Integrating metabolic scaling and coexistence theories

Serguei Saavedra[1,2*], José Ignacio Arroyo[2], Jie Deng[1],
Pablo A. Marquet[2,3,4,5], Christopher P. Kempes[2]

[1]Department of Civil and Environmental Engineering, MIT,
77 Massachusetts Av., 02139 Cambridge, MA, USA

[2]Santa Fe Institute,
Santa Fe, NM 87501, USA

[3]Department of Ecology & Evolutionary Biology, Princeton University,
Princeton, NJ 08544, USA

[4]Grupo de Biología Integrativa, Facultad de Ciencias Biológicas,
Pontificia Universidad Católica de Chile,
Santiago, 8331150, Chile

[5]Centro de Modelamiento Matemático,
Universidad de Chile, International Research Laboratory 2807, CNRS,
Santiago 8370456, Chile

*To whom correspondence should be addressed.
E-mail: sersaa@mit.edu

1

Abstract

Metabolic scaling theory has been pivotal in formalizing the limits of energy expenditures across individuals as a function of body size. Similarly, coexistence theory has provided a mathematization of the expected energy transformations across 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 the distribution of population sizes and the distribution of mean body sizes, can be explained in light of these limits and expectations. Here, we provide a tractable and scalable framework to study the feasibility of resource-mediated competing populations as a function of their mean body size. This integration reveals that the expected -3/4 power dependence of carrying capacity on body size specifies the distribution of carrying capacities that maximizes the feasibility of species coexistence under random environmental perturbations. 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). 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 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) 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 is typically exponential, $y = a \cdot e^{E/T}$, and known as the Arrhenius equation (Gillooly et al., 2001, 2002, West et al., 1997). 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 scales with its body size (m_i) and temperature (T) as

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

(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]$^{1/4}$[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 $b_i \cdot m_i^{-1} = b_0 \cdot e^{-\frac{E_i}{k \cdot T}} \cdot m_i^{-1/4}$ (known as mass-specific metabolism, dimension [time]$^{-1}$), revealing the economies of body plans (Arroyo et al., 2022, Savage et al., 2004).

In ecological research, 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 (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 average metabolic rate (Eq. 1) of population i can be written as $B_i(\theta) = B_0 \cdot e^{-\frac{E_i}{k \cdot T}} \cdot M_i^{3/4}$ (dimensions [mass][time]$^{-1}$) (Savage et al., 2004), where the environment can be specified as

$\theta = \{T\}$. 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 proved (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 $G_i \propto e^{\frac{E_i}{k \cdot T}} \cdot M_i^{\frac{1}{4}}$ (dimension [time]). Thus, the reciprocal of the maximum generation time (i.e., mortality rate) specifies the maximum growth rate of an individual in population i and can be written as

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

(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 (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 maximum biomass density of a population that can be sustained and can be approximated as

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

(dimensions $[\text{mass}][\text{area}]^{-1}$). That is, the maximum biomass of a population per unit area (or volume) decreases with both temperature and 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 some given biotic constraints ($\mathbf{A}$), can persist under different environmental contexts (θ). 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 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 $[\text{density}][\text{time}]^{-1}$). Here, $r_i(\theta) > 0$ is the intrinsic growth rate (dimension $[\text{time}]^{-1}$), $K_i(\theta) > 0$ is the environmental carrying capacity (dimension [density]). Here, θ 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. (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 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) (Hofbauer and Sigmund, 1998). This necessary condition is known as *feasibility* and it is written as (using matrix notation (Song et al., 2018, Vandermeer, 1970))

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

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 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). 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. 1) (Deng et al., 2023, 2022, Song et al., 2018). 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.

