

Energetic feasibility in ecological systems

Serguei Saavedra¹

CENTRAL QUESTION

How does ecological organization transform environmental resource inputs into system-level constraints on the energetic feasibility of multispecies systems?

ANSWER

Ecological organization transforms external resource inputs into coupled energetic constraints whose intersection defines a system-level feasibility domain. Its geometry depends on resource capture, internal routing, and productive capacity, and can generate a maximal feasible fraction at intermediate input. Recurrent microbial assemblages show a corresponding empirical signature, most frequently peaking at intermediate calorie intake.

FIELD MAP COORDINATES

Emergence; Energy, matter, and information; Persistence and fragility.

Abstract

Ecological systems persist by routing resource and energy fluxes through interacting components. Yet external supply alone does not determine whether a community can be sustained: resources must be captured, redistributed, and processed at rates that are jointly compatible across the system. Here we connect ecological energetics, consumer-resource theory, network ecology, and feasibility theory to ask which environmental conditions can energetically support a given ecological organization. This synthesis provides a common geometric representation in which saturating resource capture and internal flux routing translate component-level energetic constraints into a multispecies feasibility domain. Using microbial cross-feeding as a worked example, we show how ecological organization shapes this domain and how the fraction of feasible configurations changes with total input. Increasing input initially expands feasibility by relieving energetic limitation, whereas further input can reduce it when routed flux exceeds productive capacity and cannot be fully accommodated through storage, export, dissipation, or redistribution. This shift in the dominant constraint can generate an intermediate-input window in which the fraction of feasible configurations is maximized. A reanalysis of a longitudinal human gut microbiome reveals a corresponding empirical signature: recurrent microbial assemblages most frequently reach their highest occurrence frequencies at intermediate caloric intake across community sizes. By connecting concepts and theories that are often treated separately, this synthesis shows that energetic feasibility is a systems-level property arising from the interplay between environmental supply, internal flux routing, and ecological organization.

Introduction

Ecological organization is sustained by energy flux [1, 2]. Resources enter through particular pathways, are captured and transformed by organisms, and are transferred, secreted, recycled, respired, or exported through ecological interactions [3]. The persistence of a food web, microbial consortium, or producer–consumer system therefore depends not only on how much resource enters the environment, but also on whether the resulting flows can be accommodated across the interacting system. This idea has deep roots in trophic energetics and ecosystem ecology and underlies consumer–resource, stoichiometric, and metabolic approaches to ecological organization [1, 4–9]. Yet these traditions leave a broad systems-level question difficult to answer: given a specified ecological organization, which environmental resource-input rates can be captured and routed through the system while remaining compatible with the energetic requirements of all its components?

This question also connects ecology to a broader thermodynamic view of living organization. Living systems are open systems that acquire free energy from their environment, transform it through organized pathways, and ultimately dissipate or export energy and matter while maintaining internal organization [10–12]. Morowitz emphasized that non-equilibrium steady states require organized fluxes and cycles rather than

static energetic inventories [10], and later work developed this view of energy flow as constitutive of biological organization [11]. Importantly, thermodynamic constraints do not act alone: kinetic limits, chemical mechanisms, and the finite pathways through which living systems construct, process, store, and degrade material can impose tighter proximal constraints on realized biological fluxes [12]. At the ecological scale, this suggests that the relevant question is not only how much energy is supplied, but whether the organization of the system can capture, route, process, and dissipate the resulting flux.

This question matters because environmental inputs vary naturally and are increasingly altered by human activities. Agriculture modifies nutrient and water inputs to increase production; restoration can supplement nutrients, water, or organic matter, or food-web subsidies; eutrophication reflects altered nutrient loading; and climate change modifies the magnitude, timing, and balance of metabolic and biogeochemical fluxes [13–18]. Throughout this paper, resource supply refers specifically to an external input rate. It does not denote standing biomass or carrying capacity and should not be conflated with “enrichment” as commonly represented in the paradox-of-enrichment literature [19]. External supply, however, is only the beginning of the energetic constraint. Additional input can relieve limitation when a required resource is scarce, but resources must subsequently be captured, processed, and routed through the system. Biomass production requires complementary materials, organisms differ in maintenance and processing rates, and material that cannot be productively accommodated by one population may be secreted, exported, or become a resource for another. Microbial cross-feeding makes this distinction especially transparent: externally supplied substrates may enter only a subset of populations, whereas metabolites produced by those populations can support others that never access the original substrate directly [20–22]. Consequently, identical environmental inputs can generate very different internal energetic conditions depending on ecological organization.

The same systems logic extends beyond microbial cross-feeding, although the specific bookkeeping of transfers depends on the mechanism. In food webs, energy enters through primary production or basal resources and is redistributed through trophic interactions, with losses at each transfer [1, 3]. In mutualisms, reciprocal exchanges can couple the energetic or material budgets of interacting partners, whereas detrital systems route production through organic matter, decomposers, and recycled nutrients [3, 7]. Competitors need not exchange material directly, yet their energetic conditions become coupled through shared resource pools [5, 6]. These mechanisms differ in how flux is transferred, but they share a common systems structure: external input rates are distinct from the internal fluxes experienced by the components of an ecological system. In some systems, such as cross-feeding, secretion, or recycling, processing by one component generates usable flux for another; in others, such as direct trophic transfer, the bookkeeping must also distinguish the energy retained by the donor from that transferred to the recipient. The common systems problem is to determine how external inputs are transformed by ecological organization into the

internal fluxes experienced by interacting components.

The first step in this transformation is resource capture, which links external input to internal flux. A high external input rate does not imply an arbitrarily high biological uptake rate because functional responses, transport, handling, enzyme kinetics, and other physiological processes impose finite rates of capture [12, 23]. Ecological interactions then redistribute the flux that has entered the biological system rather than the external input itself. This distinction separates three processes that are often considered independently: external input, biological capture, and redistribution through ecological organization. Bringing them together raises the central systems-level question: can the resulting flows simultaneously satisfy the energetic requirements of all interacting components?

We call an environmental condition *energetically feasible* when the energetic requirements of all components can be met simultaneously for a specified ecological organization. Energetic feasibility therefore asks whether energetic and resource-flow constraints alone rule out a given configuration. This perspective connects the mechanistic tradition of MacArthur–Tilman consumer–resource theory and zero-net-growth isoclines with feasibility-domain approaches [6, 24–30]. Geometrically, environmental input rates define the coordinates, while component-level energetic constraints generated after capture and internal routing define the boundaries. Their intersection defines the system-level energetic-feasibility domain.

Here we develop this framework in three steps. We first formulate the mapping from environmental inputs to system-level energetic feasibility and define the corresponding feasibility domain. We then use microbial cross-feeding as a worked example to show how ecological organization shapes that domain and how its feasible cross-section changes with total input. This reveals a mechanism by which the feasible fraction can peak at intermediate input as the dominant constraint shifts from insufficient supply to limited accommodation of excess flux. Finally, we reanalyze a longitudinal human gut microbiome to ask whether recurrent assemblages show a qualitative empirical signature of this intermediate-input pattern [31]. Together, these analyses connect ecological energetics, network organization, and feasibility theory within a common systems-level framework.

From environmental input to ecological energetic flux

An external input rate is not the energetic rate experienced by an organism. Before an external resource can support growth, maintenance, or exchange, it must first be captured and converted into biologically usable flux [2]. Resource capture therefore provides the first link between external input and ecological organization. This distinction between input and capture matters because capture is often bounded: beyond some range, increasing external input need not produce a proportional increase in the rate at which organisms capture the resource [5, 6, 23].

Let

$$Q = (Q_1, \dots, Q_p)^T \geq 0 \quad (1)$$

denote the external input vector for p distinct external resources or substrates, where Q_α is the external input rate of resource α . Let $U_\alpha(Q_\alpha)$ denote the rate at which resource α is captured and e_α the efficiency with which captured resource is converted into biologically usable energetic flux. We write

$$J_\alpha(Q_\alpha) = e_\alpha U_\alpha(Q_\alpha) = J_{\alpha,\max} \frac{Q_\alpha}{K_\alpha + Q_\alpha}, \quad (2)$$

where $J_\alpha(Q_\alpha)$ is the captured energetic flux generated from external resource α , $J_{\alpha,\max}$ is its maximum value, and K_α is the external input rate at which J_α reaches one-half of $J_{\alpha,\max}$. Thus, Q_α denotes the external input rate whereas J_α denotes the part of that input captured and converted into a form available to the ecological system.

Equation (2) is a simplified mapping from external input rate to captured energetic flux: it relates the two directly without explicitly modelling the intervening resource pool or uptake dynamics. Standard Holling or Monod kinetics instead act on resource concentration. The particular saturating form is not essential to the framework. What matters for the general construction is an explicit mapping from external input to biological capture. The form used here additionally assumes $J_\alpha(0) = 0$, increasing capture over the relevant range, and a finite upper capture rate (Fig. 1).

