

Thermodynamic selection: The role of entropy waste elimination in evolution

Enno Wein,¹ Arik Avagyan^{2,*} and David B. Saakian^{2,3,†}

¹*Instigate Academy, Tsarav Aghbyur 134/1, Yerevan 0052, Armenia*

²*A.I. Alikhanyan National Science Laboratory (Yerevan Physics Institute) Foundation, 2 Alikhanian Brothers St., Yerevan 375036, Armenia*

³*Marchuk Institute of Numerical Mathematics of the Russian Academy of Sciences, Moscow 119991, Russia*



(Received 23 February 2025; accepted 11 September 2025; published 3 November 2025)

Evolution is often viewed as a competition among agents for resources, effectively the harnessing of negative entropy or free energy in nonequilibrium states. In this work, we examine how constraints on entropic waste elimination shape evolutionary outcomes and affect the choices made by competing agents. We build on the Babajanyan–Koonin–Allahverdyan model that represents agents as heat engines in a game-theoretic setting. We introduce a constraint on the system’s total cooling rate, arising from its interaction with a low-temperature heat bath that represents the system’s elimination of entropic waste. We show that imposing such a constraint modifies the Nash equilibrium solutions of the game. We identify scenarios where the cap on the combined waste-removal drives the agents toward different optimal strategies than in the unconstrained case.

DOI: [10.1103/vzwb-1fp3](https://doi.org/10.1103/vzwb-1fp3)

I. INTRODUCTION

In his famous book [1], Schrödinger underlines one of the key properties of life, delayed entropy growth. The living system exists in a nonequilibrium state [2,3], interacting with its environment to maintain a low-entropy state temporarily during its lifetime, as the increase in entropy can be delayed but not entirely prevented. The delay in entropy growth is a result of the living system’s resource consumption, which serves as the source of negative entropy, as proposed by Brillouin [4]. From this perspective, the “survival of the fittest” by Darwin can be understood as competition for neg-entropy or free energy, where the source of free energy is food. Darwin predominantly refers to species competing with other species, rather than individuals competing with other individuals; however, his statement is often interpreted as applicable to individuals as well, particularly within societies [5]. Food is typically a scarce resource, giving rise to competition between individuals. But what about the positive entropy/“entropic waste” that living beings must dispose of according to the second law of thermodynamics? Can there be competition over something so abundant? Is the elimination of entropic waste simply irrelevant for evolution, or is it a challenge that plays a role in shaping evolutionary outcomes?

In this paper, we argue that the competition for the disposal of entropic waste is a significant evolutionary factor. To explore this perspective, we modify a recent evolutionary model that represents competing agents as heat engines [6]. The

central premise of that study is that since organisms consume energy and convert it to useful work in their metabolism, they should obey the principles of nonequilibrium thermodynamics and, thus, can be modeled as heat engines. The environment consists of two thermal baths at different temperatures. The engines extract energy from the hot bath (i.e., the pool of resources) and convert it to work, releasing entropic waste into the cold bath in the process. In case of nondepletable resources (the temperatures of the baths remain constant), the engines attempt to maximize their work by tuning their efficiency. The competition between the engines arises due to a constraint on the combined flow of energy from the hot bath. No constraint is assumed on the combined flow of entropic waste into the cold bath. This premise aligns with the perspective that applies nonequilibrium thermodynamics to investigate diverse phenomena in evolutionary biology [7–19].

In this work, we extend the model introduced in [6] by incorporating a constraint on the total rate at which entropic waste is disposed of. This modification introduces competition not only for access to the shared hot bath, but also for access to the cold bath. To avoid misunderstanding the contribution of this work, it is important to clarify the limits of descriptive applicability of the model. This model is a highly idealized, minimal representation of evolutionary competition under thermodynamic constraints. We view this model as a step toward a thermodynamic framework that captures the phenomenology of cellular competition and co-operation by describing energy-consuming subsystems and their roles in driving intercellular interactions. Many of these subsystems act as microscopic heat engines, converting free energy into work while releasing entropy primarily as heat. Examples include the mitochondrial electron transport chain, ATP-powered molecular motors and ion pumps, protein synthesis, and catabolic pathways like glycolysis [20–24]. These processes dissipate energy and produce waste, analogous to heat expelled by a heat engine. Moreover, the “hot” and “cold” baths in the model need not be physical temperatures but

*Contact author: arav2492@colorado.edu

†Contact author: saakian@yerphi.am

Published by the American Physical Society under the terms of the Creative Commons Attribution 4.0 International license. Further distribution of this work must maintain attribution to the author(s) and the published article’s title, journal citation, and DOI.

can represent reservoirs of differing chemical potential [6,25]. Waste products effectively act as a low-temperature reservoir, making this framework suitable to describe energy use at the cellular level.

The model may also serve as an analogical description of competition between organisms in an ecological context. In this interpretation, competition for access to the cold bath should not be taken to imply that the cold bath functions as a consumable resource. Accordingly, the model does not apply to scenarios where waste products serve as resources for other organisms [26,27]. Second, the model does not include any form of cooperation. Unlike mutualistic or symbiotic systems in which one species aids another in eliminating waste [28,29], our setting involves purely competitive dynamics. Third, our model does not describe ecological systems where the accumulation of waste can alter the environment in significant ways, which can be exploited by some organisms to eliminate competitors that cannot survive in the altered environment. An example of such weaponization of waste is the excretion of pyrogenic litter by fire-promoting plants such as eucalypts and pines, which benefit when fire kills off competitors [30]. In contrast, our model is more appropriate for an ecological system where the environment has a maximum speed for absorbing waste, and none of the organisms benefit from a more toxic environment. Thus, the speed cap on waste removal constrains the overall growth rate of the organisms. One example of such a system is multiple ant colonies living in close proximity due to limitations of physical space. Each colony produces metabolic waste within its nesting area, and the confined nature of these nesting sites limits the diffusion and absorption of waste products, which leads to competition between the colonies [31].

The paper is organized as follows. In Sec. II, we summarize the model introduced by [6]. In Sec. III, we formulate the main features of the game between the two heat engines by introducing constraints on the combined rate of extraction of the common resource and on the combined rate of disposal of entropic waste. In this section, we also apply the Stackelberg model [32] to the game. In Sec. IV, we explore the Nash equilibrium solutions of the game under different conditions on the constraints.