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, the geometric centroid of the feasibility domain (Fig. 1) corresponds to the distribution of $\boldsymbol{K}^*(\theta)$ that maximizes the feasibility of the community under random environmental perturbations (i.e., small changes to the direction of $\boldsymbol{K}^*(\theta)$). This geometric centroid can be written 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 $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K_c}^*(\theta) = (1, 1, \ldots, 1) \in \mathcal{R}^{|\mathcal{S}|}$ (Rohr et al., 2016). 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, Yeakel et al., 2018, Yodzis and Innes, 1992, Zaoli et al., 2017). Here, we provide a tractable and scalable 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, time-independent competitive interactions (a_{ij}) can be written as a function of the average consumption rates of consumers (see Supplementary Information for details):

$$a_{ij} = a_0' \cdot \left(\frac{C_j}{C_i}\right), \tag{10}$$

where C_i corresponds to the average consumption rate for a population i (dimension [density]$^{-1}$), and a_0' is a normalization constant. 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:

$$C_i = \frac{1}{K_i\left(1 + d_i/r_i\right)}, \tag{11}$$

where d_i denotes the mortality rate. Then, following metabolic scaling theory (Eqs. 2-3), we can use the maximum of these demographics and approximate the time-independent competitive

effects as a function of body size M_i and activation energy E_i (see Supplementary Information for details):

$$a_{ij} = a_0 \cdot e^{E_i - E_j} \cdot (M_j/M_i)^{3/4}. \tag{12}$$

That is, the higher the average body size of population j relative to that of population i, the higher the time-independent competitive effect. Instead, the higher the activation energy of population j relative to that of population i, the lower the time-independent competitive effect.

To understand the link between the feasibility of a community and the distribution of body sizes, we systematically studied the possible scaling relationship β between the vector of environmental carrying capacities and the vector of body sizes (i.e., $\boldsymbol{K}(\theta) \propto \boldsymbol{M}^{\beta}$) that becomes the closest to the centroid of the feasibility domain ($\boldsymbol{K_c}(\mathbf{A})$) of a metabolically-generated competition matrix $\mathbf{A}$. To perform this task, following Eq. (10), 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 $LN(0, 2)$, and E_i values independently from a uniform distribution $U(0.5, 0.7)$ (Gillooly et al., 2001, Savage et al., 2004). These distributions can change without affecting the qualitative results. Following previous work (Bunin, 2017, Dougoud et al., 2018), we set the normalization constant 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 $\boldsymbol{K}(\theta)$ as (Medeiros et al., 2021*b*, Saavedra et al., 2017)

$$d(\mathbf{A}, \boldsymbol{K}(\theta)) = \arccos(\boldsymbol{K}(\theta) \cdot \boldsymbol{K_c}(\mathbf{A}) \cdot ||\boldsymbol{K}(\theta)||^{-1} \cdot ||\boldsymbol{K_c}(\mathbf{A})||^{-1}) \in [0, 90]. \tag{13}$$

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 the vector of environmental carrying capacities described by the scaling relationship $\boldsymbol{K}(\theta) \propto \boldsymbol{M}^{\beta=-\frac{3}{4}}$ is, in fact, the centroid of the feasibility domain (i.e., $\boldsymbol{K_c}(\mathbf{A})$, $d(\mathbf{A}, \boldsymbol{K}(\theta)) = 0$, Eq. 9) of the metabolically-generated competition matrices. This reveals that the expected -3/4 power dependence of carrying capacity on body size specifies the distribution of carrying capacities that maximizes the feasibility of species coexistence under random en-

vironmental perturbations. Furthermore, because the centroid represents the condition under which all populations have the same biomass at equilibrium (Rohr et al., 2016), 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 ($\boldsymbol{I} \propto \boldsymbol{M}^{-1}$). Thus, 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) and can be treated as a potentially maximum relationship (Segura and Perera, 2023).

Concluding remarks

We have proposed a tractable and scalable 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 observe that the expected -3/4 power dependence of carrying capacity on body size specifies the distribution of carrying capacities that maximizes the feasibility of species coexistence under random environmental perturbations. In line with empirical observations (Hatton et al., 2019), our integration conforms to the expectation that carrying capacities lead to equilibrium biomasses 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 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 (Arroyo et al., 2022). This alternative model can be adapted to our integration 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_2024`