Captured flux then enters the ecological system through particular components and is redistributed by ecological interactions (Fig. 1). Let H be the entry matrix, with $H_{i\alpha}$ denoting the fraction of captured flux from external resource α that enters population i . Thus, one external resource can be captured by several populations and one population can receive several external resources. We require $H_{i\alpha} \geq 0$ and $\sum_i H_{i\alpha} \leq 1$ for every resource α , so captured external flux is not duplicated at entry. Let T be the routing matrix describing how flux generated by processing in one population becomes usable input to another. Writing $J(Q)$ for the vector of captured energetic fluxes and I for the vector of incoming energetic fluxes, flux balance requires

$$I = HJ(Q) + TI. \quad (3)$$

Here, $HJ(Q)$ is the captured energetic flux entering populations directly from external resources, whereas TI is usable flux generated elsewhere and received through internal routing. Equation (3) is a simultaneous balance relation: processing at one component can generate a by-product or other usable flux for another component, where it contributes to the recipient's incoming energetic flux. We interpret T_{ij} as an effective routing fraction: the fraction of incoming flux processed by donor j that subsequently becomes usable input to recipient i through secretion, cross-feeding, recycling, or another by-product pathway. Physical routing requires $T_{ij} \geq 0$ and $\sum_i T_{ij} \leq 1$ for every donor j ; the remainder is retained, respired, dissipated, excreted, or exported from the routed network. In this reduced formulation, routed flux represents usable output generated by donor processing. Direct trophic transfer, in which transferred energy is no longer available to the donor, requires an explicit partition between donor retention and transfer rather than using Eq. (3) unchanged.

Rearranging the balance relation,

$$(\mathbb{I} - T)I = HJ(Q),$$

gives

$$I = (\mathbb{I} - T)^{-1} HJ(Q), \quad (4)$$

where $\mathbb{I}$ denotes the identity matrix. The inverse $(\mathbb{I} - T)^{-1}$ accounts for both direct and indirect routing through the ecological network. When repeated circulation converges,

$$(\mathbb{I} - T)^{-1} = \mathbb{I} + T + T^2 + T^3 + \dots$$

Thus, $HJ(Q)$ represents captured environmental flux at its points of entry, $THJ(Q)$ represents flux received after one internal transfer, $T^2HJ(Q)$ represents flux received after two transfers, and higher-order terms represent progressively longer internal routing sequences. Reciprocal exchange is therefore allowed, provided repeated circulation remains finite; the corresponding convergence condition is given in Methods. Equation (4) provides the systems-level link between external inputs and local energetic conditions. External input rates are first converted into captured energetic flux through $J(Q)$; ecological organization, encoded by H and T , then determines how that flux is distributed across the interacting system. The same external input vector can therefore generate different energetic conditions under different ecological organizations.

Energetic input must next be compatible with the capacities of the receiving components. Population i has a minimum energetic requirement m_i and a productive capacity C_i [7, 9, 23]. In the present reduced formulation, both constraints are applied to the incoming processing flux I_i ; that is, m_i and C_i constrain gross incoming flux rather than a separately computed post-routing retained pool. For the energetic-window formulation below, we assume $0 < m_i < C_i$; if $C_i \leq m_i$, the component has no positive-margin productive regime under this reduced description. Finite productive capacity is consistent with the broader distinction between ultimate thermodynamic constraints and tighter proximal limits imposed by kinetics, chemical mechanisms, and biological processing pathways [12]. Below m_i , incoming flux is insufficient to maintain the specified population. Between m_i and C_i , additional flux can be productively accommodated. At C_i , productive processing saturates. Importantly, crossing C_i does not itself imply energetic failure. Excess flux may instead be stored, respired, excreted, exported, or redirected through the ecological network [7, 9, 22].

We therefore distinguish excess flux from its biological consequence. To measure whether the incoming energetic flux experienced by population i is compatible with its requirements, we define an *energetic margin* $g_i(I_i)$. Below productive capacity, the margin is the incoming flux remaining after the minimum energetic requirement m_i has been met. Above C_i , the margin depends on how much of the excess flux can be accommodated without reducing energetic compatibility. Let $\epsilon_i \geq 0$ quantify the residual reduction in energetic margin per unit of excess incoming flux that remains

unaccommodated by these processes. We then write

$$g_i(I_i) = \begin{cases} I_i - m_i, & I_i \leq C_i, \\ C_i - m_i - \epsilon_i(I_i - C_i), & I_i > C_i. \end{cases} \quad (5)$$

Because g_i and I_i are expressed in the same rate units, ϵ_i is dimensionless in this formulation.

The energetic margin therefore increases while additional incoming flux relieves energetic limitation and reaches its maximum value $C_i - m_i$ when productive capacity is reached. Crossing C_i does not itself imply energetic failure. If $\epsilon_i = 0$, excess flux is fully accommodated in this reduced description and the margin remains at $C_i - m_i$. If $\epsilon_i > 0$, accommodation is incomplete and each additional unit of unresolved excess flux reduces the energetic margin by ϵ_i . The upper energetic-feasibility boundary is reached when this remaining margin is exhausted. Setting the second branch of Eq. (5) equal to zero,

$$C_i - m_i - \epsilon_i(I_i - C_i) = 0,$$

gives

$$I_i^+ = C_i + \frac{C_i - m_i}{\epsilon_i}, \quad \epsilon_i > 0. \quad (6)$$

Thus, C_i marks where excess flux begins, whereas I_i^+ marks where the energetic consequence of that excess has used up the population's entire margin. For $\epsilon_i > 0$, population i is energetically compatible with incoming rates in the interval

$$m_i < I_i < I_i^+.$$

Equation (6) therefore defines an upper energetic threshold in incoming-flux space. Whether it produces an upper boundary in external-input space depends on whether the input, capture, and routing functions can deliver sufficient flux for population i to reach I_i^+ . If the maximum attainable incoming flux remains below I_i^+ , the local upper threshold is never reached and does not generate an environmental feasibility boundary. Thus, a component-level upper threshold becomes a boundary of the environmental feasibility domain only when it is reachable through the mapping from external inputs to internally routed fluxes. Together, m_i , C_i , and ϵ_i distinguish the minimum energetic requirement, the onset of productive saturation, and the consequence of flux that cannot be productively accommodated.

The biological origins of these constraints depend on the system. Productive capacity may reflect finite handling and assimilation, metabolic throughput, stoichiometrically constrained production, or other rate-limiting processes [7, 9, 12, 23]. A positive ϵ_i arises when incoming flux exceeds productive and regulatory capacities and accommodating the residual flux carries an energetic cost. In microbes, this can occur through overflow metabolism when respiratory or biosynthetic capacity becomes limiting [32]; in consumers, stoichiometric imbalance can require respiration, excretion, or other regulatory processes [9]. Thus, ϵ_i is not a universal physiological constant or an intrinsic toxicity of high resource supply, but a reduced representation of *limited excess-flux accommodation*. If excess can be stored, exported, dissipated, or redirected without reducing the focal component's

energetic margin, $\epsilon_i = 0$ and the margin plateaus after C_i ; if accommodation is incomplete, $\epsilon_i > 0$ represents the remaining energetic burden [7, 21, 22]. Saturating resource capture alone therefore produces saturation, not impairment [23]. A high-input loss of feasibility requires finite productive capacity together with a positive consequence of unresolved excess flux.

A positive energetic margin means that the energetic requirements represented by the model can be met, $g_i = 0$ defines an energetic boundary, and $g_i < 0$ means that energetic constraints alone rule out the population in the specified configuration. We use the strict condition $g_i > 0$ to define the interior of the feasibility domain; including $g_i = 0$ adds only its boundary and does not change the volume-based quantities considered below. The margin is therefore not an invasion growth rate or a criterion for dynamical stability. It is a rate-space measure of energetic compatibility.

The component-level margins generate the system-level geometry. Through Eqs. (2), (4), and (5), every margin is ultimately a function of the external input vector,

$$Q \longrightarrow J(Q) \longrightarrow I(Q) \longrightarrow g(Q).$$

We therefore write the general system-level feasibility margin as

$$G(Q) = \min_i g_i[I_i(Q)]. \quad (7)$$

Population i permits the external-input domain

$$D_i = \{Q \geq 0 : g_i[I_i(Q)] > 0\}. \quad (8)$$

A specified ecological organization is energetically feasible only when all component requirements are satisfied simultaneously. Its energetic-feasibility domain is therefore

$$D_E = \bigcap_{i=1}^n D_i = \{Q \geq 0 : G(Q) > 0\}. \quad (9)$$

This intersection is the central systems-level object of the framework. It identifies the environmental input rates compatible with the whole ecological organization after resource capture and internal routing have transformed external supply into local energetic conditions. Its existence indicates whether compatible energetic flows are possible; its shape reveals which combinations of environmental inputs are permitted and which components constrain their boundaries.

Existence alone, however, does not indicate how restrictive the domain is. Relative to a specified environmental reference region E , we define

$$V_E = \text{Vol}(D_E \cap E), \quad \Omega_E = \frac{V_E}{\text{Vol}(E)}. \quad (10)$$

The normalized volume Ω_E measures the fraction of the external-input space under consideration that is energetically compatible with the specified ecological organization. It is a geometric measure rather than, by itself, a probability. It equals the probability of feasibility only if all input conditions within E are equally likely; otherwise, each condition must be weighted by how often it occurs [30].