II. THE HEAT ENGINE MODEL

Here we describe the model of a single engine as an agent, see [6] and [33] for more details. The schematic diagram of the engine is shown in Fig. 1. The engine operates with three states, $i = 1, 2, 3$, characterized by their respective energy levels E_i , ordered as:

$$0 = E_1 < E_2 < E_3. \quad (1)$$

The system interacts with three thermal baths at temperatures T_h , T_c , and T . Each state transition is coupled with one of these thermal baths: the transition $3 \rightarrow 1$ corresponds to the interaction with the bath at temperature T_h , $2 \rightarrow 3$ corresponds to the bath at T_c , and $1 \rightarrow 2$ corresponds to the bath at T . The temperature T is assumed to be infinite, in which case this bath plays the role of a work source. This fine point is explained in Sec. II A of [6].

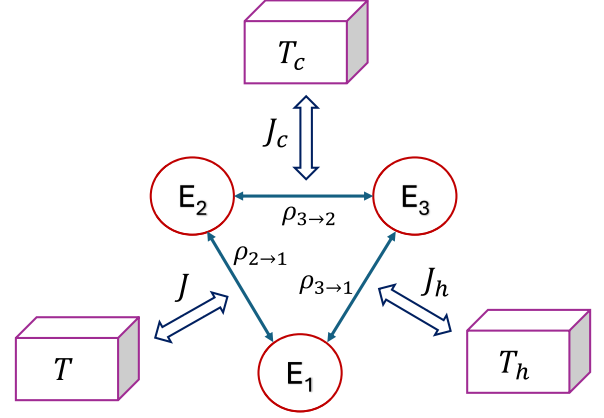


FIG. 1. A diagram of the heat engine with three energy levels E_1, E_2, E_3 interacting with three heat baths at constant temperatures. Here the suffixes h and c refer to the hot and cold baths, respectively. Thus, $T_h > T_c$, and we take $T = \infty$, which makes it play the role of a work-source. J_h and J_c denote the heat currents from the hot and cold baths, respectively, while $-J$ corresponds to the power of the engine. Each heat bath is coupled to one of the energy transitions of the engine. For example, the heat flow from the hot bath causes the transition from E_1 to E_3 .

The dynamics are assumed to be Markovian, so that the system is governed by a continuous-time Markov process:

$$\frac{dp_i}{dt} = \sum_j \rho_{j \rightarrow i} p_j - p_i \sum_j \rho_{i \rightarrow j}, \quad (2)$$

where p_i denotes the probability of being in the i 'th state, and $\rho_{i \rightarrow j}$ denotes the rate of the transition from state i to state j . Further, the characteristic equilibration times are assumed to be much faster than the contact times with each bath. Thus, the engine is considered to be in a thermal equilibrium when it is in contact with a given bath. This implies that the system obeys the detailed balance condition for all transitions. For example, for the transition between states 2 and 3, we require $\rho_{3 \rightarrow 2} e^{-E_3/T_c} = \rho_{2 \rightarrow 3} e^{-E_2/T_c}$. This condition ensures that there are no net fluxes between the states i and j when the system is coupled to the corresponding bath.

The model is studied in the stationary state. The conservation of the average energy in this state reads

$$\sum_i E_i \frac{dp_i}{dt} = J_{31} + J_{12} + J_{23} = 0. \quad (3)$$

Here J_{31}, J_{12}, J_{23} represent the energy currents (the average energy per unit time) from the baths at temperatures T_h, T, T_c , respectively. They are given by

$$J_{ij} = (E_i - E_j)(\rho_{j \rightarrow i} p_j - \rho_{i \rightarrow j} p_i). \quad (4)$$

Hereafter, we denote J_{31}, J_{12}, J_{23} by J_h, J, J_c , respectively. To relate this to the central idea of the paper, J_h represents the rate at which the free energy resource is extracted, $-J_c$ represents the rate of waste energy elimination, and $-J$ corresponds to the engine's power output (average work per unit time). The minus signs arise due to the definition of the J_{ij} as representing the flows into the engine. It can be seen that in order for

the system to function as a heat engine, it is necessary that

$$J < 0, J_h > 0, J_c < 0. \quad (5)$$

Then, the efficiency of the engine is defined as the ratio of the extracted power to the current supplied by the hot bath:

$$\eta = \frac{-J}{J_h} = \frac{E_2}{E_3} \leq 1 - \frac{\beta_h}{\beta_c}. \quad (6)$$

In the stationary state, the left-hand sides of Eq. (2) are zero, which allows to solve for the p_i in terms of the $\rho_{i \rightarrow j}$, and substitute those expressions into Eq. (3) to obtain the J_{ij} as expressions of the E_i and the $\rho_{i \rightarrow j}$. In the high temperature limit, $E_i/T_c \ll 1$ and $E_i/T_h \ll 1$ for all i , it is possible to obtain simpler expressions for the currents that do not depend on the specifics of transition rates. In particular,

$$\begin{aligned} -J &= \beta_c \rho E_3^2 \eta (1 - \theta - \eta), \\ J_h &= -\frac{E_3}{E_2} J, \quad J_c = \frac{E_3 - E_2}{E_2} J \end{aligned} \quad (7)$$

where we introduced the parameter $\theta = \frac{\beta_h}{\beta_c}$, and $\rho = 1/Z(\rho_{1 \rightarrow 2} \rho_{3 \rightarrow 1} \rho_{2 \rightarrow 3})|_{\beta_c, \beta_h \rightarrow 0}$. From Eq. (6), the system achieves maximum efficiency when $E_2 = E_3$, resulting in $\theta = 0$. Substituting these values into the expression for J , we find that the power output drops to zero, in agreement with the standard theory of heat engines.

We find it convenient to redefine E_2 and E_3 as $E_2 \leftarrow E_2 \sqrt{\beta_c \rho}$ and $E_3 \leftarrow E_3 \sqrt{\beta_c \rho}$, respectively. Then, the power output becomes $J = -E_3^2 \eta (1 - \theta - \eta)$, and the expressions for J_h and J_c in Eq. (7) retain their form.

