Integrating metabolic scaling and coexistence theories

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Open Research: The code supporting the results is archived on `Github:\https://github.com/MITEcology/Scaling_Coexistence_2024`

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Abstract

Metabolic scaling theory has been pivotal in formalizing the expected energy expenditures across populations as a function of body size. Coexistence theory has provided a mathematization of the tolerated effects of environmental perturbations on a given set of interacting populations as a function of interspecific interactions. Yet, it has been challenging to explain how coexistence patterns observed in ecological communities, such as the inverse relationship between population abundance and mean body size, can be unified under both theories. Here, we provide the foundation for a tractable, scalable, and extendable framework to study the coexistence of resource-mediated competing populations as a function of their mean body size. For a fixed thermal domain and response, this integration reveals that the metabolically predicted -3/4 power dependence of carrying capacity on body size specifies the distribution of environmental carrying capacities that tends to maximize the tolerance to random environmental perturbations within large communities. In line with empirical observations, our integration predicts that such a distribution leads to equilibrium biomasses that are independent from body size, and consequently, to equilibrium abundances that are inversely related to body size. This integration opens new opportunities to increase our understanding of how metabolic scaling relationships at the population level can 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) (Kleiber, 1932). 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 (Arroyo et al., 2022, Kempes et al., 2011, Maurer, 1996, Shestopaloff, 2024). In this line, metabolic scaling theory (Brown et al., 2004) 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 (Gillooly et al., 2001, West et al., 1997). These dependencies are described 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) β phenomenologically represent the physico-chemical constraints operating at the individual level (Gillooly et al., 2001, 2002, West et al., 1997). On the other hand, the temperature response has been typically modeled as exponential, $y = a \cdot e^{E/T}$, and known as the Arrhenius equation (Gillooly et al., 2001, 2002, West et al., 1997). Although, recently this response has been empirically and theoretically shown to be unimodal (Arroyo et al., 2022, Dell et al., 2011).

Put together, it has been shown (Gillooly et al., 2001, 2002, West et al., 1997) that the metabolic rate (b_i) of an individual i is expected to scale with its body size (m_i) under a given temperature and thermal response as

$$b_i = b_0 \cdot m_i^{3/4} \tag{1}$$

(dimensions [mass][time]$^{-1}$), where b_0 is an effective parameter reflecting a taxon-specific response (dimensions [mass]$^{1/4}$[time]$^{-1}$). Eq. 1 reveals that larger individuals are expected to be characterized by higher energy requirements per unit of time over a given thermal domain and response. These requirements, however, are expected to decrease non-linearly per unit of mass as $b_i \cdot m_i^{-1} = b_0 \cdot m_i^{-1/4}$ (known as mass-specific metabolism, dimension [time]$^{-1}$), revealing the economies of body plans (Arroyo et al., 2022, Savage et al., 2004).

In community ecology (Vellend, 2016), populations (rather than individuals) are typically the basic units of living matter organization (Odum and Barrett, 2005, Vellend, 2016). Assuming a fixed growth rate of a population i under a constant environment, 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 average metabolic rate (Eq. 1) of population i can be written as $B_i = B_0 \cdot M_i^{3/4}$ (dimensions [mass][time]$^{-1}$) (Savage et al., 2004), where B_0 is an effective parameter for a given temperature and thermal response (dimension [mass]$^{1/4}$[time]$^{-1}$). These metabolic scaling relationships have been confirmed by multiple empirical data across different taxa (Belgrano et al., 2002, Bernhardt et al., 2018, Damuth, 1987). 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 (Arroyo et al., 2022, Dell et al., 2011, Gillooly et al., 2001). 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 (DeLong et al., 2010).

Similarly, it can then be predicted (Gillooly et al., 2002, Savage et al., 2004) that the maximum generation time (or lifespan) of an individual from population i becomes proportional to the scaling relationship $G_i \propto M_i^{\frac{1}{4}}$ (dimension [time]). Thus, the reciprocal of maximum generation time (i.e., mortality rate) is expected to be proportionally related to the maximum growth rate of an individual in population i and can be written as

$$\frac{1}{G_i} \propto r_i = r_0 \cdot M_i^{-1/4} \tag{2}$$

(dimension [time]$^{-1}$), where r_0 is an effective parameter for a given temperature and thermal response (dimension [mass]$^{1/4}$[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 (Savage et al., 2004).

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 (Damuth, 1987)), it has been shown (Savage et al., 2004) that it is possible to derive the mass and temperature dependence of a population's environmental carrying capacity. This is the predicted, maximum, biomass density of a population in isolation that can be sustained and can be written as

$$K_i = K_0 \cdot M_i^{-3/4} \tag{3}$$

(dimensions [mass][area]$^{-1}$), where K_0 is an effective parameter (dimension [mass]$^{3/4}$). That is, under a given temperature and thermal response, the maximum biomass of a population in isolation per unit area (or volume) is expected to decrease with size.

