# Linking power, efficiency, and bifurcations in ecological systems

Serguei Saavedra[1,2,*], Yuguang Yang[1], Christopher P. Kempes[2], Chengyi Long[1], Ricard Solé[2,3,4], Tomo Yoshino[1], and Marco Tulio Angulo[5,*]

[1] *Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Avenue, Cambridge, MA 02139, USA*

[2] *Santa Fe Institute, Santa Fe, NM 87501, USA*

[3] *Complex Systems Lab, Universitat Pompeu Fabra, Dr Aiguader 88, 08003 Barcelona, Spain*

[4] *Institució Catalana de Recerca i Estudis Avançats, Lluís Companys 23, 08010 Barcelona, Spain*

[5] *Institute of Mathematics, Universidad Nacional Autónoma de México,, Juriquilla, Querétaro, México*

[*] *To whom correspondence should be addressed. E-mail: sersaa@mit.edu, mangulo@im.unam.mx*

## Abstract

Understanding the selecting and generating forces operating across the self-organization of ecological systems is synonymous with understanding principles of life itself. Three prominent hypotheses in ecological research—Lotka's *Maximum Power Principle*, Odum and Pinkerton's *Intermediate Efficiency Principle*, and Morowitz's *Biological Cycle Principle*—have independently attempted to explain these forces. However, how these hypotheses interconnect at the ecosystem scale remains unclear. Using a classical consumer-resource model, we reveal a formal property of ecological systems that leads them to maximize power exchange with intermediate efficiency while undergoing bifurcations from attracting points to attracting cycles. Our work reiterates the importance of ecosystem science rooted in energy flux, while illuminating a potential link between optimal thermodynamic properties and biological self-organization.

## Introduction

Complex living systems belong to a class of systems known as dissipative systems (Prigogine, 1962). These are open systems that obtain *free* energy from an external source (i.e., an ultimate constraint) and typically operate far from thermal equilibrium (not to be confused with steady state (Denbigh, 1951)), thus increasing the entropy of its environment (Boltzmann, 1964). Although dissipative systems can be biotic or abiotic, living dissipative systems tend to store energy and develop a level of thermodynamic autonomy from immediate changes in their environment (Kondepudi et al., 2020, Margalef, 1968, Schrödinger, 1944). This intermediate thermodynamic autonomy is typically achieved through internal structures characterized by physicochemical laws (i.e., proximal constraints) (Solé et al., 2024). Due to the generality of these observations and their significance for life itself, there is considerable value in understanding the presence and implications of biological self-organization (Deng et al., 2024, Solé et al., 2024). It is also necessary to move these thermophysical ideas from principles (or hypotheses) to theorems to provide not only a conceptual but also a quantitative understanding of natural phenomena (Everitt and Anner, 1956, Poincaré, 1905).

Ecological systems, ranging from microbiomes to rainforests, are among the most complex, living, dissipative systems in nature (de Castro and McShea, 2022, Murphy and O'Neill, 1995, Odum, 1983). For example, energy from the Sun is first converted by plants, then transferred to herbivores that feed on plants, and subsequently to carnivores that feed on herbivores, continuing through the interconnected web of life (Odum and Barrett, 2005, Olff et al., 2009, Pielou, 2001). This ecological complexity has been addressed over the years following different theoretical approaches (Solé and Bascompte, 2005). In most cases, non-linear dynamical systems have provided a solid framework for exploring the nature of ecological attractors at the population level (Case, 1999, Strogatz, 2014). However, ecological systems are also open systems, where energy flows (such as the input of solar radiation and the dissipation of metabolic heat) govern processes of self-organization, trophic interactions, and long-term stability (Svirezhev, 2000). Both sides of the coin have been treated in the context of a system view of complexity, where out-of-equilibrium phenomena appear to be described in terms of bifurcations and phase transitions (Haken, 1987, Nicolis and Prigogine, 1989). How are nonlinear dynamics and thermodynamics related to each other in the context of ecology and evolution?

To answer the question above, scientists have interpreted the laws of nature in terms of energetic principles (Lindeman, 1942). In particular, three prominent hypotheses have endured the test

of time. In the 1920s, Lotka (Lotka, 1922) (following Boltzmann's ideas) reasoned that, under a competitive struggle for free energy, organisms should be selected based on their ability to capture and transform more energy for growth, reproduction, and maintenance—a principle now known as *the Maximum Power Principle*. Under this principle, natural selection was a maximum power organizer. This hypothesis was later rediscovered in the 1950s by Odum and Pinkerton (Odum and Pinkerton, 1955), who realized that it could also operate at the level of groups of organisms to structure the ecological systems we observe in nature. Their analysis was performed in systems close to thermodynamic equilibrium (although real ecosystems are far from this equilibrium). Following physical laws that operate in electrical circuits, they propose that maximum power exchange cannot be achieved under perfect conversion efficiency—this is known as *the Intermediate Efficiency Principle*. This hypothesis can be understood as a selective influence on ecological systems, filtering those that are most likely to persist (i.e., attractor systems that best balance efficiency and power) under different environmental conditions (Levin, 1998, Lotka, 1922, Saavedra, 2024, Solé et al., 2024). In the 1960s, Morowitz (Morowitz, 1966) proposed that in all living systems, energy flux should lead to persistent material cycling—this was termed *The Biological Cycle Principle*. This other hypothesis can be understood as a generating influence on ecological systems, determining the existence and abundance of material upon which selection can act (Levin, 1998, Lotka, 1922, Saavedra, 2024, Solé et al., 2024).

However, to this day, we still lack a complete understanding of how these three hypotheses can be linked under a common quantitative framework in ecological systems (Hall and McWhirter, 2023). Yet, this unification can emphasize the generality of these ideas and guide further developments towards our understanding of natural systems. Here, we show that these three prominent hypotheses can be linked using a classical consumer-resource model. First, we describe our formalism, starting with the model and then with the three principles ordered such that the mathematical exposition can have a linear flow. Then, we show the unification of these principles using a numerical example. We discuss the potential implications of our study for future work.