III. FORMULATION OF THE GAME

Here, we formulate a game involving two heat engines as agents. The heat engines interact with the same thermal baths in the high temperature limit and attempt to maximize their work. An additional index is added to the relevant parameters to differentiate between the engines. For example, the current from the hot bath to engine 1 is denoted by $J_{h,1}$, or the highest energy state of engine 2 is denoted by $E_{3,2}$. An effective parameter $\epsilon = \frac{(E_{3,2})^2}{(E_{3,1})^2}$ is introduced to encapsulate the differences between the engines. We assume Eq. (4) is satisfied for the individual currents of both engines.

For a given game, the highest energy states ($E_{3,k}$) of the engines are fixed, and not necessarily equal. Engine k can control its efficiency η_k by effectively tuning its intermediate energy state $E_{2,k}$, according to Eq. (5). The game includes two constraints, one on the combined current from the hot bath, and one on the combined current to the cold bath. Our analysis also includes scenarios in which one of the constraints is removed, effectively corresponding to the limit where the combined current is allowed to become arbitrarily large.

A. Constraint on the free energy current

The combined current from the hot bath obeys the constraint

$$J_{h,1} + J_{h,2} \leq A. \quad (8)$$

Here

$$J_{h,k} = -\frac{E_{3,k}}{E_{2,k}} J_k = \frac{E_{3,k}^3}{E_{2,k}} \eta_k (1 - \eta_k - \theta), \quad (9)$$

We introduce the parameters $x_k = \frac{\eta_k}{1-\theta}$, $k = 1, 2$, to represent the actions taken by the agents in the game. Then, Eq. (8) can be written as

$$x_1 + \epsilon x_2 \geq a(1 + \epsilon), \quad (10)$$

where

$$a = 1 - \frac{A}{(1-\theta)(1+\epsilon)E_3^2}. \quad (11)$$

See [6] for a detailed derivation. To exclude trivial game-theoretic solutions, the authors of [6] impose a constraint $0.5 < a < 1$, which we also adopt when this constraint is present.

B. Constraint on the waste disposal rate

The second constraint is imposed on the combined current of waste energy: $|J_{c,1}| + |J_{c,2}| \leq B$, where

$$\begin{aligned} J_{c,k} &= \frac{(E_{3,k} - E_{2,k})}{E_{2,k}} J_k = \frac{(E_{3,k} - E_{2,k}) E_{3,k}^2}{E_{2,k}} \frac{E_{2,k}}{E_{3,k}} (1 - \eta_k - \theta) \\ &= E_{3,k}^2 (1 - \eta_k) (1 - \eta_k - \theta). \end{aligned} \quad (12)$$

The absolute values for the $J_{c,k}$ are used for convenience, in order to have $B > 0$. Substituting $\eta_k = (1 - \theta)x_k$ and $E_{3,2}^2 = \epsilon E_{3,1}^2$, we can rewrite the above as:

$$\begin{aligned} f(x_1) + \epsilon f(x_2) &\leq b, \\ f(x) &= (1 - (1 - \theta)x)(1 - x) \\ &= (1 - \theta)x^2 - (2 - \theta)x + 1, \end{aligned} \quad (13)$$

where $b = B/(E_{3,1}^2(1 - \theta))$. The extracted power by agent k is given by

$$W_k \sim x_k(1 - x_k). \quad (14)$$

We can now state the game as follows. Each agent aims to maximize their payoff W_k by selecting action x_k , subject to the constraints in Eqs. 10 and 13.

Hereafter, we refer to Eq. (10) as the first constraint, and to Eq. (13) as the second constraint.

C. Stackelberg model

Here, we analyze the choice of actions by agents 1 and 2 using a Stackelberg model. In this framework, agent 1 acts as the leader, choosing their action first, while agent 2, as the follower, optimizes their response. Note that $W_i(x_1, x_2)$ are concave functions with an absolute maximum at $x_i = 1/2$. Thus, agent 1 chooses the action $x_1 = 1/2$. Then, if both constraints are enforced, the action space of agent 2 is restricted as follows:

$$\begin{aligned} \epsilon x_2 &\geq a(1 + \epsilon) - \frac{1}{2}, \\ (1 - \theta)x_2^2 - (2 - \theta)x_2 - (b/\epsilon - \frac{1}{4\epsilon}(1 + \theta)) &\leq 0 \end{aligned} \quad (15)$$

Let us define

$$\begin{aligned} X_1 &= \frac{1}{\epsilon} \left[a(1 + \epsilon) - \frac{1}{2} \right], \\ X_2 &= \frac{(1 - \frac{\theta}{2}) - \sqrt{(1 - \frac{\theta}{2})^2 + (1 - \theta)(\frac{b}{\epsilon} - \frac{1}{4\epsilon}(1 + \theta))}}{(1 - \theta)}, \\ X_3 &= \frac{(1 - \frac{\theta}{2}) + \sqrt{(1 - \frac{\theta}{2})^2 + (1 - \theta)(\frac{b}{\epsilon} - \frac{1}{4\epsilon}(1 + \theta))}}{(1 - \theta)}. \end{aligned} \quad (16)$$

Then, we can express the constraints in Eq. (15) as

$$x_2 \geq X_1, \quad X_2 \leq x_2 \leq X_3. \quad (17)$$

We say that the outcome of the game is positive when both agents get positive payoffs, and the outcome is successful when both agents get maximum payoffs (that is, the second agent can choose $x_2 = 1/2$). If the first constraint is imposed, the outcome of the game cannot be successful. This is because $0.5 < a < 1$, which implies $\epsilon x_2 > 1/2(1 + \epsilon) - 1/2 = \epsilon/2$, so $x_2 > 1/2$. If only the second constraint is imposed, the game might have a successful outcome. It can be seen that the positive outcome is excluded if $X_1 \geq 1$, which we can rewrite as

$$a \geq (\epsilon + \frac{1}{2})/(1 + \epsilon). \quad (18)$$

For a given ϵ , we denote the right-hand side as the critical value a_c . The positive outcome is also excluded when either (1) $X_2 \geq 1$ or (2) the discriminant inside the square roots in Eq. (16) is negative. A bit of algebra shows that condition (1) in fact follows from condition (2). Thus, a positive outcome becomes possible if condition (1) is violated, namely, when $X_2 < 1$. The latter can be expressed as

$$b > \frac{1 + \theta}{4} - \epsilon. \quad (19)$$

For a given ϵ and θ we denote the right-hand side as the critical value b_1 .

