# Integrating metabolic scaling and coexistence theories

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# Abstract

Metabolic scaling and coexistence theories have been pivotal in mathematizing both the energy expenditures and transformations across individuals and populations. Yet, it is unclear how the sustainability of biodiversity depends on metabolic scaling relationships. Here, we provide a tractable and scalable perspective to study how the possibilities for multispecies coexistence (i.e., feasibility) change as a function of the dependence of a population's metabolism on body size. This integration predicts that, regardless of body size distribution among populations, there is a reciprocal relationship between the scaling exponents defining the dependence of competitive effects and expected carrying capacities on body size. In line with empirical observations, our integration predicts that expected carrying capacities lead to equilibrium biomasses that are independent from body size, and consequently, to equilibrium abundances that are inversely related to body size. We show that this even distribution of equilibrium biomasses increases the possibilities for multispecies coexistence under random environmental perturbations. Additionally, this integration establishes that the possibilities for multispecies coexistence is maximized when no species has an energetic competitive advantage. This integration opens new opportunities to increase our understanding of how metabolic scaling relationships at the individual and population levels shape processes at the community level.

## Metabolic scaling theory

Metabolism is the sum of the total biochemical reactions governing the flow of energy in an individual (organism) [1]. Therefore, knowing how and why metabolism changes across individuals has become central in our understanding of the energy requirements driving the sustainability of different forms of life on Earth [2, 3]. In this line, metabolic scaling theory [4] has been instrumental in explaining and predicting the extent to which the rate of energy expenditure in an individual scales with its body size (body mass) and temperature. The size and temperature dependence is expected as the result of the fractal-like design of the resource supply system and the kinetics of the metabolic reactions [5]. These dependencies are governed by simple equations. On the one hand, the size dependence is typically allometric (not proportional) power-law relationships of the form $y = a \cdot x^{\beta}$, where $a$ is the constant of proportionality (normalization constant), and the sign and magnitude of the exponent (power) $\beta$ phenomenologically represent the physico-chemical constraints operating at the individual level [5–7]. On the other hand, the temperature response is typically exponential, $y = a \cdot e^{\frac{E}{T}}$, and known as the Arrhenius equation [5–7]. Put together, it has been shown [5–7] that the metabolic rate ($b_i$) of an individual $i$ scales with its body size ($m_i$) and temperature ($T$) as

$$b_i = b_0 \cdot e^{-\frac{E_i}{k \cdot T}} \cdot m_i^{\frac{3}{4}} \tag{1}$$

(dimensions [mass][time]$^{-1}$), where $E_i$ is the activation energy (dimension [eV]), $k$ is the Boltzmann's constant (dimensions [eV][K]$^{-1}$), $T$ is the absolute temperature (dimension [K]), and $b_0$ is a taxon-specific normalization constant (dimensions [mass]$^{\frac{1}{4}}$[time]$^{-1}$). Eq. (1) reveals that larger individuals are characterized by higher energy requirements per unit of time. These requirements, however, decrease non-linearly per unit of mass as $b_i \cdot m_i^{-1} = b_0 \cdot e^{-\frac{E_i}{k \cdot T}} \cdot m_i^{-\frac{1}{4}}$ (known as mass-specific metabolism, dimension [time]$^{-1}$), revealing the economies of body plans [3, 8].

In ecological research, populations (rather than individuals) are typically the basic units of living matter organization [9, 10]. Assuming a fixed growth rate of a population $i$ under a constant environment ($\theta$), and that a stable age and size distribution have been reached, the average value of mass per individual ($M_i$) becomes time independent and the metabolic rate (Eq. 1) of population $i$ can be written as $B_i(\theta) = B_0 \cdot e^{-\frac{E_i}{k \cdot T}} \cdot M_i^{\frac{3}{4}}$ (dimensions [mass][time]$^{-1}$) [8], where the environment can be specified as $\theta = \{T\}$. These metabolic scaling relationships have been confirmed by multiple empirical data across different taxa [11–13]. However, the specific parameter values characterizing the metabolic dependence on temperature and size can vary as a function of the species and taxonomic group, respectively [3, 6, 14]. For instance, it has been

shown that for metazoans, protists, and prokaryotes, the scaling dependence of metabolic rate on body size ranges from sub-linear, linear, to super-linear, respectively [15].