# Methods

## Model

We illustrate our approach using the classical Rosenzweig-MacArthur consumer–resource model (Rosenzweig and MacArthur, 1963), defined by the differential equations

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{k}\right) - y\frac{cx}{x+a}, \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \varepsilon\, y\frac{cx}{x+a} - d\, y, \tag{1}$$

where $x$ and $y$ denote the biomass of the resource and consumer, respectively (both with dimensions [mass]). The parameters $r$ and $k$ represent the intrinsic growth rate of the resource (dimension $[\text{time}]^{-1}$) and the carrying capacity (dimension [mass]), respectively. These are phenomenological parameters that reflect the net environmental effect on population growth, which captures the balance of resource uptake, assimilation, and mortality under supply constraints. The consumer–resource interaction follows a Holling Type II functional response. Here, $c$ is the maximum consumption rate per unit biomass of the consumer ($[\text{time}]^{-1}$), and $a$ is the half-saturation constant ([mass]). We assume that $k > a$. In this formulation, $c$ represents the intake rate when the resource is abundant. The parameter $\varepsilon \in [0, 1)$ denotes the assimilation efficiency of the consumer (dimensionless), and $d$ is its per capita mortality rate ($[\text{time}]^{-1}$).

The system admits an internal equilibrium at $x^* = ad/(c\varepsilon - d)$, $y^* = \varepsilon\, ar\, \big[(c\varepsilon - d) - ad/k\big]/(c\varepsilon - d)^2$. For this equilibrium to be feasible (i.e., with positive $x^*$ and $y^*$), the following condition must hold:

$$c\,\varepsilon > \left(1 + \frac{a}{k}\right) d. \tag{2}$$

The product $c\varepsilon$ represents the maximum assimilated consumption rate per unit of consumer biomass. Feasibility requires that this rate not only compensates for the consumer's mortality ($d$), but also exceeds it by a buffer term $(a/k)d$ that accounts for intake saturation and finite carrying capacity of the resource. This condition is both necessary and sufficient for stable coexistence of the consumer and the resource (Supplementary Information).

## Limit cycle bifurcation

In the context of the Biological Cycle Principle (Morowitz, 1966), the coupled consumer-resource system of Eq. (1) can exhibit either an asymptotically stable equilibrium at $(x^*, y^*)$, or a a stable limit cycle around this equilibrium point that emerges through a Hopf bifurcation (Bieg et al., 2023, Strogatz, 2014). The transition between these two regimes occurs when the real part of the

eigenvalues of the Jacobian matrix, evaluated at the equilibrium, crosses zero (Supplementary Information). From this condition, we derive that oscillations occur if and only if

$$c\,\varepsilon \geq \left(1 + \frac{2a}{k-a}\right) d. \tag{3}$$

The emergence of oscillations depends solely on the maximum assimilated consumption rate $c\varepsilon$. The above inequality sets a strict lower bound on this rate: oscillations arise only when the consumer assimilates energy at a rate high enough to overcome both mortality $d$ and the damping effects $2ad/(k-a)$ introduced by resource saturation and limited carrying capacity. By rewriting $2ad/(k-a) = (ad/k)[2k/(k-a)]$, we can note that $2k/(k-a)$ is a decreasing function of $k$ when $k > a$ and $2k/(k-a) > 2$. Therefore, oscillations naturally require feasibility since $2ad/(k-a) \geq 2ad/k > ad/k$.

## Average long-term power and efficiency

In the context of the Intermediate Efficiency Principle and following Odum and Pinkerton (1955), we measure power as biomass (force) multiplied by specific growth (flux). In Eq. (1), the instantaneous input power is $rx$, representing the rate at which energy enters the system through resource production. Note that this bioenergetic input is different from the one expected under classical, abiotic, chemical systems (Kempes et al., 2021). The instantaneous output power is $\varepsilon cxy/(x+a)$, corresponding to the rate at which assimilated energy flows into the consumer population. Energy dissipation occurs via three pathways: crowding losses in the resource ($-rx^2/k$), consumer mortality ($-dy$), and incomplete assimilation—where a fraction $(1-\varepsilon)$ of the extracted resource energy is lost. The specific definitions of input and output power are not unique, but can be expressed in terms of different levels of energy flux.

We estimate the long-term average input power as (Supplementary Information)

$$P_{\text{in}} := \lim_{T\to\infty} \frac{1}{T}\int_0^T r\ x(t)\mathrm{d}t \approx a\ dr\frac{1}{c\varepsilon - d}.$$

The feasibility condition in Eq. (2) bounds this input power strictly between zero and an upper limit $rk$, which corresponds to the maximum energy input when the resource saturates at its carrying capacity. Similarly, the (long-term average) output power is

$$P_{\text{out}} := \lim_{T\to\infty} \frac{1}{T}\int_0^T \varepsilon y(t)\frac{cx(t)}{x(t)+a}\mathrm{d}t \approx \varepsilon\ a\ dr\ \frac{(c\varepsilon - d) - ad/k}{(c\varepsilon - d)^2}. \tag{4}$$

In contrast to the input power, feasibility only requires that $P_{\text{out}} > 0$; no upper bound is implied by feasibility constraints.