Understanding how these different scaling relationships at the individual (or population level) are linked to ecological processes at the community level (the collection of different interacting populations in a given place and time) is challenging, and while there has been significant empirical and theoretical work using metabolic scaling theory at the community level (Basset and Angelis, 2007, Brose et al., 2006, Marquet et al., 2004, 1990, 2005, Tabi et al., 2023, Vasseur and McCann, 2005, Yeakel et al., 2018, Yodzis and Innes, 1992), several important challenges for theoretical integration and simplification still remain open. A clear example is the relationship between the distribution of body sizes and the coexistence of multiple populations, which has been typically studied for a specific set of model parameters (Brose et al., 2006, Yodzis and Innes, 1992). As a consequence, it continues to be debated the extent to which the distribution of body sizes determines both the possibilities for coexistence of multiple populations and the distribution of population abundances (Bideault et al., 2021, Brose et al., 2006, DeLong et al., 2010, Hatton et al., 2019, Savage et al., 2004). Similarly, there is still theoretical work to be done in order to increase our understanding of how metabolic scaling relationships at the individual or population levels affect coexistence processes at the community level (Arim et al., 2007, Basset and Angelis, 2007, Hatton et al., 2024, Savage et al., 2004).

Coexistence theory

In general, coexistence theory in ecology (Chesson, 2000, MacArthur and Levins, 1967, Saavedra et al., 2017, Vandermeer, 1970) aims to investigate the possibility that a community $\mathcal{S}(\mathbf{A})$, formed by $|\mathcal{S}|$ populations and characterized by an interaction matrix ($\mathbf{A}$), can persist under different environmental contexts. Although not exclusively, this analysis has been mainly performed under generalized Lotka-Volterra dynamics (Case, 2000), which in line with metabolic scaling theory (Brown et al., 2004), can be derived from thermodynamics principles, from principles of conservation of mass and energy, and from chemical kinetics in large populations (Logofet, 1993, Lotka, 1920, Michaelian, 2005, Täuber, 2011). In particular, in the Lotka-Volterra competition model (Arditi et al., 2021, Medeiros et al., 2021*a*), the per capita growth rate of a population's biomass density can be written as

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

(dimension $[\text{time}]^{-1}$), where N_i is the population biomass density (dimension [mass][area] or [individuals][area]) and $\dot{N}_i$ is the time derivative (dimensions $[\text{density}][\text{time}]^{-1}$). Here, $r_i > 0$ is the maximum intrinsic growth rate (dimension $[\text{time}]^{-1}$), $K_i > 0$ is the environmental

carrying capacity (dimension [density]). 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. (Arditi et al., 2021)) 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 (Arditi et al., 2021). 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) (Logofet, 1993). Then, the environmental carrying capacity of a population i under a given environment can be expressed as a function of its intrinsic growth rate and time-dependent self-regulation as

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

The necessary condition for persistence under Lotka-Volterra equilibrium dynamics (i.e., $\dot{N}_i = 0$) becomes the existence of positive solutions in population densities (Hofbauer and Sigmund, 1998). This necessary condition is known as *feasibility* and takes the form of a linear equation in matrix notation (Song et al., 2018*b*, Vandermeer, 1970))

$$\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K}^* > 0, \tag{7}$$

where the vector $\boldsymbol{N}^*$ represents the distribution of population densities at equilibrium, $\mathbf{A}^{-1}$ corresponds to the inverse of the interaction matrix, and the vector $\boldsymbol{K}^*$ is the distribution (relationship) of environmental carrying capacities compatible with the feasibility of community $\mathcal{S}(\mathbf{A})$. Notice that it is possible to multiply the vector $\boldsymbol{K}^*$ by any positive scalar ($\lambda > 0$) and the feasibility condition (i.e., $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K}^*\lambda > 0$) does not change. This is true because the relationship among carrying capacities within the community does not change (i.e., all values are either increased or decreased proportionally). Of course, if λ approaches zero, the loss of feasibility can happen due to stochasticity (Hofbauer and Sigmund, 1998). This implies that given an interaction matrix, the feasibility of a community is determined by the direction rather than the magnitude of the vector (Saavedra et al., 2017). In other words, feasibility depends on the relationship (or distribution) among carrying capacities within the community.

Importantly, there can be more than one compatible vector $\boldsymbol{K}^*$. This possible set of vectors is known as the feasibility domain (D_F) (Logofet, 1993, Saavedra et al., 2017). Formally,

rearranging Eq. 7 and solving for $\boldsymbol{K}^*$, this feasibility domain can be expressed as

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

where $\mathbf{a}_j$ is the jth column vector of the interaction matrix $\mathbf{A}$ (Logofet, 1993, Song and Saavedra, 2018). Each column j represents the time-independent competitive effect of population j on all other populations (including itself). The feasibility domain specifies all the possible distributions (vector directions) of $\boldsymbol{K}$ (Eq. 6) that are compatible with the interaction matrix $\mathbf{A}$ 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. 1) (Deng et al., 2023, 2022, Song et al., 2018*b*). Overall, the interaction matrix $\mathbf{A}$ determines the size of the feasibility domain. The stronger the mean competition in a community ($\langle a_{ij} \rangle$), the smaller the feasibility domain (Saavedra et al., 2017).

For a given community characterized by a particular interaction matrix (and feasibility domain), the location of a given vector $\boldsymbol{K}^*$ inside the feasibility domain provides information about the extent to which this feasible community can tolerate random (all directions are equally likely) perturbations to the direction of $\boldsymbol{K}^*$ without losing feasibility ($\boldsymbol{N}^* > 0$). Thus, the geometric centroid of the feasibility domain (Fig. 1) corresponds to the distribution of $\boldsymbol{K}^*$ that maximizes the feasibility of the community under random perturbations to the direction of $\boldsymbol{K}^*$. This statement makes the assumption that the elements of the vector of environmental carrying capacities are independent from each other and free to vary due to external factors other than temperature. It is worth mentioning that because we are interested in the impact of environmental perturbations on the direction of carrying capacities (i.e., these perturbations need to modify the relationship among carrying capacities), these perturbations need to act differently on the structure (or parameters) that define the carrying capacities within the community (this is known as structural or parameter perturbations). For example, these perturbations can be reflected as long-term changes in species habitats.