A complementary measure asks how feasibility changes with total environmental input [33]. Let

$$Q_{\text{tot}} = \sum_{\alpha=1}^P Q_{\alpha}, \quad S_E(Q_{\text{tot}}) = \left\{ Q \in E : \sum_{\alpha=1}^P Q_{\alpha} = Q_{\text{tot}} \right\}. \quad (11)$$

The slice $S_E(Q_{\text{tot}})$ contains all allocations among external resources having the same total input. We define the conditional feasible fraction

$$\Phi_E(Q_{\text{tot}}) = \frac{\text{Vol}_{p-1}[D_E \cap S_E(Q_{\text{tot}})]}{\text{Vol}_{p-1}[S_E(Q_{\text{tot}})]}. \quad (12)$$

This quantity is defined for values of Q_{tot} such that $\text{Vol}_{p-1}[S_E(Q_{\text{tot}})] > 0$. Whereas Ω_E measures the overall extent of the energetic-feasibility domain, $\Phi_E(Q_{\text{tot}})$ measures the fraction of allocation space that remains feasible at a given total input. For two external resources, the fixed-total-input set is a line segment; for three it is a triangle; and for general p it is a $(p-1)$ -dimensional simplex in the nonnegative orthant [28]. Its intersection with E defines the potentially truncated slice $S_E(Q_{\text{tot}})$ [30]. This distinction between the

full feasibility domain and its constant-input cross-sections will allow us to ask when increasing external input expands the set of energetically compatible configurations and when it instead contracts it.

Figure 1 summarizes the framework using the six-population routing topology developed later as a worked example. External input rates Q_{α} are converted into captured energetic fluxes $J_{\alpha}(Q_{\alpha})$, the entry matrix H determines which populations receive those captured resources directly, and the routing matrix T redistributes usable by-product flux through the ecological network. The resulting incoming energetic flux I_i determines the component margin $g_i(I_i)$, and the ecological organization is energetically feasible only when all component margins are positive. We now make each transformation explicit using the smallest system in which internal routing alters component-level energetic conditions: two populations linked by reciprocal cross-feeding. Because this system has a single external input, the full sequence from capture and routing to component constraints and joint feasibility can be followed analytically before extending the same construction to a multispecies network.

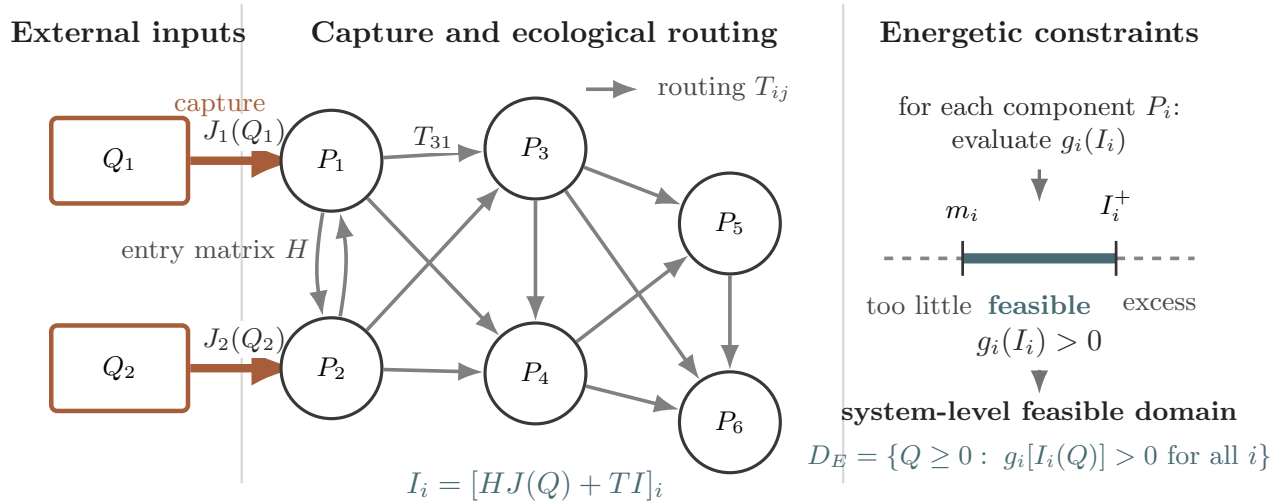


Figure 1: From external input to system-level energetic feasibility. External resource inputs Q_{α} are converted by capture functions into captured energetic fluxes $J_{\alpha}(Q_{\alpha})$. The entry matrix H determines which ecological components receive those resources directly, while the routing matrix T redistributes usable by-product flux among components. Each component P_i therefore experiences an incoming energetic flux I_i , which is mapped to a component energetic margin $g_i(I_i)$. In the six-population microbial example developed below, the generic components $P_1, \dots, P_6$ correspond to populations $M_1, \dots, M_6$. The system-level energetic-feasibility domain is $D_E = \{Q \geq 0 : g_i[I_i(Q)] > 0 \text{ for all } i\}$. Routing fractions for the illustrated topology are given in Methods.

A reciprocal two-population example

Consider two microbial populations, M_1 and M_2 . Only M_1 directly captures an external substrate supplied at rate Q . Following Eq. (2), let the resulting usable energetic flux be

$$J(Q) = 3.2 \frac{Q}{1.15 + Q}. \quad (13)$$

Thus, increasing environmental supply initially increases captured flux, but $J(Q)$ approaches the finite limit 3.2 as Q becomes large.

The captured flux is subsequently redistributed through reciprocal cross-feeding. Population M_1 makes a fraction $a = 0.12$ of its processed flux available to M_2 , while M_2 returns a fraction $b = 0.10$ through a different metabolite. The total incoming energetic rates satisfy the simultaneous

balance relations

$$I_1 = J(Q) + bI_2, \quad I_2 = aI_1. \quad (14)$$

Solving these equations gives

$$I_1(Q) = \frac{J(Q)}{1-ab}, \quad I_2(Q) = \frac{aJ(Q)}{1-ab}. \quad (15)$$

Because $ab = 0.012 < 1$, successive rounds of reciprocal routing converge. The factor $(1-ab)^{-1}$ accounts for direct and repeated contributions of this exchange, analogous to the network inverse in Eq. (4). Reciprocal routing therefore recirculates part of the captured flux without generating energy: only a fraction of processed flux remains available at each transfer. Equations (13)–(15) make the first two transformations of the framework explicit. Environmental input Q first becomes the bounded captured flux $J(Q)$; ecological routing then transforms that flux into the local incoming rates $I_1(Q)$ and $I_2(Q)$. As $Q \rightarrow \infty$, $J(Q) \rightarrow 3.2$, and both incoming rates consequently approach finite limits.

We next ask which environmental input rates make these routed flows compatible with both populations. Let $(m_1, C_1) = (0.62, 2.20)$ and $(m_2, C_2) = (0.20, 0.60)$ and, for illustration, set $\epsilon_1 = \epsilon_2 = 3.0$. Substituting Eq. (15) into the energetic-margin definition gives

$$g_1(Q) = \begin{cases} I_1(Q) - 0.62, & I_1(Q) \leq 2.20, \\ 1.58 - 3.0[I_1(Q) - 2.20], & I_1(Q) > 2.20, \end{cases} \quad (16)$$

and

$$g_2(Q) = \begin{cases} I_2(Q) - 0.20, & I_2(Q) \leq 0.60, \\ 0.40 - 3.0[I_2(Q) - 0.60], & I_2(Q) > 0.60. \end{cases} \quad (17)$$

At low incoming flux, each margin increases as additional energy relieves limitation. The margin is largest when incoming flux reaches productive capacity C_i . Beyond that point, productive use has saturated and unresolved excess reduces the margin at rate ϵ_i . Importantly, C_i is not itself a feasibility boundary: a population remains energetically compatible with the specified organization until its margin reaches zero at I_i^+ .

The environmental feasibility window can now be obtained analytically. At low input, M_2 sets the system-level boundary. Because M_2 receives no external resource directly, its minimum energetic requirement can be met only through flux routed from M_1 . Setting $I_2(Q_{\text{low}}) = m_2$ in Eq. (15) first gives the captured flux required at the boundary,

$$J_{\text{low}} = \frac{m_2(1-ab)}{a}.$$

For the capture function $J(Q) = J_{\text{max}}Q/(K+Q)$, inversion gives

$$Q = K \frac{J}{J_{\text{max}} - J}.$$

Therefore,

$$Q_{\text{low}} = K \frac{J_{\text{low}}}{J_{\text{max}} - J_{\text{low}}} \simeq 1.22.$$

This expression makes explicit that the low-input boundary depends on the minimum requirement of the recipient and on the routing fraction a . Below this value, insufficient routed flux reaches M_2 , so the specified two-population organization is energetically infeasible even though the externally supplied population M_1 can already satisfy its own requirement.

At high input, the system-level boundary is instead set by M_1 . From Eq. (6),

$$I_1^+ = C_1 + \frac{C_1 - m_1}{\epsilon_1} = 2.20 + \frac{2.20 - 0.62}{3} \simeq 2.727.$$

Setting $I_1(Q_{\text{high}}) = I_1^+$ in Eq. (15) gives

$$J_{\text{high}} = (1-ab)I_1^+,$$

and hence

$$Q_{\text{high}} = K \frac{(1-ab)I_1^+}{J_{\text{max}} - (1-ab)I_1^+} \simeq 6.12.$$

Beyond this input, the energetic consequence of excess flux exhausts the margin of M_1 , making the specified two-population organization energetically infeasible. At this boundary, M_2 has not crossed its own local energetic boundary. This does not mean that M_2 remains independently viable: its incoming flux depends on processing and routing by M_1 . Once the constraint on M_1 is violated, the coupled organization containing both populations is no longer energetically feasible. The framework identifies which component sets a system-level boundary; it does not describe the subsequent dynamics of community collapse.