Similarly, it can then be proved [7, 8] that the average generation time (or lifespan) of an individual from population $i$ becomes proportional to the scaling relationship $G_i(\theta) \propto e^{\frac{E_i}{k \cdot T}} \cdot M_i^{\frac{1}{4}}$ (dimension [time]). Thus, the reciprocal of the average generation time specifies the maximum growth rate of an individual in population $i$ under a given environment $\theta$ and can be written as

$$\frac{1}{G_i(\theta)} = r_i(\theta) \propto e^{-\frac{E_i}{k \cdot T}} \cdot M_i^{-\frac{1}{4}} \tag{2}$$

(dimension $[\text{time}]^{-1}$). These relationships have been used to show how the metabolic processes at the level of individuals can affect the metabolic and ecological processes at the level of populations under a local environment [8]. Moreover, assuming that individuals from a population with different body sizes capture on average the same amount of resources or energy in their environment (i.e., the energetic equivalence rule [11]), it has been shown [8] that it is possible to derive the mass and temperature dependence of a population's environmental carrying capacity. This is the maximum biomass density of a population that can be sustained by a specific local environment $\theta$ and can be approximated as

$$K_i(\theta) \propto e^{\frac{E_i}{k \cdot T}} \cdot M_i^{-\frac{3}{4}} \tag{3}$$

(dimensions $[\text{mass}][\text{space}]^{-1}$). That is, the maximum biomass of a population per unit area (or volume) decreases with both temperature and size.

Therefore, it has become central to understand how these different scaling relationships at the individual or population level are linked to ecological processes at the community level (the collection of different coexisting populations in a given place and time). While there has been significant work using metabolic theory at the ecosystem level [16–21], many opportunities remain open for theoretical integration and simplification. A clear example of these opportunities is the relationship between metabolism and multispecies coexistence, which has been typically studied for a specific set of model parameters [18, 22]. As a consequence, it continues to be debated the extent to which the possibilities for multispecies coexistence are mainly determined by the distribution of body sizes or by the exponents (constraints) determining the dependence of interaction processes on body size [8, 15, 18, 23]. Similarly, it is still missing a tractable and scalable framework that can increase our understanding of how metabolic scaling relationships at the individual or population levels affect processes at the community level [8, 17].

## Coexistence theory

In general, coexistence theory in ecology [24–27] aims to investigate the possibilities that a community $\mathcal{S}(\mathbf{A})$, formed by $|\mathcal{S}|$ populations and characterized by some given biotic constraints ($\mathbf{A}$), can persist under different environmental contexts ($\theta$). Although not exclusively, this analysis has been mainly performed under generalized Lotka-Volterra dynamics [28], which in line with metabolic scaling theory [4], can be derived from thermodynamics principles, from principles of conservation of mass and energy, and from chemical kinetics in large populations [29–32]. In particular, in the Lotka-Volterra competition model [33, 34], the per capita growth rate of a population's density can be written as

$$\frac{\dot{N}_i}{N_i} = \frac{r_i(\theta)}{K_i(\theta)}(K_i(\theta) - \sum_j a_{ij} \cdot N_j), \forall i \in \mathcal{S}(\mathbf{A}), \tag{4}$$

(dimension $[\text{time}]^{-1}$), where $N_i$ is the population density (dimension [mass][area] or [individuals][area]) and $\dot{N}_i$ is the time derivative (dimensions $[\text{density}][\text{time}]^{-1}$). Per competition, $r_i(\theta) > 0$ is the intrinsic growth rate (dimension $[\text{time}]^{-1}$), $K_i(\theta) > 0$ is the environmental carrying capacity (dimension [density]). Here, $\theta$ represents the phenomenological joint effect of the abiotic and biotic environmental factors, not explicitly considered in the model, acting on the per-capita growth rate of each particular population. Then, $\mathbf{A} = (a_{ij}) \geq 0 \in \mathbb{R}^{|\mathcal{S}|\times|\mathcal{S}|}$ is the per capita, time-independent, competitive effect (dimensionless, but see Ref. [34]) of a population $j$ on an individual of population $i$. Note that