Formally, the geometric centroid can be calculated as (Medeiros et al., 2021*b*, Song and Saavedra, 2018, Tabi et al., 2020)

$$\boldsymbol{K_c}(\mathbf{A}) = |\mathcal{S}|^{-1} \boldsymbol{a}_1 + \cdots + |\mathcal{S}|^{-1} \boldsymbol{a}_n. \tag{9}$$

Moreover, by definition, the centroid $\boldsymbol{K_c}(\mathbf{A})$ yields the solution (Rohr et al., 2016)

$$\boldsymbol{N}^* = \mathbf{A}^{-1} \boldsymbol{K}_{\boldsymbol{c}}^* = (1, 1, \ldots, 1) \in \mathcal{R}^{|\mathcal{S}|}. \tag{10}$$

That is, while the elements of the vector of carrying capacities defining the centroid of the feasibility domain can be different from each other, the populations' biomasses become the same at equilibrium and independent from body size.

Integrating theories

The link between metabolic scaling and coexistence theories has been performed under different frameworks, each answering specific ecological questions (Basset and Angelis, 2007, Brose et al., 2006, Campillay-Llanos et al., 2022, Harte et al., 2008, Parain et al., 2019, Vasseur and McCann, 2005, Yeakel et al., 2018, Yodzis and Innes, 1992, Zaoli et al., 2017). Here, we provide a tractable, scalable, and extendable framework to study the effect of body size on the feasibility of resource-mediated competing populations. Specifically, we aim to investigate the possibility that a community of competing populations characterized by a given distribution of body sizes can coexist under different environmental contexts. To this end, our framework is based on Lotka-Volterra competition dynamics (Vandermeer and Goldberg, 2013).

Under resource-mediated competition models, it is assumed that the dynamics of resources are faster than that of consumers. While this is a strong assumption, classic and recent work has shown promising approximations to empirical competition dynamics (MacArthur and Levins, 1967, Medeiros et al., 2021*a*, Parain et al., 2019, Song et al., 2018*a*). Following this premise, time-independent competitive interactions (a_{ij}) can be written as a function of the average consumption rates of consumers (Fig. 1, see Supplementary Information for details):

$$a_{ij} = a_0' \cdot \left(\frac{C_j}{C_i} \right), \tag{11}$$

where C_i corresponds to the average consumption rate for a population i (dimension [density]$^{-1}$), and a_0' is an *effective* parameter representing the overall effect of intrinsic properties (dimensionless), such as consumers' conversion rates and resources' carrying capacities (Parain et al., 2019). Similarly, following single population models (Deng et al., 2024), the average consumption rate of consumer i can be expressed as a function of its demographics (Fig. 1, see Supplementary Information for details):

$$C_i = \frac{1}{K_i \left(1 + d_i/r_i\right)}, \tag{12}$$

where d_i denotes the mortality rate (dimension [time]$^{-1}$), and K_i and r_i represent again the carrying capacity and maximum growth rate of consumer i, respectively. Then, we can integrate

metabolic scaling theory (Eqs. 2-3) and coexistence theory (Eq. 12) to write

$$C_i = C_0 \cdot M_i^{3/4}, \tag{13}$$

where C_0 is a new effective parameter (dimensions $[\text{mass}]^{-3/4}[\text{density}]^{-1}$). Thus, for a fixed temperature and thermal response, we can integrate Eqs. 11 and 13 as

$$a_{ij} = a_0 \cdot (M_j/M_i)^{3/4}, \tag{14}$$

where a_0 is yet again a new effective parameter (dimensionless). In sum, for a given thermal domain and response, it is expected that the higher the average body size of population j relative to that of population i, the higher the time-independent competitive effect.

Next, we investigated the link between the feasibility of a community and the distribution of body sizes for a fixed temperature in metabolically-generated competition matrices $\mathbf{A}$. In particular, we systematically studied the scaling relationship β between the vector of environmental carrying capacities and the vector of body sizes ($\boldsymbol{K} = \boldsymbol{K_0} \cdot \boldsymbol{M}^{\beta}$) that makes $\boldsymbol{K}$ close to the centroid of the feasibility domain ($\boldsymbol{K_c}(\mathbf{A})$). Recall that the centroid corresponds to the location inside the feasibility domain that can tolerate the largest random perturbations to the direction (distribution) of environmental carrying capacities (assuming elements of such a vector are free to vary due to external factors other than temperature and independent from each other). This vector determines the feasibility of a community as expressed in Eq. 7.

