Linking metabolic scaling and coexistence theories

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Abstract

Energy is life's main currency. Understanding the requirements, flow, and availability of energy among organisms then becomes synonym for our understanding of the sustainability of biodiversity. In this regard, metabolic scaling and coexistence theories have been pivotal in mathematizing the energy consumption by an organism and the energy transformation across organisms, respectively. Yet, a simple formal integration of these theories has remained overdue. Here, we provide a tractable and scalable framework to link metabolic scaling relationships at the population level and the persistence of ecological communities under different environmental conditions. Specifically, this framework focuses on exploring the dependence of community feasibility on body size. This integration predicts that the exponent defining the dependence of pairwise interaction effects on body sizes, but not the distribution of body sizes itself, is linked to the optimal distribution of environmental carrying capacities compatible with community persistence. Additionally, this integration predicts that the compatibility between community persistence and distributions of environmental carrying capacities is maximized when interaction effects are homogeneous across all pairs of interacting populations. We believe this integration can open up new opportunities to increase our understanding of how metabolic scaling relationships at the population level have evolved to optimize process at the community level.

Metabolic scaling theory

Metabolism is the sum of the total biochemical reactions governing the flow of energy in an individual (or 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 (or 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 (or normalization constant), and the sign and magnitude of the power or exponent β phenomenologically represent the physico-chemical constraints operating at the individual level [5–7]. On the other hand, the temperature response is typically exponential, $y = a \cdot e^{(E/T)}$, 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 mass (m_i) and temperature (T) approximately as

$$b_i \sim e^{-E_i/kT} \cdot m_i^{3/4} \tag{1}$$

(dimensions [mass][time]$^{-1}$), where E_i is the activation energy (dimension [eV]), k is the Boltzmann's constant (dimensions [eV][K]$^{-1}$), and T is the absolute temperature (dimension [K]). Notably, 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 approximately as $b_i \cdot m_i^{-1} \sim e^{-E_i/kT} \cdot m_i^{-1/4}$ (known as mass-specific metabolism, dimension [time]$^{-1}$), revealing the economies of body plans [3, 8].

In ecological research, populations (rather than individuals) are the basic units of living matter organization [9, 10]. Assuming a fixed growth rate of a population i under a constant environment (θ), 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 approximately written as $B_i(\theta) \sim e^{-E_i/kT} \cdot M_i^{3/4}$ (dimensions [mass][time]$^{-1}$) [8], where the environment can be specified as $\theta = \{T\}$. 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 $G_i(\theta) \propto e^{E_i/kT} \cdot M_i^{1/4}$ (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 θ and can be written as

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

(dimension [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 organisms 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 density of a population that can be sustained

by a specific local environment θ and can be written as

$$K_i(\theta) \propto e^{E_i/kT} \cdot M_i^{-3/4} \tag{3}$$

(dimensions [space]$^{-1}$[mass]). That is, the maximum number of individuals (or biomass) of a population per unit area (or volume) decreases with both temperature and size (or mass). These aforementioned scaling relationships (Eqs. 1-3) 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].

Therefore, it has become central to understand how these different scaling relationships at the 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 community and ecosystem levels [16–21], many opportunities remain open for theoretical integration and simplification. An example of these opportunities is the relationship between metabolism and the persistence of ecological communities, which has been typically studied numerically using models with a large number of parameters [18, 22]—losing tractability [23, 24]. As a consequence, it is debated the extent to which the compatibility of a community's persistence under different environmental conditions is mainly determined by the distribution of body sizes or the exponents (constraints) determining the dependence of interaction processes on body size [8, 15, 18, 25]. Similarly, it is still missing a tractable and scalable framework that can increase our understanding of how metabolic scaling relationships at the population level have evolved to optimize process at the community level [8, 17].