From these expressions, we define the power efficiency of the coupled system as the ratio of output to input power:

$$\eta := \frac{P_{\text{out}}}{P_{\text{in}}} \approx \left(1 - \frac{ad}{k}\frac{1}{c\varepsilon - d}\right)\varepsilon. \tag{5}$$

Because the term in parentheses is positive and strictly less than one under the feasibility condition, it follows that $\eta < \varepsilon$. Therefore, the power efficiency of the consumer–resource system is strictly lower than the consumer's assimilation efficiency, due to structural losses associated with finite carrying capacity and resource saturation. Note that if we combine the uptake rate ($c$) and the assimilation efficiency ($\epsilon$) into a single variable (i.e., $b = c\epsilon$), the power efficiency would be simply the consumer's efficiency, i.e., $\eta = b/c = \epsilon$ (this do not alter the qualitative results shown in Fig. 1 other than than the fact that $\eta$ would scale linearly with $\epsilon$).

## Maximum output power

In the context of the Maximum Power Principle (Lotka, 1922), we consider the resource is given and ask for the conditions under which the consumer attains maximum power. We focus our analysis on the assimilation efficiency $\varepsilon$ and consumption rate $c$ as traits that the consumer can change, assuming the half-saturation constant $a$ is determined by the resource. Maximizing $P_{\text{out}} = P_{\text{out}}(\varepsilon, c)$ of Eq. (3) with respect to $c$ at a fixed $\varepsilon$ yields the best response

$$c^*(\varepsilon) = \left(1 + \frac{2a}{k}\right)\frac{d}{\varepsilon},$$

attaining an output power $P^*_{\text{out}}(\varepsilon) := P_{\text{out}}(c^*(\varepsilon), \varepsilon) = \varepsilon k r/4$, which is independent of $a$ and $d$ (Supplementary Information). Note that $\varepsilon c^* - d = 2da/k > da/k$, so $c^*$ is always feasible according to Eq. (2).

Alternatively, maximizing over $\varepsilon$ at a fixed $c$ subject to the constraint $\varepsilon \in [0, 1]$ gives the best response

$$\varepsilon^*(c) = \begin{cases} \dfrac{k+a}{k-a}\dfrac{d}{c}, & \text{if } c > \dfrac{k+a}{k-a}d \\ 1, & \text{otherwise} \end{cases}$$

The condition in the first line of the above equation yields an intermediate optimal assimilation efficiency $0 < \varepsilon^* < 1$. In this case, $\varepsilon^*$ is feasible because $\varepsilon^* c - d = (da/k)[2k/(k-a)] > da/k$ since $k > a$. When this condition is not satisfied, the output power becomes an increasing function of $\varepsilon$, and its maximum is attained at the boundary $\varepsilon^* = 1$. In this case, it is possible

that $\varepsilon^*$ is not feasible. With the optimum assimilation efficiency, the output power is

$$P^*_{\text{out}}(c) := P_{\text{out}}(\varepsilon^*(c), c) = \begin{cases} \frac{1}{4}\frac{drk}{c}\left(1+\frac{a}{k}\right)^2 & \text{if } c > \frac{k+a}{k-a}d \\ a\ dr\ \frac{(c-d)-ad/k}{(c-d)^2} & \text{otherwise.} \end{cases}$$

Note that the products $\varepsilon\ c^*(\varepsilon)$ and $c\ \varepsilon^*(c)$ are both constant.

Substituting the best responses in Eq. (4) yields the power efficiencies

$$\eta^*(\varepsilon) := \eta(\varepsilon, c^*(\varepsilon)) = \frac{1}{2}\varepsilon, \quad \eta^*(c) := \eta(\varepsilon^*, c) = \begin{cases} \frac{1}{2}\frac{(k+a)^2}{k(k-a)}\frac{d}{c} & \text{if } c > \frac{k+a}{k-a}d, \\ 1 - \frac{ad}{k}\frac{1}{c-d} & \text{otherwise.} \end{cases}$$

Since $c - d > c\varepsilon - d > 0$ by feasibility, the efficiencies are well-posed. The efficiency $\eta^*(\varepsilon)$ with the optimal consumption rate $c^*$ is simply half the assimilation efficiency of the consumer, which coincides exactly with the results of Odum and Pinkerton (Odum and Pinkerton, 1955). That is, at maximum power exchange, efficiency is exactly half of its maximum.

## Results

Holding the consumption rate $c$ fixed, the optimal assimilation efficiency $\varepsilon^*$ satisfies $c\varepsilon^* = d + 2ad/(k+a)$—the lower bound in Eq. (3). Thus, the efficiency that maximizes output power coincides with the Hopf bifurcation that triggers oscillations. Holding the assimilation rate $\varepsilon$ fixed, the optimal consumption rate $c^*$ satisfies $c^*\varepsilon = (2a+k)(d/k)$, which lies below $d + 2ad/(k+a)$ provided $k > a$. Consequently, the system remains on the pre-bifurcation side, and every trajectory converges to the interior equilibrium.

Figure 1 numerically confirms this result: as $\varepsilon$ increases, the power curve peaks precisely where the equilibrium loses stability and a limit cycle emerges. After $\varepsilon$ reaches the feasibility threshold (i.e., $x^* > 0$ and $y^* > 0$, Supplementary Information), the system first has a stable equilibrium and then a stable limit cycle. The output power is maximized at $\varepsilon^*$. That is, output power is maximized exactly at the Hopf bifurcation where the resource and consumer starts to oscillate. In summary, $\varepsilon^*(c)$ acts as a "triple point": it delivers maximum output power, entails intermediate efficiency, and marks the onset of oscillations.

We can draw evolutionary insights by treating assimilation efficiency $\varepsilon$ and consumption rate $c$ as adaptive traits of the consumer. Because $\varepsilon\ c^*(\varepsilon) \neq c\ \varepsilon^*(c)$, no single pair $(\varepsilon, c)$ simultaneously

maximizes output power for both traits —only in the limit $k \to \infty$ of infinite carrying capacity both best responses coincide (in line with classical chemical systems (Kempes et al., 2021)). When traits evolve on different timescales, evolutionary theory predicts that the faster trait will swiftly reach its adaptive optimum while the slower one tracks its reaction norm (Cortez and Ellner, 2010, Hofbauer and Sigmund, 1998). Thus, if assimilation efficiency $\varepsilon$ adapts more rapidly than consumption rate $c$, the system converges to the "triple point" defined by $\varepsilon^*$. Conversely, if $c$ changes more quickly than $\varepsilon$, the system settles at a "double point" $c^*$ that maximizes power exchange at intermediate efficiency, but looses oscillations.

