers' task preference and ultimately specialisation [24]. Most studies regard inherent inter-individual differentiation as the main cause [39]. Some studies have shown that specialisation can arise in colonies of initially identical workers either from reinforcement via individual experience [57] or from spatially localised task demands [59, 41]. Our results show an new alternative driver for specialisation, namely social interaction between individuals (see Fig 2 and Fig 3).

There is clear evidence that social learning matters in social insect colonies [20, 30]. However, little is known about the exact mechanisms of social learning in relation to task allocation, and there is a clear need for further empirical work in this regard. For our models we have assumed one of the most basic forms of social learning. Since there is insufficient knowledge about the details of the real biological mechanisms that may be at work, this provides a reasonable starting point. Importantly, the dynamics that these assumptions lead to, so-called replicator dynamics [31], is qualitatively stable for a reasonably broad range of changes in the detailed mechanisms of learning. Replicator dynamics arises in a surprisingly wide range of different learning scenarios [53, 34]. It thus provides a good basis for a hypothetical discussion in the absence of more precise knowledge.

Interpreted from an optimality perspective, our results suggest that individual learning leads to higher colony performance in a broader range of environments and, conversely, that social learning achieves high efficiency only in a

limited range of environment types. One may thus expect that social learning is selected against in environment types where it does not achieve high efficiency. However, social learning arguably provides other benefits to the colony, most importantly a mechanism to spread information through the colony in the absence of local cues. Empirical studies suggest that workers can recognise the tasks that others perform simply by chemical cues or antennal contact [21, 25]. Spatial movement is widely observed and is likely to influence task allocation in social insects [22, 9, 54, 40, 8]. It is thus conceivable that these benefits outweigh the potential price that is paid in terms of overall performance.

In environment types where both weak and strong specialisation can exist, weak specialisation can be more efficient than strong specialisation (see social learning in Fig 6). This seems to contradict the traditional assumption that strong specialisation is one of the ways how colonies achieve higher efficiency [47, 10]. Our models show strong specialisation may, in some circumstances, be an emergent byproduct of the proximate mechanisms that determine individual task selection rather than a fitness improving outcome (and thus directly selected for).

However, strong specialisation in a social learning context may convey a fitness benefit in the presence of environmental fluctuations. Weakly-specialised colonies must depend on individual-based exploration of the strategy space by a small proportion of workers to adjust to changing conditions. In contrast, strongly-specialised colonies can benefit from imitation between different specialised group to adjust the ratio of workers. In the dynamics of game theory, the process of exploring new strategies is generally assumed to occur on a much longer timescale than strategy imitation [6]. It is thus not unreasonable to expect that strongly specialised colonies may adapt faster and more flexibly to changing conditions.

Our task-allocation game is similar to a continuous Snowdrift game [12], in which the benefit is shared by all individuals at the group level, but the costs are strategy-dependent at the individual level and tend to be different across individuals. Both games can be used to explore features of cooperation and illustrate a principle called "Tragedy of the Commune" [12]. This principle describes non-uniform investment across a group that receives uniform benefit: some individuals significantly contribute to generating a common good, while some "free loaders" invest less or nothing and still reap the same benefits.

There are some factors that may influence the outcomes of the modelled process and whose influence remains to be investigated in more detail. One of these is the "interaction range" of individuals. It is well known that individuals

in a colony, due to their physical or spatial limitations, typically sample and respond to localised cues as a proxy for the global situation [21]. In our model this is reflected by letting individuals interact in smaller subgroups (the games), to which their information gathering is limited at any point of time. The size of a game then is a proxy for the scale of interaction in the colony. Game size is a factor that can influence the ultimate outcomes of the EGT models [5], and the impact of games size on our models remains to be investigated. The strength of our modelling approach is that it gives us a principled way to investigate the influence of such factors.

As a starting point we have modelled the allocation between a homeostatic task and a maximising task. While this addresses some fundamental aspects, the range of possible task types is obviously much larger. Different cost and benefit functions, associated with different task types, must be expected to have a significant influence on the outcomes of the models. Game theory research has shown that a qualitative classification of games can go a long way in determining long-term behaviour [1]. This allows us to abstract from the exact quantitative nature of these functions and to switch to a qualitative perspective. This is a powerful concept, since the exact qualitative nature of cost and benefit functions can usually not be ascertained. The hope is that switching to a qualitative view will allow us to focus the discussion on different fundamental types of tasks that are competing for attention.