We now consider when the successful outcome of the game is possible in the absence of the first constraint. It can be seen that $X_2 \leq 1/2$ is a sufficient condition. This condition is equivalent to

$$b \geq \frac{1 + \theta}{4} - \epsilon \frac{3 - \theta}{4}. \quad (20)$$

We denote the right-hand side as the critical value b_2 . Thus, if $b \geq b_2$, the successful outcome is possible. In particular, if ϵ and θ are such that $b_2 \leq 0$, then the successful outcome occurs. To illustrate the different outcome regimes of the model, we plot its phase structure — specifically, the types of outcomes across the ranges of constraints a and b for various values of the parameters ϵ and θ (Figs. 2–4). The straight lines separate the phase space into regions according to the critical values a_c, b_1, b_2 . The outcomes in each region are shown for two different scenarios: either the first constraint is applied and the second is absent, or vice versa. The left symbol indicates the outcome in the former scenario, and the right symbol indicates the outcome in the latter scenario. In each case + implies a positive outcome, – implies the exclusion of the positive outcome, and ! indicates a successful outcome. If

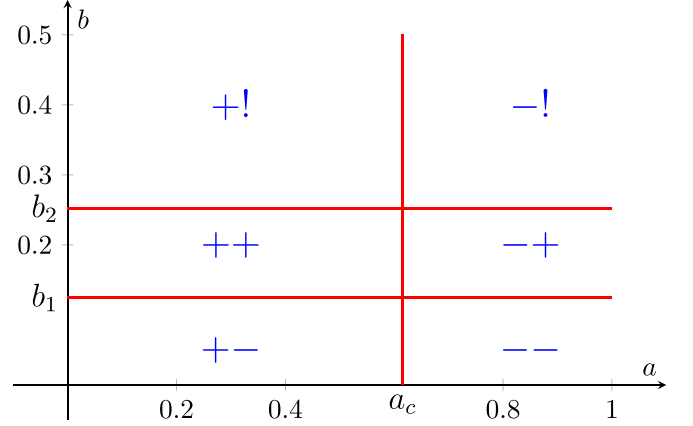


FIG. 2. The phase structure of the model for different values of a and b . Here $\theta = 0.7$ and $\epsilon = 0.3$, for which the critical values are $a_c = 8/13$, $b_1 = 0.125$ and $b_2 = 0.2525$. Each of the two symbols and their color in each region delineated by the straight lines indicate the resulting outcomes in the absence of one of the constraints. More specifically, the left symbol (+ or –) indicates the outcome in the absence of the second constraint, with + implying a positive outcome and – implying the exclusion of a positive outcome. Similarly, the right symbol (+ or – or !) indicates the outcome in the absence of the first constraint, with ! implying a successful outcome.

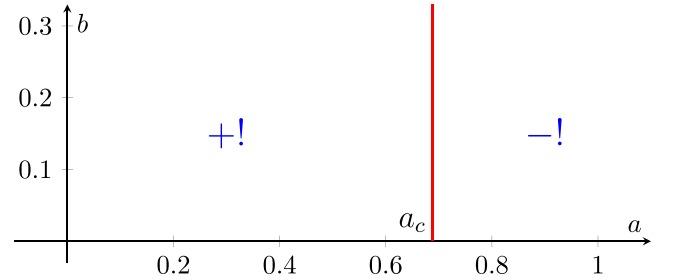


FIG. 3. The phase structure of the model for different values of a and b . Here $\theta = 0.5$ and $\epsilon = 0.6$, for which the critical values are $a_c = 0.6875$ and $b_2 = 0$. Thus, the successful outcome occurs when the first constraint is absent.

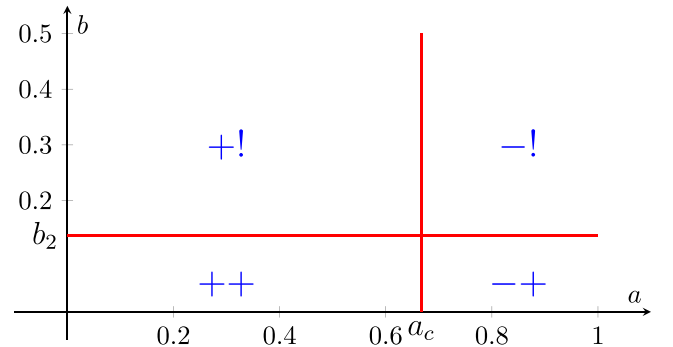


FIG. 4. The phase structure of the model for different values of a and b . Here $\theta = 0.7$ and $\epsilon = 0.5$, for which the critical values are $a_c = 2/3$, $b_1 < 0$ and $b_2 = 0.1375$.

both constraints are present, the outcome is the more exclusive of the two outcomes for the two scenarios. More specifically, if one of the symbols is $-$, the outcome is negative; if one of the symbols is $+$ and none is $-$, the outcome is positive.

How should the outcomes of the game be interpreted? Given the constraints, the first agent selects the efficiency that maximizes its work output per unit time. In doing so, it effectively chooses the largest allowable shares of the total current from the hot bath and to the cold bath that yield its most favorable efficiency. The second agent must then select its best possible strategy from the remaining portions of the current. For instance, if the constraints allow the first agent to claim the entire current from the hot bath, the second agent is left with zero input from the hot bath and is thus unable to perform any work, resulting in a negative outcome. This situation arises, for example, when the constraint on the cold bath current is absent, but the hot bath constraint satisfies $a > a_c$, as indicated by the left symbols in the right-hand regions of all figures.

IV. NASH EQUILIBRIUM POINTS

In this section, we investigate the Nash equilibrium points of the game [34–36]. The actions x_1^* and x_2^* taken by agents 1 and 2, respectively, represent a Nash equilibrium if neither agent can achieve a higher payoff by unilaterally changing their action. Namely, the following conditions are satisfied:

$$\begin{aligned} W_1(x_1^*, x_2^*) &\geq W_1(x_1, x_2^*), \\ W_2(x_1^*, x_2^*) &\geq W_2(x_1^*, x_2). \end{aligned} \quad (21)$$

Note that, since the $W_i(x_1, x_2)$ reach an absolute maximum at $x_i = 1/2$, the point $(x_1, x_2) = (1/2, 1/2)$ would be the only Nash equilibrium if it satisfied the constraints of the game. Since $a > 1/2$, it can be seen that this point violates Eq. (10). We denote the line $x_1 + \epsilon x_2 = a(1 + \epsilon)$ by L . To identify the set of Nash equilibrium points, we first analyze the solutions of the game in the absence of the second constraint. In other words, we take $b = \infty$. An extended discussion of this game can be found in [6].