## Conclusions

Energy flux has been a central theme in biology, allowing us to understand the behavior of complex living systems under a common lens (Lindeman, 1942, Morowitz and Smith, 2007). In fact, three prominent principles rooted in energy fluxes, the Maximum Power Principle (Lotka, 1922), the Intermediate Efficiency Principle (Odum and Pinkerton, 1955), and the Biological Cycle Principle (Morowitz, 1966)—have provided a roadmap for understanding the emergence, selection, and transformation of such complex living systems. Although debatable, these three principles suggest a natural tendency of evolution, a selecting influence on the structure of living systems, and a generating influence on the material of living systems, respectively. However, the gap between a principle and a theorem limits our quantitative understanding of how energy shapes the systems that we observe in nature. For example, it is unclear whether ecological systems exhibit a fundamental tradeoff between power transfer and efficiency, and whether this tradeoff occurs under critical transitions that lead to oscillatory dynamics.

Here, we have shown how these three principles can be unified under an ecosystem perspective. Our results suggest a formal property of ecological systems, namely, to maximize power exchange without maximizing efficiency while undergoing bifurcations from attracting points to attracting cycles. More broadly, our results suggest a potential relationship between critical states (along the lines of self-organized criticality (Munoz, 2018, Solé and Bascompte, 2005)) and optimal thermodynamic properties. Confirming this hypothesis could lead to a better understanding of the tendency of dissipative living systems to approach critical points, which have been suggested to have adaptive potential (Mora and Bialek, 2011). These results, however, follow two central assumptions: (1) In the context of ecological systems, we define thermodynamic power as the product of biomass (acting as force) and growth rate (acting as flux). (2) The system can be reduced to a consumer-resource model with self-regulation of resources and a nonlinear

functional response of consumers. These assumptions differ from classical chemical systems (Kempes et al., 2021), implying that these triple points could be a derivative of emergent ecologies. Yet, future work can explore different power definitions (albeit remaining coherent with power units) and extensions to multi-dimensional systems.

Moreover, our findings can have real-world applications in ecosystem management and restoration, where we may aim to maximize energy flow or productive potential of the ecosystem (and expect to observe minor periodic behavior) instead of focusing on the genetic engineering of higher conversion efficiencies of each component (Odum, 1969). This work aims to reiterate the importance of ecosystem science rooted in external energy flux and internal energy exchange, while illuminating a potential link between maximum thermodynamic properties and critical states in ecological systems.

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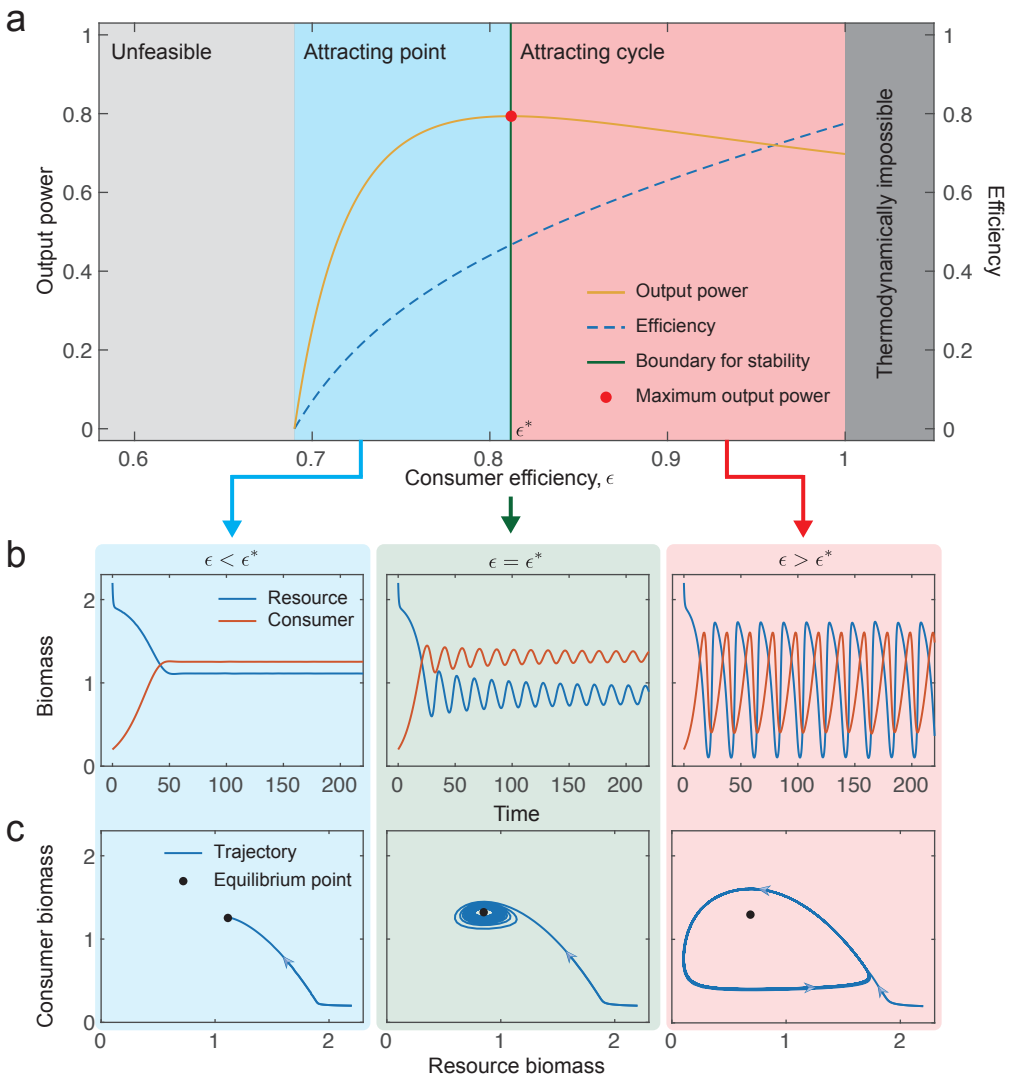