For this two-population system, the general system-level margin in Eq. (7) becomes

$$G(Q) = \min\{g_1(Q), g_2(Q)\}. \quad (18)$$

The two-population system is therefore energetically feasible only over the bounded external-input interval

$$Q_{\text{low}} < Q < Q_{\text{high}}, \quad 1.22 \lesssim Q \lesssim 6.12. \quad (19)$$

This simple result illustrates why energetic feasibility is a property of the ecological organization rather than of any component considered in isolation. Different populations set opposite boundaries of the same system-level window: M_2 determines the minimum environmental input required to sustain the coupled organization, whereas M_1 determines its maximum. Violation of either component constraint makes the entire specified organization infeasible.

Figure 2 follows this construction from external input to system-level feasibility. Fig. 2A shows the sequence $Q \mapsto J(Q) \mapsto I_i(Q)$: external input is first transformed by saturating capture and then redistributed by reciprocal routing. Fig. 2B shows how those incoming rates determine the component-level margins and their minimum $G(Q)$. The shaded interval identifies the environmental conditions for which both margins are positive. Saturating capture bounds the amount of energetic flux entering the system, whereas C_i marks the onset of productive saturation after that flux has been routed. Neither mechanism alone makes high input

detrimental. The upper feasibility boundary appears only because excess flux is not fully accommodated ($\epsilon_i > 0$). If storage, export, dissipation, or redistribution were sufficient

to make $\epsilon_i = 0$, the high-input branch would plateau rather than decline.

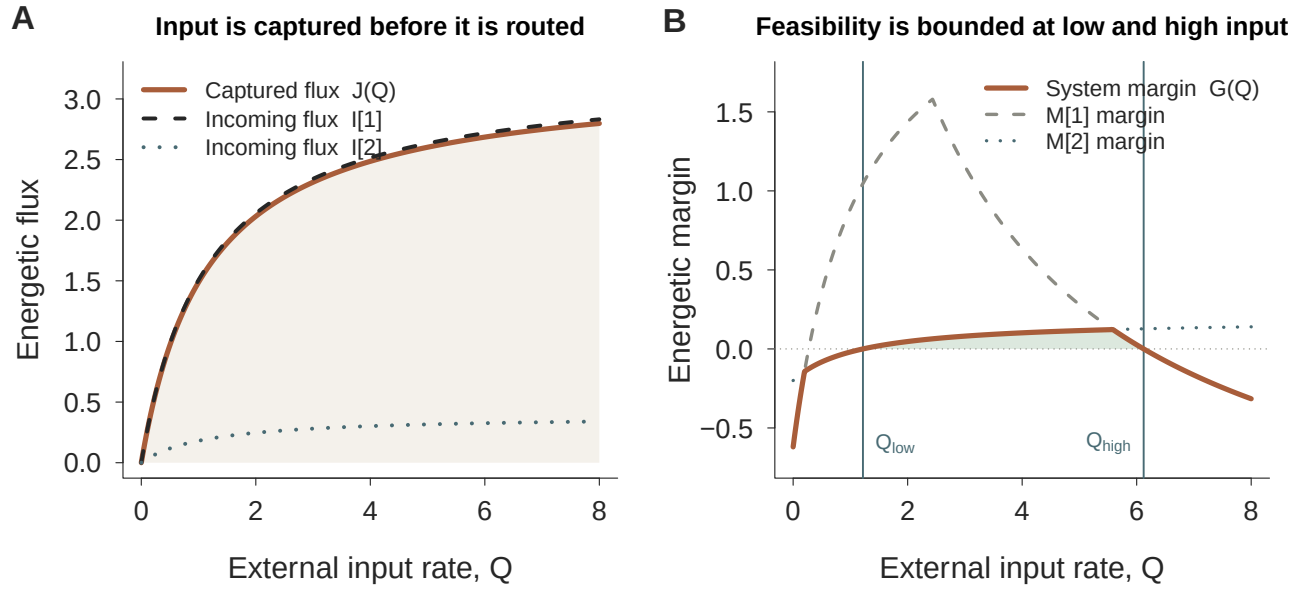


Figure 2: A bounded energetic-feasibility window emerges from capture, routing, and component-level constraints. A, environmental input Q is converted into the saturating captured flux $J(Q)$ and redistributed by reciprocal routing into the incoming rates $I_1(Q)$ and $I_2(Q)$. **B,** the resulting energetic margins define a bounded system-level feasibility window. At low input, the boundary is set by insufficient routed flux reaching M_2 ($Q_{low} \approx 1.22$); at high input, it is set by the energetic consequence of excess flux at M_1 ($Q_{high} \approx 6.12$). The thick curve is the system-level margin $G(Q) = \min\{g_1(Q), g_2(Q)\}$, and the shaded region denotes $G(Q) > 0$. Violation of either component constraint makes the coupled organization energetically infeasible.

The two-population example reduces the full framework to a single external-input axis, making each transformation and both feasibility boundaries analytically visible. With several external resources and a larger network, however, these one-dimensional boundaries become surfaces whose intersection defines a multidimensional domain. Multiple bounded inputs can converge on the same population, different components can constrain different parts of the boundary, and changing ecological organization can reshape the set of environmental conditions compatible with the whole system. We therefore turn next to a multi-population microbial network to construct and measure this energetic-feasibility geometry explicitly.

A worked multispecies microbial network

The reciprocal pair shows how a bounded feasibility window can emerge along a single environmental axis. With several external inputs and a larger network, the same component-level constraints generate a multidimensional object: different combinations of environmental inputs produce different routed fluxes, and the ecological system is feasible only where all component requirements are satisfied simultaneously. We illustrate this geometry with six microbial populations and two externally supplied substrates (Fig. 3). The parameters are illustrative rather than fitted to a particular consortium; their purpose is to make the construction transparent while retaining the systems structure of multiple inputs, internal

routing, and coupled energetic constraints.

Let Q_1 be an external substrate captured directly by M_1 and Q_2 a second substrate captured directly by M_2 . Following Eq. (2), their captured energetic fluxes are

$$J_1(Q_1) = 3.2 \frac{Q_1}{1.15 + Q_1}, \quad J_2(Q_2) = 3.0 \frac{Q_2}{1.35 + Q_2}. \quad (20)$$

The remaining four populations receive no environmental substrate directly and are supported entirely by internally routed flux. The environmental system therefore has only two input coordinates, (Q_1, Q_2) , but ecological organization transforms them into six local energetic conditions.

For the routing network specified in Methods, Eq. (4) gives

$$\begin{aligned} I_1 &= 1.01215J_1 + 0.10121J_2, \\ I_2 &= 0.12146J_1 + 1.01215J_2, \\ I_3 &= 0.25992J_1 + 0.16599J_2, \\ I_4 &= 0.15879J_1 + 0.28988J_2, \\ I_5 &= 0.06989J_1 + 0.05971J_2, \\ I_6 &= 0.05814J_1 + 0.07603J_2. \end{aligned} \quad (21)$$

These coefficients summarize the direct and indirect routing pathways connecting environmental capture to each population. They are determined by the network rather than fitted

as response slopes. Because J_1 and J_2 saturate, every incoming rate I_i remains bounded even as the corresponding environmental input rates continue to increase. At the particular environmental condition $(Q_1, Q_2) = (2, 2)$, for example, Eq. (20) gives $J_1 = 2.0317$ and $J_2 = 1.7910$, yielding

$$I = (2.2377, 2.0596, 0.8254, 0.8418, 0.2489, 0.2543)^T. \quad (22)$$

Thus, two environmental input rates become six distinct energetic conditions after capture and network routing. A different ecological organization exposed to the same (Q_1, Q_2) would generally generate a different vector I .

To determine whether these incoming rates are compatible with the specified community, we assign

$$m = (0.62, 0.60, 0.35, 0.34, 0.23, 0.10)^T, \quad (23)$$

and

$$C = (2.20, 2.15, 0.95, 0.95, 0.33, 0.27)^T, \quad (24)$$

$$\epsilon_i = 3.0 \quad \text{for all } i.$$

As in the two-population example, these values are illustrative. Population M_5 is assigned a comparatively high minimum requirement ($m_5 = 0.23$) relative to the flux it receives through the network. This makes it a restrictive downstream component and allows the multispecies example to show explicitly how adding component-level constraints can contract the system-level feasibility domain. The common value $\epsilon_i = 3.0$ makes the energetic consequence of unresolved excess explicit rather than representing a universal physiological parameter.