In this paper, we introduce evolutionary game theory as a powerful alternative modelling framework into the study of task allocation, which gives important insights to advance this field. It has the potential to address some of the most central open questions in social insect task allocation.

Appendix A Details of the payoff function

As Task T needs to be controlled at a certain level, under or over performing Task T can reduce $B_T(X)$. We use a simple way to model

$$B_T(X) = -\frac{4}{n^2} \cdot \big(\sum_{j=1}^{n} x_j\big)^2 + \frac{4}{n} \cdot \sum_{j=1}^{n} x_j.$$

Here $B_T(X)$ is assumed to achieve the maximum value, which is normalised between 0 and 1, when half of the workforce in the game is engaged in Task T and to be 0 when none or all of workers in the game are engaged. As Task F is a maximising task, which implies, for example, the more food is collected, the more brood can survive, $B_F(X)$ is simply assumed to be linear

$$B_F(X) = b \cdot \sum_{j=1}^{n} (1 - x_j)$$

where b is coefficient ratio between the benefit of Task F and the cost of Task F.

We assume the cost of a homeostatic task to be linear in individual effort and thus define

$$C_T(x_i) = r \cdot x_i$$

where r is coefficient ratio of the costs between Task T and Task F. We assume that $C_F(x_i)$ is marginally decreasing with the effort in Task F, indicating the scenarios in which foragers initially need to spend more effort exploring their neighbourhood and once they become familiar with the surrounding areas of food resources, the cost for them tend to be less than the initial stage. As a result, we simply assume

$$C_F(x_i) = -(1 - x_i)^2 + 2(1 - x_i).$$

Here the cost of Task F for a worker who engage fully in Task F per time-period is assumed to be 1 unit.

Appendix B Theoretical analysis

B.1 Analysis of the Nash equilibrium

We give a mathematical analysis of our task-allocation game for a symmetric Nash equilibrium [62]. In a game of size n, with $n-1$ type-I individuals of their mean strategy x and 1 type-II individual of strategy y ($x, y \in [0,1]$), the strategy of the type-II individual converges to x^* where $x^* \in [0,1]$ is the solution of

$$\begin{aligned}\left.\frac{\partial \Pi\Big(y,(n-1)x\Big)}{\partial y}\right|_{y=x} &= \left.\frac{\partial\Big(\frac{1}{n}\,B_T(y+(n-1)x)\cdot B_F(y+(n-1)x)-C_T(y)-C_F(y)\Big)}{\partial y}\right|_{y=x}\\ &= \frac{1}{n}\,B_T^{'}(n\,x)\cdot B_F(n\,x)+\frac{1}{n}\,B_T(n\,x)\cdot B_F^{'}(n\,x)\\ &\quad - C_T^{'}(x)-C_F^{'}(x)=0.\end{aligned}$$

Fig 7 illustrates how close the mean of individual strategies in colonies based on individual learning and social learning is to the Nash equilibrium for a range of b and r.

B.2 Analysis based on adaptive dynamics

Here we give a mathematical analysis based on the work by [12]. In a game of size n, with $n-1$ type-I workers of strategy x and 1 type-II worker of strategy y ($x, y \in [0,1]$), the growth rate of the type-II worker is