Figure 1: **Unifying the principles of maximum power, efficiency, and biological cycles.** Numerical example (Supplementary Information). **(a)** Output power and efficiency analysis. As the consumer efficiency $\epsilon$ increases, the system's efficiency increases (blue dashed line), while the output power (yellow line) first increases and then decreases. Colored regions represent distinct system behaviors: the left-most light-gray region is unfeasible, the blue region corresponds to an attracting fixed point (i.e., local asymptotic stability), the red region indicates an attracting limit cycle, and the dark gray region is thermodynamically impossible (i.e., $\epsilon > 1$). The green vertical line marks the boundary between the blue and red regions. The red dot denotes the point of maximum output power, which occurs at the green boundary; the corresponding assimilation (consumption) efficiency is denoted by $\epsilon^*$. **(b-c)** Illustration of the system's dynamic behavior as $b$ increases. Panel **b** shows the biomass time series, while panel **c** displays the corresponding phase portraits. The left-most blue region illustrates the attracting fixed point behavior for $\epsilon < \epsilon^*$; the green region represents the transition point at $\epsilon = \epsilon^*$, where cyclic behavior emerges; and the red region depicts persistent cyclic behavior for $\epsilon > \epsilon^*$.

# —SUPPLEMENTARY INFORMATION—
# LINKING POWER, EFFICIENCY, AND BIFURCATIONS IN ECOLOGICAL SYSTEMS

Contents


**1 Equilibria and feasibility analysis** . . . . . **2**

**2 Hopf bifurcation** . . . . . **3**

**3 Long-term average power** . . . . . **4**

3.1 Theoretical accuracy of the approximation . . . . . 5

3.2 Numerical verification of the approximation . . . . . 6

**4 Maximum output power** . . . . . **7**

4.1 Optimal maximum intake . . . . . 7

4.2 Optimal assimilation efficiency . . . . . 7

**References** . . . . . **8**

## 1. Equilibria and feasibility analysis

The consumer-resource system we study is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1-\frac{x}{k}\right) - y\frac{cx}{x+a}, \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \varepsilon\, y\frac{cx}{x+a} - d\, y, \tag{S1}$$

where $x$ and $y$ denote the biomass of the resource and consumer, respectively (dimensions [mass]). The parameters $r$ and $k$ are the regeneration rate (dimension $[\text{time}]^{-1}$) and carrying capacity (dimension [mass]) of the resource. Both are phenomenological considering the net environmental effect on growth rate (i.e., the balance between uptake, assimilation, and mortality rates under supply constraints). The resource and the consumer interact via a Holling Type II functional response. The parameters $c$ and $a$ are the consumption rate (dimensions $[\text{time}]^{-1}$) and the half-saturation constant (dimension [mass]). Note that the consumption rate represents the per-unit-consumer intake when the resource is abundant. The parameter $\varepsilon \in [0,1)$ is the consumer's assimilation efficiency (dimensionless), and $d$ its mortality (dimensions $[\text{time}]^{-1}$). Table 1 below summarizes the model parameters and typical values used in our study.

The equilibria $(x^*, y^*)$ of the system are determined by the system of equations $\mathrm{d}x/\mathrm{d}t = 0$ and $\mathrm{d}y/\mathrm{d}t = 0$. This system of equations has a trivial solution $x^* = y^* = 0$ where neither the resource nor the consumer are present, a boundary solution $x^* = k, y^* = 0$ where only the resource is present, and the equilibrium

$$x^* = \frac{ad}{c\varepsilon - d}, \quad y^* = \varepsilon\, ar\, \frac{(c\varepsilon - d) - ad/k}{(c\varepsilon - d)^2}. \tag{S2}$$

we study in our work. Feasibility characterizes the conditions under which this last equilibrium satisfies $x^* > 0, y^* > 0$, which are

$$c\,\varepsilon > \left(1 + \frac{a}{k}\right) d, \tag{S3}$$

which is Eq. (2) of the main text.

For numerical results, use following parameter value which are plausible for a lynx-hare system in the Hudson-Bay.

Table 1. Model parameters (biomass units: $\mathrm{kg\,km^{-2}}$ for $x, y$; $\mathrm{yr^{-1}}$ for rates).

| **Symbol** | **Meaning (units)** | **Plausible range** | **Working value** |
|---|---|---|---|
| $r$ | Intrinsic resource growth rate ($\mathrm{yr^{-1}}$) | 1.2–1.8 | 1.6 |
| $k$ | Carrying capacity ($\mathrm{kg\,km^{-2}}$) | 850–1200 | 1000 |
| $c$ | Per-lynx max intake ($\mathrm{yr^{-1}}$) | 50–70 | 60 |
| $a$ | Half-saturation prey biomass ($\mathrm{kg\,km^{-2}}$) | 40–80 | 60 |
| $\varepsilon$ | Assimilation efficiency (–) | 0.10–0.25 | 0.15 |
| $d$ | Adult lynx mortality ($\mathrm{yr^{-1}}$) | 0.20–0.45 | 0.30 |

## 2. Hopf bifurcation

To study when a limit cycle appears due to a Hopf bifurcation, we calculate the conditions under which the Jacobian $J$ of Eq. (S1) evaluated at the interior equilibrium of Eq. (S2) has purely imaginary eigenvalues. Because system has only two states, this condition is equivalent to when the trace of the Jacobian is zero. Indeed, recall the characteristic polynomial in this case is

$$\lambda^2 - \text{trace}(J)\ \lambda + \det(J) = 0,$$

where the solutions $\lambda$ of the above equation represents the eigenvalues of the system at the equilibrium.