At $(Q_1, Q_2) = (2, 2)$, all six populations have positive energetic margins. Population M_1 lies slightly above its productive capacity, whereas the remaining populations lie below theirs. Thus, the second branch of Eq. (5) applies to M_1 and the first branch to M_2 – M_6 . For example,

$$g_1 = 2.20 - 0.62 - 3.0(2.2377 - 2.20) = 1.4669, \quad (25)$$

$$g_5 = 0.2489 - 0.23 = 0.0189.$$

and the complete margin vector is

$$g = (1.4669, 1.4596, 0.4754, 0.5018, 0.0189, 0.1543)^T. \quad (26)$$

All six margins are positive, so this environmental condition lies inside the community energetic-feasibility domain. The smallest margin belongs to M_5 , identifying it as the component closest to the system-level boundary at this particular point. This does not imply that M_5 defines every boundary of the domain: as environmental inputs change, different populations can become limiting.

The distinction between productive capacity and energetic

failure remains important in the multispecies system. If, for example, $I_5 = 0.35 > C_5 = 0.33$, then

$$g_5 = (0.33 - 0.23) - 3.0(0.35 - 0.33) = 0.040. \quad (27)$$

Population M_5 therefore remains energetically compatible even though its productive capacity has been exceeded. It reaches its upper energetic boundary only when the consequence of unresolved excess exhausts the margin $C_5 - m_5$. Productive capacity C_i consequently marks a change in energetic regime rather than the edge of the feasibility domain.

Each population translates this local energetic window into a constraint on environmental input space. For M_1 , Eq. (6) gives $I_1^+ = 2.7267$, so

$$0.62 < 1.01215J_1(Q_1) + 0.10121J_2(Q_2) < 2.7267. \quad (28)$$

For M_5 , $I_5^+ = 0.3633$, giving

$$0.23 < 0.06989J_1(Q_1) + 0.05971J_2(Q_2) < 0.3633. \quad (29)$$

The remaining populations generate analogous constraints. Each therefore permits a region of (Q_1, Q_2) space bounded below by insufficient energetic input and, when $\epsilon_i > 0$, above by the energetic consequence of excess flux. The contour $I_i = C_i$ lies inside this region and marks the onset of productive saturation, not energetic failure. Because environmental input is transformed through saturating capture before routing, these boundaries are curved in (Q_1, Q_2) space even though Eq. (21) is linear in the captured fluxes.

The system-level energetic-feasibility domain is the intersection of all six population-specific regions (Fig. 3). Fig. 3A illustrates the geometric logic using the first two populations: their constraints define a relatively broad joint region of environmental conditions. Analogously to Eq. (10), we denote the normalized area of this two-component intersection by $\Omega_{12} = \text{Vol}[(D_1 \cap D_2) \cap E] / \text{Vol}(E)$. Fig. 3B then imposes all six population constraints simultaneously. The downstream requirement of M_5 removes a substantial portion of the region permitted by M_1 and M_2 , making explicit how an additional component can become restrictive at the system level. The resulting intersection is D_E , the set of environmental input combinations that can be captured and routed through the specified organization while maintaining positive energetic margins for every component. Different portions of its boundary can therefore be set by different populations, generalizing the switch between M_2 and M_1 that bounded the one-dimensional window in Figure 2. Correspondingly, the normalized feasible area decreases from $\Omega_{12} \approx 0.341$ for the first two component constraints to $\Omega_E \approx 0.207$ when all six constraints are imposed.

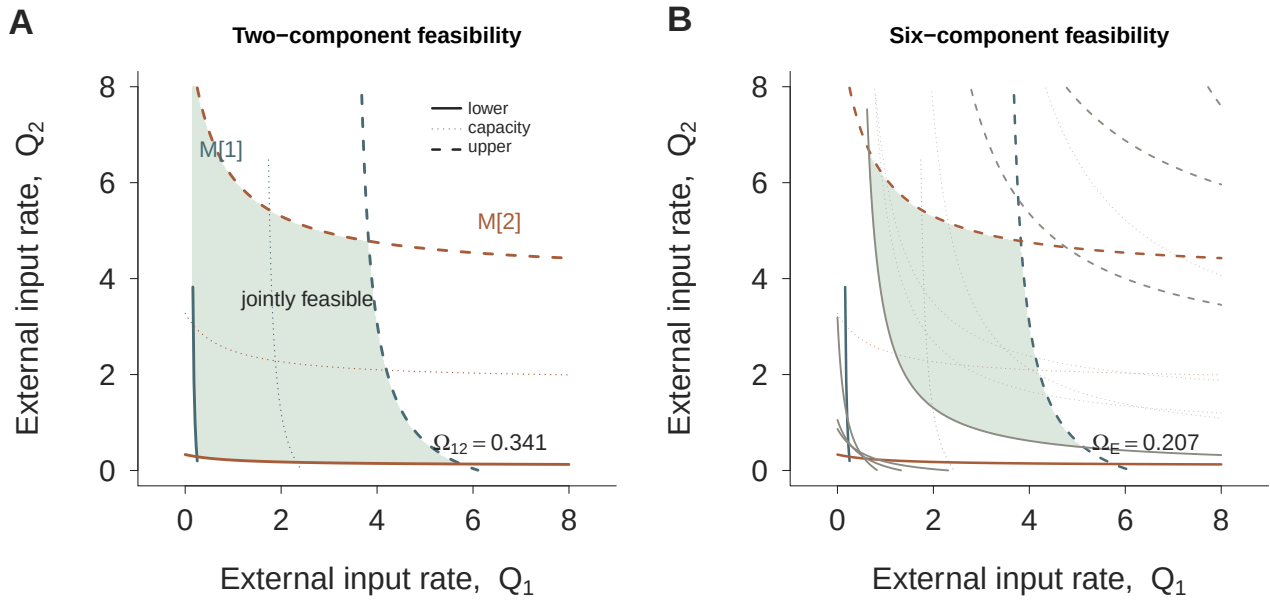


Figure 3: Component-level energetic constraints intersect to define a multispecies feasibility domain. **A**, the constraints of M_1 and M_2 define a relatively broad region of environmental input combinations compatible with both populations. **B**, adding the remaining component constraints contracts this region; in the illustrative parameterization, the comparatively high minimum requirement of downstream population M_5 is particularly restrictive. The six-population system is energetically feasible only where all six population-specific regions overlap. Solid and dashed curves denote lower and upper energetic-feasibility boundaries, respectively. Productive-capacity contours lie within these regions and mark the onset of excess rather than feasibility boundaries. Saturating resource capture makes the boundaries curved in environmental input space. The shaded intersection is the system-level energetic-feasibility domain D_E .

A nonempty domain establishes that some environmental conditions can support the specified organization, but it does not indicate how restrictive those conditions are. A narrow and a broad domain are both nonempty, yet they imply very different ranges of compatible environmental variation. Relative to the reference region $E = [0, 8]^2$, whose area is 64, Eq. (10) gives

$$V_E \approx 13.23, \quad \Omega_E \approx 0.207. \quad (30)$$

Thus, approximately 20% of the environmental input combinations within this stated reference region satisfy all six energetic constraints simultaneously. The numerical value is specific to the illustrative parameterization and to the chosen reference region. The general quantity Ω_E provides a way to compare how restrictive different ecological organizations are when evaluated over the same environmental domain.

The geometry now allows a second question. Ω_E measures the overall extent of environmental conditions compatible with the system, but environmental change is often described in terms of the *total* amount of resource supplied [33]. A fixed total input does not specify how that input is distributed among external resources. The same total supply can correspond to many combinations of (Q_1, Q_2) , each of which is routed differently through the ecological network. We therefore turn from the full feasibility domain to its constant-total-input cross-sections.

Energetic feasibility across total environmental input

For the two-input microbial system above, let

$$Q_{\text{tot}} = Q_1 + Q_2. \quad (31)$$

At a fixed Q_{tot} , varying the allocation between Q_1 and Q_2 traces a line through environmental input space. The intersection of this line with D_E contains the allocations that remain energetically feasible. Writing $\ell_E(Q_{\text{tot}})$ for the length of this feasible portion and $\ell_S(Q_{\text{tot}})$ for the length of the corresponding slice within the reference region, Eq. (12) becomes

$$\Phi_E(Q_{\text{tot}}) = \frac{\ell_E(Q_{\text{tot}})}{\ell_S(Q_{\text{tot}})}. \quad (32)$$

For $0 < Q_{\text{tot}} \leq 8$, the entire constant-total-input segment from $(0, Q_{\text{tot}})$ to $(Q_{\text{tot}}, 0)$ lies within $E = [0, 8]^2$. For $8 < Q_{\text{tot}} < 16$, the reference region truncates this segment to the portion between $(Q_{\text{tot}} - 8, 8)$ and $(8, Q_{\text{tot}} - 8)$. At $Q_{\text{tot}} = 16$ the slice reduces to the point $(8, 8)$, and for $Q_{\text{tot}} > 16$ it does not intersect E . Because the line-based denominator in Eq. (32) has zero length at $Q_{\text{tot}} = 16$, $\Phi_E(Q_{\text{tot}})$ is formally defined for $0 < Q_{\text{tot}} < 16$ in this reference region. Within that range, it measures the fraction of allocations available at a given total input that remain compatible with the entire ecological organization.

Figure 4 shows two complementary views of this dependence on total input. Fig. 4A follows the equal-allocation

path,

$$Q_1 = Q_2 = \frac{Q_{\text{tot}}}{2},$$

and tracks the six component-level energetic margins. The minimum of these margins identifies the active system-level constraint along this particular environmental trajectory. Which population is limiting can change as total input increases, just as different populations define different portions of the boundary in Figure 3.