$$f_x(y) = \Pi\Big(y,(n-1)x\Big) - \Pi\Big(x,(n-1)x\Big)$$

where

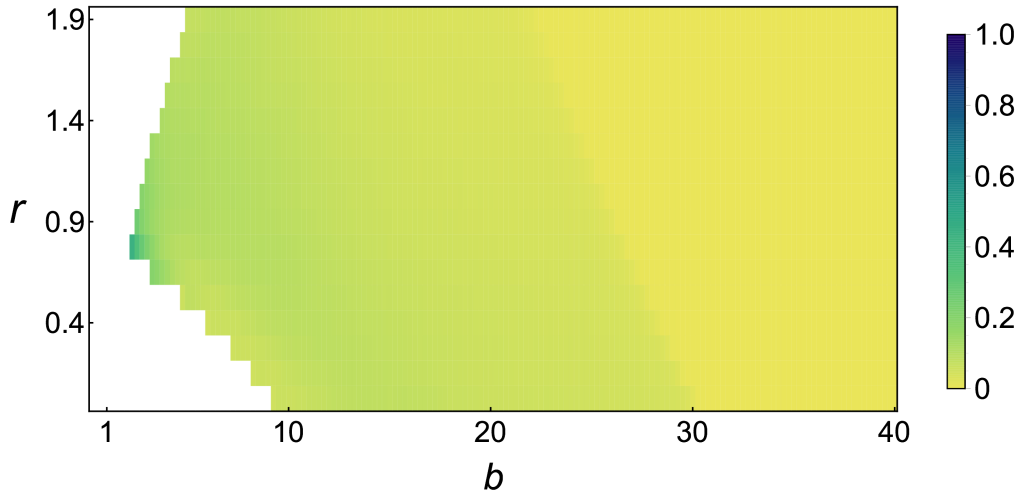
$$\Pi\Big(y,(n-1)x\Big) = \frac{1}{n}\,B_T(y+(n-1)x)\cdot B_F(y+(n-1)x)-C_T(y)-C_F(y)$$

and

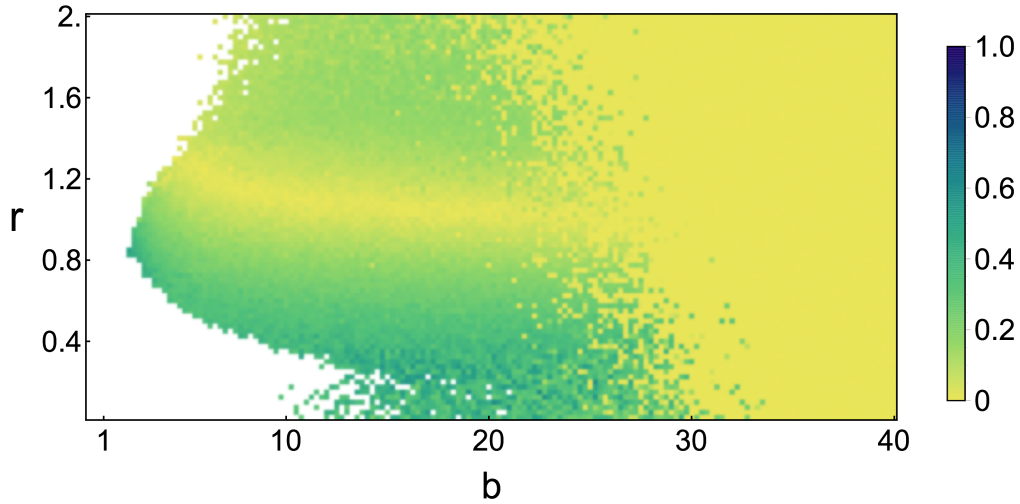
$$\Pi\Big(x,(n-1)x\Big) = \frac{1}{n}\,B_T(n\,x)\cdot B_F(n\,x)-C_T(x)-C_F(x).$$

Thus, the replication gradient is

$$\begin{aligned}D(x) &= \left.\frac{\partial f_x(y)}{\partial y}\right|_{y=x}\\ &= \frac{1}{n}\,B_T^{'}(n\,x)\cdot B_F(n\,x)+\frac{1}{n}\,B_T(n\,x)\cdot B_F^{'}(n\,x)-C_T^{'}(x)-C_F^{'}(x)\end{aligned}$$



(a) Individual learning



(b) Social learning

Fig 7. The absolute difference between the mean of individual strategies in a colony and the Nash equilibrium ($n = 10$). This analysis only applies to the cases when the colony is not inviable.

