An energetic unification of ecological theory

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Abstract

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Ecological communities can persist for long periods despite strong competition and environmental variability, yet they can also reorganize or collapse abruptly after seemingly modest change. Explaining persistence, diversity, and collapse has produced several major traditions in ecology, including species-interaction models, consumer–resource theory, coexistence theory, feasibility analysis, and stability theory. These approaches are often developed separately, even though they all describe systems that capture energy from the environment, redistribute it through ecological interactions, and lose it through metabolism. Here I propose an energetic framework that helps place these traditions in a common language. The central idea is that ecological communities persist only when external energy supply can support both the maintenance of biomass and the losses associated with internal redistribution, while remaining within finite supply and throughput limits. For flux-based ecological models, this perspective yields an exact aggregate balance identity; for other model classes, the mapping is partial or reduced-form and depends on how the system boundary is defined. This framework clarifies why persistence is conditional on energetic compatibility, why enrichment need not always promote persistence, and how feasibility, coexistence, stability, and early warning signals can be interpreted as related aspects of the same underlying constraint. It also shows how finite supply and throughput can bound energetically compatible community states, while superlinear scaling of internal throughput provides one simple special case that yields transparent reduced-form limits on community size and, with additional assumptions, on ecological complexity. More broadly, the framework offers a physically grounded way to connect historically separate areas of ecological theory.

Introduction

Ecological communities exhibit a striking duality. They can persist for long periods despite intense competition, predation, and environmental variability, yet they can also reorganize or collapse abruptly following seemingly modest environmental change (Carpenter et al., 2011, Dakos et al., 2012, Holling, 1973, Scheffer et al., 2009, 2001). Explaining how interacting assemblages of organisms remain coherent—and why that coherence sometimes fails—has long been a central challenge in ecology (Elton, 1927, Levin, 1998, MacArthur, 1955, Margalef, 1968). Over the past century, this problem has generated major theoretical traditions focused on species interactions, resource limitation, coexistence mechanisms, structural feasibility, and dynamical stability (Allesina and Tang, 2012, Barabás et al., 2018, Chesson, 2000, Lotka, 1925, MacArthur and Levins, 1967, MacArthur, 1970, May, 1972, 1973, Saavedra et al., 2017, Tilman, 1982, Volterra, 1926).

Early mathematical ecology approached these questions through interaction-based dynamics. The Lotka–Volterra equations formalized competition and predator–prey regulation through interaction coefficients and feedback structure (Lotka, 1925, Volterra, 1926). Consumer–resource theory then made environmental supply explicit, showing how coexistence can arise through differential exploitation of limiting resources, trade-offs in uptake, and packing along resource axes (MacArthur and Levins, 1967, MacArthur, 1970, Tilman, 1982, 1985). Later work sharpened the analysis of persistence itself. Coexistence theory framed persistence in terms of invasion growth rates, niche differences, and stabilizing versus equalizing mechanisms (Barabás et al., 2018, Chesson, 2000, Hutchinson, 1961); stability theory examined how interaction strength, connectance, and sign structure shape dynamical robustness (Allesina and Tang, 2012, May, 1972, 1973); and structural approaches focused on the existence of positive equilibria and the parameter domains supporting them (Deng et al., 2024, Rohr et al., 2014, Saavedra, 2024, Saavedra et al., 2017, Song et al., 2018).

In parallel, ecosystem ecology developed a complementary perspective centered on flows of energy and matter. Lindeman's trophic-dynamic view identified energy transfer across trophic levels as a basic organizing principle (Lindeman, 1942). Odum emphasized ecosystem metabolism and system-level energy budgets (Odum, 1969), while network approaches analyzed how energy is routed through complex ecological systems (Ulanowicz, 1986). Related systems perspectives connected energy flow, nutrient cycling, resilience, and whole-system organization (DeAngelis, 1980). Together, these traditions established that ecosystems can be understood as open systems in which energy and matter are captured, redistributed, and dissipated (DeAngelis, 1980, Levin, 1992, Lindeman, 1942, Odum, 1969, Ulanowicz, 1986).

Despite their shared concern with persistence, these traditions are still often treated as separate explanatory frameworks. Interaction-based models emphasize pairwise effects, resource-based models emphasize environmental supply and renewal, coexistence theory centers on invasion criteria, stability theory focuses on Jacobian structure, and feasibility analyses characterize the parameter regions that permit positive equilibria (Allesina and Tang, 2012, Barabás et al., 2018, Chesson, 2000, May, 1972, Rohr et al., 2014, Saavedra et al., 2017, Song et al., 2018, Tilman, 1982). Ecosystem energetics, by contrast, focuses on the magnitude and organization of trophic fluxes (DeAngelis, 1980, Lindeman, 1942, Odum, 1969, Ulanowicz, 1986). Because these approaches arose from different analytical viewpoints, ecology still lacks a common language that makes clear how they are related (Godoy et al., 2018, Levin, 1998, Levins, 1966, Marquet et al., 2014).

Yet all ecological communities share the same physical foundation. They are open dissipative systems that capture energy from the environment, redistribute it internally through ecological interactions, and lose it irreversibly through metabolism (Brown et al., 2004, DeAngelis, 1980, Lindeman, 1942, Odum, 1969). In population models, these processes are often implicit: interaction terms encode transfers among species, resource uptake terms encode flows from the environment into populations, and mortality or maintenance terms encode energetic loss (Holling, 1959, Lotka, 1925, MacArthur, 1970, Tilman, 1982, Volterra, 1926, Yodzis and Innes, 1992). In ecosystem models, the same structure appears explicitly as fluxes through trophic networks (Odum, 1969, Ulanowicz, 1986). Although this energetic architecture has long been recognized qualitatively, it is rarely treated as the organizing principle linking the major branches of ecological theory (Godoy et al., 2018, Levin, 1998, Lindeman, 1942, Odum, 1969).

Here I argue that making this energetic structure explicit provides a useful unifying foundation for ecological theory. More precisely, I propose a common energetic framework within which models of species interactions, resource dynamics, invasion-based persistence, feasibility conditions, and stability analyses can be compared as different mathematical projections of a shared energetic constraint: compatibility between external energy capture, internal redistribution, dissipative loss, and finite admissible throughput. The paper does not claim a universal theorem reducing all ecological models to a single scalar law. Instead, it develops a common energetic language, identifies an exact aggregate balance identity for flux-based formulations, and makes finite admissible supply and throughput the central structural condition for persistence.

Reduced-form scaling closures are then introduced only as transparent special cases that summarize how energetic burden may rise with biomass or complexity over a specified range. This perspective also connects naturally to several longstanding ecological patterns. It offers a structural interpretation of diversity–productivity relationships (Loreau et al., 2001, Tilman, 1985), provides a mechanism linking enrichment to abrupt ecosystem collapse (Carpenter et al., 2011, Rosenzweig, 1971, Scheffer et al., 2001), gives a physical interpretation of instability (Allesina and Tang, 2012, May, 1972), and suggests a structural counterpart to early warning signals preceding regime shifts (Dakos et al., 2012, Scheffer et al., 2009, Yang et al., 2025). In particular, the framework makes explicit that increasing external energy capture does not necessarily relax ecological constraints: by increasing standing biomass and activating stronger or more numerous interaction pathways, enrichment can also intensify internal throughput and push systems closer to structural energetic limits.

The remainder of the paper develops this argument in three steps. First, I formalize ecological communities as open dissipative networks governed by external energy capture, internal redistribution through species interactions, and metabolic dissipation. Second, I show that persistence requires not only energetic balance but also compatibility with finite admissible supply and throughput capacities, because ecological flows are constrained by biological and physical limits at the level of interaction channels. Third, I show that several major ecological frameworks can be interpreted as different mathematical perspectives on this same energetic constraint. Consumer–resource models describe mechanisms of energy capture, interaction models encode redistribution among species, coexistence theory characterizes invasion conditions within the feasible energetic domain, and stability analyses describe how systems behave as energetic limits are approached. A reduced-form scaling closure is then introduced as one convenient special case that yields especially transparent scalar expressions for biomass bounds and overload under enrichment. In this view, diversity–productivity relationships, enrichment-driven instability, structural feasibility limits, trophic cascades, and early warning signals can be interpreted as different manifestations of the same underlying condition of energetic compatibility. The contribution of this paper is therefore not a universal reduction theorem, but a common energetic language that makes explicit the assumptions often left implicit across otherwise distinct theoretical frameworks.