Fig. 4B removes the restriction to equal allocation and evaluates all allocations at each Q_{tot} . At low total input, few or no allocations provide sufficient routed flux to every component. As total input increases in this example, the feasible fraction of

the constant-input slice increases. At still higher input, upper energetic boundaries remove an increasing fraction of the available allocations and $\Phi_E(Q_{\text{tot}})$ declines. The intermediate maximum therefore arises because the feasible fraction of the constant-input slice first increases and later decreases as the slice traverses the system-level feasibility domain. We denote the maximizing total input by $Q_{\text{tot}}^* = \arg \max_{Q_{\text{tot}}} \Phi_E(Q_{\text{tot}})$; this is the input at which the feasible allocation fraction is largest, not an upper limit beyond which total input is impossible. It is not an imposed response curve, nor is it a necessary outcome for every ecological organization: other domain geometries can produce saturating, monotonic, or more complex relationships.

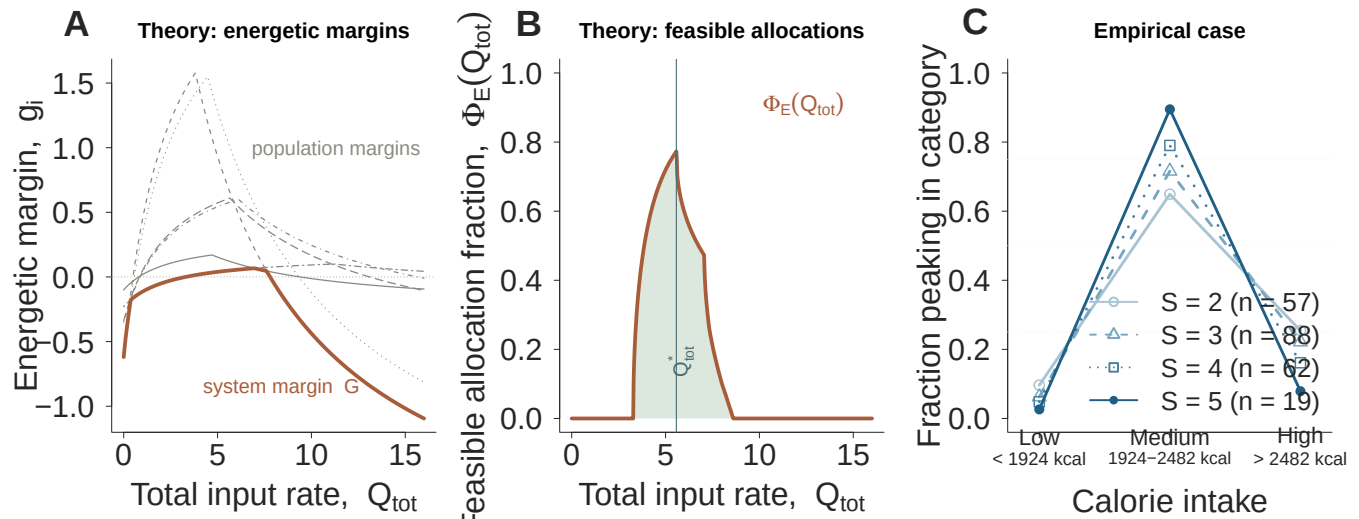


Figure 4: The feasible allocation fraction can be maximized at intermediate total input. **A**, component-level energetic margins along the equal-allocation path $Q_1 = Q_2 = Q_{\text{tot}}/2$. Thin curves denote individual population margins and the thick terracotta curve is the system-level margin $G(Q_{\text{tot}}) = \min_i g_i$. **B**, the conditional feasible fraction $\Phi_E(Q_{\text{tot}})$ measures the fraction of allocations at each total input that lie within the six-population energetic-feasibility domain. Its intermediate maximum arises from the geometry of constant-input cross-sections through D_E . **C**, qualitative empirical signature from a longitudinal human gut microbiome [31]. For each assemblage size $S = 2, 3, 4, 5$, curves show the fraction of recurrent assemblages whose within-category occurrence frequency is maximal at low, medium, or high caloric intake; n denotes the number of recurrent assemblages contributing to each curve. Caloric intake is a coarse proxy for environmental resource supply, and assemblage occurrence is not equivalent to energetic feasibility.

The geometric result suggests a qualitative empirical signature. If ecological organizations are more likely to be observed under environmental conditions compatible with their energetic requirements, recurrent assemblages might be concentrated around intermediate rather than extreme levels of resource input [33]. We examined this possibility using the longitudinal Subject A human gut microbiome dataset [31]. Microbial observations were aggregated at the Order level, daily caloric intake was divided into low, medium, and high tertiles, and recurrent assemblages were defined from simultaneous occurrence on more than one valid day. For each recurrent assemblage, we calculated its occurrence frequency within each calorie category and identified the category in which that frequency was maximal (Methods).

Across assemblage sizes $S = 2, 3, 4, 5$, recurrent assemblages most frequently reached their maximum occurrence at intermediate caloric intake (Fig. 4C). The concentration in the medium-calorie category became stronger with assemblage size, with 57, 88, 62, and 19 recurrent assemblages contributing to the $S = 2, 3, 4, 5$ curves, respectively. Larger assemblages were too sparsely represented for an informative comparison: at $S = 6$, only two recurrent assemblages remained. We therefore restrict the empirical comparison to $S \leq 5$. Within this range, the pattern is qualitatively consistent with the intermediate-input window generated by the feasibility geometry.

The comparison should not be interpreted as a direct test of the theory. Daily caloric intake is not the environmen-

tal input rate Q_{tot} : digestion, absorption, host metabolism, spatial structure, and resource composition intervene before dietary resources become available to gut microbes. Nor is repeated observation equivalent to energetic feasibility; demographic, ecological, and host-mediated processes also determine whether an assemblage is observed. Figure 4C therefore illustrates an empirical signature consistent with the geometric prediction rather than validating the underlying energetic mechanism. A direct test would instead estimate environmental inputs, capture functions, internal routing, and component-level energetic constraints independently, construct the predicted feasibility domain, and ask whether observed ecological organizations preferentially occupy it.

Discussion

The central conclusion of this synthesis is that energetic feasibility is a property of ecological organization, not of environmental supply alone. Resources supplied by the environment must first be captured and then routed through interacting components, each with its own energetic requirements and processing constraints. Feasibility therefore emerges from the compatibility of these coupled flows across the system. This perspective connects ecological energetics, consumer–resource theory, network ecology, and feasibility theory within a common sequence: environmental supply determines what is available, biological capture determines what enters the system, ecological organization determines where that flux goes, and component-level constraints determine whether the resulting flows are mutually compatible.

This distinction changes how resource supply should be interpreted. The same total supply can be partitioned among external resources in different ways, and identical external inputs can generate different local conditions when routed through different ecological organizations. In our formulation, H determines where environmental inputs enter and T determines how captured flux is redistributed. Changing either can therefore reshape the energetic-feasibility domain D_E without changing total environmental supply.

Microbial cross-feeding makes this distinction transparent because metabolites produced by one population can support others that do not directly access the external resource [20–22]. The same systems logic applies more broadly to trophic and detrital networks and to competitors coupled through shared resources [1, 3, 5–7], although the bookkeeping of transfers must respect the underlying mechanism. Equation (3) is most direct for secretion, cross-feeding, recycling, and related cases in which donor processing generates a usable secondary flux. Direct trophic transfer instead requires an explicit partition between donor retention and transferred energy.

Internal routing can both relieve and create energetic constraints. It can deliver resources to components that would otherwise remain limited, while also providing destinations for flux that cannot be productively accommodated where it first arrives. The parameter ϵ_i summarizes the energetic consequence of excess that remains unresolved locally. Positive values are most plausible when incoming flux exceeds assimilation or regulatory capacity, as under stoichiometric imbalance in consumers or overflow metabolism in microbes [9, 32]. A more mechanistic model could make these pro-

cesses and the fate of excess explicit.

This distinction clarifies the intermediate-input result. Saturating capture alone does not make high resource input detrimental; it only limits the rate at which environmental supply enters the biological system. Nor does crossing productive capacity C_i imply failure. A high-input boundary arises only when routed flux reaches an upper energetic threshold because excess cannot be fully accommodated, so that $\epsilon_i > 0$. Saturating capture shapes the geometry of the feasibility domain but is not required for such a boundary: a non-saturating increasing capture function can generate the same qualitative low–high feasibility window if routed flux reaches the upper threshold of at least one component. The intermediate maximum in $\Phi_E(Q_{\text{tot}})$ is therefore conditional rather than imposed; depending on capture, routing, productive capacity, and excess-flux accommodation, the response may be unimodal, saturating, monotonic, or more complex. Different components can also determine different portions of the system-level boundary, as illustrated by the reciprocal pair.

The feasibility geometry builds on, but is distinct from, established consumer–resource approaches. Resource requirements, zero-net-growth isoclines, supply points, and coexistence geometry provide mechanistic representations of ecological constraints in resource space [5, 6, 24, 25, 29]. Here the coordinates are external input rates, while the boundaries arise only after those inputs have been captured and routed through a specified ecological network. Energetic feasibility is also narrower than coexistence, invasion growth, or dynamical stability [34–36]. It asks whether energetic constraints alone rule out a specified organization. A configuration inside D_E may still fail because of demographic, dynamical, spatial, or evolutionary processes.