A. Nash equilibria with unconstrained waste disposal rate

In the absence of constraints, the space of actions can be graphically represented as a square, with corners $(x_1, x_2) = (0, 0), (0, 1), (1, 0), (1, 1)$ (see Fig. 5). Note the four sub-squares, S_i , $i = 1, \dots, 4$, in the figure; hereafter, when referring to S_i , we mean the set of points that lie within the interior and on the boundary of S_i . The first constraint is associated with a straight line (L) positioned strictly above and to the right of S_1 (e.g., the red line in Fig. 5). The set of (x_1, x_2) values satisfying this constraint can only belong to S_2 , S_3 , or S_4 . Now, consider a point (x'_1, x'_2) within the interior of S_3 that satisfies the constraint. We argue that this point cannot be a Nash equilibrium. Since (x'_1, x'_2) lies in the interior of S_3 , agent 1 can choose a point $x''_1 > x'_1$ such that (x''_1, x'_2) is again within S_3 . Given that W_1 is independent of x_2 and is strictly increasing as a function of x_1 for $x_1 \in [0, 1/2]$, the payoff for agent 1 at (x''_1, x'_2) would be greater than at (x'_1, x'_2) . Similarly, a point located within the interior of S_2 cannot be a Nash equilibrium either, as a parallel argument applies.

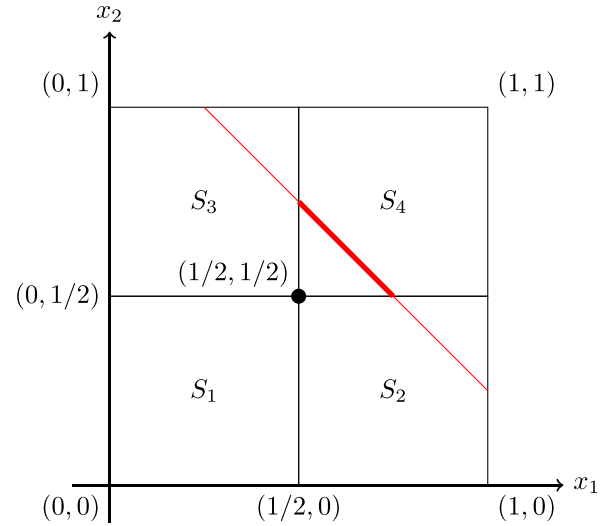


FIG. 5. The space of actions available to the agents in the game with unconstrained entropy output is the right triangle with a hypotenuse corresponding to the red line segment and with a right angle vertex at $(1, 1)$. The thick segment of the red line corresponds to the set of Nash equilibria.

Now consider a point (x'_1, x'_2) on S_4 that satisfies the strict inequality in the constraint, i.e., is not on L . If this point lies on the line $x_2 = 1/2$, then agent 1 can increase its payoff by changing its action to some $x''_1 < x'_1$ such that the new point still satisfies the constraint. Thus, such a point cannot be a Nash equilibrium. Similarly, (x'_1, x'_2) cannot be a Nash equilibrium if $x'_1 = 1/2$. If (x'_1, x'_2) lies in the interior of S_4 , agent 1 (agent 2) can unilaterally move leftward (downward) on the figure to increase its payoff. Therefore, the Nash equilibrium point(s) must lie on the segment of L within S_4 (e.g. the thick segment of the red line in Fig. 5). It can be seen that each point on this segment is a Nash equilibrium, as any unilateral move by one of the agents results in a point that no longer lies on L , and we have already demonstrated that such a point cannot be a Nash equilibrium. Thus, to find the set of Nash equilibrium points, it suffices to determine the segment of L that belongs to S_4 . The endpoints of this segment are given by $(1/2, \frac{1}{\epsilon}[a(1 + \epsilon) - 1/2])$ and $(a(1 + \epsilon) - \epsilon/2, 1/2)$.

B. Nash equilibria with constraint on waste disposal rate

We now consider the game where $b \neq \infty$. Introducing $\eta_c = 1 - \theta$ as the Carnot efficiency, the second constraint can be written as

$$\begin{aligned} \eta_c \left(x_1 - \frac{1 + \eta_c}{2\eta_c} \right)^2 + \epsilon \eta_c \left(x_2 - \frac{1 + \eta_c}{2\eta_c} \right)^2 \\ - \frac{(\eta_c - 1)^2}{4\eta_c} (1 + \epsilon) \leq b, \end{aligned} \quad (22)$$

where we have completed the square for both x_1 and x_2 . It can be seen that the set of points satisfying this constraint forms an ellipse along with its interior. We denote $h = \frac{1 + \eta_c}{2\eta_c}$. The center of the ellipse is located at $(x_1, x_2) = (h, h)$, so it lies on the line $x_2 = x_1$ in Fig. 5. Since $0 < \eta_c \leq 1$, the derivative of $\frac{1 + \eta_c}{2\eta_c}$ is negative for $\eta_c \in (0, 1]$ and diverges as $\eta_c \rightarrow 0$.

Thus $h \in [1, \infty)$, with $h = 1$ when $\eta_c = 1$. This means that the center lies along half-line $x_2 = x_1$ with its endpoint at $(1, 1)$. As the center moves further up the half-line, the size of the ellipse increases. Any action by the agents must simultaneously satisfy two conditions: (1) it must lie either on the ellipse or within its interior, and (2) it must lie either on L or to the right of it. Thus, it is nontrivial to determine the set of Nash equilibrium points for general values of η_c , ϵ , b and a .

Nevertheless, the set of Nash equilibria for different choices of the parameters η_c , ϵ , β , a can be divided into several classes that can be described graphically. Our first goal is to determine the conditions for L to intersect, be tangent to, or remain separate from the ellipse. The slope of L is equal to $\frac{dx_2}{dx_1} = -1/\epsilon$. To determine these conditions, it suffices to identify the point $(\bar{x}_1, \bar{x}_2)$ on the lower-left side of the ellipse where the tangent line has a slope of $-1/\epsilon$. If this point lies on L , then L is the tangent line of the ellipse at that point. If $\bar{x}_1 + \epsilon\bar{x}_2 > a(1 + \epsilon)$, L does not intersect the ellipse. Conversely, if $\bar{x}_1 + \epsilon\bar{x}_2 < a(1 + \epsilon)$, part of L lies within the interior of the ellipse.