Energy balance: a common ecological identity

Any ecological community can be viewed as a system that captures energy from its environment, redistributes that energy among constituent species through ecological interactions, and dissipates energy irreversibly through metabolism (Brown et al., 2004, DeAngelis, 1980, Lindeman, 1942, Odum, 1969, Ulanowicz, 1986). Figure 1 provides a schematic summary of this argument. To keep the notation dimensionally consistent, all variables entering the aggregate energetic balance are understood after conversion to a common energetic currency. Let x denote the full state of the chosen focal aggregate system. Write B for the summed stock over the variables included in that aggregate balance. When only living nodes are aggregated, B coincides with total community biomass; when explicit resources or substrates are included, B should be read as the corresponding aggregate energetic stock. The mapping below is therefore exact only relative to the chosen aggregate boundary.

I distinguish five objects. First, $Q(x)$ denotes energetic input across the boundary of the focal aggregate state. Second, $D(x)$ denotes dissipative loss associated with metabolism, maintenance, and other irreversible processes. Third, $\Phi(x)$ denotes gross internal throughput, that is, the total rate at which energy is transferred through interaction-mediated channels internal to the focal aggregate state. Fourth, $L(x)$ denotes the dissipative energetic cost generated by sustaining that throughput. Fifth, $C(x, \Theta)$ denotes an effective structural capacity summary when such a scalar representation is useful. In general, $L(x)$ need not be determined by $\Phi(x)$ alone. A notation such as $L(\Phi)$ should therefore be understood only as a reduced-form closure imposed under additional assumptions; Appendix A gives the exact state-dependent formulation for flux-based models. With this distinction, the aggregate energetic balance can be written as

$$\dot{B} = Q(x) - D(x) - L(x). \tag{1}$$

Equation (1) does not introduce a new dynamical model. Rather, it is an aggregate relation that can be used to compare ecological models whenever their state variables and flows are expressed in a common currency and the aggregate boundary is explicit. For flux-based models, Appendix A shows that equation (1) can be obtained exactly by summing node-level balances and collecting the non-retained fraction of internal transfers. What differs among model classes is how external input, internal throughput, and dissipation are represented or approximated (Lotka, 1925, MacArthur, 1970, Tilman, 1982, Ulanowicz, 1986, Volterra, 1926, Yodzis and Innes, 1992).

The term $Q(x)$ represents the pathways through which energy enters the focal aggregate state from the environment or, more generally, across the chosen system boundary. In systems dominated by primary producers, Q corresponds to primary production, which depends on environmental drivers such as light, nutrients, and temperature (Lindeman, 1942, Odum, 1969). In microbial communities it may correspond to the inflow of metabolic substrates (Monod, 1949). In detrital systems it may include external organic inputs, while in subsidized food webs it can incorporate cross-ecosystem transfers of energy or materials (Pace et al., 1999, Ulanowicz, 1986). Dissipative losses $D(x)$ aggregate the energetic costs required to maintain living biomass and, when nonliving pools are included in the focal aggregate state, may also include abiotic turnover losses. Gross internal throughput $\Phi(x)$ captures the total rate of interaction-mediated transfer through trophic interactions, resource uptake, and other ecological processes that move energy among species or between species and explicit resource pools within the chosen boundary (Holling, 1959, MacArthur, 1970, Tilman, 1982, Yodzis and Innes, 1992). The corresponding function $L(x)$ captures the dissipative burden associated with sustaining that redistribution. Its form depends on transfer efficiencies, handling costs, transport losses, and the structure of the underlying functional responses.

At ecological equilibrium, the total aggregate stock is constant and the system must satisfy

$$Q(x^*) = D(x^*) + L(x^*). \tag{2}$$

This condition expresses a fundamental requirement of energetic compatibility: the energy captured across the system boundary must support both the dissipative maintenance of biomass and the energetic losses generated by internal redistribution (DeAngelis, 1980, Lindeman, 1942, Odum, 1969, Ulanowicz, 1986). In explicit flux-based settings, however, balance alone is not sufficient: the realized internal transfers must also remain inside the set of admissible flows determined by finite supply and channel capacities, as formalized below. Classical analyses of coexistence, feasibility, stability, and ecological tipping implicitly assume that such compatibility can be achieved (Barabás et al., 2018, Chesson, 2000, May, 1972, Rohr et al., 2014, Saavedra et al., 2017, Scheffer et al., 2001). By writing the balance explicitly, we can instead ask under what conditions a compatible configuration exists and how those conditions depend on network structure, functional responses, environmental supply, and admissible throughput (Song et al., 2018, Tilman, 1982, Yodzis and Innes, 1992).

A reduced-form scaling closure for dissipation and internal throughput

The core energetic framework does not require a specific scaling law for persistence to be constrained: finite admissible supply and throughput capacities already define a boundary of energetic compatibility. Nevertheless, reduced-form scaling closures provide a useful special case because they summarize in a compact scalar form how energetic burden may rise with community size over a specified regime. This interpretation is most natural when the focal aggregate stock B tracks living biomass or another stock tightly coupled to it over the regime of interest.

Dissipation represents the metabolic and maintenance costs required to sustain living biomass and is commonly approximated as proportional to total biomass:

$$D(x) \approx c_1 B, \tag{3}$$

where B is the aggregate biomass or stock of interest and c_1 is an average per-biomass maintenance coefficient. This approximation is supported by metabolic theory, which documents regular scaling relationships between metabolic rate, body mass, and temperature (Brown et al., 2004, West et al., 1997), and underlies classical ecosystem energy-budget approaches (Lindeman, 1942, Odum, 1969). At the community level, maintenance costs therefore tend to accumulate approximately linearly with total biomass (Brown et al., 2004).

Gross internal throughput, by contrast, arises from ecological interactions that redistribute energy among species and between species and their resources. Because these processes depend on encounter rates and trophic transfers, aggregate throughput can increase more rapidly than biomass over relevant ranges of state space (May, 1972, 1973, Yodzis and Innes, 1992). Under mass-action encounters, pairwise transfer rates scale with the product of species densities, $F_{ij} \propto N_i N_j$. Summing across interaction channels therefore generates terms that scale quadratically with biomass under homogeneous conditions and, more generally, motivates a reduced-form exponent $\gamma > 1$ when interactions compound across complex networks:

$$\Phi(x) \approx c_\Phi B^\gamma, \qquad \gamma > 1, \tag{4}$$

where c_Φ is an effective coefficient summarizing the average intensity of interaction-mediated throughput across the network. The effective exponent γ depends on network connectivity, species-level scaling, functional responses, and spatial structure (Allesina and Tang, 2012, Holling, 1959, Levin, 1992, May, 1972, 1973, Yodzis and Innes, 1992). Even when individual functional responses saturate, the number of active interaction channels can still increase with community richness, which may produce aggregate superlinear scaling in total throughput.

Equation (4) is a reduced-form hypothesis, not a universal consequence of ecological interactions. The effective exponent may depend on state, topology, and functional response, and the regime of interest here is the one in which an effective superlinear scaling provides a reasonable approximation over the range considered. If the dissipative cost of processing is approximately proportional to throughput over the relevant range,

$$L(x) \approx \ell\,\Phi(x), \tag{5}$$

with $\ell > 0$ an effective dissipation-per-throughput coefficient, then substituting these approximations into the steady-state energetic balance (2) yields

$$Q(x^*) \approx c_1 B + (\ell c_\Phi) B^\gamma. \tag{6}$$

Absorbing the product ℓc_Φ into a single coefficient c_2 gives the common reduced form

$$Q(x^*) \approx c_1 B + c_2 B^\gamma. \tag{7}$$

Equation (7) should therefore be read as a reduced form applying under explicit assumptions on scaling and over a specified range, rather than as a universal ecological law or as the foundation of the framework itself. Appendix A states a general sufficient condition for a finite biomass or aggregate-stock bound under a coercive energetic burden; the superlinear reduced form in equation (7) is one transparent special case. In particular, that argument also requires a uniform upper bound on external capture, $Q(x, \theta) \leq \bar{Q}(\theta)$.