Specifically, following Eq. 14, we generated an ensemble of 10^6 competition 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 values independently from a lognormal distribution $LN(0, 2)$. These distributions can change without affecting the qualitative results. Following previous work (Bunin, 2017, Dougoud et al., 2018), we set the effective parameter of competitive effects to $a_0 = |\mathcal{S}|^{-1/2}$ for $i \neq j$, otherwise $a_0 = 1$. This assumption follows the rationale that empirical interactions tend to be weak, stabilizing communities (Gellner et al., 2023, McCann et al., 1998). The greater the value of a_0, the greater the overall competition, and the smaller the feasibility domain. Then, for regular intervals between $\beta \in [-2, 2]$ (used as representative values), we calculated the average distance between $\boldsymbol{K_c}(\mathbf{A})$ and $\boldsymbol{K}$ as (Medeiros et al., 2021*b*, Saavedra et al., 2017)

$$d(\mathbf{A}, \boldsymbol{K} = \arccos(\boldsymbol{K} \cdot \boldsymbol{K_c}(\mathbf{A}) \cdot ||\boldsymbol{K}||^{-1} \cdot ||\boldsymbol{K_c}(\mathbf{A})||^{-1}) \in [0, 90]. \tag{15}$$

Note that the normalization constant K_0 of environmental carrying capacities does not affect this distance and can be omitted from the equation (Rohr et al., 2016).

Figure 2 reveals that, for large communities, the vector of environmental carrying capacities described by the scaling relationship $\boldsymbol{K} \propto \boldsymbol{M}^{\beta=-\frac{3}{4}}$ gets close to the centroid of the feasibility domain of the metabolically-generated competition matrices for a given thermal domain and response. For few competing species (e.g., two), it will be exactly the centroid only for a particular value of a_0 (see Supplementary Information). This reveals that the expected -3/4 power dependence of environmental carrying capacity on body size specifies the distribution of carrying capacities that tends to maximize the feasibility of multispecies coexistence under random environmental perturbations acting on the direction (relationship among) of such carrying capacities.

Furthermore, because the centroid represents the condition under which all populations have the same biomass at equilibrium (Eq. 10), 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 implies that our framework 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 (Hatton et al., 2019, Marquet et al., 1990), which can be treated as an extreme value (Segura and Perera, 2023).

Concluding remarks

We have proposed an tractable, scalable, and extendable integration of metabolic scaling theory (Brown et al., 2004) and coexistence theories (Chesson, 2000, MacArthur and Levins, 1967, Saavedra et al., 2017, Vandermeer, 1970) in order to systematically link metabolic scaling relationships at the population level to community dynamics (Deng et al., 2021, 2022, Saavedra et al., 2020). 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 show that the metabolically predicted -3/4 power dependence of carrying capacity on body size specifies the distribution of carrying capacities that tends to maximize the feasibility of multispecies coexistence under random environmental perturbations. Additionally, in line with empirical observations (Hatton et al., 2019), our integration conforms to the expectation that equilibrium biomasses are independent from body size, and consequently, to equilibrium abundances that are inversely related to body size. Therefore, our framework can be used to link competitive

effects to metabolism and, consequently, to body size, helping to capture important theoretical derivations and empirical observations (Hatton et al., 2019, Savage et al., 2004).

It is worth mentioning that our efforts to integrate metabolic scaling and coexistence theories have been simplified under a formalism that uses a set of relevant assumptions. In particular, we have focused on resource-mediated competition assuming that the dynamics of resources are faster than that of consumers. While there is a strong tradition on this type of competition systems, this does not take into account other type of much richer dynamics, such as as trophic interactions. However, previous efforts on these forms of dynamics (Parain et al., 2019, Vasseur and McCann, 2005) can be compatible with our framework (Saavedra et al., 2016). Similarly, we have exclusively focused on feasibility (the necessary condition for species coexistence under equilibrium dynamics) without systematically investigating dynamically stability (Song and Saavedra, 2018). Yet, future work can expand our work in order to investigate the role of the effective parameter a_0 acting on interspecific effects and its ecological interpretation in shaping the dynamical stability of communities. Additionally, while our results on the distance to the centroid of the feasibility domain are valid for a fixed thermal domain and response, feasibility itself can change as a function of temperature via changes in interspecific effects. Thus, for cases where the interest is to predict how a population or community will respond to temperature, it would be useful to use a model that accounts for the curvature of temperature response curve (Arroyo et al., 2022). This alternative model can be adapted to our integration (by separating the role of temperature from the effective parameters) to explore temperature-related questions, such as how the variation in optimum temperatures of populations in a community would affect its feasibility or how global warming may alter communities. Lastly, we have assumed that, in a the community, perturbations on environmental carrying capacities are independent from each other and free to vary due to external factors other than temperature. This can also be relaxed by incorporating different priors to such perturbations or to the probability of each vector's direction inside the feasibility domain (Grilli et al., 2017, Saavedra et al., 2020, Song et al., 2018*b*). 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_2024`