Coexistence theory

In general, coexistence theory in ecology [26–29] aims to investigate the possibility and probability that a community $\mathcal{S}(\mathbf{A})$, formed by $|\mathcal{S}|$ populations and characterized by some given ecological constraints ($\mathbf{A}$), can persist under different environmental contexts (θ). Although not exclusively, this analysis has been mainly performed under generalized Lotka-Volterra dynamics [30], 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 [31–34]. In particular, in the Lotka-Volterra competition model [35, 36], 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 [time]$^{-1}$), where N_i is the population density (dimension [density$_i$]) and $\dot{N}_i$ is the time derivative (dimensions [density$_i$][time]$^{-1}$). Per competition, $r_i(\theta) > 0$ is the intrinsic growth rate

(dimension $[\text{time}]^{-1}$), $K_i(\theta) > 0$ is the carrying capacity (dimension $[\text{density}_i]$). Here, θ represents the phenomenological joint effect of the internal and abiotic factors acting on the per-capita growth rate of each particular species. Then, $\mathbf{A} = (a_{ij}) \geq 0 \in \mathbb{R}^{|\mathcal{S}|\times|\mathcal{S}|}$ is the per capita, time-independent, interaction effect (dimensionless, but see Ref. [36]) 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, pairwise, interaction effect and self-regulation, respectively (dimensions $[\text{time}]^{-1}[\text{density}_i]^{-1}$). It follows that $a_{ii} = 1$ per definition [36]. 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) [33]. Then, the carrying capacity of a population i under a local environment θ 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) [37]. This necessary condition is known as community feasibility and it is written as (using matrix notation [27, 38])

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

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 jth column vector of the pairwise interaction matrix $\mathbf{A}$ [33, 39]. Each column j represents the time-independent, pairwise, interaction effect of population j on all other populations (including itself). Thus, the feasibility domain specifies all the possible distributions of $\boldsymbol{K}(\theta)$ (Eq. 6) that are compatible with a given set of pairwise interactions $\mathbf{A}$ 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) [38, 40]. Overall, the ecological constraints $\mathbf{A}$ determine the size of the feasibility domain. For example, the stronger the mean competition in a community ($\langle a_{ij}\rangle$), the smaller the feasibility domain.

Assuming that all values of θ are equally likely and there is a one-to-one mapping between the environmental contexts θ and the vectors of carrying capacities $\boldsymbol{K}(\theta)$, it also follows that the larger the feasibility domain, the larger the probability that a community is feasible [35, 41]. Specifically, for a competition community, the probability of feasibility (i.e., the normalized size of the feasibility

domain) can be estimated as

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

where $\Theta^{|\mathcal{S}|}$ is the $(|\mathcal{S}| - 1)$-dimensional closed unit sphere in dimension $|\mathcal{S}|$ [35, 38]. Because $\Omega(\mathcal{S}(\mathbf{A}))$ decreases exponentially with the dimension of the community $|\mathcal{S}|$ [39, 42], it is practical to use the size-specific probability $\omega(\mathcal{S}(\mathbf{A})) = \Omega(\mathcal{S}(\mathbf{A}))^{1/|\mathcal{S}|}$, which can be interpreted as the probability of feasibility per population [38, 43, 44]. Additionally, the location of a given vector $\boldsymbol{K}^*(\theta)$ inside the feasibility domain provides information about the extent to which a feasible community can tolerate small random variations in its distribution of environmental carrying capacities without losing feasibility ($\boldsymbol{N}^* > 0$). Assuming that all directions of variations in $\boldsymbol{K}^*(\theta)$ are equally likely, it has been shown that the distribution of environmental carrying capacities with the highest tolerance becomes the geometric centroid of the feasibility domain (Fig. 1A) [39, 45, 46]

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

Linking theories

The link between metabolic scaling and coexistence theories has been performed under different frameworks, each answering specific ecological questions [16–19, 22, 47]. Here, we are interested in developing a tractable and scalable framework to link metabolic scaling relationships at the population level with community persistence under different environmental conditions. To this end, first we parameterize the pairwise interaction matrix $\mathbf{A}$ using metabolic scaling theory with a minimum set of assumptions. Then, we investigate the association of metabolic scaling relationships with the optimal and largest distribution of environmental carrying capacities compatible with community persistence.