$$a_{ij} = \frac{\hat{a}_{ij}}{\hat{a}_{ii}}, \tag{5}$$

where $\hat{a}_{ij}$ and $\hat{a}_{ii}$ are the time-dependent competitive effects (dimensions $[\text{time}]^{-1}[\text{density}_j]^{-1}$) and self-regulation (dimensions $[\text{time}]^{-1}[\text{density}_i]^{-1}$), respectively. It follows that $a_{ii} = 1$ per definition [34]. In other words, $a_{ij}$ specifies the time-independent rate of biomass (energy) converted from a population $i$ to a population $j$ (or resources used by $j$ instead of $i$) [31]. Then, the environmental carrying capacity of a population $i$ under a local environment $\theta$ can be expressed as a function of its intrinsic growth rate and time-dependent self-regulation as

$$K_i(\theta) = \frac{r_i(\theta)}{\hat{a}_{ii}}. \tag{6}$$

The necessary condition for persistence under Lotka-Volterra equilibrium dynamics becomes the existence of positive solutions in Eq. (4) [35]. This necessary condition is known as *feasibility*

and it is written as (using matrix notation [25, 36])

$$\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K}^*(\theta) > 0. \tag{7}$$

Subsequently, the environmental carrying capacities ($\boldsymbol{K}^*(\theta)$) compatible with the feasibility of community $\mathcal{S}(\mathbf{A})$ (known as the feasibility domain $D_F$) are given by

$$D_F(\mathcal{S}(\mathbf{A})) = \left\{ \boldsymbol{K}^*(\theta) = \sum_{j\in\mathcal{S}} N_j^* \mathbf{a}_j : \mathbf{A} = [\mathbf{a}_1\ \mathbf{a}_2\ \cdots\ \mathbf{a}_{|\mathcal{S}|}], N_j^* \in \mathbb{R}_{>0} \right\} \in \mathbb{R}^{|\mathcal{S}|}, \tag{8}$$

where $\mathbf{a}_j$ is the $j^{\text{th}}$ column vector of the interaction matrix $\mathbf{A}$ [31, 37]. Each column $j$ represents the time-independent competitive effect of population $j$ on all other populations (including itself). Thus, the feasibility domain specifies all the possible distributions (vector directions) of $\boldsymbol{K}(\theta)$ (Eq. 6) that are compatible with biotic constraints $\mathbf{A}$ as written in Eq. (7). Geometrically, the feasibility domain is the convex hull of the $|\mathcal{S}|$ spanning vectors in $|\mathcal{S}|$-dimensional space (Fig. 1A) [36, 38]. Overall, the interaction matrix $\mathbf{A}$ determine the size of the feasibility domain. The stronger the mean competition in a community ($\langle a_{ij}\rangle$), the smaller the feasibility domain.

Assuming that all values of $\theta$ are equally likely and there is a one-to-one mapping between the environmental contexts $\theta$ and the vectors of environmental carrying capacities $\boldsymbol{K}(\theta)$, it also follows that the larger the feasibility domain, the larger the possibilities for multispecies coexistence [33, 39]. Specifically, for a competition system, the normalized size of the feasibility domain can be estimated as

$$\Omega(\mathcal{S}(\mathbf{A})) = \frac{2^{|\mathcal{S}|}}{\text{vol}(\Theta^{|\mathcal{S}|})} \cdot \text{vol}(D_F(\mathcal{S}(\mathbf{A})) \cap \Theta^{|\mathcal{S}|}) \in [0, 1], \tag{9}$$

where $\Theta^{|\mathcal{S}|}$ is the $(|\mathcal{S}| - 1)$-dimensional closed unit sphere in dimension $|\mathcal{S}|$ [33, 36]. Because $\Omega(\mathcal{S}(\mathbf{A}))$ decreases exponentially with the dimension of the community $|\mathcal{S}|$ [37, 40], it is practical to use the *population-specific feasibility* $\omega(\mathcal{S}(\mathbf{A})) = \Omega(\mathcal{S}(\mathbf{A}))^{1/|\mathcal{S}|}$, which can be interpreted as the possibilities for survival of a random population within the community [36, 41, 42].