Equation (7) nevertheless reveals a useful structural tension. For small B, the linear dissipation term dominates and energetic balance is readily satisfied. As biomass increases, however, the superlinear contribution generated by internal throughput grows increasingly important. Unless external energy capture Q, or the associated structural capacity discussed below, scales comparably with B^γ, equation (7) admits only finite solutions for B. In other words, superlinear throughput provides one sufficient route to limits on the total biomass that a community can sustain and, under additional assumptions on biomass allocation or minimum viable biomass, on the richness and complexity of ecological networks.

This reduced-form scaling closure provides a structural interpretation of several well-known ecological patterns. Diversity–productivity relationships that saturate at high productivity (Loreau et al., 2001, Tilman, 1985) may arise because increasing productivity elevates biomass and the number of interaction pathways, steepening internal throughput until capacity constraints limit further diversity gains. More generally, enrichment does not simply relax energetic limitation. By increasing standing biomass and activating more or stronger interaction pathways, higher external supply can also increase internal throughput and the associated dissipative burden. When this induced increase in $\Phi(x)$ outpaces the available structural capacity, additional energy input can push the system closer to loss of energetic compatibility rather than farther from it. In this sense, the paradox of enrichment can be interpreted as a demand–capacity imbalance generated by excessive external supply (Carpenter et al., 2011, Rosenzweig, 1971, Scheffer et al., 2001). More generally, what matters is how demanded throughput responds to biomass, enrichment, and network structure relative to the admissible capacity of the system; reduced-form scaling is one convenient way to summarize that response. As illustrated schematically in Figure 1A,B, this closure naturally produces a common scaled energetic form and shows how enrichment can push systems toward the admissible throughput boundary once structural capacity is imposed.

Structural capacity: throughput constraints and admissible flows

Whether or not one adopts a reduced-form scaling closure, ecological flows are constrained by biological and physical mechanisms that cap the rates of interaction channels. Handling times limit per-capita ingestion (Holling, 1959, Yodzis and Innes, 1992), enzyme kinetics limit microbial uptake (Monod, 1949), resource renewal limits extraction rates (MacArthur, 1970, Tilman, 1982), and spatial structure constrains encounter frequencies (Levin, 1992). Network topology and the presence of recycling pathways further influence how energy can be routed through ecological systems (Ulanowicz, 1986). Together, these constraints impose finite throughput capacities on ecological networks (DeAngelis, 1980, Ulanowicz, 1986). These capacities, rather than any particular scaling ansatz, provide the general structural engine of the framework.

To formalize these limits, consider the gross transfer of energy from node i to node j, denoted F_{ij}. At the node level, the dynamic relation can be written as

$$\dot{N}_i = Q_i + \sum_j \varepsilon_{ji} F_{ji} - D_i - \sum_k F_{ik}, \tag{8}$$

where Q_i denotes external capture by node i, D_i denotes dissipative loss, F_{ij} denotes gross outgoing transfer, and $0 < \varepsilon_{ji} \leq 1$ is the transfer efficiency from node j to node i. At equilibrium this reduces to the steady-state balance

$$Q_i + \sum_j \varepsilon_{ji} F_{ji} = D_i + \sum_k F_{ik}. \tag{9}$$

Structural constraints impose upper bounds on each interaction channel,

$$0 \leq F_{ij} \leq F_{ij}^{\max}(x, \Theta), \tag{10}$$

where Θ denotes the collection of biological and environmental parameters governing channel capacities, such as handling times, attack rates, resource renewal rates, and spatial overlap among species (Holling, 1959, Levin, 1992, Tilman, 1982, Yodzis and Innes, 1992). These constraints reflect the finite rates at which energy can be processed along each ecological pathway.

The total gross internal throughput is therefore

$$\Phi(x) = \sum_{i,j} F_{ij}(x). \tag{11}$$

An effective structural capacity summary can then be defined as the maximum aggregate throughput compatible with both steady-state balance and channel constraints:

$$C(x, \Theta) = \sup \sum_{i,j} F_{ij} \quad \text{subject to (9) and } 0 \leq F_{ij} \leq F_{ij}^{\max}(x, \Theta). \tag{12}$$

For notational simplicity, the main text sometimes suppresses part of the state dependence and writes an effective scalar summary such as C_{eff}, but the exact object is the state-dependent quantity in equation (12). Appendix A gives the more general formulation in terms of an admissible flow set and a state-dependent scalar summary $C(x, \theta)$.

Energetic feasibility therefore requires that equilibrium throughput satisfy

$$\Phi(x^*) \leq C(x^*, \Theta). \tag{13}$$

Unlike the reduced-form scaling closure above, equation (13) does not require any specific exponent or aggregate law. It states directly that persistence requires the realized energetic transfers implied by the equilibrium to lie inside the admissible set of flows.

Thus, increasing Q is not unconditionally stabilizing (Rosenzweig, 1971): if the associated rise in throughput exceeds the rise in admissible capacity, enrichment can reduce persistence by driving the system toward $\Phi(x^*) \approx C(x^*, \Theta)$. When the throughput implied by species abundances approaches this structural boundary, the space of admissible flow configurations becomes increasingly restricted (Saavedra, 2024, Saavedra et al., 2017). If demanded throughput exceeds the network's effective capacity, no energetically compatible equilibrium of the focal formulation exists, and the system may reorganize through species loss, reduced biomass, or qualitative dynamical change (Holling, 1973, Rohr et al., 2014, Saavedra et al., 2017, Scheffer et al., 2001).

These constraints appear explicitly in many ecological models. In consumer–resource frameworks, resource inflow I_α bounds total uptake while handling times cap per-capita ingestion, generating explicit limits on interaction channels (Holling, 1959, MacArthur, 1970, Tilman, 1982). In bioenergetic food-web models, Holling-type functional responses impose per-link throughput limits (Yodzis and Innes, 1992). In chemostat systems, substrate inflow and dilution rates constrain processing capacity (Monod, 1949). Stoichiometric frameworks show that elemental constraints, for example phosphorus limitation, can become binding even when energetic supply is high (Sterner and Elser, 2002). Spatially structured systems impose additional local throughput limits within habitat patches, so that regional persistence requires compatibility among patch-level capacities (Levin, 1992). Structural capacity therefore provides a mechanistic explanation for intrinsic limits on ecological complexity. Interactions that increase throughput demand—such as increased connectance, stronger trophic fluxes, or higher biomass—can drive systems toward their throughput limits. When these limits are approached, the system can become increasingly sensitive to perturbations and may ultimately lose energetic compatibility if required throughput exceeds effective structural capacity.

Explicit mapping to classical model classes

This unifying framework should show not only that classical ecological models are compatible with energetic reasoning, but also exactly how their variables and constraints map onto the core quantities of the theory: external capture Q, dissipative loss D, gross internal throughput Φ, processing loss L, and structural capacity C. Because these mappings depend on the aggregate system boundary, it is useful to distinguish two cases. When explicit resource or substrate pools are included in the focal aggregate state, raw environmental inflows into those pools contribute directly to Q, and abiotic turnover contributes to D. When the focal aggregate state contains only consumer or living biomass, the direct input into that focal state is the boundary-crossing retained or assimilated flux into biomass, not necessarily the raw environmental inflow. The mappings below are structural correspondences in a shared energetic language rather than exact dynamical isomorphisms for every model class. Table 1 summarizes this correspondence for the principal dynamical model classes discussed below, while Table 2 summarizes how the major analytical traditions in ecology correspond to different mathematical operations on the same energetic structure. A concrete illustration of how the framework maps onto a standard ecological model is provided in the worked example below for a one-resource, two-consumers system.