To parameterize the Lotka-Volterra competition model (Eq. 4), we replace $r_i(\theta) \propto e^{-E_i/kT} \cdot M_i^{-1/4}$ and $K_i(\theta) \propto e^{E_i/kT} \cdot M_i^{-3/4}$ by their corresponding metabolic upper-limit approximations (Eq. 2 and Eq.3, respectively). Then, we rewrite the time-dependent self-regulation $\hat{a}_{ii} = r_i \cdot K_i^{-1}$ (Eq. 6) as $\hat{a}_{ii} \propto e^{-2E_i/kT} \cdot M_i^{1/2}$. Following this rationale, we define the time-dependent pairwise interaction effects as $\hat{a}_{ij} = r_i \cdot K_j^{-1}$, and rewrite it as $\hat{a}_{ij} \propto e^{-(E_i+E_j)/kT} \cdot M_i^{-1/4} \cdot M_j^{3/4}$. Thus, from Eq. (5), the time-independent, pairwise, interaction effect can be estimated as

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

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

effect.

To investigate the optimal distribution (in relation with tolerance to random variations) of environmental carrying capacities compatible with community persistence, we study the scaling exponent (β) 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 pairwise interaction matrix $\mathbf{A}$ as defined in Eq. (11). To perform this task, we generate an ensemble of 10^6 matrices $\mathbf{A}$ characterizing the time-independent, pairwise, interaction 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 [48, 49], we set the normalization constant of interaction effects to $a_0 = |\mathcal{S}|^{-1/2}$ for $i \neq j$, otherwise $a_0 = 1$. Indeed, it has been shown that biological interaction networks tend to be weak in empirical food webs and they tend to stabilize theoretical communities [50]. The greater the value of a_o, the greater the overall competition, and the smaller the feasibility domain [41]. Then, for each value of the scaling exponent $\beta \in [-2, 2]$, we calculate the average distance between $\boldsymbol{K_c}(\mathbf{A})$ and $\boldsymbol{K}$ as [29]

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

Note that the normalization constant K_0 of environmental carrying capacities does not affect this distance and can be omitted from the equation [41].

Figure 1B (blue solid line) reveals that the vector of environmental carrying capacities generated by the scaling relationship $\boldsymbol{K} \propto \boldsymbol{M}^{\beta=-3/4}$ is, in fact, the centroid ($\boldsymbol{K_c}(\mathbf{A})$, Eq. 10) of the feasibility domain (i.e., $d(\mathbf{A}, \boldsymbol{K}) = 0$, Eq. 10) of the metabolically-generated community characterized by Eq. (11). This implies that the decrease of environmental carrying capacities with body mass given by $\beta = -3/4$ is the scaling relationship with the strongest tolerance to small random variations in the environment θ (recall that we are assuming a one-to-one mapping between θ and $\boldsymbol{K}(\theta)$) when the dependence of pairwise interaction on body mass increases by the power-law $\alpha = 3/4$. However, as mentioned before, it is expected that the specific details (value of β) of metabolic scaling relationships may change across different taxa [2, 3, 15]. Notably, our framework is compatible with these differences. Figure 1B (resp. 1C) shows that the value of α (resp. β) constrains the value of β (resp. α) that minimizes the distance to the centroid of the feasibility domain. In fact, the value of β is analytically linked to the dependence of pairwise interactions on body mass as $\beta = -\alpha$ (derived from Eq. 6 and Eq. 11). This further implies that the exponent defining the dependence of pairwise interaction effects on body sizes, but not the distribution of body sizes itself, is linked to the optimal distribution of environmental carrying capacities compatible with community persistence. This is also in agreement with empirical and theoretical results showing the importance of size ratios in food web stability and length [18, 51, 52].