Additionally, the location of a given vector $\boldsymbol{K}^*(\theta)$ inside the feasibility domain (a feasible distribution of environmental carrying capacities) provides information about the extent to which a feasible community can tolerate small random environmental perturbations without losing feasibility ($\boldsymbol{N}^* > 0$). For example, assuming that all directions of environmental perturbations in $\boldsymbol{K}^*(\theta)$ are equally likely, it logically follows that the distribution of environmental carrying capacities with the highest possibilities for multispecies coexistence under random environmental

perturbations is the geometric centroid of the feasibility domain (Fig. 1A) [37, 43, 44]

$$\boldsymbol{K_c}(\mathbf{A}) = |\mathcal{S}|^{-1}\boldsymbol{a}_1 + \cdots + |\mathcal{S}|^{-1}\boldsymbol{a}_n. \tag{10}$$

By definition, the centroid $\boldsymbol{K_c}(\mathbf{A})$ is the expected vector of environmental carrying capacities of a feasible community and corresponds to the parameter values that provide the solution $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K_c^*}(\theta) = (1, 1, \ldots, 1) \in \mathcal{R}^{|\mathcal{S}|}$ [39]. In other words, while the elements of the vector defining the expected carrying capacities (the centroid of the feasibility domain) can be different from each other, the populations' biomasses become the same at equilibrium. This implies that the equilibrium biomass of a population is independent from the population's body size.

## Integrating theories

The link between metabolic scaling and coexistence theories has been performed under different frameworks, each answering specific ecological questions [16–19, 22, 45, 46]. Here, we are interested in developing a tractable and scalable perspective to investigate the association of metabolic scaling relationships with the possibilities for multispecies coexistence. To this end, first we parameterized the interaction matrix $\mathbf{A}$ using metabolic scaling theory with a minimum set of assumptions. Specifically, to parameterize the Lotka-Volterra competition model (Eq. 4), we replaced $r_i(\theta) \propto e^{-\frac{E_i}{k \cdot T}} \cdot M_i^{-\frac{1}{4}}$ and $K_i(\theta) \propto e^{\frac{E_i}{k \cdot T}} \cdot M_i^{-\frac{3}{4}}$ by their corresponding metabolic upper-limit approximations (Eq. 2 and Eq.3, respectively). Then, we can rewrite the time-dependent self-regulation $\hat{a}_{ii} = r_i \cdot K_i^{-1}$ (Eq. 6) as $\hat{a}_{ii} \propto e^{-2\frac{E_i}{k \cdot T}} \cdot M_i^{\frac{1}{2}}$. Following standard unit conversions [34], we defined the time-dependent competitive effects as $\hat{a}_{ij} = r_i \cdot K_j^{-1}$, and rewrite them as $\hat{a}_{ij} \propto e^{-\frac{E_i + E_j}{k \cdot T}} \cdot M_i^{-\frac{1}{4}} \cdot M_j^{\frac{3}{4}}$. Next, from Eq. (5), the time-independent competitive effect can be estimated as

$$a_{ij} = a_0 \cdot e^{E_i - E_j} \cdot (M_j/M_i)^{\alpha = \frac{3}{4}}, \tag{11}$$

where $a_0$ is a normalization constant and $\alpha = 3/4$ is the derived dependence of time-independent competitive effects on body size. In other words, the higher the mass of population $j$ relative to the mass of population $i$, the higher the time-independent competitive effect. Instead, the higher the activation energy of population $j$ relative to the activation energy of population $i$, the lower the time-independent competitive effect.

To investigate the expected distribution of environmental carrying capacities compatible with the feasibility of a given community (centroid of feasibility domain), we studied the scaling exponent ($\beta$) that makes the vector of environmental carrying capacities (from Eq. 3, $\boldsymbol{K} =$