Then the singular strategies are given as solutions of

$$D(x^*) = \frac{1}{n} B_T^{'}(n\,x^*) \cdot B_F(n\,x^*) + \frac{1}{n} B_T(n\,x^*) \cdot B_F^{'}(n\,x^*) - C_T^{'}(x^*) - C_F^{'}(x^*) = 0$$

Both strong specialisation and weak specialisation require the condition that there exists such $x^* \in [0,1]$ that x^* is convergency stable

$$\begin{aligned}\left.\frac{dD(x)}{dx}\right|_{x=x^*} &= B_T^{''}(n\,x^*) \cdot B_F(n\,x^*) + 2\,B_T^{'}(n\,x^*) \cdot B_F^{'}(n\,x^*) + B_T(n\,x^*) \cdot B_F^{''}(n\,x^*) \\ &\quad - C_T^{''}(x^*) - C_F^{''}(x^*) < 0.\end{aligned}$$

In addition to the above condition, strong specialisation emerges if

$$\begin{aligned}\left.\frac{\partial^2 f_{x^*}(y)}{\partial y^2}\right|_{y=x^*} &= \frac{1}{n} B_T^{''}(n\,x^*) \cdot B_F(n\,x^*) + \frac{2}{n} B_T^{'}(n\,x^*) \cdot B_F^{'}(n\,x^*) + \frac{1}{n} B_T(n\,x^*) \cdot B_F^{''}(n\,x^*) \\ &\quad - C_T^{''}(x^*) - C_F^{''}(x^*) > 0\end{aligned}$$

and weak specialisation requires

$$\begin{aligned}\left.\frac{\partial^2 f_{x^*}(y)}{\partial y^2}\right|_{y=x^*} &= \frac{1}{n} B_T^{''}(n\,x^*) \cdot B_F(n\,x^*) + \frac{2}{n} B_T^{'}(n\,x^*) \cdot B_F^{'}(n\,x^*) + \frac{1}{n} B_T(n\,x^*) \cdot B_F^{''}(n\,x^*) \\ &\quad - C_T^{''}(x^*) - C_F^{''}(x^*) < 0.\end{aligned}$$

In other cases such as when x^* is convergency unstable, colonies tend to become inviable based on our payoff function, as one task out of the two is abandoned.

Appendix C Classification of simulation results

For the models with individual learning and social learning, the colonies with the non-positive mean of workers' payoffs are classified under being inviable (for details of the mean of individual payoffs, see Fig 8 and Fig 11). The other colonies are tentatively regarded under strong specialisation if the standard deviation of workers' strategies exceeds a certain level (set as 0.1) or weak specialisation otherwise (for details of the standard deviation of individual strategies, see Fig 9 and Fig 12).

However, a large standard deviation of individual strategies cannot guarantee strong specialisation, as a colony with a wide span of strategies may belong to weak specialisation and correspond to a large standard deviation as well. To capture the span of individual strategies, we verify the above temporary region

classification by the Shannon entropy (for details, see Fig 10 and Fig 13). For both models, the entropies of individual strategies in colonies with large standard deviation are smaller than those with small standard deviation, which in turn confirms our temporary region classifications. In order to highlight the variation under different environmental conditions, each of the three figures have a unique colour scheme for both individual learning and social learning.