Generalized Lotka–Volterra (GLV)

The generalized Lotka–Volterra model is commonly written

$$\dot{N}_i = r_i N_i + \sum_j a_{ij} N_i N_j,$$

where r_i is the intrinsic per-capita growth rate of species i and a_{ij} is the interaction coefficient describing the effect of species j on species i. Writing $r_i = q_i - m_i$, where q_i is the per-capita gain associated with external input and m_i is the per-capita maintenance or mortality term, gives

$$\dot{N}_i = q_i N_i - m_i N_i + \sum_j a_{ij} N_i N_j.$$

Summing over species yields

$$\sum_i \dot{N}_i = \underbrace{\sum_i q_i N_i}_{Q} - \underbrace{\sum_i m_i N_i}_{D} + \underbrace{\sum_{i,j} a_{ij} N_i N_j}_{\text{net interaction contribution}} .$$

Thus GLV admits only a partial energetic mapping. External gain and maintenance dissipation are represented explicitly by

$$Q = \sum_i q_i N_i, \qquad D = \sum_i m_i N_i.$$

By contrast, the signed interaction sum is a reduced-form net interaction contribution rather than an explicitly nonnegative throughput variable. Bare GLV therefore does not by itself define a positive gross-throughput quantity Φ or a structural capacity. Those arise only after augmenting the model with explicit resources, saturating uptake, or bounded directional fluxes

(Lotka, 1925, May, 1973, Volterra, 1926). In this sense GLV captures supply and dissipation directly, while treating redistribution in reduced form.

MacArthur consumer–resource and Tilman competition

Consumer–resource models make the energetic decomposition particularly transparent because environmental capture and internal transfers are represented explicitly. In MacArthur's formulation (MacArthur, 1970),

$$\dot{R}_\alpha = I_\alpha - w_\alpha R_\alpha - \sum_i c_{i\alpha} N_i R_\alpha, \qquad \dot{N}_i = N_i\Big(\sum_\alpha e_{i\alpha} c_{i\alpha} R_\alpha - m_i\Big),$$

where R_α is the abundance of resource α, I_α is its external inflow or renewal rate, w_α is its turnover or loss rate, $c_{i\alpha}$ is the uptake coefficient of species i on resource α, $e_{i\alpha}$ is conversion efficiency, and m_i is maintenance or mortality. Defining the uptake flow

$$F_{i\alpha} = c_{i\alpha} N_i R_\alpha,$$

the natural energetic quantities depend on the aggregate boundary. If resources are included in the aggregate state, then

$$Q = \sum_\alpha I_\alpha, \qquad \Phi = \sum_{i,\alpha} F_{i\alpha}, \qquad D = \sum_i m_i N_i + \sum_\alpha w_\alpha R_\alpha,$$

and conversion inefficiencies contribute to L. If instead the aggregate state contains consumers only, then the direct input into consumer biomass is the assimilated boundary-crossing flux

$$Q = \sum_{i,\alpha} e_{i\alpha} F_{i\alpha},$$

while resource turnover is external to D for that focal aggregate state. In either representation, Φ is the total internal throughput associated with resource extraction and transfer. At equilibrium, the resource equation implies the exact identity

$$\sum_i F^*_{i\alpha} = I_\alpha - w_\alpha R^*_\alpha \leq I_\alpha,$$

so resource renewal imposes a supply bound, while handling times or uptake ceilings generate throughput bounds summarized by an effective capacity term.

Bioenergetic trophic models

Bioenergetic food-web models make both Φ and structural limits especially explicit. Writing biomass as N_i for consistency with the notation of this paper, a Yodzis–Innes type formulation (Yodzis and Innes, 1992) uses ingestion

$$g_{ij}(N) = \frac{a_{ij} N_i N_j}{1 + \sum_\ell h_{i\ell} a_{i\ell} N_\ell},$$

where N_i is the biomass of species i, a_{ij} is the attack rate of consumer i on prey j, and $h_{i\ell}$ is the handling-time parameter associated with consumer i and resource ℓ. Gross internal throughput is then naturally

$$\Phi(N) = \sum_{i,j} g_{ij}(N),$$

while external capture is determined by basal production or external subsidy,

$$Q = \sum_{i \in \mathcal{B}} q_i N_i,$$

and dissipation is given by metabolic expenditure,

$$D = \sum_i x_i N_i.$$

Here $\mathcal{B}$ denotes the set of basal species, q_i their per-unit-biomass external capture rate, and x_i the metabolic dissipation coefficient of species i. Because ingestion saturates, handling times impose explicit throughput bounds on each consumer and link, so these models include a natural structural capacity summary (Holling, 1959, Yodzis and Innes, 1992). The corresponding processing loss L reflects the fraction of throughput not converted into retained biomass.

Chemostats and microbial kinetics

Chemostat models also admit a direct energetic interpretation. A standard formulation is

$$\dot{S} = D_{\mathrm{dil}}(S_{\mathrm{in}} - S) - \sum_i \frac{1}{Y_i} \mu_i(S) N_i, \qquad \dot{N}_i = \mu_i(S) N_i - D_{\mathrm{dil}} N_i,$$

where S is substrate concentration, S_{in} is inflow substrate concentration, D_{dil} is the dilution rate, Y_i is the yield coefficient of species i, and $\mu_i(S)$ is the substrate-dependent growth function, typically bounded above by $\mu_i^{\max}$. Define

$$F_i = \frac{1}{Y_i}\mu_i(S)N_i.$$

Then F_i is substrate-processing throughput, while retained biomass production is

$$Y_i F_i = \mu_i(S)N_i.$$

If substrate is included in the focal aggregate state, then

$$Q = D_{\text{dil}}S_{\text{in}}, \qquad D = D_{\text{dil}}S + D_{\text{dil}}\sum_i N_i$$

(after conversion to a common energetic currency, with maintenance added where appropriate), and

$$\Phi = \sum_i F_i.$$

If the aggregate state contains microbial biomass only, then the direct boundary-crossing input into that focal state is retained biomass production,

$$Q = \sum_i \mu_i(S)N_i = \sum_i Y_i F_i,$$

whereas raw substrate inflow $D_{\text{dil}}S_{\text{in}}$ enters through the environmental compartment. In both cases, capacity arises from supply,

$$\sum_i F_i \le D_{\text{dil}}S_{\text{in}},$$

and from kinetic throughput limits via $\mu_i^{\max}$ (Monod, 1949). Chemostats therefore provide one of the clearest empirical settings in which Q, D, Φ, and active limits on structural capacity can all be measured directly once the aggregate boundary is specified.

Stoichiometric and multi-element constraints

Stoichiometric models generalize the energetic framework by tracking several conserved currencies simultaneously. If $F_{ij}^{(E)}$ denotes the transfer of element E, then each element has its own capture, dissipation, and throughput terms,

$$Q^{(E)}, \qquad D^{(E)}(x), \qquad \Phi^{(E)}(x) = \sum_{i,j} F_{ij}^{(E)}.$$

In this setting, the relevant structural condition is not a literal minimum across unnormalized element-specific capacities, because different currencies generally carry different units and biological meanings. Instead, feasibility is determined by the joint satisfaction of the element-specific admissible constraints. Equivalently, if one introduces normalized dimensionless capacities $\widetilde{C}_E(\Theta)$ relative to a common limiting scale, then an effective scalar summary may be taken from the most restrictive normalized constraint,

$$\widetilde{C}_{\text{eff}}(\Theta) = \min_E \widetilde{C}_E(\Theta).$$

Thus the same logic still applies, but Q, D, Φ, and capacity must be understood as element-specific quantities coupled through stoichiometric balance and, when aggregated further, through an explicitly normalized summary (Sterner and Elser, 2002).

Spatial and metacommunity systems

In spatially structured systems, capture, dissipation, and throughput occur locally, while dispersal redistributes biomass and energetic demand among patches. A generic form is

$$\dot{N}_{i,x} = G_{i,x}(N_{\cdot,x}) + \sum_y m_{xy}(N_{i,y} - N_{i,x}),$$

where x indexes location, $G_{i,x}(N_{\cdot,x})$ denotes the local demographic contribution to species i in patch x, m_{xy} is the dispersal rate from patch y to patch x, and $N_{\cdot,x}$ denotes the vector of species abundances in patch x. Each patch has its own local energetic quantities,

$$Q_x, \qquad D_x(N_{\cdot,x}), \qquad \Phi_x(N_{\cdot,x}),$$

and its own local structural capacity $C_x(\Theta_x)$. Regional persistence therefore requires that

$$\Phi_x(N_{\cdot,x}) \leq C_x(\Theta_x) \qquad \text{for all } x,$$

while dispersal determines how energetic pressure is redistributed across patches. In this sense, spatial structure does not remove the Q–D–Φ–C logic; it replicates it locally and couples it across space (Levin, 1992, 1998).