Because the dependence of pairwise interaction effects on body sizes (α, Eq. 11) has important implications for the distribution of environmental carrying capacities, it also becomes paramount to understand how metabolic scaling relationships at the population level may have evolved to optimize process at the community level. To shew new light onto this question, we study the link between α and the size of the feasibility domain (Eq. 8). Specifically, we quantify the size of the feasibility domain by the probability of feasibility per population in community $\mathcal{S}(\mathbf{A})$ (i.e., $\omega(\mathcal{S}(\mathbf{A})) = \Omega(\mathcal{S}(\mathbf{A}))^{1/|\mathcal{S}|}$, Eq. 9). Recall that this probability is a function of the pairwise interaction matrix $\mathbf{A}$, which is in turn characterized by the dependence of time-independent, pairwise, interaction effects on body mass. For this purpose, we follow our previous analysis generating an ensemble of 10^6 matrices $\mathbf{A}$ characterizing the pairwise interaction effects (a_{ij}) between five populations (higher dimensions yield similar conclusions), where 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). We set the normalization constant of interaction effects to $a_0 = |\mathcal{S}|^{-1/2}$ for $i \neq j$, otherwise $a_0 = 1$. Then, for each value of the scaling exponent $\alpha \in [-2, 2]$, we calculate the average probability of feasibility per population ($\omega(\mathcal{S}(\mathbf{A}))$). Figure 1C shows that the maximum value of $\omega(\mathcal{S}(\mathbf{A}))$ is attained when $\alpha = 0$. This reveals that the compatibility between community persistence and distributions of environmental carrying capacities is maximized when interaction effects are homogeneous across all interacting populations. This is also consistent with previous models linking metabolic theory and food web dynamics that have show the existence of an optimal predator prey ratio [52].

Concluding remarks

We have proposed a tractable and scalable integration of metabolic scaling theory [4] and coexistence theories [26–29] in order to systematically link metabolic scaling relationships at the population level and the persistence of ecological communities under different environmental conditions [40, 43, 44]. Our framework has been based on understanding how body-size restrictions operating on pairwise interactions affect the parameter space of environmental carrying capacities compatible with the coexistence of multiple populations. For example, we have found that the dependence of pairwise interaction effects on body sizes is linked to the dependence of the environmental carrying capacity on body size. This link specifies the distribution of carrying capacities that can tolerate the largest random variations (i.e., the centroid of the feasibility domain). Therefore, linking interaction strength to metabolism and size can help to capture important asymmetries in density and explain known symmetries, such as the energetic equivalence rule [11]. Additionally, we have found that the highest compatibility of a community's persistence with different environmental carrying capacities (but relatively similar activation energies) is achieved when pairwise interaction effects are homogeneous ($\alpha = 0$, $a_{ij} = c$). Under this homogeneous scenario, our framework predicts that the optimal distribution of environmental carrying capacities should also be homogeneous ($\beta = -\alpha$, $K_i = c$). This homogeneous property should be more expected under the context that community stability is better

associated with the size of the feasibility domain [53]. Recall that weaker competition leads to larger feasibility domains [41] (i.e., lower $a_{ij} = c$). A fundamental question, however, is to what extent communities may benefit from a balance between the compatibility to environmental variations and the ability to change to different compositions (e.g., adaptability versus evolvability) [54–56].

It is worth mentioning that our effort to integrate metabolic scaling and coexistence theories has been focused on exploring the dependence of 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 population level have evolved to optimize process at the community level.

Data accessibility . The code supporting the results are archived on Github: `https://github.com/MITEcology/Scaling_Coexistence_2003`