C.1 Individual learning simulation

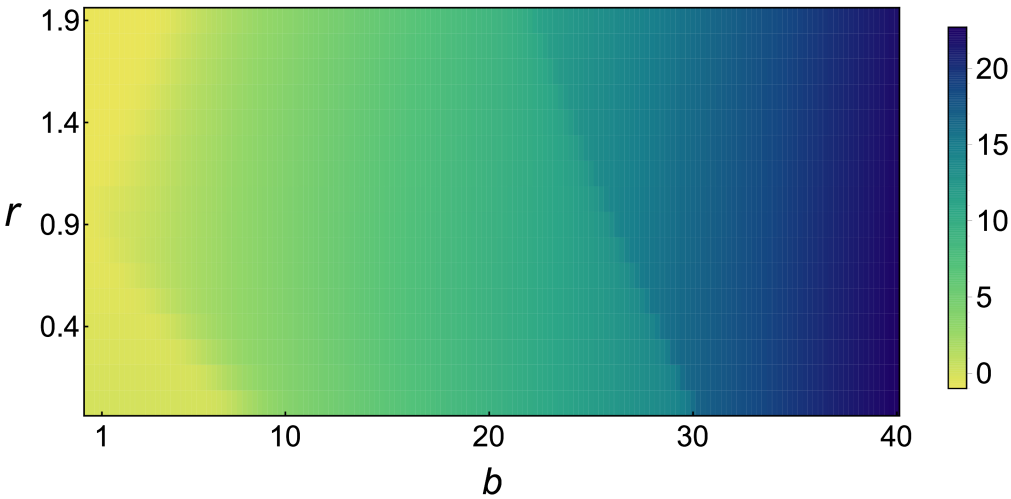


Fig 8. Mean payoff of the model with individual learning ($N = 2000$, $t_{end} = 100000$, $n = 10$, $\beta = 0.001$, $\gamma = 0.1$).

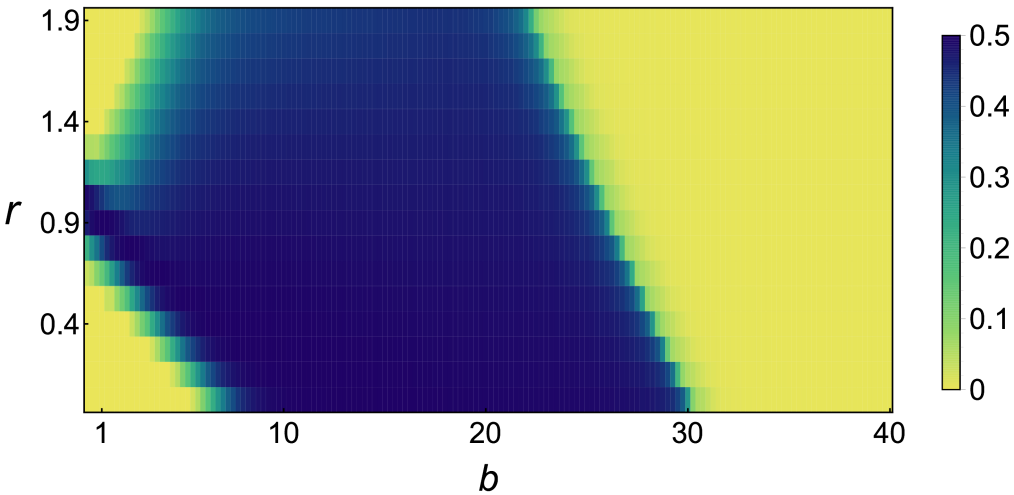


Fig 9. Standard deviation of the model with individual learning ($N = 2000$, $t_{end} = 100000$, $n = 10$, $\beta = 0.001$, $\gamma = 0.1$).

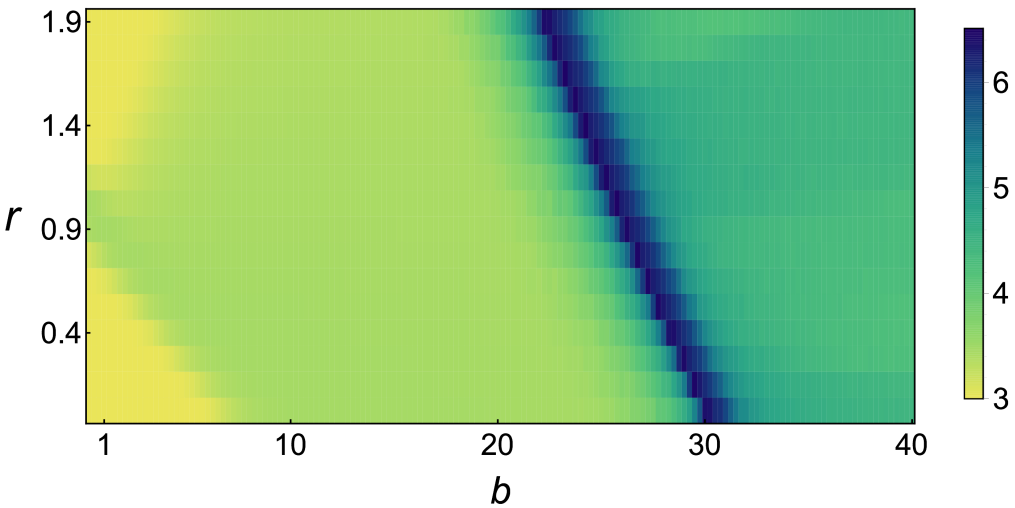


Fig 10. Shannon entropy of the model with individual learning ($N = 2000$, $t_{end} = 100000$, $n = 10$, $\beta = 0.001$, $\gamma = 0.1$).