Coexistence interpreted through energetic marginal effects

To express coexistence explicitly within the energetic framework, let N denote the species-biomass vector and x the full state. Write the species-level dynamics as

$$\dot{N}_i = G_i(x) - D_i(x) - L_i(x), \qquad i = 1, \ldots, S, \tag{14}$$

where $G_i(x)$ denotes the total energetic gain term for species i. Unlike the community-level quantity Q, the term $G_i(x)$ may include assimilated internal transfers in addition to externally captured input. With aggregate quantities

$$G(x) = \sum_i G_i(x), \qquad D(x) = \sum_i D_i(x), \qquad L(x) = \sum_i L_i(x),$$

and structural compatibility condition given by equation (13), coexistence theory corresponds to the marginal energetic performance of a species when rare. Define the per-capita net growth of species i as

$$g_i(x) = \frac{G_i(x) - D_i(x) - L_i(x)}{N_i},$$

whenever this quantity, or its limit, is well defined near $N_i = 0$. If $x^{-i,*}$ denotes the resident equilibrium of the full state with species i absent, the invasion growth rate of species i is

$$r_i^{\text{inv}} = \lim_{N_i \to 0^+} g_i(x) \Big|_{x_{-i} = x_{-i}^{-i,*}}. \tag{15}$$

When the numerator vanishes linearly in N_i near rarity, this expression reduces to the derivative form used in standard linearizations.

This decomposition makes explicit how classical coexistence mechanisms arise from the energetic components (Barabás et al., 2018, Chesson, 2000). Equalizing mechanisms act primarily through reducing differences in the marginal net energetic advantage of species when rare. Stabilizing mechanisms, by contrast, arise from the way species modify the marginal energetic burden created by redistribution. They are therefore encoded not in the scalar value of aggregate throughput alone, but in the derivative structure of the species-level net-growth terms, particularly in their self- and cross-effects. In model classes where self- and cross-effects can be compared directly, negative frequency dependence emerges when an increase in a species' own abundance raises its own marginal energetic burden more strongly than it raises that of competitors (Barabás et al., 2018, Chesson, 2000). This is an energetic interpretation of coexistence mechanisms, not a replacement for the full generality of Chesson's partition.

Crucially, these conditions are local. They describe whether a rare species has positive marginal growth in the resident energetic environment, but they do not by themselves guarantee that the full assemblage can be sustained globally (Saavedra et al., 2017). Even if all species satisfy positive invasion conditions, coexistence may still fail if the corresponding full equilibrium state x^* violates the energetic compatibility condition

$$\Phi(x^*) \leq C(x^*, \Theta).$$

Mutual invasibility is therefore a necessary but not sufficient condition for persistence when ecological systems operate under finite supply and throughput limits (Chesson, 2000, Godoy et al., 2018, Saavedra et al., 2017).

Feasibility domains as regions of energetic compatibility

Within the energetic framework, feasibility is the existence problem for ecological energetics. A community is feasible only if there exists a positive equilibrium $N^* > 0$ and a compatible full state x^* such that, for every species,

$$G_i(x^*) - D_i(x^*) - L_i(x^*) = 0,$$

while simultaneously satisfying the system-level compatibility condition in equation (13). Feasibility is therefore a global property of the energetic components: gain must match the combined demands of dissipation and processing loss, and the implied throughput must remain inside the admissible capacity of the system (Rohr et al., 2014, Saavedra et al., 2017, Song et al., 2018).

This formulation clarifies the energetic meaning of feasibility domains (Rohr et al., 2014, Saavedra et al., 2017, Song et al., 2018). They are regions of parameter space in which the system admits positive abundance vectors that satisfy both energetic balance and structural bounds. Parameters that increase capture enlarge this domain, whereas parameters that increase dissipation, raise demanded throughput, or reduce structural capacity shrink it. In settings where a reduced-form scaling closure is appropriate, a steeper throughput exponent provides one convenient way of representing this contraction. Structural stability may then be understood as the persistence of these energetically compatible states under perturbation (Rohr et al., 2014, Saavedra et al., 2017). Recent efforts to integrate niche and network perspectives reinforce this interpretation by showing that coexistence, interaction structure, and feasibility are best understood as coupled aspects of the same ecological organization (Deng et al., 2024, Godoy et al., 2018).

When feasibility is analyzed in the reduced species system, the relevant derivative object is

$$J_{ij}(x) = \frac{\partial}{\partial N_j}\big(G_i(x) - D_i(x) - L_i(x)\big). \tag{16}$$

In models with additional state variables, this matrix forms part of the full regularity matrix of the coupled equilibrium conditions. At regular feasible equilibria the relevant regularity matrix is nonsingular. At fold-type or other regularity-breaking feasibility boundaries its determinant may vanish, indicating that the system is losing the ability to sustain a positive compatible state (Medeiros et al., 2021). This condition should be understood as a local diagnostic of regular interior boundaries, not as an exhaustive characterization of every way feasibility may fail; feasibility can also be lost at positivity boundaries or when inequality constraints bind. Feasibility domains can thus be interpreted geometrically as the set of parameter combinations for which the coupled G–D–L–C conditions admit a positive solution.

Stability and complexity

If feasibility concerns the existence of an energetically compatible equilibrium, stability concerns the response of that equilibrium to perturbation (Medeiros et al., 2021). Local stability is governed by the full Jacobian $\mathcal{J}(x^*)$ of the coupled dynamical system evaluated at equilibrium. The species-level block contains derivatives of the energetic components in equation (14), including the matrix in equation (16) (Song and Saavedra., 2021). This makes explicit how stability emerges from the same energetic ingredients. The derivatives of D_i typically contribute local damping, since dissipative losses increase with abundance and oppose perturbations. The derivatives of G_i describe how gain changes with species abundances, while the derivatives of L_i describe how perturbations propagate through redistribution-associated energetic burden. Stability is therefore determined by the local balance between dissipative damping and interaction-driven amplification (Allesina and Tang, 2012, May, 1972, 1973).

This recovers the main intuition of classical stability theory in energetic form. Increasing interaction strength, connectance, or heterogeneity increases the magnitude and complexity of the redistribution-mediated derivative terms, thereby shrinking the margin by which damping dominates amplification. Complexity therefore destabilizes communities not because interaction matrices are intrinsically abstract, but because richer and stronger interaction structure amplifies the local energetic consequences of redistribution relative to dissipation. Stability analysis is thus a second-order perspective on the same energetic architecture that underlies coexistence and feasibility.

Stochastic dynamics and early warning signals

Early warning signals arise when stochastic perturbations act on systems that are approaching the boundary of energetic compatibility. Linearizing the full dynamics near a feasible equilibrium x^* gives

$$\dot{z} = \mathcal{J}(x^*)z + \eta(t),$$

where z denotes the vector of deviations from equilibrium, $\mathcal{J}(x^*)$ is the full Jacobian evaluated at equilibrium, and $\eta(t)$ represents stochastic forcing. Classical critical slowing down occurs when the dominant eigenvalue of $\mathcal{J}(x^*)$ approaches zero from below, so that perturbations decay more slowly and variance and autocorrelation increase (Carpenter et al., 2011, Dakos et al., 2012, Scheffer et al., 2009, Yang et al., 2025).

Within the energetic framework, these statistical signatures reflect the fact that perturbations increasingly alter redistribution-associated energetic burdens relative to the gain and dissipative mechanisms that restore equilibrium. In this sense, conventional early warning indicators diagnose the local dynamical consequences of a weakening restoring structure near the compatibility boundary (Dakos et al., 2012, Scheffer et al., 2009). For the stationary covariance matrix V of fluctuations under noise covariance Σ, the linearized dynamics satisfy the continuous Lyapunov equation

$$\mathcal{J}(x^*)V + V\mathcal{J}(x^*)^\top + \Sigma = 0.$$

The energetic framework also suggests a complementary structural precursor. If external input is used as a control parameter and the equilibria form a differentiable branch $x^*(Q)$, then

$$\frac{d\Phi^*}{dQ}$$

measures the marginal throughput response to added supply, while

$$\frac{d}{dQ}\left(\frac{\Phi^*(Q)}{C_{\mathrm{eff}}(Q)}\right)$$

measures the rate at which the system approaches an effective structural boundary. As these quantities increase, additional external input is converted increasingly into internal throughput rather than energetic slack.