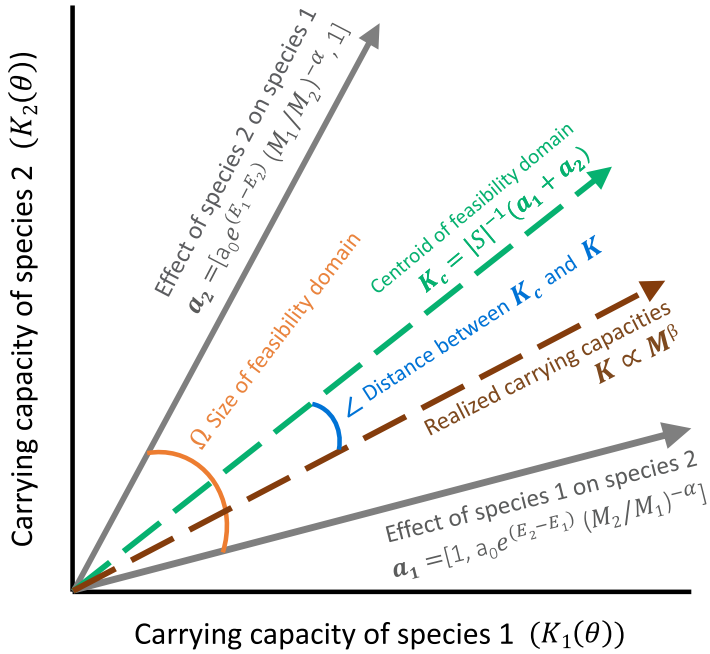

Figure 1: **A graphical integration of metabolic scaling and coexistence theories**. For an illustrative example of a community with $|S| = 2$ populations under Lotka-Volterra competition dynamics (Eq. 4), we show the parameter space of carrying capacities $K_i(\theta)$ (as a function of the environmental context θ). The solid gray arrows correspond to the column vectors of the interaction matrix ($\mathbf{A} = [\mathbf{a_1}; \mathbf{a_2}]$) parameterized using metabolic scaling relationships (Eq. 10). In this parameterization, a_0 corresponds to a normalization constant, E_i specifies the activation energy of population i, M_i represents the average body size of population i, and α is a scaling exponent. 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 green vector depicts the geometric centroid of the feasibility domain (Eq. 9, $\mathbf{K_c}$), representing the expected distribution of $\mathbf{K}(\theta)$ that increase coexistence of multiple competing population under random environmental perturbations acting on $\mathbf{K}(\theta)$. 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 $\boldsymbol{N}^* = \mathbf{A}^{-1}\boldsymbol{K_c^*}(\mathbf{A}) = (1, 1)$.

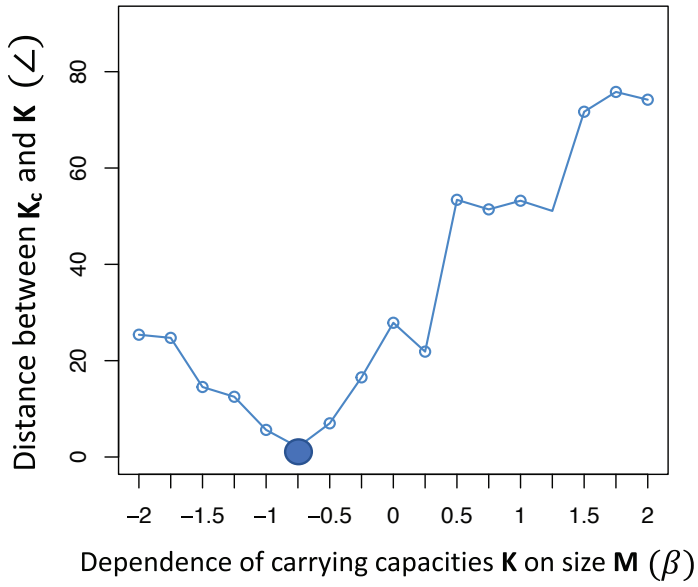

Figure 2: **Theoretical predictions**. (**A**) For an ensemble of 10^6 communities with $|S = 5|$ populations, the blue solid line shows the average distance (Eq. 13, blue small curve in Figure 1) between the centroid of the feasibility domain $\mathbf{K_c}$ and the possible vectors of carrying capacities ($\boldsymbol{K}(\theta) \propto \boldsymbol{M}^{\beta}$) as a function of body size and the power exponent $\beta \in [-2, 2]$. For each community, the interaction matrix (Eq. 10) is defined by $\alpha = 3/4$ and $a_0 = |S|^{-1/2}$. The values of M_i are drawn independently from a lognormal distribution $LN(0, 2)$, and E_i values are drawn independently from a uniform distribution $U(0.5, 0.7)$. Note that $\beta = -3/4$ (large blue symbol) is the value that minimizes the distance.