$K_0 \cdot \boldsymbol{M}^{\beta}$, where $K_0$ is a normalization constant) the closest to the centroid of the feasibility domain ($\boldsymbol{K_c}(\mathbf{A})$) of a metabolically-generated interaction matrix $\mathbf{A}$ as defined in Eq. (11). To perform this task, we generated an ensemble of $10^6$ interaction matrices $\mathbf{A}$ characterizing the time-independent competitive effects ($a_{ij}$) between five populations (higher dimensions yield similar conclusions). Each matrix was formed by drawing $M_i$ and $E_i$ values independently from uniform distributions $\in [0, 1]$ and $\in [0.5, 0.7]$, respectively [6, 8] (these distributions can change without affecting the qualitative results). Following previous work [47, 48], we set the normalization constant of interaction effects to $a_0 = |\mathcal{S}|^{-\frac{1}{2}}$ for $i \neq j$, otherwise $a_0 = 1$. This assumption follows the rationale that interactions tend to be weak in empirical food webs, stabilizing theoretical communities [49, 50]. The greater the value of $a_o$, the greater the overall competition, and the smaller the feasibility domain [39]. Then, for each value of the scaling exponent $\beta \in [-2, 2]$, we calculated the average distance between $\boldsymbol{K_c}(\mathbf{A})$ and $\boldsymbol{K}$ as [27]

$$d(\mathbf{A}, \boldsymbol{K}) = \arccos(\boldsymbol{K} \cdot \boldsymbol{K_c}(\mathbf{A}) \cdot ||\boldsymbol{K}||^{-1} \cdot ||\boldsymbol{K_c}(\mathbf{A})||^{-1}). \tag{12}$$

Note that the normalization constant $K_0$ of environmental carrying capacities does not affect this distance and can be omitted from the equation [39].

Figure 1B (blue solid line) reveals that the vector of environmental carrying capacities generated by the scaling relationship $\boldsymbol{K} \propto \boldsymbol{M}^{\beta=-\frac{3}{4}}$ is, in fact, the centroid of the feasibility domain (i.e., $\boldsymbol{K_c}(\mathbf{A})$, $d(\mathbf{A}, \boldsymbol{K}) = 0$, Eq. 10) of the metabolically-generated interaction matrices (Eq. 11)). This implies that the decrease of environmental carrying capacities with body size given by $\beta = -3/4$ is the scaling relationship that increases the possibilities for multispecies coexistence under random environmental perturbations when the dependence of competitive effects on body size increases by the power law $\alpha = 3/4$. However, as mentioned before, it is expected that the specific details (value of $\beta$) of metabolic scaling relationships may change across different taxa [2, 3, 15]. Notably, our framework is compatible with these differences. Figure 1B-C shows that the values of $\alpha$ and $\beta$ are reciprocal (i.e., $\beta = -\alpha$, Eqs. 6 and 11). This further implies that the exponent defining the dependence of competitive effects on body sizes, but not the distribution of body sizes itself, is linked to the expected distribution of environmental carrying capacities compatible with the feasibility of a community (the centroid of the feasibility domain). It is worth recalling that the centroid represents the condition under which all populations have the same biomass at equilibrium [39]. Furthermore, this result implies that dividing the equilibrium biomasses ($\boldsymbol{N^*}$) by the corresponding average body size $\boldsymbol{M}$, the number of individuals per area ($\boldsymbol{I}$) become inversely related to body size ($\boldsymbol{I} \propto \boldsymbol{M}^{-1}$). This is in agreement with empirical

observations showing that at the community level (or over a much larger size range of life) population density scales inversely with body size [51] and can be treated as a potentially maximum relationship [52].

Because the dependence of competitive effects on body size (the exponent $\alpha$ in Eq. 11) has important implications for feasibility in a community, it becomes paramount to understand when are these competitive effects maximizing the possibilities for multispecies coexistence. To this end, we investigated the extent to which the size of the feasibility domain, measured by the population-specific feasibility (i.e., $\omega(\mathcal{S}(\mathbf{A})) = \Omega(\mathcal{S}(\mathbf{A}))^{1/|\mathcal{S}|}$, Eq. 9), changes as a function of the interaction matrix. We followed our previous analysis generating an ensemble of $10^6$ interaction matrices $\mathbf{A}$ characterizing the competitive effects ($a_{ij}$) between five populations (higher dimensions yield similar conclusions), where each interaction matrix was formed by drawing $M_i$ and $E_i$ values independently from uniform distributions $\in [0, 1]$ and $\in [0.5, 0.7]$, respectively [6, 8] (these distributions can change without affecting the qualitative results). We set the normalization constant of competitive effects to $a_0 = |\mathcal{S}|^{-\frac{1}{2}}$ for $i \neq j$, otherwise $a_0 = 1$. Then, for each value of the scaling exponent $\alpha \in [-2, 2]$, we calculated the population-specific feasibility. Figure 1C shows that the maximum value of $\omega(\mathcal{S}(\mathbf{A}))$ is attained when $\alpha = 0$. This reveals that the possibilities for multispecies coexistence is achieved when no population has a competitive advantage, supporting the relevance of an energetic equivalence rule [11].