If this structural approach to the boundary coincides with a local stability boundary or bifurcation, then the dominant eigenvalue of $\mathcal{J}(x^*)$ approaches zero and classical critical slowing down occurs. Structural saturation does not by itself guarantee critical slowing down in every model. The ratio $\Phi^*(Q)/C_{\text{eff}}(Q)$ should therefore be interpreted as a structural indicator of boundary approach, not as a universal distance-to-collapse metric and not as equivalent to conventional dynamical early warning statistics. Thus classical early warning signals and energetic precursor indicators describe two related aspects of the same phenomenon: the former capture the local dynamical consequences of weakened stability, whereas the latter quantify structural approach to the supply or throughput limits that bound ecological persistence. The boxed worked example below illustrates this connection explicitly for a simple consumer–resource system, showing how feasibility, invasion, local stability, and energetic boundary approach can all be written in the same formal language.

Discussion

The central synthesis is straightforward. Interaction models, consumer–resource theory, coexistence theory, feasibility-domain analysis, and stability theory can be read as different mathematical perspectives on a shared energetic constraint. Ecological communities must balance external energy capture, dissipative loss, and redistribution while remaining within finite supply and throughput limits. What differs across frameworks is not the underlying physical structure, but the property emphasized: existence of compatible equilibria, marginal responses to perturbations, or local dynamical behavior near equilibrium (Chesson, 2000, Godoy et al., 2018, May, 1972, Rohr et al., 2014, Saavedra et al., 2017). The contribution of this paper is therefore not a universal reduction theorem, but an exact balance identity for flux-based models together with a general admissible-flow condition for persistence and a set of reduced-form closures useful when scalar summaries are informative.

This perspective also sharpens the interpretation of classical results. May's complexity–stability threshold reflects increasing marginal amplification associated with redistribution as interaction richness and variance grow (Allesina and Tang, 2012, May, 1972). Coexistence mechanisms correspond to local derivative properties of net energetic balance that generate stabilizing or equalizing effects (Barabás et al., 2018, Chesson, 2000). Feasibility domains describe the regions of parameter space where energetic balance can be satisfied globally and where the implied throughput remains admissible (Rohr et al., 2014, Saavedra et al., 2017, Song et al., 2018). Early warning signals arise when dynamical responses slow as systems approach local stability boundaries, while ratios such as Φ/C can track structural saturation of admissible flow when an appropriate effective capacity summary is available. From this perspective, empirical patterns such as diversity saturating with productivity, enrichment-driven ecosystem collapse, and trophic cascades can be interpreted through the way redistribution demand and admissible capacity respond to environmental supply. Reduced-form scaling laws such as equation (7) provide one especially transparent summary when empirically justified (Loreau et al., 2001, Pace et al., 1999, Scheffer et al., 2001, Tilman, 1985). The main change is therefore not to the validity of classical theories, but to the lens through which they are connected.

This energetic unification also suggests concrete empirical directions. Quantifying aggregate internal throughput alongside environmental inputs and per-link throughput limits would allow direct estimation of $\Phi(x)$ and effective structural capacity summaries. Advances in ecological network reconstruction, metabolic flux measurements, and ecosystem metabolism provide increasingly feasible ways to estimate these quantities in natural systems (DeAngelis, 1980, Odum, 1969, Ulanowicz, 1986). Monitoring the ratio $\Phi(x)/C_{\text{eff}}(x, \Theta)$ through time could provide a mechanistic indicator of fragility: as the ratio approaches unity, the system approaches the boundary of energetic compatibility. This structural signal could complement statistical indicators such as variance or autocorrelation (Carpenter et al., 2011, Dakos et al., 2012, Scheffer et al., 2009). Manipulative experiments that increase connectance or interaction strength—through species additions, nutrient enrichment, or altered trophic structure—should therefore test whether throughput demand rises faster than capacity. Under the energetic framework, such manipulations are predicted to push systems toward structural limits even when classical coexistence conditions remain locally satisfied. Comparative analyses across ecosystems may also reveal systematic variation in the effective scaling exponent γ where a reduced-form closure is appropriate. Systems with strong functional-response saturation, modular interaction networks, or spatial compartmentalization should exhibit weaker superlinear scaling of throughput and therefore sustain greater richness for a given level of productivity. By contrast, highly connected or strongly interacting systems should approach throughput limits more rapidly.

The framework also has clear limitations. It assumes that aggregate dissipation and throughput can be represented by functions $D(x)$ and $\Phi(x)$, that the dissipative burden of processing can be summarized by $L(x)$ (or approximated in reduced form through a throughput-dependent closure), and that a structural capacity summary can be defined and estimated. In practice, these quantities may vary across environmental conditions and timescales (Brown et al., 2004, Levin, 1992). Adaptive and evolutionary processes can modify throughput limits by altering traits such as attack rates, metabolic efficiencies, or resource acquisition strategies. Spatial heterogeneity and metacommunity dynamics can redistribute energetic demand across landscapes, effectively relaxing local capacity constraints (Levin, 1992, 1998). Multiple energetically feasible equilibria may also exist within the compatibility domain; the energetic framework identifies necessary conditions for persistence but does not determine which feasible state will be realized (Holling, 1973, Saavedra et al., 2017). Likewise, when a reduced-form closure is used, the effective scaling exponent γ depends on network topology, functional responses, and spatial structure. Precise predictions therefore remain system-specific. The energetic perspective should thus be viewed as complementary to, rather than a replacement for, detailed analyses of species traits, evolutionary feedbacks, and historical contingency.

Ecological communities exist within fundamental physical constraints. Energy enters ecosystems from the environment, is redistributed through networks of interacting organisms, and is ultimately dissipated through metabolic processes (Brown et al., 2004, Lindeman, 1942, Odum, 1969). The balance between external supply, internal redistribution, and dissipative loss places structural limits on the biomass, complexity, and diversity that ecological systems can sustain. By making this energetic architecture explicit, I have argued that several central branches of ecological theory can be compared within a common framework. Coexistence theory describes the local marginal effects of species on energetic balance (Barabás et al., 2018, Chesson, 2000). Feasibility analysis identifies the parameter regions where compatible equilibria exist (Rohr et al., 2014, Saavedra et al., 2017, Song et al., 2018). Stability theory evaluates the robustness of these equilibria to perturbations (Allesina and Tang, 2012, May, 1972). Complexity results and early-warning signals describe how systems behave as energetic compatibility is approached or lost (Dakos et al., 2012, Scheffer et al., 2009).

This perspective does not overturn classical ecological theory; it integrates diverse insights within a common structural framework. Recognizing the energetic foundations of ecological dynamics highlights the basic tension between the demand imposed by interaction networks and the finite capacity through which energy can flow. That demand–capacity relationship provides a simple organizing principle linking ecosystem energetics, community dynamics, and network structure. Developing a structural ecology grounded in energetic compatibility may therefore help bridge historically separate traditions in ecological theory while suggesting new empirical approaches to measuring system fragility. Ultimately, the persistence of ecological communities depends on matching environmental energy supply to the energetic architecture through which that energy is redistributed. Understanding this architecture remains one of the central challenges of ecological theory.