C.2 Social learning simulation

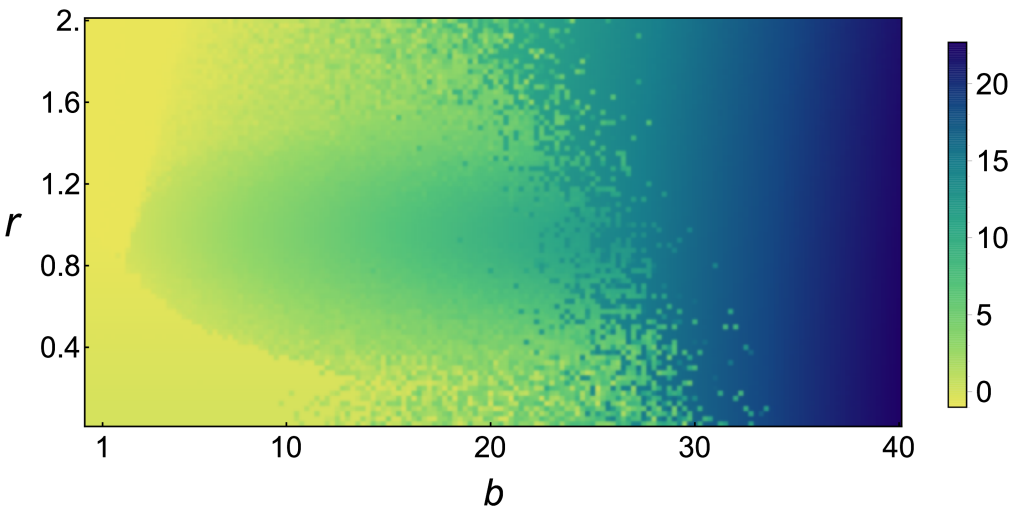


Fig 11. Mean payoff of the model with social learning ($N = 2000$, $t_{end} = 30000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$).

Appendix D Optimal payoff for efficiency analysis

To evaluate the efficiency achieved by our models, we need to know the optimal level associated with different environmental conditions (illustrated in Fig 14). Particularly, for each pair of b and r, we optimise the mean of individual payoffs with potentially different strategies in a game of size n using Differential

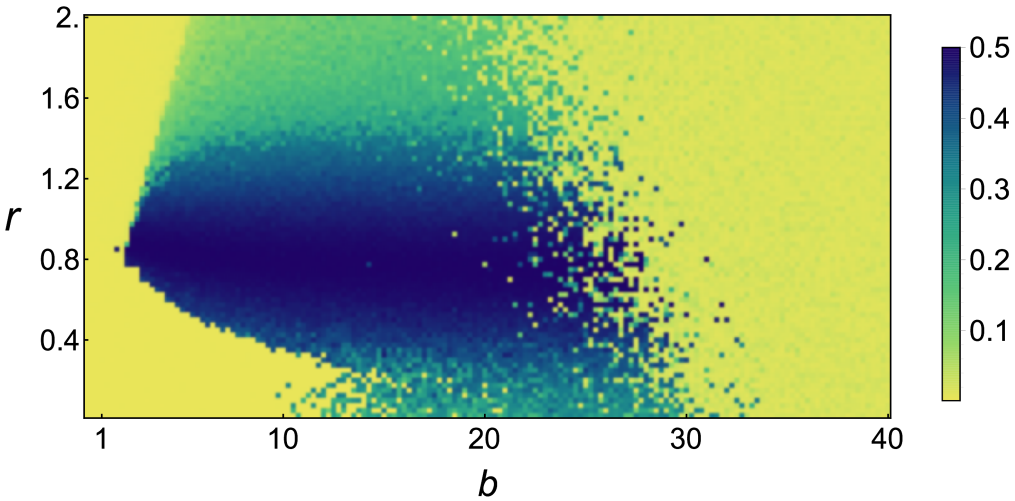


Fig 12. Standard deviation of the model with social learning ($N = 2000$, $t_{end} = 30000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$).