Now, the slope of the tangent line at any point on the ellipse can be found by implicitly differentiating the equality case in Eq. (22):

$$\begin{aligned} & \frac{d}{dx_1} [\eta_c(x_1 - h)^2 + \epsilon\eta_c(x_2 - h)^2] \\ &= \frac{d}{dx_1} \left[\frac{(\eta_c - 1)^2}{4\eta_c} (1 + \epsilon) + b \right] \\ &\Rightarrow 2\eta_c(x_1 - h) + 2\epsilon\eta_c(x_2 - h) \frac{dx_2}{dx_1} = 0 \\ &\Rightarrow \frac{dx_2}{dx_1} = -\frac{1}{\epsilon} \frac{x_1 - h}{x_2 - h}. \end{aligned} \quad (23)$$

This implies $\frac{dx_2}{dx_1} = -1/\epsilon$ when $x_2 = x_1$. Therefore, $\bar{x}_1 = \bar{x}_2 \equiv \bar{x}$. To find $\bar{x}$, we plug it in the equation for the ellipse:

$$\begin{aligned} & \eta_c(\bar{x} - h)^2 + \epsilon\eta_c(\bar{x} - h)^2 \\ &= \frac{(\eta_c - 1)^2}{4\eta_c} (1 + \epsilon) + b \\ &\Rightarrow (\bar{x} - h)^2 = \frac{(\eta_c - 1)^2}{4\eta_c^2} + \frac{b}{\eta_c(1 + \epsilon)} \\ &\Rightarrow \bar{x} = h - \sqrt{\frac{(\eta_c - 1)^2}{4\eta_c^2} + \frac{b}{\eta_c(1 + \epsilon)}}. \end{aligned} \quad (24)$$

The condition for L to be tangent to the ellipse at $(x_1, x_2) = (\bar{x}, \bar{x})$ is $\bar{x} + \epsilon\bar{x} = a(1 + \epsilon)$. Solving for $\bar{x}$, we obtain $\bar{x} = a$. In conclusion, in terms of the original parameters, if

$$\frac{1 + \eta_c}{2\eta_c} - \sqrt{\frac{(\eta_c - 1)^2}{4\eta_c^2} + \frac{b}{\eta_c(1 + \epsilon)}} \geq a, \quad (25)$$

then all points satisfying the second constraint also satisfy the first constraint. Alternatively, if

$$\frac{1 + \eta_c}{2\eta_c} - \sqrt{\frac{(\eta_c - 1)^2}{4\eta_c^2} + \frac{b}{\eta_c(1 + \epsilon)}} < a, \quad (26)$$

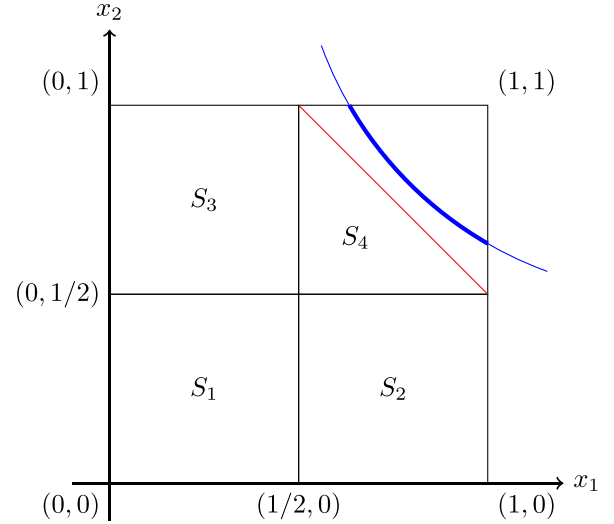


FIG. 6. When L does not intersect the ellipse, the Nash equilibrium points correspond to the part of the ellipse that lies within S_4 (depicted by the thick segment). Here the parameters are $\epsilon = 1$, $\eta_c = 0.5$, $a = 0.75$ and $b = 0.25$.

then there exist points that satisfy the second constraint but not the first constraint.

We are now ready to discuss the set of Nash equilibrium points under different parameter regimes. If the parameters satisfy Eq. (25), then the set of Nash equilibrium points lies on the part of the ellipse that resides in S_4 . The reasoning is similar to how we found the Nash equilibria in the previous subsection. Since the segment of the ellipse residing in S_4 is a convex curve on the $x_1 - x_2$ coordinate grid, any point on it must be a Nash equilibrium. This is because the allowed unilateral movements are either to the right by agent 1, or up by agent 2, and such a movement results in a smaller payoff for the moving agent. See Fig. 6 for an illustrative example. This example demonstrates that the second constraint prevents solutions where one agent receives the entire payoff while the other receives nothing (i.e., the points $(x_1, x_2) = (1/2, 1)$ and $(x_1, x_2) = (1, 1/2)$). Relating this to the core idea of the paper, the constraint on combined waste disposal rate compels the agents to select from a set of strategies that is entirely different from the set of strategies that are available without this restriction.

If the parameters satisfy Eq. (26), then there are several interesting scenarios. In this case L intersects the ellipse at two points. Denote the upper-left point by (x_1^L, x_2^L) , and the lower-right point by (x_1^R, x_2^R) , see Fig. 7 for reference. Recall that the endpoints of the part of L that lies within S_4 are $(1/2, \frac{1}{\epsilon}[a(1 + \epsilon) - 1/2])$ and $(a(1 + \epsilon) - \epsilon/2, 1/2)$ (thick red segment in Fig. 5). If this segment lies in the region composed of the ellipse and its boundary, then the set of Nash equilibria remains identical to the case where the second constraint is absent. Namely, the set of Nash equilibria corresponds to the points on the segment of L that lies in S_4 . This happens when $x_1^L \leq 1/2$ and $x_2^R \leq 1/2$. In other words, the two points of intersection of the ellipse with L lie outside of the interior of S_4 . See Fig. 7 for an illustrative example. We see that in this case the second constraint does not have an effect on the set of optimal strategies available to the agents.