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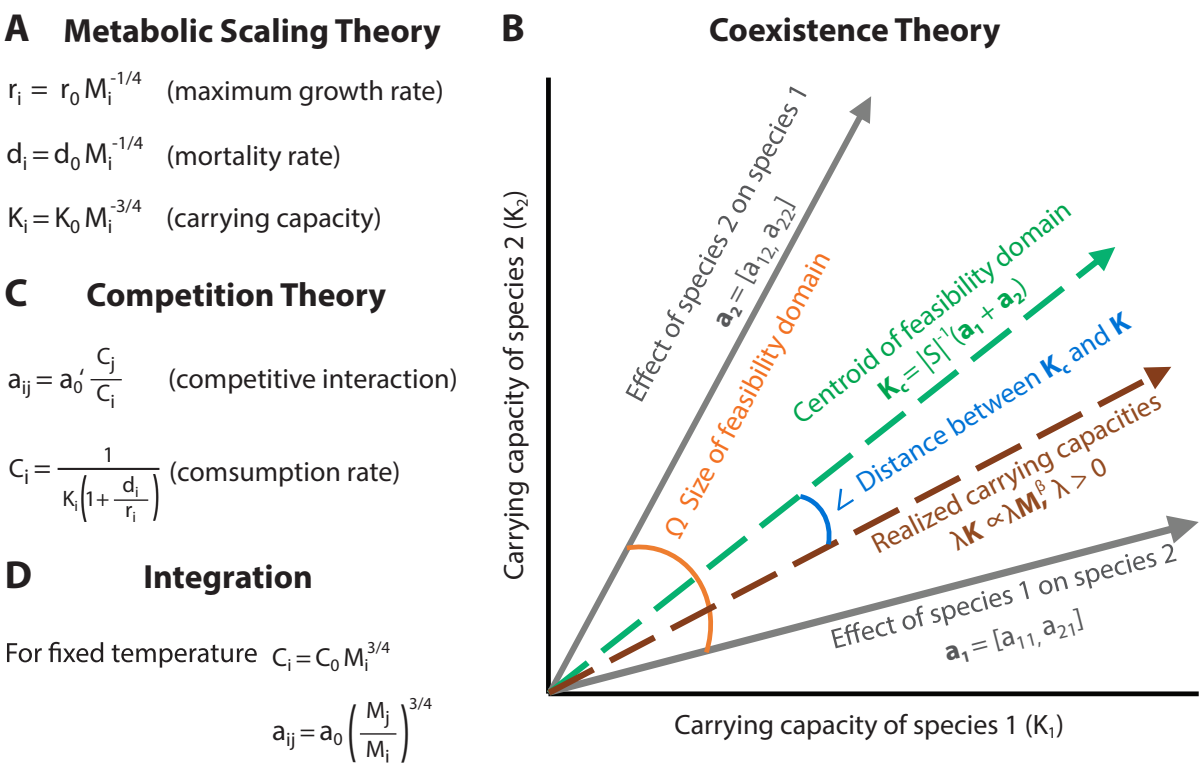

Figure 1: **A graphical integration of metabolic scaling and coexistence theories**. (**A**) Following metabolic scaling theory, for a given temperature and thermal response, maximum growth rate, mortality rate, and carrying capacities are predicted to scale as a function of body mass. (**B**) Following coexistence theory and under Lotka-Volterra competition dynamics (see main text), the feasibility (i.e., positive abundances at equilibrium) of a community will be defined by having the relationship (vector direction) among carrying capacities inside the domain constrained by species interactions. As an illustrative example, we show the parameter space (Cartesian coordinate system) of carrying capacities K_i of a community with $|S| = 2$ populations. The outer solid gray arrows correspond to the column vectors of the interaction matrix ($\mathbf{A} = [\mathbf{a_1}; \mathbf{a_2}]$). The angle (orange large curve) formed by the two column vectors corresponds to the feasibility domain $D_F(\mathcal{S}(\mathbf{A}))$ (Eq. 8). Inside the two column vectors, any direction of environmental carrying capacities $\mathbf{K}$ is compatible with positive densities at equilibrium (Eq. 7). In this sense, the direction (rather than the magnitude) defines the feasibility of a community. The centered green vector depicts the geometric centroid of the feasibility domain (Eq. 9, $\mathbf{K_c}$), representing the expected relationship or distribution of $\mathbf{K}$ that increase coexistence of multiple competing population under random environmental perturbations (other than temperature) acting on $\mathbf{K}$. While the elements of $\boldsymbol{K_c}(\mathbf{A})$ can be different from each other, the centroid corresponds to the environmental carrying capacities that provide the solution $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K_c^*}(\mathbf{A}) = (1, 1)$. (**C**) Following competition theory (see main text), we can define the competitive effect (a_{ij}) of species j on i as a function of the average consumption rates, which can also be expressed as a function the maximum growth rate, mortality rate, and carrying capacity. (**D**) Integrating theories (see main text), for a fixed temperature, we can then express both the average consumption rates and the competitive effect as a power law function of body size.