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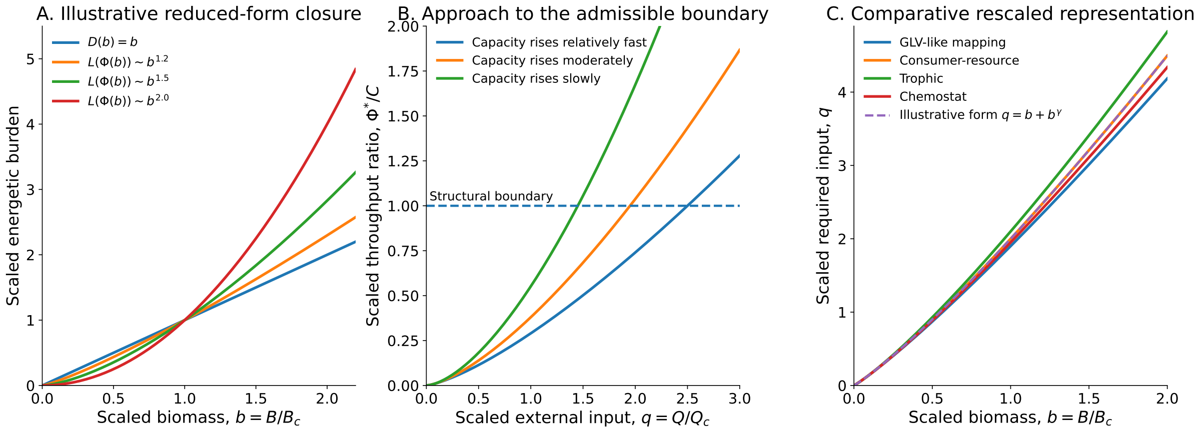

Figure 1: Illustrative reduced-form scaling closure and energetic comparison across ecological models. (**A**) Illustrative scaling asymmetry between dissipation and redistribution-associated energetic burden. Dissipative losses scale linearly with biomass, $D(b) = b$, whereas the reduced-form processing loss generated by internal throughput increases more rapidly, shown as $L_{\mathrm{rf}}(\Phi(b)) \sim b^\gamma$ for $\gamma = 1.2$, 1.5, and 2.0, with scaled biomass $b = B/B_c \in [0, 2.2]$. This panel is intended as a reduced-form closure, not as the foundation of the framework. (**B**) Illustrative approach to the admissible throughput boundary. The plotted quantity is the scaled equilibrium throughput relative to an effective structural capacity, $\Phi^*(Q)/C_{\mathrm{eff}}(Q)$, as a function of scaled external input $q = Q/Q_c \in [0, 3]$. The dashed horizontal line marks the structural boundary $\Phi^*(Q)/C_{\mathrm{eff}}(Q) = 1$. The three trajectories illustrate cases in which capacity rises relatively fast, moderately, or slowly with enrichment; when throughput demand rises faster than admissible capacity, the system is driven toward overload. (**C**) After rescaling, representative model classes align approximately with a common illustrative energetic form, $q = b + b^\gamma$, showing how distinct ecological models can be compared within a shared energetic framework when a reduced-form closure is introduced. This alignment is illustrative rather than an exact universality result.

Table 1: Energetic mapping of explicit dynamical model classes onto the core components of the framework: external capture Q, dissipation D, gross internal throughput Φ, processing loss L, and the dominant class of binding energetic constraint. The entries summarize the natural interpretation of each model class. Because the mapping depends on the aggregate system boundary, consumer–resource and chemostat entries distinguish the cases in which explicit resources are included in the aggregated state from those in which only consumer or microbial biomass is aggregated. Note that in bare generalized Lotka–Volterra models the interaction term is a signed net effect, not an explicit nonnegative throughput variable, so the mapping is only partial.

Model class	Canonical form	Q	D	Φ	L	Binding constraint
Generalized Lotka–Volterra (GLV)	$\dot{N}_i = r_i N_i + \sum_j a_{ij} N_i N_j$	$\sum_i q_i N_i$, with $r_i = q_i - m_i$	$\sum_i m_i N_i$	not explicit; signed net interaction term	implicit in reduced form	Supply
MacArthur consumer–resource / Tilman competition	Consumer growth from resource uptake	if resources aggregated: $\sum_\alpha I_\alpha$; if consumers only: $\sum_{i,\alpha} e_{i\alpha} F_{i\alpha}$	if resources aggregated: $\sum_i m_i N_i + \sum_\alpha w_\alpha R_\alpha$; if consumers only: $\sum_i m_i N_i$	$\sum_{i,\alpha} F_{i\alpha}$, $F_{i\alpha} = c_{i\alpha} N_i R_\alpha$	conversion and uptake inefficiencies	Supply + throughput
Bioenergetic trophic models	$g_{ij}(N)$ with Holling-type saturation	$\sum_{i \in \mathcal{B}} q_i N_i$	$\sum_i x_i N_i$	$\sum_{i,j} g_{ij}(N)$	unassimilated and dissipative fraction of throughput	Supply + throughput
Chemostat / microbial kinetics	Substrate inflow, Monod uptake, dilution	if substrate aggregated: $D_{\text{dil}} S_{\text{in}}$; if microbes only: $\sum_i \mu_i(S) N_i = \sum_i Y_i F_i$	if substrate aggregated: $D_{\text{dil}} S + D_{\text{dil}} \sum_i N_i$ (plus maintenance); if microbes only: $D_{\text{dil}} \sum_i N_i$ (plus maintenance)	$\sum_i F_i$, $F_i = \frac{1}{Y_i} \mu_i(S) N_i$	yield losses and maintenance	Supply + throughput
Stoichiometric / multi-element models	Element-specific flux balances	$Q^{(E)}$	$D^{(E)}(x)$	$\Phi^{(E)}(x) = \sum_{i,j} F_{ij}^{(E)}$	currency-specific processing losses	Joint element-specific constraints or normalized effective minimum
Spatial / metacommunity systems	Local dynamics plus dispersal	$\sum_x Q_x$	$\sum_x D_x(N_{\cdot,x})$	$\sum_x \Phi_x(N_{\cdot,x})$ plus dispersal transfers	local redistribution losses	Local patch constraints

Table 2: Energetic mapping of major analytical frameworks onto the common energetic structure of the system. Here $G_i(x)$, $D_i(x)$, and $L_i(x)$ denote species-level gain, dissipation, and redistribution-associated loss terms, with aggregate compatibility constrained by $\Phi(x^*) \leq C(x^*, \Theta)$ or by a corresponding effective capacity summary.

Framework	Primary object	Energetic expression	Interpretation
Coexistence theory	Invasion growth rate	$r_i^{\text{inv}} = \lim_{N_i \to 0^+} \left. \frac{G_i - D_i - L_i}{N_i} \right\|_{x_{-i} = x_{-i}^{-i,*}}$	Rare-species marginal balance
Feasibility analysis	Positive equilibrium	$G_i(x^*) - D_i(x^*) - L_i(x^*) = 0 \ \forall i, \quad \Phi(x^*) \leq C(x^*, \Theta)$	Existence of a compatible state
Local stability analysis	Full Jacobian	$\mathcal{J}(x^*)$, with species block $J_{ij}(x^*) = \left. \frac{\partial}{\partial N_j} (G_i - D_i - L_i) \right\|_{x = x^*}$	Local damping vs. amplification
May / random matrix theory	Spectrum of $\mathcal{J}$	$\Re(\lambda_k(\mathcal{J})) < 0 \quad \forall k$	Complexity-dependent stability margin
Early warning signals	Linear stochastic response	$\dot{z} = \mathcal{J}(x^*) z + \eta(t), \qquad \mathcal{J}(x^*) V + V \mathcal{J}(x^*)^\top + \Sigma = 0$	Slowing recovery near a local stability boundary
Energetic precursor indicator	Marginal boundary approach	$\frac{d\Phi^*}{dQ}, \qquad \frac{d}{dQ} \left(\frac{\Phi^*}{C_{\text{eff}}} \right)$	Structural approach to the throughput boundary

BOX 1: Worked example of two consumers and one resource

Consider two consumers N_1, N_2 feeding on one resource R: $\dot{R} = I - wR - F_1(R, N_1) - F_2(R, N_2)$ and $\dot{N}_i = e_i F_i(R, N_i) - m_i N_i$, $i = 1, 2$, with Holling-II uptake $F_i(R, N_i) = a_i R N_i/(1 + a_i h_i R)$. Here I is resource inflow, w abiotic resource loss, a_i attack rate, h_i handling time, e_i conversion efficiency, and m_i mortality. Define total throughput as $\Phi = F_1 + F_2$. Because $F_i \leq N_i/h_i$, handling times imply the capacity summary $C_h(N) = N_1/h_1 + N_2/h_2$; with an optional hard cap $\bar{C} > 0$, the admissible throughput is $\Phi \leq C(N) := \min\{C_h(N), \bar{C}\}$.