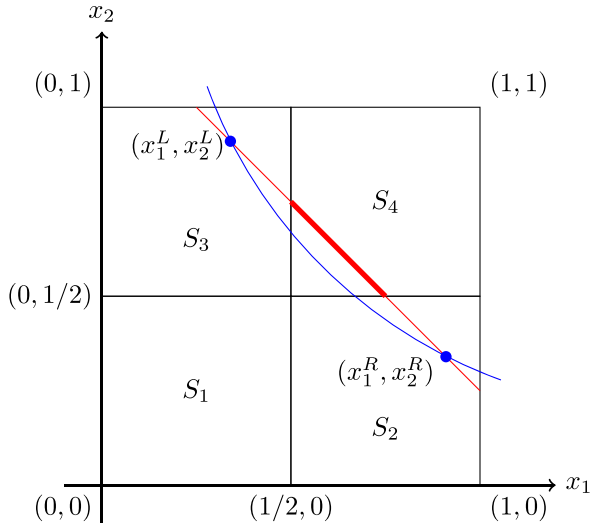


FIG. 7. When the segment of L in S_4 lies in the region enclosed by the ellipse, the set of Nash equilibrium points are the same as in the absence of the constraint on the total entropy output (shown in thick line). Here the parameters are $\epsilon = 1$, $\eta_c = 0.5$, $a = 5/8$ and $b = 0.595$.

A different variety of Nash equilibria occur when one or both of the intersection points of L with the ellipse are in the interior of S_4 . In this case, the set of Nash equilibria consists of the portion of L in S_4 that lies within the ellipse, along with the segment of the ellipse in S_4 that lies outside the two intersection points. See Fig. 8 for an illustrative example where both points are in the interior of S_4 . In this example, the constraint on combined waste disposal rate prevents the extreme strategies in which one agent obtains all of the payoff while the other receives nothing.

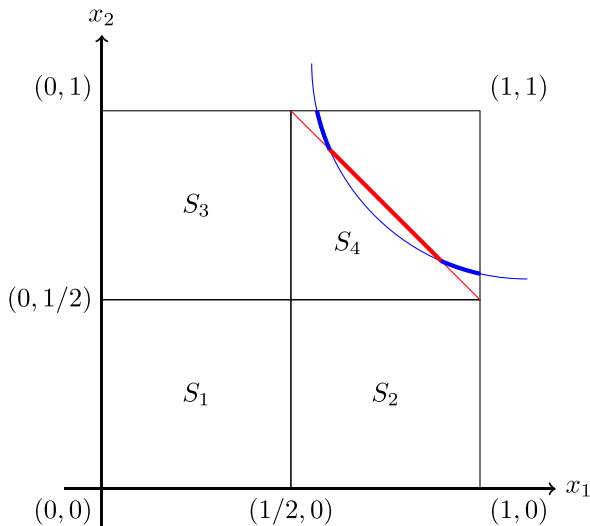


FIG. 8. When the ellipse intersects L within S_4 , the Nash equilibria are given by the thick segment in the figure. The points in thick red correspond to the Nash equilibria when the constraint on the free energy current prevails over the constraint on the waste current, while the points in thick blue represent the converse case. Here the parameters are $\epsilon = 1$, $\eta_c = 0.8$, $a = 0.75$, and $b = 0.23492$.

V. CONCLUSION

Evolution is often viewed as a competition between biological agents for shared energy resources, which, in thermodynamic terms, can be described as free energy. According to the laws of thermodynamics, the process of extraction of free energy and its storage or conversion to useful work must generate excess entropy that the organism must dispose of. Here, we explore the idea that the mechanism of elimination of entropic waste is subject to evolutionary pressure due to an environmental constraint on the shared rate of waste elimination. We employ a recently proposed thermodynamic model that describes the competition between heat engines for a finite free energy current (represented as an interaction with a high-temperature bath) [6]. We modify the model by including a constraint on the current of waste energy (represented as an interaction with a low-temperature bath). Thus, in our case, the agents also compete for access to the low-temperature bath, resulting in significantly richer dynamics.

We analyze the competition between two heat engines using game theory. Using the Stackelberg model, where one of the agents (the “first” agent) has the choice to make the move resulting in the highest payoff (extracted work per unit time), the set of options available to the second agent is determined by the Carnot efficiency, the highest energy states of each engine, and the constraints on the free energy and waste energy currents. We find that, if the constraint on the free energy current is loosened, the set of outcomes available to the second agent can range from no payoff to the highest payoff possible. This range depends on two thresholds that are determined by the Carnot efficiency and the highest energy states of the engines, Eqs. (19) and (20). If the constraint on the waste energy current is above/in-between/below both thresholds then the highest/positive/no payoff is obtained (Figs. 2–4).

We then analyzed the Nash equilibrium solutions of the game. Similar to the Stackelberg model, we found that two thresholds, depending on the constraints on both currents, determine the set of Nash equilibria. If the constraint on the waste energy current is too tight, the set of Nash equilibria entirely differ from the set without this constraint (Fig. 6), and if the constraint on the waste energy current is too loose, the set of Nash equilibria is not affected (Fig. 7). In the intermediate regime, the set of Nash equilibria is a hybrid of points resulting from each constraint (Fig. 8). These results show that the trade-off between the payoffs becomes non-linear when the constraint on waste elimination is comparable or tighter than the constraint on resource extraction.

Our model is deliberately simple and should be viewed as a motivating step toward formulating a thermodynamic description of both intra-cellular and intercellular evolutionary dynamics, where the engines represent energy-consuming, work-performing, and waste-generating organelles and complexes within cells, or, in appropriate contexts, the cells themselves. Future work should aim to develop more realistic formulations that capture aspects of this complexity. As a first step, one could consider a molecular motor that transduces ATP into ADP and inorganic phosphate (P), as in Ref. [25]. That work presents a thermodynamically consistent model of molecular biomotors. In analogy with our framework, the ATP reservoir corresponds to the hot bath, while the ADP

and P reservoirs act as cold baths. Within this setting, one could explore game-theoretic interactions between multiple biomotors operating under a constraint on the total rate at which the “waste” products, ADP and P, are recycled. Another promising direction is to investigate how successive generations of competing heat-engine “species” evolve—examining how offspring strategies are shaped by their predecessors’ performance and by changing environmental conditions, such as variations in total currents to the hot and cold baths—inspired by results such as those in Ref. [37].