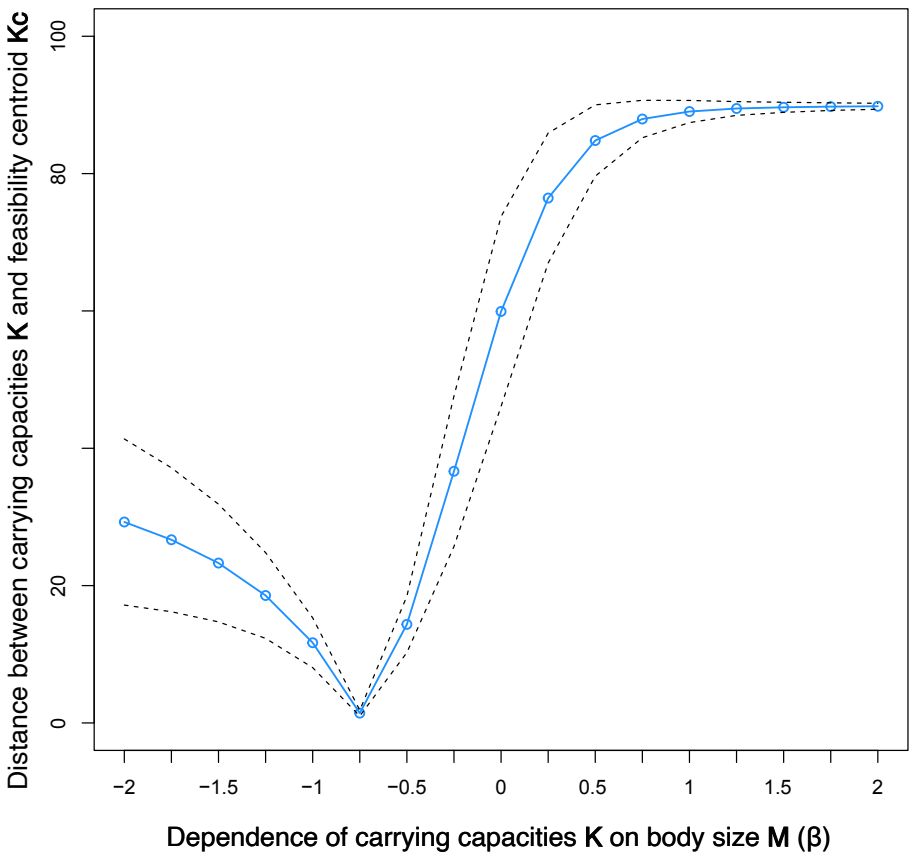

Figure 2: **Theoretical predictions**. For an ensemble of 10^6 communities with $|S = 50|$ populations, the blue solid line shows the average distance (Eq. 15, blue small curve in Figure 1) between the centroid of the feasibility domain $\mathbf{K_c}$ and the possible vectors of carrying capacities ($\boldsymbol{K} \propto \boldsymbol{M}^{\beta}$) as a function of body size and the power exponent $\beta \in [-2, 2]$. The black dashed lines correspond to the average plus minus two standard deviations. For each community, the interaction matrix (Eq. 11) is defined by $\alpha = 3/4$ and $a_0 = |S|^{-1/2}$. The values of M_i are drawn independently from a lognormal distribution $LN(0, 2)$. For large communities, $\beta = -3/4$ tends to be the closest to the centroid.

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Supplementary Information

The estimation of competitive interactions a_{ij} is derived by translating classic consumer-resource dynamics into Lotka-Volterra competition dynamics following Vandermeer and Goldberg (2013).

Let us assume that there are two self-replicating resources:

$$\begin{cases} \dfrac{\mathrm{d}R_1}{\mathrm{d}t} = r_{\mathrm{rsc}_1} R_1 \left[\left(\dfrac{k_1 - R_1}{k_1} \right) - c_{11} N_1 - c_{12} N_2 \right], \\ \dfrac{\mathrm{d}R_2}{\mathrm{d}t} = r_{\mathrm{rsc}_2} R_2 \left[\left(\dfrac{k_2 - R_2}{k_2} \right) - c_{21} N_1 - c_{22} N_2 \right], \end{cases} \tag{16}$$

where R_i is the density (or biomass) of the resource i, r_{rsc_i} is the intrinsic rate of increase of resource i, k_i is the carrying capacity of the resource i, c_{ij} is the rate at which the resource i is consumed by the jth consumer, and N_i is the population density of the ith consumer.

Then, considering two consumers, we can write the consumer equations:

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1 \left(b_{11} R_1 + b_{12} R_2 - d_1 \right), \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2 \left(b_{21} R_1 + b_{22} R_2 - d_2 \right), \end{cases} \tag{17}$$

where b_{ij} is the relative conversion of a unit of resource j by consumer i, and d_i is the death rate of the ith consumer. Note that b_{ij} is different from mass/energy transformation efficiency.

Assuming that the dynamics of the resources occur significantly faster than those of the consumers (MacArthur and Levins, 1967), we can equate the derivatives of Eqs. (16) to zero and solve for the equilibrium values R_1^* and R_2^* of the two resources:

$$\begin{aligned} R_1^* &= k_1(1 - c_{11} N_1 - c_{12} N_2), \\ R_2^* &= k_2(1 - c_{21} N_1 - c_{22} N_2). \end{aligned} \tag{18}$$

Then, we can substitute R_1 and R_2 in Eqs. (17) by R_1^* and R_2^*, respectively. That is,

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1 \left[b_{11} k_1 (1 - c_{11} N_1 - c_{12} N_2) + b_{12} k_2 (1 - c_{21} N_1 - c_{22} N_2) - d_1 \right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2 \left[b_{21} k_1 (1 - c_{11} N_1 - c_{12} N_2) + b_{22} k_2 (1 - c_{21} N_1 - c_{22} N_2) - d_2 \right], \end{cases} \tag{19}$$

which can also be written as

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1\left[b_{11}k_1 + b_{12}k_2 - d_1 - (b_{11}k_1c_{11} + b_{12}k_2c_{21})N_1 - (b_{11}k_1c_{12} + b_{12}k_2c_{22})N_2\right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2\left[b_{21}k_1 + b_{22}k_2 - d_2 - (b_{21}k_1c_{11} + b_{22}k_2c_{21})N_1 - (b_{21}k_1c_{12} + b_{22}k_2c_{22})N_2\right]. \end{cases} \tag{20}$$