Energetic decomposition. For this worked example, include the resource in the focal aggregate state and let $B = R + N_1 + N_2$. Summing the equations gives $\dot{B} = I - wR - m_1 N_1 - m_2 N_2 - (1 - e_1)F_1 - (1 - e_2)F_2$. Hence $\dot{B} = Q - D - L$ with $Q = I$, $D = wR + m_1 N_1 + m_2 N_2$, $L = (1 - e_1)F_1 + (1 - e_2)F_2$, and structural constraint $\Phi^* = F_1^* + F_2^* \leq C(N^*)$. If one instead aggregated consumers only, then the direct boundary-crossing input into the focal state would be the assimilated flux $e_1 F_1 + e_2 F_2$, not the raw inflow I.

Feasibility. A positive coexistence equilibrium (R^*, N_1^*, N_2^*) must satisfy $I - wR^* - F_1^* - F_2^* = 0$, $e_i F_i^* - m_i N_i^* = 0$ for $i = 1, 2$, and $\Phi^* \leq C(N^*)$. Thus finite capacity shrinks the parameter region that supports coexistence and reduces structural stability in the sense of Saavedra et al. (2017).

Coexistence and stability. The rare-species per-capita growth of consumer i is $g_i(x) = \big(e_i F_i(R, N_i) - m_i N_i\big)/N_i$. Equalizing effects reduce differences in g_i when species are rare. In this consumer–resource setting, stabilizing effects can be interpreted as stronger self-limitation than cross-limitation. Local stability is determined by the full Jacobian $\mathcal{J}^*$ at (R^*, N_1^*, N_2^*); all eigenvalues must have negative real part.

Structural limit and early warning. Increasing inflow I generally raises biomass and throughput $\Phi^* = F_1^* + F_2^*$. A coexistence equilibrium may therefore satisfy local invasion and local stability conditions yet still fail globally if enrichment drives $\Phi^* > C(N^*)$. Loss of compatibility can then be expressed through exclusion, biomass decline, or dynamical reorganization, depending on the model. If the approach to the structural boundary $\Phi^*/C(N^*) \to 1$ coincides with a local stability boundary, the dominant eigenvalue of $\mathcal{J}^*$ approaches 0^- and conventional early warning signals strengthen.

Appendices

Formal setting and core results

This appendix makes precise the scope of the main-text claims. The purpose is not to force all ecological models into a single exact dynamical form, but to identify one formal setting in which the energetic balance is exact and in which general sufficient conditions for bounded compatible states can be stated. The reduced-form superlinear scaling closure used in the main text is then recovered as one transparent special case.

Consider a system with focal stock variables $X_1, \ldots, X_S$ expressed in a common energetic currency. Depending on the chosen aggregate boundary, these may represent biomasses alone or a mixture of biomasses with explicit resource or substrate pools. Let

$$B = \sum_{i=1}^{S} X_i$$

denote the aggregate energetic stock of those focal variables. Additional state variables may also be present in the full state x, but all exact identities below hold relative to the chosen focal aggregate state.

Assume that the dynamics of the focal stock variables can be written as

$$\dot{X}_i = q_i(x,\theta) + \sum_j \varepsilon_{ji}(x,\theta) f_{ji}(x,\theta) - d_i(x,\theta) - \sum_k f_{ik}(x,\theta), \tag{17}$$

where x denotes the full state, θ the parameter vector, $q_i \geq 0$ the externally captured input into node i, $d_i \geq 0$ the dissipative loss of node i, $f_{ij} \geq 0$ the gross transfer from node i to node j, and $0 < \varepsilon_{ij} \leq 1$ the corresponding transfer efficiency.

Define the aggregate quantities

$$Q(x,\theta) = \sum_i q_i(x,\theta), \qquad D(x,\theta) = \sum_i d_i(x,\theta),$$

$$\Phi(x,\theta) = \sum_{i,j} f_{ij}(x,\theta), \qquad L(x,\theta) = \sum_{i,j} \big(1 - \varepsilon_{ij}(x,\theta)\big) f_{ij}(x,\theta).$$

Because all stock variables have already been converted to a common energetic currency, L is the non-retained fraction of gross internal transfers.

Proposition A1 (Exact aggregate balance). Under equation (17), the aggregate stock satisfies

$$\dot{B} = Q - D - L.$$

Summing equation (17) over i gives

$$\dot{B} = \sum_i q_i + \sum_{i,j} \varepsilon_{ji} f_{ji} - \sum_i d_i - \sum_{i,j} f_{ij}.$$

Relabeling indices in the transfer term yields

$$\sum_{i,j} \varepsilon_{ji} f_{ji} = \sum_{i,j} \varepsilon_{ij} f_{ij},$$

so

$$\dot{B} = Q - D - \sum_{i,j} (1 - \varepsilon_{ij}) f_{ij} = Q - D - L.$$

This is equation (1) in exact form.

Admissible flow set and derived capacity summary. At a given state x and parameter vector θ, define the admissible flow set

$$\mathcal{A}(x,\theta) = \left\{ F = (f_{ij}) \,:\, q_i + \sum_j \varepsilon_{ji} f_{ji} = d_i + \sum_k f_{ik} \ \forall i, \quad 0 \le f_{ij} \le f_{ij}^{\max}(x,\theta) \right\}.$$

A scalar capacity summary can then be defined by

$$C(x,\theta) = \sup_{F \in \mathcal{A}(x,\theta)} \sum_{i,j} f_{ij}.$$

The main text sometimes writes a simpler effective notation when the dependence on state can be suppressed or summarized. When multiple conserved currencies are tracked simultaneously, the exact admissible condition is the intersection of the corresponding currency-specific admissible sets; any additional scalar capacity summary requires an explicit normalization choice.

Proposition A2 (Necessary condition for a feasible equilibrium). If x^* is a feasible equilibrium of the focal aggregate state, then

$$Q(x^*,\theta) = D(x^*,\theta) + L(x^*,\theta)$$

and the realized flow vector belongs to the admissible set:

$$F(x^*, \theta) \in \mathcal{A}(x^*, \theta).$$

In particular,

$$\Phi(x^*, \theta) \leq C(x^*, \theta).$$

The equilibrium identity follows from Proposition A1 with $\dot{B} = 0$. Membership of the realized flow vector in $\mathcal{A}(x^*, \theta)$ follows directly from the node-level steady balances and channel bounds. The capacity inequality is then immediate from the definition of $C(x, \theta)$.

Proposition A3 (Finite aggregate-stock bound under coercive energetic burden). Assume there exist $B_0 \geq 0$ and an increasing function $\psi : [B_0, \infty) \to [0, \infty)$ with $\psi(B) \to \infty$ as $B \to \infty$ such that, for all feasible states with $B \geq B_0$,

$$D(x, \theta) + L(x, \theta) \geq \psi(B).$$

Assume also that external capture is uniformly bounded above,

$$Q(x, \theta) \leq \bar{Q}(\theta) < \infty.$$

Then every feasible equilibrium satisfies $B \leq B_{\max}(\theta) < \infty$.

At equilibrium, Proposition A2 gives $Q = D + L$. Therefore any feasible equilibrium with $B \geq B_0$ must satisfy

$$\bar{Q}(\theta) \geq \psi(B).$$

Because $\psi(B) \to \infty$ as $B \to \infty$, this inequality can hold only for B below the largest solution of

$$\psi(B) = \bar{Q}(\theta).$$

Taking the maximum of that solution and B_0 gives a finite bound $B_{\max}(\theta)$.

The reduced-form superlinear closure used in the main text,

$$D(x, \theta) + L(x, \theta) \geq c_1 B + c_2 B^{\gamma}, \qquad c_1, c_2 > 0,\ \gamma > 1,$$

is one transparent special case of Proposition A3.

Proposition A4 (Richness bound requires an additional biomass-floor assumption). Suppose, in addition to Proposition A3, that the aggregate stock relevant for richness is the summed biomass of persisting species and that every persisting species satisfies a minimum biomass requirement

$$N_i^* \geq \underline{N} > 0.$$

Then the number of persisting species satisfies

$$S \leq \frac{B_{\max}(\theta)}{\underline{N}}.$$

Since $B^* = \sum_i N_i^* \geq S\underline{N}$, the result follows immediately from $B^* \leq B_{\max}(\theta)$.

Proposition A4 explains why the main text treats limits on richness and complexity conditionally. A bound on total biomass alone does not imply a bound on richness unless one adds an assumption linking persistence to a minimum biomass scale or to a particular rule of biomass allocation across species.

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