## Concluding remarks

We have proposed a tractable and scalable integration of metabolic scaling theory [4] and coexistence theories [24–27] in order to systematically link metabolic scaling relationships at the population level and community dynamics [38, 41, 42]. Our framework has been based on understanding how body-size constraints operating on competitive effects modulate the parameter space of environmental carrying capacities compatible with multispecies coexistence. This integration has allowed us to observe that the dependence of competitive effects on body size is reciprocal to the dependence of environmental carrying capacities on body size. This link in particular specifies the expected distribution of carrying capacities (i.e., the centroid of the feasibility domain), which in turn is the distribution that can increase the possibilities for multispecies coexistence under random environmental perturbations. In line with empirical observations [51], our integration predicts that expected carrying capacities lead to equilibrium biomasses that are independent from body size, and consequently, to equilibrium abundances that are inversely related to body size. Therefore, linking competitive effects to metabolism and,

consequently, to body size can help to capture important theoretical derivations and empirical observations [8, 51].

It is worth mentioning that our effort to integrate metabolic scaling and coexistence theories has been focused on exploring the dependence of the possibilities for multispecies coexistence (feasibility) on body size. For this purpose, we have used the Arrhenius equation (Eq. 1) to describe the exponential phase of temperature response. However, for cases where the interest is to predict how a population or community will respond to temperature beyond that phase, it would be useful to use a model that accounts for the curvature of temperature response curve [3]. This alternative model can be adapted to our integration in order to explore temperature-related questions, such as how the variation in optimum temperatures of populations in a community would affect its feasibility. In general, we believe the proposed integration can open up new opportunities to increase our understanding of how metabolic scaling relationships at the individual and population levels shape processes at the community level.

**Code accessibility**. The code supporting the results is archived on Github: `https://github.com/MITEcology/Scaling_Coexistence_2023`

**Acknowledgments**. We would like to thank the Santa Fe Institute scaling and NETI working groups, Jie Deng, Lucas Medeiros, Rudolf Rohr, Chuliang Song, and Andrea Tabi for insightful comments that led to the improvement of this work.