Multiplying and dividing the two equations in Eqs. (20) by

$$\begin{aligned} &b_{11}k_1 + b_{12}k_2 - d_1, \\ &b_{21}k_1 + b_{22}k_2 - d_2, \end{aligned} \tag{21}$$

respectively, we obtain

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = (b_{11}k_1 + b_{12}k_2 - d_1)N_1\left[\dfrac{b_{11}k_1 + b_{12}k_2 - d_1 - (b_{11}k_1c_{11} + b_{12}k_2c_{21})N_1 - (b_{11}k_1c_{12} + b_{12}k_2c_{22})N_2}{b_{11}k_1 + b_{12}k_2 - d_1}\right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = (b_{21}k_1 + b_{22}k_2 - d_2)N_2\left[\dfrac{b_{21}k_1 + b_{22}k_2 - d_2 - (b_{21}k_1c_{11} + b_{22}k_2c_{21})N_1 - (b_{21}k_1c_{12} + b_{22}k_2c_{22})N_2}{b_{21}k_1 + b_{22}k_2 - d_2}\right]. \end{cases} \tag{22}$$

Again, dividing both the numerator and denominator of the fractions on the right sides of the two equations in Eqs. (22) by

$$\begin{aligned} &b_{11}k_1c_{11} + b_{12}k_2c_{21}, \\ &b_{21}k_1c_{12} + b_{22}k_2c_{22}, \end{aligned} \tag{23}$$

respectively, gives us

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = (b_{11}k_1 + b_{12}k_2 - d_1)N_1\left[\dfrac{\frac{b_{11}k_1+b_{12}k_2-d_1}{b_{11}k_1c_{11}+b_{12}k_2c_{21}} - N_1 - \frac{b_{11}k_1c_{12}+b_{12}k_2c_{22}}{b_{11}k_1c_{11}+b_{12}k_2c_{21}}N_2}{\frac{b_{11}k_1+b_{12}k_2-d_1}{b_{11}k_1c_{11}+b_{12}k_2c_{21}}}\right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = (b_{21}k_1 + b_{22}k_2 - d_2)N_2\left[\dfrac{\frac{b_{21}k_1+b_{22}k_2-d_2}{b_{21}k_1c_{12}+b_{22}k_2c_{22}} - \frac{b_{21}k_1c_{11}+b_{22}k_2c_{21}}{b_{21}k_1c_{12}+b_{22}k_2c_{22}}N_1 - N_2}{\frac{b_{21}k_1+b_{22}k_2-d_2}{b_{21}k_1c_{12}+b_{22}k_2c_{22}}}\right]. \end{cases} \tag{24}$$

Essentially, Eqs. (24) are the Lotka-Volterra competition dynamics, which can be easily recognized if we make the following substitutions

$$\begin{aligned} r_1 &\triangleq b_{11}k_1 + b_{12}k_2 - d_1, \\ r_2 &\triangleq b_{21}k_1 + b_{22}k_2 - d_2, \\ K_1 &\triangleq \frac{b_{11}k_1 + b_{12}k_2 - d_1}{b_{11}k_1c_{11} + b_{12}k_2c_{21}}, \\ K_2 &\triangleq \frac{b_{21}k_1 + b_{22}k_2 - d_2}{b_{21}k_1c_{12} + b_{22}k_2c_{22}}, \end{aligned} \tag{25}$$

and

$$
\begin{aligned}
a_{12} &\triangleq \frac{b_{11}k_1c_{12} + b_{12}k_2c_{22}}{b_{11}k_1c_{11} + b_{12}k_2c_{21}} = \frac{C_2(b_{11}k_1n_{12} + b_{12}k_2n_{22})}{C_1(b_{11}k_1n_{11} + b_{12}k_2n_{21})} = \frac{C_2}{C_1} \cdot \text{normalization constant}, \\
a_{21} &\triangleq \frac{b_{21}k_1c_{11} + b_{22}k_2c_{21}}{b_{21}k_1c_{12} + b_{22}k_2c_{22}} = \frac{C_1(b_{21}k_1n_{11} + b_{22}k_2n_{21})}{C_2(b_{21}k_1n_{12} + b_{22}k_2n_{22})} = \frac{C_1}{C_2} \cdot \text{normalization constant},
\end{aligned}
\tag{26}
$$

where r_i is the rate of natural increase in isolation of consumer i, K_i is the carry capacity of consumer i in the absence of all competitors, and a_{ij} is the competition coefficient measuring the competitive effect of consumer j on consumer i. Specifically, C_j is the average rate at which consumer j consumes resources. Furthermore, it is typically observed that the relative conversion b_{ij} of a unit of resource j by consumer i and the carrying capacity k_j of resource j have limited variations for a given consumer i across different resources j and can be assumed constant for the sake of model simplification (Brown et al., 2004). Therefore, as indicated by Eq. (26), it is important to note that the competition coefficient a_{ij} is proportional to the ratio of consumption rates C between consumer j and consumer i. Formally, we can represent it as

$$
a_{ij} = a_0' \left(\frac{C_j}{C_i} \right), \tag{27}
$$

where a_0' is an *effective* parameter representing the overall effect of intrinsic properties, such as consumers' conversion rates and resources' carrying capacities (Parain et al., 2019).

To further estimate the average rate C_i at which consumer i consumes resources, we can simplify the previous scenario by considering a streamlined framework that involves only one consumer (also predator, either consumer j or consumer i) and one resource (also prey). Specifically, if the resource is self-replicating, then the resource equation with a logistic growth is

$$
\frac{\mathrm{d}R}{\mathrm{d}t} = rR \left[\left(\frac{k - R}{k} \right) - cN \right], \tag{28}
$$

where R is the density of the resource, r is its per capita rate of increase, k is the carrying capacity of the resource, c is the rate at which the resource is consumed by the consumer, and N is the population density of the consumer.