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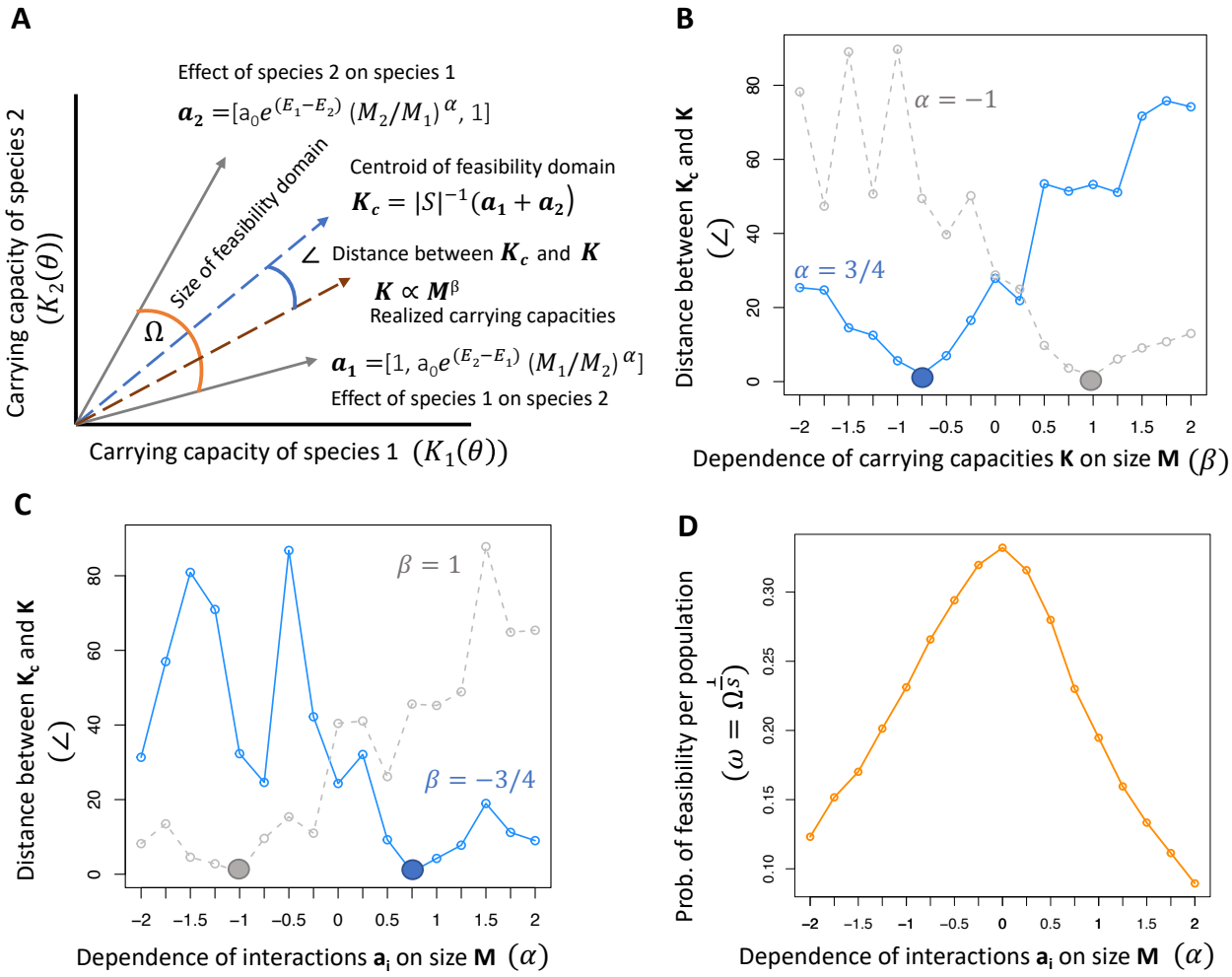

Figure 1: **Linking metabolic scaling and coexistence theories**. Panel **A**. For an illustrative example of a community with $|S| = 2$ populations under Lotka-Volterra competition dynamics (Eq. 4), we show the parameter space of carrying capacities $K_i(\theta)$ (as a function of the environmental context θ). The solid gray arrows correspond to the column vectors of the pairwise interaction matrix ($\mathbf{A} = [\mathbf{a_1}; \mathbf{a_2}]$) parameterized using metabolic 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 body mass 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 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 combination of $\mathbf{K}(\theta)$ that are more robust to external random variations. 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 mass 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 pairwise interaction effects on body mass 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 probability of 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 rescaled 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 $\alpha = 0$ (homogeneous interaction effects).

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