The Jacobian of the system at the interior equilibrium is

$$J = \begin{pmatrix} \frac{dr\left(\frac{2a}{d-c\varepsilon}+\frac{a+k}{c\varepsilon}\right)}{k} & -\frac{d}{\varepsilon} \\ r\left(\varepsilon - \frac{d(a+k)}{ck}\right) & 0 \end{pmatrix}.$$

Note that

$$\det(J) = dr\left(1 - \frac{d(a+k)}{ck\varepsilon}\right) > 0,$$

if the feasibility condition of Eq. (S3) is satisfied. Therefore, a limit cycle will appear when $\text{trace}(J) \geq 0$.

From the Jacobian matrix, note that $\text{trace}(J) \geq 0$ is equivalent to

$$\frac{2a}{d-c\varepsilon} + \frac{a+k}{c\varepsilon} \geq 0.$$

Solving for $c\varepsilon$ yields

$$c\,\varepsilon \geq \left(1 + \frac{2a}{k-a}\right) d, \tag{S4}$$

which is Eq. (3) of the main text.

## 3. Long-term average power

We begin by introducing some notation and clarifying the energetic bookkeeping. For an (integrable) function $g(t)$, define the long-term average operator as

$$\langle g \rangle = \lim_{T\to\infty} \frac{1}{T} \int_0^T g(t)\mathrm{d}t.$$

This operator is linear. When the consumer-resource system of Eq. (S1) is feasible, its trajectories either (i) approach the interior equilibrium, or (ii) settle on a limit cycle around the equilibrium point born at the Hopf bifurcation. Both cases are periodic. The equilibrium can be regarded as a degenerate 0-period orbit. Therefore, the time average of every time derivative is zero. Using the consumer population as example and taking $T$ to be the period

$$\frac{1}{T}\int_0^T \dot{y}(t)\mathrm{d}t = \frac{1}{T}[y(T) - y(0)] = 0,$$

and thus in the limit $T \to \infty$ we obtain $\langle \dot{y} \rangle = 0$.

With this notation, the long-term average input and output power defined in the main text can be written as

$$P_{\text{in}} := \langle rx \rangle, \quad P_{\text{out}} := \left\langle \varepsilon y \frac{cx}{x+a} \right\rangle. \tag{S5}$$

For simplicity, we refer to this expression as input and output power from here on.

Applying the long-term average operator to both sides of the of Eq. (S1) yields

$$\begin{aligned} 0 &= r\langle x \rangle - \frac{r}{k}\langle x^2 \rangle - \left\langle y \frac{cx}{x+a} \right\rangle, \\ 0 &= \left\langle \varepsilon y \frac{cx}{x+a} \right\rangle - d\langle y \rangle. \end{aligned}$$

The second line immediately yields a convenient expression for the output power

$$P_{\text{out}} = d\langle y \rangle,$$

showing that output power is proportional to the long-term average biomass of the consumer. The first line of the above equation yields

$$P_{\text{out}} = \varepsilon \left( P_{\text{in}} - \frac{r}{k}\langle x^2 \rangle \right),$$

where $P_{\text{in}} = r\langle x \rangle$. Here, $r\langle x^2 \rangle / k$ plays the role of an internal dissipation term caused by logistic self-limitation, so that net power equals gross assimilation minus dissipation, scaled by the assimilation efficiency $\varepsilon$.

In the limit when $k \to \infty$ and the consumer-resource interact with a Holling Type I functional response, the Volterra principle asserts that time averages coincide with equilibrium values: $\langle x \rangle = x^*, \langle y \rangle = y^*$ [1, pp. 16]. Substituting this equilibrium in Eq. (S5) yields

$$P_{\text{in}} = a\ dr \frac{1}{c\varepsilon - d}, \quad P_{\text{out}} = \varepsilon\ a\ dr\ \frac{(c\varepsilon - d) - ad/k}{(c\varepsilon - d)^2}. \tag{S6}$$

When $k < \infty$ or the functional response is of Holling Type II (i.e., saturated), these formulas remain exact as long as the interior equilibrium is stable, i.e. before the Hopf bifurcation. This happens because $\langle x \rangle = x^*, \langle y \rangle = y^*$ when trajectories converge to the equilibrium point.

Next we show that Eq. (S6) still approximates the long-term powers with an error $O(\mu^2)$ once the bifurcation is passed:

$$r\langle x\rangle = rx^* + O(\mu^2), \quad d\langle y\rangle = dy^* + O(\mu^2)$$

where $\mu = c\varepsilon - (c\varepsilon)_H$, $(c\varepsilon)_H := \left(1 + \frac{2a}{k-a}\right) d$, measures the distance to the Hopf bifurcation.

3.1. **Theoretical accuracy of the approximation.** At a super-critical Hopf bifurcation, standard results of bifurcation theory (Poincaré–Dulac procedure) shows that the vector field on the centre manifold can always be written in the complex normal form

$$\dot{z} = iw_0 z + \alpha\mu z - \beta|z|^2 z + \text{H.O.T.},$$

where $z \in \mathbb{C}$ and $\alpha, \beta$ are some real coefficients [2]. The amplitude of the resulting limit cycle satisfies

$$|z| = R = \sqrt{\alpha/\beta}\sqrt{\mu}.$$

Note that $R = O(\sqrt{\mu})$. This expression is general, and does not depend on any ecological details.