Then, we can write the consumer equation as

$$
\frac{\mathrm{d}N}{\mathrm{d}t} = (bR - d)N, \tag{29}
$$

where b is the predation rate and d is the death rate of the consumer.

Assuming again that the resource dynamics are very fast compared to the consumer dynamics (MacArthur and Levins, 1967), we can solve the equilibrium value of R:

$$R^* = k(1 - CN), \tag{30}$$

and then substitute R^* in place of R in the consumer equation Eq. (29). We obtain

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [bk(1 - CN) - d]N, \tag{31}$$

which can also be written as

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(bk - d - bkCN). \tag{32}$$

Multiplying and dividing Eq. (32) by $(bk - m)$ gives us

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (bk - d)N\left(\frac{bk - d - bkCN}{bk - d}\right). \tag{33}$$

Next, dividing both the numerator and the denominator of the fraction on the right side of the Eq. (33) by bkC, we have

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (bk - m)N\left(\frac{\frac{bk-d}{bkC} - N}{\frac{bk-d}{bkC}}\right). \tag{34}$$

If we denote

$$\begin{aligned} r &\triangleq bk - d, \\ K &\triangleq \frac{bk - d}{bkC}, \end{aligned} \tag{35}$$

then Eq. (34) can be written as the classic population model with logistic growth:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{K - N}{K}\right), \tag{36}$$

where again r is the rate of natural increase in isolation of the consumer and K is the carrying capacity of the consumer without competitors.

Importantly, Eqs. (35) indicate that the consumption rate C increases monotonically with the intrinsic growth rate r (Deng et al., 2024). Formally, by substituting the expression for bk as $(r + d)$ from the first equation into the second equation, we obtain

$$C = \frac{1}{K\left(1 + \frac{d}{r}\right)}. \tag{37}$$

The consumption rate C exhibits a monotonically decreasing behavior with respect to the carrying capacity K. Note that the relationship between carrying capacity K and intrinsic growth rate r appears to be complex and context-dependent (Marshall et al., 2023). Therefore, instead of establishing relationships between r and K, our primary focus lies on K due to its role in the feasibility of Lotka-Volterra competition dynamics for developed communities (Odum, 1969). However, the focus can be shifted to r if one is interested in developing communities (Deng et al., 2024).

Following metabolic scaling theory (Eqs. 2-3 in main text), one can write the average consumption rate of population i (Eq. 35) as a function of body size (M_i). Note that mortality rate (d_i) is the reciprocal of generation time (G_i) and proportional to growth rate (r_i). For a fixed thermal domain and response, we can replace the parameters in Eq. 37 with the following equivalences: $r_i = r_0 \cdot M_i^{-1/4}$, $d_i = d_0 \cdot M_i^{-1/4}$, $K_i = K_0 \cdot M_i^{-3/4}$, where r_0, d_0, and K_0 are normalization constants. Thus, Eq. (35) can be expressed as:

$$C_i = a_0'' \cdot M_i^{3/4}. \tag{38}$$

Eventually, by combining Eq. (27) with Eq. (36), we can derive an estimation of competitive interaction strength a_{ij} for a fixed thermal domain and response as:

$$a_{ij} = a_0 \cdot (M_j/M_i)^{3/4}, \tag{39}$$

where a_0', a_0'', and a_0 are normalization constants. Based on this estimation, we can generate the competition matrix $\mathbf{A}$ for the Lotka-Volterra competition dynamics in Eq. (4) in main text.

Under $a_{ij} = a_0 \cdot (M_j/M_i)^{3/4}$ (Eq. 39), Figure 2 (main text) shows that if the environmental carrying capacities are defined as $K_i = K_0 \cdot M_i^{-3/4}$, then they are the closest to the centroid of the feasibility domain. However, these carrying capacities $\boldsymbol{K}$ are expected to become exactly the centroid only under a specific value of a_0. For example, following Eq. 39 and for two competing species, the maximum and minimum feasible carrying capacities for species 2 (corresponding to the spanning vectors of the feasibility domain in Fig. 1) can be defined as $K_{2\max} = (a_{22}/a_{12})K_1$ and $K_{2\min} = (a_{21}/a_{11})K_1$, where $K_1 = K_0 \cdot M_1^{-3/4}$ is the environmental carrying capacity of species 1 per metabolic scaling theory. Then, following Eq. 9, the carrying capacity for species 2 that belongs to the centroid of the feasibility domain becomes:

$$K_{2\mathrm{c}} = \frac{1}{2}(K_{2\max} + K_{2\min}). \tag{40}$$

Note that in the centroid the distance beteween K_{2c} and K_1 should be the absolute minimum, i.e., $K_{2c}/K_1 = 1$. Thus, diving Eq. 40 by the environmental carrying capacities of species 1 (K_1) and rearranging it yields:

$$(M_2/M_1)^{-3/4} = \frac{1}{2} \cdot \frac{1 + a_0^2}{a_0} \cdot (M_2/M_1)^{-3/4}. \tag{41}$$

This implies that the equality is satisfied if and only if the factor $\frac{1+a_0^2}{2a_0} = 1$. Since a_0 also affects the dynamical stability of the community, future work can investigate the possible trade-offs between stability and feasibility under this framework.