ACKNOWLEDGMENTS

The work was supported by the Higher Education and Science Committee of the Republic of Armenia, Grants No. 24IRF/2-1C001 and No. 10-27/24FP-1D009. D.B.S. thanks also Russian Science Foundation Grant No. 23-11-00116. We thank A. Allahverdyan and S. Babajanyan for helpful discussions.

DATA AVAILABILITY

No data were created or analyzed in this study.

- [1] E. Schrödinger, *What Is Life? The Physical Aspect of the Living Cell* (Cambridge University Press, Cambridge, 1944).
- [2] I. Prigogine, Dissipative structures, dynamics, and life [Nobel lecture], in *Nobel Lectures, Chemistry 1971–1980* (World Scientific, Singapore, 1977), pp. 246–265.
- [3] L. Peliti and S. Pigolotti, *Stochastic Thermodynamics: An Introduction* (Princeton University Press, Princeton, NJ, 2021).
- [4] L. Brillouin, The negentropy principle of information, *J. Appl. Phys.* **24**, 1152 (1953).
- [5] P. Turchin, *Ultrasociety: How 10, 000 Years of War Made Humans the Greatest Cooperators on Earth* (Beresta Books, Los Angeles, CA, 2016).
- [6] S. G. Babajanyan, E. V. Koonin, and A. E. Allahverdyan, Thermodynamic selection: Mechanisms and scenarios, *New J. Phys.* **24**, 053006 (2022).
- [7] A. J. Lotka, Contribution to the energetics of evolution, *Proc. Natl. Acad. Sci. USA* **8**, 147 (1922).
- [8] I. Svirezhev and D. O. Logofet, *The Stability of Biological Communities* (Mir Publishers, Moscow, 1978).
- [9] H. T. Odum and R. C. Pinkerton, Time’s speed regulator: The optimum efficiency for maximum power output in physical and biological systems, *Am. Sci.* **43**, 331 (1955).
- [10] H. T. Odum, *Systems Ecology: An Introduction* (John Wiley & Sons, New York, NY, 1983).
- [11] H. T. Odum, Efficiencies, size of organisms, and community structure, *Ecology* **37**, 592 (1956).
- [12] S. E. Jørgensen and Y. M. Svirezhev, *Towards a Thermodynamic Theory for Ecological Systems* (Elsevier, Amsterdam, 2004).
- [13] G. Sella and A. E. Hirsh, The application of statistical physics to evolutionary biology, *Proc. Natl. Acad. Sci. USA* **102**, 9541 (2005).
- [14] B. Drossel, Biological evolution and statistical physics, *Adv. Phys.* **50**, 209 (2001).
- [15] H. P. De Vlarar and N. H. Barton, The contribution of statistical physics to evolutionary biology, *Trends Ecol. Evol.* **26**, 424 (2011).
- [16] Y. I. Wolf, M. I. Katsnelson, and E. V. Koonin, Physical foundations of biological complexity, *Proc. Natl. Acad. Sci. USA* **115**, E8678 (2018).
- [17] E. D. Schneider and J. J. Kay, Life as a manifestation of the second law of thermodynamics, *Math. Comput. Modell.* **19**, 25 (1994).
- [18] L. M. Martyushev and V. D. Seleznev, Maximum entropy production principle in physics, chemistry, and biology, *Phys. Rep.* **426**, 1 (2006).
- [19] P. Ao, Laws in Darwinian evolutionary theory, *Phys. Life Rev.* **2**, 117 (2005).
- [20] D. G. Nicholls, The molecular machinery of Keilin’s respiratory chain and proton leak, *Biochem. Soc. Trans.* **31**, 1238 (2003).
- [21] A. Lervik, F. Bresme, S. Kjelstrup, and J. M. Rubí, On the thermodynamic efficiency of Ca^{2+} -ATPase molecular machines, *Biophys. J.* **103**, 1218 (2012).
- [22] M. Nakano, H. Imamura, M. Toei, M. Tamakoshi, M. Yoshida, and K. Yokoyama, ATP hydrolysis and synthesis of a rotary motor V-ATPase from *Thermus Thermophilus*, *J. Biol. Chem.* **283**, 20789 (2008).
- [23] W. Hwang and C. Hyeon, Energetic costs, precision, and transport efficiency of molecular motors, *J. Phys. Chem. Lett.* **9**, 513 (2018).
- [24] T. L. Hill, *Free Energy Transduction in Biology* (Academic Press, New York, San Francisco, London, 1977).
- [25] T. Schmiedl and U. Seifert, Efficiency of molecular motors at maximum power, *Europhys. Lett.* **83**, 30005 (2008).
- [26] *Dung Beetle Ecology*, edited by I. Hanski and Y. Cambefort (Princeton University Press, Princeton, NJ 1991).
- [27] B. Momeni, A. J. Waite and W. Shou, Spatial self-organization favors heterotypic cooperation over cheating, *elife*, **2**, e00960 (2013).
- [28] I. M. Côté, Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology, Annu. Rev.* **38**, 311 (2000).
- [29] L. McNally, H. K. Johansen, and R. C. MacLean, Cooperativity and cheating in microbial social interactions, *Proc. Natl. Acad. Sci. USA* **114**, 4130 (2017).
- [30] W. J. Bond and J. J. Midgley, Kill thy: An individualistic argument for the evolution of flammability, *Oikos* **73**, 79 (1995).
- [31] A. G. Hart and F. L. W. Ratnieks, Waste management in the leaf-cutting ant *atta colombica*, *Behav. Ecol.* **13**, 224 (2002).
- [32] H. von Stackelberg, *The Theory of Market Economy* (Oxford University Press, Oxford, UK, 1952).
- [33] A. E. Allahverdyan, S. G. Babajanyan, N. H. Martirosyan, and A. V. Melkikh, Adaptive heat engine, *Phys. Rev. Lett.* **117**, 030601 (2016).
- [34] J. F. Nash, Non-cooperative games. *Annals of Mathematics*, **54**, 286 (1951).
- [35] R. D. Luce and H. Raiffa, *Games and Decisions: Introduction and Critical Survey*, 1st ed. (John Wiley & Sons, New York, NY, 1957).
- [36] R. B. Myerson, *Game Theory: Analysis of Conflict* (Harvard University Press, Cambridge, MA 1991).
- [37] S. Cavallero, A. Rousselot, R. Pugatch, L. Dinis, and D. Lacoste, The trade-off between growth and risk in Kelly’s gambling and beyond, *Physica A* **659**, 130316 (2025).