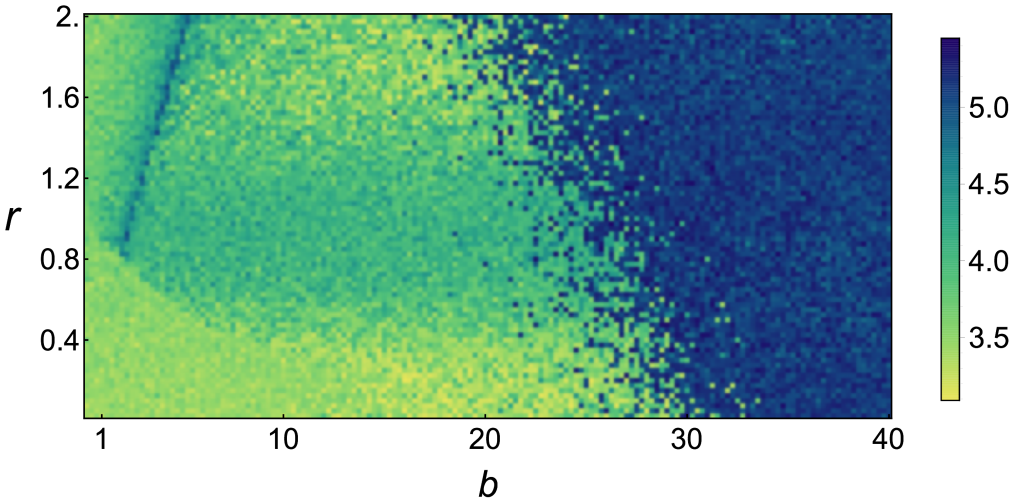


Fig 13. Shannon entropy of the model with social learning ($N = 2000$, $t_{end} = 30000$, $n = 10$, $\alpha = 2.5$, $\beta = 0.01$, $\gamma = 0.005$).

Evolution [56], a stochastic population-based heuristic method for global optimisation (implemented by *differential_evolution* in the package *optimize* of Scipy, Version 0.19.0).

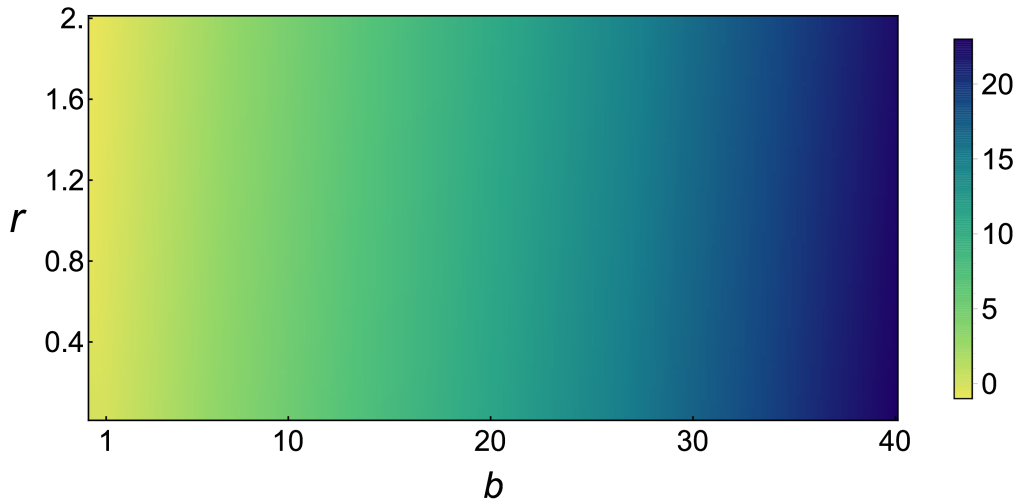


Fig 14. Optimal individual payoff. This diagram gives the optimal payoff that an individual can achieve in a game ($n = 10$) under in a range of values for parameters b and r.

Appendix

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