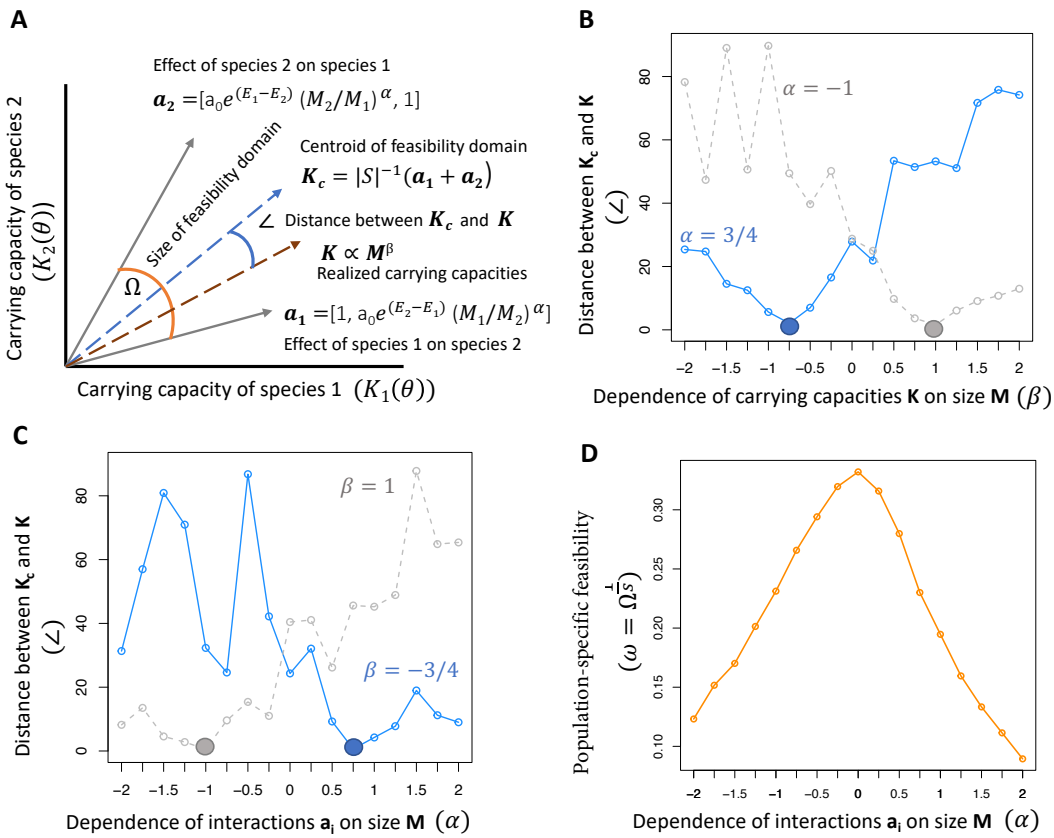


Figure 1: **Linking metabolic scaling and coexistence theories**. Panel **A**. For an illustrative example of a community with $|S| = 2$ populations under Lotka-Volterra competition dynamics (Eq. 4), we show the parameter space of carrying capacities $K_i(\theta)$ (as a function of the environmental context $\theta$). The solid gray arrows correspond to the column vectors of the interaction matrix ($\mathbf{A} = [\mathbf{a_1}; \mathbf{a_2}]$) parameterized using metabolic scaling relationships (Eq. 11). In this parameterization, $a_0$ corresponds to a normalization constant, $E_i$ specifies the activation energy of population $i$, and $M_i$ represents the average body size of population $i$. The angle (orange large curve) formed by the two column vectors corresponds to the feasibility domain $D_F(\mathcal{S}(\mathbf{A}))$ (Eq. 8). That is, inside the two column vectors, any vector of environmental carrying capacities $\mathbf{K}(\theta)$ is compatible with positive densities at equilibrium (Eq. 7). The centered blue vector depicts the geometric centroid of the feasibility domain (Eq. 10, $\mathbf{K_c}$), representing the expected distribution of $\mathbf{K}(\theta)$ that increase multispecies coexistence under random environmental perturbations. Panel **B**. For an ensemble of $10^6$ communities with $|S = 5|$ populations, the blue solid line shows the average distance (Eq. 12, blue small curve in Panel A) between the centroid of the feasibility domain and the generated vectors of carrying capacities as a function of body size and the power exponent $\beta \in [-2, 2]$ (Eq. 6). For each community, the interaction matrix is defined by $\alpha = 3/4$ and $a_0 = |S|^{-1/2}$. The values of $M_i$ and $E_i$ are independently drawn from uniform distributions $\in [0, 1]$ and $\in [0.5, 0.7]$, respectively. Note that $\beta = -3/4$ (large blue symbol) is the value that minimizes the distance. Instead, the gray dotted line shows that $\beta = 1$ (large gray symbol) is the value that minimizes the distance when the dependence of competitive effects on body size is $\alpha = -1$. Panel **C**. Equivalent to Panel B, but here we vary $\alpha \in [-2, 2]$ while keeping fixed $\beta = -3/4$ (blue solid line) and $\beta = 1$ (gray dotted line). This reveals that $\beta = -\alpha$ (derived from Eq. 6 and Eq. 11). Panel **D**. For the same metabolically-generated communities of Panel B, we show the relationship between $\alpha \in [-2, 2]$ and the feasibility per population (Eq. 9, $\omega(\mathcal{S}(\mathbf{A})) = \Omega(\mathcal{S}(\mathbf{A}))^{1/|\mathcal{S}|}$, large orange curve in Panel A). Note that $\omega(\mathcal{S}(\mathbf{A}))$ is the re-scaled angle characterizing the feasibility domain (large orange curve in Panel A). Theory predicts that the maximization of $\omega(\mathcal{S}(\mathbf{A}))$ is achieved with $\alpha = 0$ (no population has a competitive advantage).

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