Consider now the deviations from the equilibrium

$$u = x - x^*, \quad v = y - y^*.$$

The linear change of basis that takes $(u, v)$ to $z$ and its complex conjugate is orthogonal up to order $R$, so

$$u(t) = R\cos\theta(t) + O(R^2), \quad v(t) = R\sin\theta(t) + O(R^2),$$

where $\dot{\theta} = \omega_0 + O(\mu)$. Importantly, note this implies that

$$\langle u\rangle = \langle v\rangle = 0, \tag{S7}$$

up to order $R$ because the averages of $\cos\theta$ and $\sin\theta$ over one period vanish.

Consider any smooth observable $\varphi$ near the equilibrium $(x^*, y^*)$. Using a Taylor expansion, this observable can be written as a linear combination of: i) an order 1 term $\varphi(x^*, y^*)$; ii) linear terms $\{\langle u\rangle, \langle v\rangle\}$ of order $R$, quadratic terms $\{\langle u^2\rangle, \langle uv\rangle, \langle v^2\rangle\}$ of order $R^2$; and so on.

From Eq. (S7) above, the linear terms $\{\langle u\rangle, \langle v\rangle\}$ vanish. The quadratic average $\langle u^2\rangle$ is of order $R^2 = \mu$. But crucially, note it enters the consumer and the resource only through the combination

$$r\langle x\rangle - \frac{r}{k}\langle x^2\rangle.$$

Re-expanding $\langle x^2\rangle = (x^* + u)^2$ and collecting the $\mu$-terms, we find the coefficient in front of $\mu$ is proportional to $r - 2rx^*/k$. This expression is exactly zero at the Hopf bifuctaction because $x^* = (k - a)/2$ there. A similar cancellation occurs in the consumer thanks to the identity $\varepsilon x x^* y^*/(x^* + a) = dy^*$. Consequently, every contribution generated by the quadratic terms disappears. Consequently

$$\langle x\rangle = x^* + O(\mu^2), \quad \langle y\rangle = y^* + O(\mu^2).$$

Multiplying by $r$ and $d$ respectively gives the desired power relations. Note that no explicit form of the limit cycle is needed. Only the universal amplitude law and the algebraic identities at the Hopf bifurcation are needed.

The above argument can also be intepretd as follows: the Volterra principle acts by approximating the limit cycle by an ellipse. Indeed, the limit cycle $|z|^2 = R^2$ can be expressed in the original variables as the ellipse

$$(x - x^*)^2 + \kappa\,(y - y^*)^2 = R^2,$$

where the parameters

$$\kappa = \frac{c^2 k(k-a)^2}{dar(k+a)^2}, \quad R = \frac{(k-a)^3}{8ark}\mu,$$

are derived from the normal form. A convenient parametrization is therefore

$$x(t) = x^* + R\cos\theta(t), \quad y(t) = y^* + \frac{R}{\sqrt{\kappa}}\sin\theta(t),$$

with $\dot{\theta} = \omega_0 + O(\mu)$.

3.2. **Numerical verification of the approximation.** We compared the input and output power estimated using the analytical approximation of Eq. (S6) with results obtained by numerically integrating the consumer-resource model of Eq. (S1) for a large time $T = 1200$. We find a good agreement between the analytical approximation and the exact numerical results across different consumption rates and assimilation efficiencies (Fig. S1).

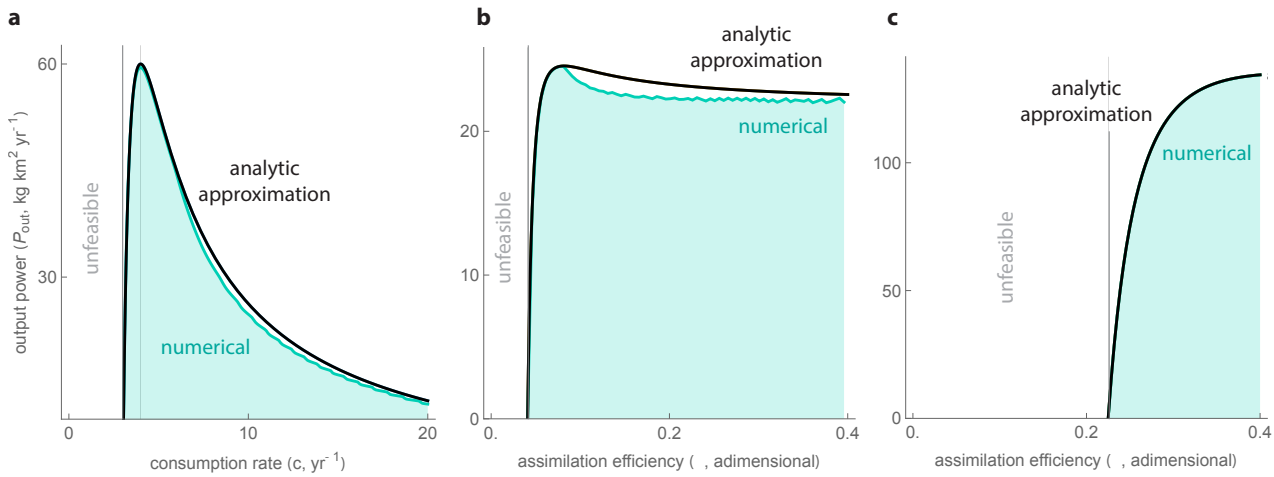


FIGURE S1. **Accuracy of the approximated input and output power.** Panels compare the analytic approximation of Eq. (S6) with estimation constructed by numerically integrating the differential equation of Eq. (6) for $T = 1200$ time units. Unless indicated otherwise, parameters of the model are as in Supplementary Table 1. **a.** Output power as a function of the consumption rate. **b.** Output power as a function of the assimilation efficiency $\varepsilon$. **c.** Output power as a function of the assimilation efficiency with a lower consumption rate $c = 2$.