The present formulation makes several simplifying assumptions. Capture is represented by reduced-form saturating functions, routing coefficients are fixed, and feasibility is evaluated for a specified ecological organization rather than through explicit population and resource dynamics. In particular, the framework tracks energetic fluxes but not the population stocks that generate and respond to them. Routing is therefore donor-controlled in the present formulation, without feedback from recipient abundance or energetic state, while the minimum requirements m_i and productive capacities C_i are fixed rather than functions of population biomass. In a dynamical population model, changes in abundance could alter energetic requirements, capture, and transfer rates, so the amount of flux considered excess could itself depend on ecological state. These assumptions characterize the illustrative implementation rather than the feasibility construction itself. In this sense, the framework is model-agnostic: alternative consumer–resource, stoichiometric, metabolic, or dynamic models can provide the mapping from environmental inputs and ecological state to component-level energetic conditions without changing the system-level construction. Stoichiometric models can provide mechanistic productive constraints [7, 9, 37]; metabolic relationships can inform heterogeneous energetic requirements [8, 38, 39]; and dynamic consumer–resource models can make capture, routing, and energetic requirements explicitly state-dependent [25].

The central construction remains the simultaneous satisfaction of all component constraints for a specified ecological organization.

This perspective may be particularly useful for understanding environmental change and restoration. A renewed systems ecology has been argued to require greater attention to ecological systems in transformation rather than only to the maintenance of stable configurations [40]. Environmental inputs can represent light, nutrients, organic matter, food subsidies, or other resource fluxes once their capture and conversion are specified. Agriculture, eutrophication, restoration, and global change alter such inputs in different ways [14–18, 41]. Changing environmental supply moves a given ecological organization through input space, potentially across the boundaries of its existing D_E , whereas changing species, interactions, or functional pathways reshapes the domain itself. Restoration may therefore require not only restoring resource supply but also rebuilding the pathways through which resources are captured, transferred, and recycled [13–15].

The microbiome analysis provides a deliberately limited empirical illustration. Recurrent assemblages preferentially reached their highest occurrence frequencies at intermediate caloric intake across the community sizes for which sufficient observations were available. This pattern is consistent with the intermediate-input signature generated by the feasibility geometry, but caloric intake is only a coarse proxy for microbial resource supply and assemblage recurrence is not energetic feasibility. A direct test would independently estimate environmental inputs, capture functions, internal transfers, and component-level constraints, use them to predict D_E , and then ask whether observed ecological organizations preferentially occupy that domain.

More broadly, the underlying systems question is whether external conditions permit internally compatible flows for a specified organization. Living systems persist by acquiring, transforming, redistributing, storing, and dissipating energy and materials [11, 12], although the relevant mechanisms differ across levels of organization. The broader synthesis is therefore not that ecological systems require an optimal amount of energy, but that external supply and internal organization cannot be understood independently when asking whether an organized system can be energetically sustained. Environmental change can move a system through input space, whereas ecological reorganization can reshape the feasibility domain itself.

Methods

Routing and bidirectional flows

For n populations and p external resources, $H \in \mathbb{R}_+^{n \times p}$ maps captured energetic fluxes to their points of entry in the ecological system, and $T \in \mathbb{R}_+^{n \times n}$ describes internal routing among populations. We interpret $H_{i\alpha}$ as the fraction of captured flux from external resource α entering population i , and require

$$H_{i\alpha} \geq 0, \quad \sum_i H_{i\alpha} \leq 1$$

for every external resource α , so that captured external flux is not duplicated at entry. As in the main text, T_{ij} is the fraction

of flux processed by donor j that becomes usable input to recipient i . In this reduced formulation, these routing fractions are fixed properties of the specified ecological organization and do not depend on recipient abundance or energetic state. We likewise require

$$T_{ij} \geq 0, \quad \sum_i T_{ij} \leq 1$$

for every donor j , so that routed output cannot exceed processed donor flux. Any remainder is retained, respired, dissipated, excreted, or exported from the routed network. In the present cross-feeding interpretation, $T_{ij}I_j$ is a usable by-product generated by processing at donor j ; the donor margin is therefore based on its incoming processing flux I_j . Direct trophic transfer would require an additional retention/transfer partition before evaluating donor energetic availability.

For repeated routing to remain finite, the spectral radius of T must satisfy

$$\rho(T) < 1.$$

Under this condition,

$$(\mathbb{I} - T)^{-1} = \mathbb{I} + T + T^2 + \dots$$

converges, and the flux-balance relation in Eq. (3) has the nonnegative solution given by Eq. (4). The column-sum conditions on H and T constrain physical allocation at environmental entry and internal routing, respectively, whereas $\rho(T) < 1$ ensures convergence of repeated transfers. Reciprocal and cyclic pathways are therefore permitted provided these conditions are satisfied.

Six-population microbial example

Populations are ordered $(M_1, \dots, M_6)$. External resource Q_1 enters only through M_1 , whereas Q_2 enters only through M_2 , giving

$$H = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{pmatrix}. \quad (33)$$

The nonzero internal routing fractions are

$$\begin{aligned} T_{21} &= 0.12, & T_{12} &= 0.10, & T_{31} &= 0.24, \\ T_{32} &= 0.14, & T_{41} &= 0.10, & T_{42} &= 0.26, \\ T_{43} &= 0.10, & T_{53} &= 0.22, & T_{54} &= 0.08, \\ T_{63} &= 0.08, & T_{64} &= 0.20, & T_{65} &= 0.08. \end{aligned}$$

For this routing structure,

$$(\mathbb{I} - T)^{-1}H = \begin{pmatrix} 1.012146 & 0.101215 \\ 0.121457 & 1.012146 \\ 0.259919 & 0.165992 \\ 0.158785 & 0.289879 \\ 0.069885 & 0.059709 \\ 0.058141 & 0.076032 \end{pmatrix}, \quad (34)$$

which gives the incoming-rate relations reported in the main text.

The minimum energetic requirements are

$$m = (0.62, 0.60, 0.35, 0.34, 0.23, 0.10)^\top,$$

and the productive capacities are

$$C = (2.20, 2.15, 0.95, 0.95, 0.33, 0.27)^\top.$$

All six parameter pairs satisfy $0 < m_i < C_i$. For the illustrative calculation, $\epsilon_i = 3.0$ for all six populations. This common value is not an empirical estimate; it represents a regime in which flux beyond productive capacity is not fully accommodated. The minimum requirement of M_5 is set to $m_5 = 0.23$, making this downstream population deliberately restrictive relative to the flux delivered to it by the network; this choice is used to illustrate how adding a component constraint can visibly contract the multispecies feasibility domain. Equation (6) then gives the upper energetic-feasibility rates

$$I^+ = (2.7267, 2.6667, 1.1500, 1.1533, 0.3633, 0.3267)^\top.$$

All domain calculations use the environmental reference region $E = [0, 8]^2$.

Domain area and conditional feasible fraction

For the two-input example, the area of the energetic-feasibility domain within the reference region is

$$V_E = \int_E \mathbf{1}_{D_E}(Q_1, Q_2) dQ_1 dQ_2, \quad (35)$$

where $\mathbf{1}_{D_E}(Q_1, Q_2) = 1$ when all six energetic margins are positive and is zero otherwise. We evaluate this integral numerically using midpoint quadrature on a regular partition of E . Each grid cell is represented by its center, and V_E is estimated by summing the areas of cells whose centers lie within D_E . The calculation is repeated at increasing grid resolutions to verify numerical convergence. The normalized domain size is then calculated as $\Omega_E = V_E / \text{Vol}(E)$.

For the conditional feasible fraction, total environmental input is

$$Q_{\text{tot}} = Q_1 + Q_2.$$

In this illustrative example, Q_1 and Q_2 are expressed in the same abstract input-rate currency, so their sum is well defined. For external inputs expressed in different physical currencies, the corresponding total-input coordinate would require explicit conversion weights. At each Q_{tot} , the corresponding slice within $E = [0, 8]^2$ is parameterized by

$$Q_1 \in [\max(0, Q_{\text{tot}} - 8), \min(8, Q_{\text{tot}})], \quad Q_2 = Q_{\text{tot}} - Q_1.$$

We evaluate the six energetic constraints at evenly spaced midpoint allocations along this segment. The conditional feasible fraction $\Phi_E(Q_{\text{tot}})$ is the length of the feasible portion divided by the total length of the truncated segment, as in Eq. (32). Figure 4A instead evaluates the six margins along the single equal-allocation trajectory $Q_1 = Q_2 = Q_{\text{tot}}/2$.

Longitudinal microbiome analysis

We reanalyzed the Subject A longitudinal human gut microbiome dataset [31]. Microbial reads were aggregated at the taxonomic Order level and matched to daily dietary records. Daily caloric intake was taken from variable V64 of the associated .proc file, and only days containing both caloric-intake and microbiome observations were retained.