## 4. Maximum output power

Here we calculate the maximum intake and assimilation efficiency that maximize output power. For this, we write

$$P_{\text{out}}(\varepsilon, c) = \varepsilon\ a\ dr\ \frac{(c\varepsilon - d) - ad/k}{(c\varepsilon - d)^2},$$

and calculate the first order conditions for optimality subject to the inherent constraints of each parameter.

4.1. **Optimal maximum intake.** The optimal maximum intake is $c^*(\varepsilon) = \max_c P_{\text{out}}(\varepsilon, c)$ subject to the feasibility condition of Eq. (S3). The first order condition $\mathrm{d}P_{\text{out}}/\mathrm{d}c = 0$ and solving for $c$ yields

$$c^*(\varepsilon) = \left(1 + \frac{2a}{k}\right)\frac{d}{\varepsilon} \tag{S8}$$

attaining $P^*_{\text{out}}(\varepsilon) = \varepsilon k$. The second derivative is

$$\frac{\mathrm{d}^2 P_{\text{out}}}{\mathrm{d}c^2} = -\frac{2adr\varepsilon^3(3ad + k(d - c\varepsilon))}{k(d - c\varepsilon)^4} < 0,$$

because feasibility implies $c\varepsilon - d > 0$. This implies that $c^*$ is indeed a maximum. Figure S2a illustrates the form of $P_{\text{out}}$ as a function of $c$, and the location of its maximum.

4.2. **Optimal assimilation efficiency.** The optimal maximum intake is $\varepsilon^*(c) = \max_\varepsilon P_{\text{out}}(\varepsilon, c)$ subject to the feasibility condition of Eq. (S3) and to $\varepsilon \in [0, 1]$. A similar calculation shows that

$$\varepsilon^*(c) = \begin{cases} \dfrac{k+a}{k-a}\dfrac{d}{c}, & \text{if } k > a \text{ and } c \geq \dfrac{k+a}{k-a}d \\ 1, & \text{otherwise} \end{cases} \tag{S9}$$

Figure S2b shows the three qualitatively different behaviors of $P_{\text{out}}$ as a function of $\varepsilon$. Note that $P_{\text{out}} = 0$ for $\varepsilon = 0$. When, $k < a$ the output power becomes an increasing function of $\varepsilon$ after the feasibility point. Thus, the optimal assimilation efficiency is $\varepsilon^* = 1$ (purple in Fig. S2b). When $c < \dfrac{k+a}{k-a}d$ the output power is a decreasing function of $\varepsilon$, so the system is never feasible (orange in Fig. S2b). Only when $k > a$ and $c \geq \dfrac{k+a}{k-a}d$ the output power has an interior maximum $\varepsilon^*$.

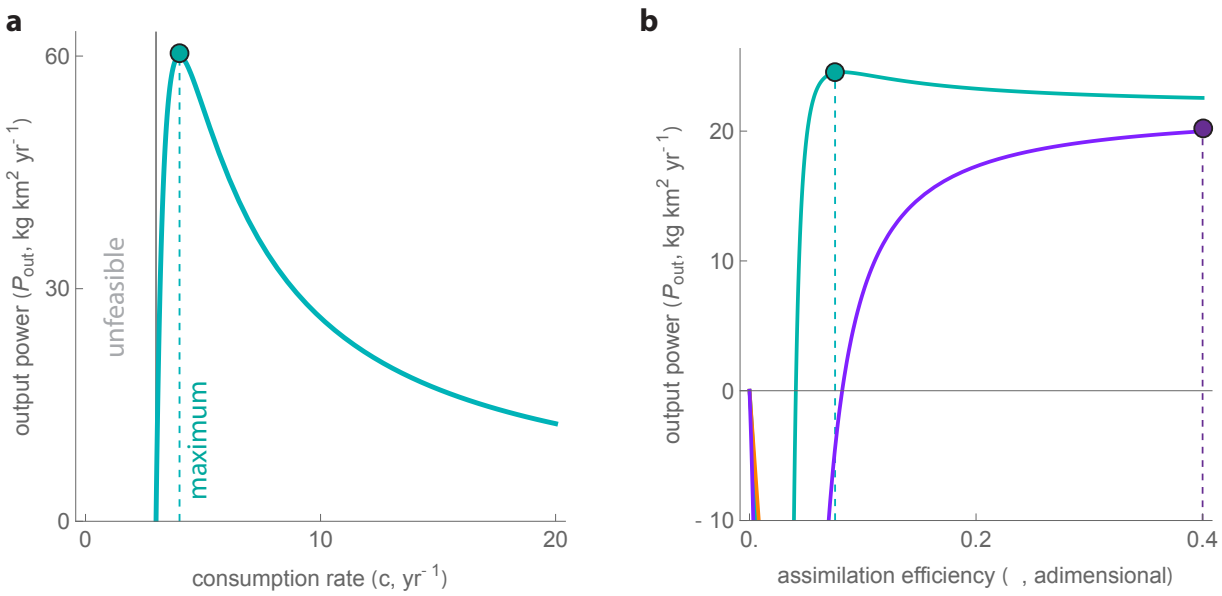


FIGURE S2. **Maximum output power.** Output power $P_{\text{out}}$ as a function of consumption rate $c$ and assimilation efficiency $\varepsilon$. Parameters are as in Table 1, expect for panel b ($k = a/2$ for the purple line, and $c = 0.5\frac{k+a}{k-a}d$ for the orange line).

## REFERENCES

[1] Hofbauer J, Sigmund K (1998) *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge).

[2] Kuznetsov YA, Kuznetsov IA, Kuznetsov Y (1998) *Elements of applied bifurcation theory* (Springer) Vol. 112.