For each valid day, Order-level relative abundances were calculated by dividing each Order's read count by the total Order-level read count. An Order was considered present when its relative abundance was at least 10^{-3} . Unresolved Order-level taxonomic assignments were excluded. We further retained only Orders that crossed the presence threshold during the time series, meaning that they were present on at least one valid day and absent on at least one valid day. This procedure yielded 18 candidate Orders.

Daily caloric intake was divided into Low, Medium, and High categories using the one-third and two-thirds quantiles of the valid calorie observations. For each assemblage size $S \in \{2, 3, 4, 5\}$, we generated all combinations of S candidate Orders and recorded the days on which all members were simultaneously present. Assemblages observed on more than one valid day were classified as recurrent and retained for Figure 4C. This yielded

$$N_2 = 57, \quad N_3 = 88, \quad N_4 = 62, \quad N_5 = 19$$

recurrent assemblages. Larger assemblages were too sparsely represented for an informative comparison; only two recurrent assemblages remained at $S = 6$.

For recurrent assemblage c and calorie category $k \in \{\text{Low, Medium, High}\}$, the within-category occurrence frequency was

$$f_{c,k} = \frac{\#\{\text{valid days in } k \text{ with } c \text{ present}\}}{\#\{\text{valid days in } k\}}. \quad (36)$$

For each assemblage, we identified the calorie category in which $f_{c,k}$ was maximal. If two or more categories shared the maximum, the assemblage was divided equally among those categories. Specifically, let $w_{c,k} = 1$ when k is the unique maximum, $w_{c,k} = 0$ when it is not a maximum, and $w_{c,k} = 1/r$ when k is one of r tied maxima. Figure 4C reports

$$P_S(k) = \frac{1}{N_S} \sum_{c=1}^{N_S} w_{c,k}, \quad (37)$$

the fraction of recurrent assemblages of size S whose occurrence frequency peaks in each calorie category.

This empirical quantity is intentionally distinct from $\Phi_E(Q_{\text{tot}})$. Caloric intake is used as a coarse empirical proxy for external resource supply, and $P_S(k)$ describes the distribution of observed assemblage recurrence across intake categories rather than the volume of a mechanistically estimated energetic-feasibility domain.

More than two external resources

The two-dimensional environmental domain is a visualization choice rather than a restriction of the framework. For $p = 3$,

fixed total input Q_{tot} defines the triangle

$$Q_1 + Q_2 + Q_3 = Q_{\text{tot}}, \quad Q_\alpha \geq 0,$$

whose intersection with the chosen environmental reference region E gives the potentially truncated slice $S_E(Q_{\text{tot}})$. More generally, fixed total input defines a $(p - 1)$ -dimensional simplex in the nonnegative orthant, and its intersection with E defines the slice used in Eq. (12). The conditional feasible fraction is the portion of that slice lying within D_E . These quantities can be evaluated numerically using deterministic simplex quadrature or uniform sampling over the simplex [28].

References

- [1] R. L. Lindeman. “The trophic-dynamic aspect of ecology”. *Ecology* 23, 399–417 (1942).
- [2] E. C. Pielou. *The Energy of Nature*. The University of Chicago Press, Chicago (2001).
- [3] E. P. Odum. “The Strategy of Ecosystem Development”. *Science* 164, 262–270 (1969).
- [4] R. Margalef. *Perspectives in Ecological Theory*. University of Chicago Press (1968).
- [5] R. MacArthur. “Species packing and competitive equilibrium for many species”. *Theoretical Population Biology* 1, 1–11 (1970).
- [6] D. Tilman. *Resource Competition and Community Structure*. Princeton University Press (1982).
- [7] R. W. Sterner, J. J. Elser. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press (2002).
- [8] J. H. Brown et al. “Toward a metabolic theory of ecology”. *Ecology* 85, 1771–1789 (2004).
- [9] T. R. Anderson et al. “Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers”. *The American Naturalist* 165, 1–15 (2005).
- [10] H. J. Morowitz. “Physical background of cycles in biological systems”. *Journal of Theoretical Biology* 13, 60–62 (1966).
- [11] H. Morowitz, E. Smith. “Energy flow and the organization of life”. *Complexity* 13, 51–59 (2007).
- [12] R. Solé et al. “Fundamental constraints to the logic of living systems”. *Interface Focus* 14, 20240010 (2024).
- [13] J. J. Cairns, J. R. Heckman. “Restoration ecology: the state of an emerging field”. *Annual Review of Energy and the Environment* 21, 167–189 (1996).
- [14] R. J. Hobbs, V. A. Cramer. “Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change”. *Annual Review of Environment and Resources* 33, 39–61 (2008).
- [15] G. D. Gann, T. McDonald, B. Walder, et al. “International principles and standards for the practice of ecological restoration. Second edition”. *Restoration Ecology* 27, S1–S46 (2019).
- [16] J. Peñuelas, B. Poulter, J. Sardans, et al. “Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe”. *Nature Communications* 4, 2934 (2013).
- [17] T. L. Greaver, C. M. Clark, J. E. Compton, et al. “Key ecological responses to nitrogen are altered by climate change”. *Nature Climate Change* 6, 836–843 (2016).
- [18] W. Zhang et al. “The Economics of Nutrient Pollution from Agriculture”. *Annual Review of Resource Economics* 15 (2023).
- [19] M. L. Rosenzweig. “Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time”. *Science* 171, 385–387 (1971).
- [20] J. E. Goldford et al. “Emergent simplicity in microbial community assembly”. *Science* 361, 469–474 (2018).
- [21] G. D’Souza et al. “Ecology and evolution of metabolic cross-feeding interactions in bacteria”. *Natural Product Reports* 35, 455–488 (2018).
- [22] A. R. Pacheco, M. Moel, D. Segrè. “Costless metabolic secretions as drivers of interspecies interactions in microbial ecosystems”. *Nature Communications* 10, 103 (2019).
- [23] C. S. Holling. “Some characteristics of simple types of predation and parasitism”. *The Canadian Entomologist* 91, 385–398 (1959).
- [24] J. M. Chase, M. A. Leibold. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press (2003).
- [25] T. Koffel et al. “Geometrical envelopes: Extending graphical contemporary niche theory to communities and eco-evolutionary dynamics”. *Journal of Theoretical Biology* 407, 271–289 (2016).
- [26] R. P. Rohr, S. Saavedra, J. Bascompte. “On the structural stability of mutualistic systems”. *Science* 345, 1253497 (2014).
- [27] J. Grilli et al. “Feasibility and coexistence of large ecological communities”. *Nature Communications* 8, 14389 (2017).
- [28] S. Saavedra et al. “A structural approach for understanding multispecies coexistence”. *Ecological Monographs* 87, 470–486 (2017).
- [29] E. Blumenthal et al. “Geometry of ecological coexistence and niche differentiation”. *Physical Review E* 108, 044409 (2023).
- [30] S. Saavedra. “The feasibility principle in community ecology”. *Oikos*, e11355 (2026).
- [31] L. A. David et al. “Host lifestyle affects human microbiota on daily timescales”. *Genome Biology* 15, R89 (2014).
- [32] M. Basan et al. “Overflow metabolism in *Escherichia coli* results from efficient proteome allocation”. *Nature* 528, 99–104 (2015).
- [33] C. Long et al. “Energetic constraints shape the diversity of feasible ecological networks”. *PLOS Computational Biology* 22, e1014330 (2026).
- [34] P. Chesson. “Mechanisms of maintenance of species diversity”. *Annual Review of Ecology and Systematics* 31, 343–366 (2000).
- [35] T. N. Grainger, J. M. Levine, B. Gilbert. “The invasion criterion: a common currency for ecological research”. *Trends in Ecology & Evolution* 34, 925–935 (2019).
- [36] R. Ranjan, T. Koffel, C. A. Klausmeier. “The three-species problem: Incorporating competitive asymmetry and intransitivity in modern coexistence theory”. *Ecology Letters* 27, e14426 (2024).
- [37] G. I. Ågren. “Stoichiometry and Nutrition of Plant Growth in Natural Communities”. *Annual Review of Ecology, Evolution, and Systematics* 39, 153–170 (2008).
- [38] V. M. Savage et al. “Effects of body size and temperature on population growth”. *The American Naturalist* 163, 429–441 (2004).
- [39] J. P. DeLong et al. “Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life”. *Proceedings of the National Academy of Sciences* 107, 12941–12945 (2010).
- [40] D. M. Gordon. “The future of systems ecology”. *Systems Ecology* 1:002 (2026).
- [41] M. T. Angulo et al. “Quantifying ecosystem degradation via energetic deficits”. *Royal Society Open Science* 13, 260268 (2026).

Editor: Shaopeng Wang

Acknowledgements

The author thanks the editor and reviewers for constructive comments that improved the manuscript.

Data and code availability

No new data were generated in this paper. The longitudinal microbiome and dietary data analyzed here are from [31]. Code used to generate the numerical illustrations, compute feasibility measures, perform the empirical analysis, and reproduce the quantitative figures is provided as Supporting Information.

Funding

SS acknowledges support from the National Science Foundation under Grant No. DEB-2436069.

Competing interests

The author declares no competing interests.

AI use statement

AI-assisted tools were used for English editing and plot refinement. All research design and mathematical derivations are the product of the author.

¹ Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, Massachusetts 02139, USA; Santa Fe Institute, Santa Fe, New Mexico 87501, USA; sersaa@mit.edu