References

Arditi, R., Tyutyunov, Y. V., Titova, L. I., Rohr, R. P., and Bersier, L. F. 2021. The dimensions and units of the population interaction coefficients. Frontiers Ecol. Evol. 9:775754.

Arim, M., Bozinovic, F., and Marquet, P. A. 2007. On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. Oikos 116:1524–1530.

Arroyo, J. I., Díez, B., Kempes, C. P., West, G. B., and Marquet, P. A. 2022. A general theory for temperature dependence in biology. PNAS 119:e2119872119.

Basset, A. and Angelis, D. L. 2007. Body size mediated coexistence of consumers competing for resources in space. Oikos 116:1363–1377.

Belgrano, A., Allen, A. P., Enquist, B. J., and Gillooly, J. F. 2002. Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. Ecology Letters 5:611–613.

Bernhardt, J. R., Sunday, J. M., and O'Connor, M. I. 2018. Metabolic theory and the temperature-size rule explain the temperature dependence of population carrying capacity. The American Naturalist 192:687–697.

Bideault, A., Galiana, N., Zelnik, Y. R., Gravel, D., Loreau, M., Barbier, M., and Sentis, A. 2021. Thermal mismatches in biological rates determine trophic control and biomass distribution under warming. Global Change Biology 27:257–269.

Brose, U., Williams, R. J., and Martinez, N. D. 2006. Allometric scaling enhances stability in complex food webs. Ecology Letters 9:1228–1236.

Brown, J. H., Gillooly, J. F., Allen, A. P., M., V., and West, G. B. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Bunin, G. 2017. Ecological communities with Lotka-Volterra dynamics. Physical Review E 95:042414.

Campillay-Llanos, W., Córdova-Lepe, F. D., and Moreno-Gómez, F. N. 2022. Coexistence, energy, and trophic cascade in a three-level food chain integrating body sizes. Frontiers in Ecol. and Evol. 10:821176.

Case, T. J., 2000. An Illustrated Guide to Theoretical Ecology. Oxford Univ. Press, Oxford.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics 31:343–366.

Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. Biological Journal of the Linnaean Society 31:193–246.

Dell, A. I., Pawar, S., and Savage, V. M. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. USA 108:10591–10596.

DeLong, J. P., Okie, J. G., Moses, M. E., Sibly, R. M., and Brown, J. H. 2010. Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. Proceedings of the National Academy of Sciences 107:12941–12945.

Deng, J., Angulo, M. T., and Saavedra, S. 2021. Generalizing game-changing species across microbial communities. ISME Communications 1:1–8.

Deng, J., Cordero, O. X., Fukami, T., Levin, S. A., Pringle, R. M., Solé, R., and Saavedra, S. 2024. The development of ecological systems along paths of least resistance. Biorxiv doi.org/10.1101/2024.06.24.600194.

Deng, J., Taylor, W., Levin, S. A., and Saavedra, S. 2023. On the limits to invasion prediction using coexistence outcomes. J. of Theoretical Biology 577:111674.

Deng, J., Taylor, W., and Saavedra, S. 2022. Understanding the impact of third-party species on pairwise coexistence. PLoS Comput. Biol. 18:e1010630.

Dougoud, M., Vinckenbosch, L., Rohr, R. P., Bersier, L. F., and Mazza, C. 2018. The feasibility of equilibiria in large ecosystems: a primary but neglected concept in the complexity-stability debate. PLOS Computational Biology 14:e1005988s.

Gellner, G., McCann, K., and Hastings, A. 2023. Stable diverse food webs become more common when interactions are more biologically constrained. PNAS 120:e2212061120.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Gillooly, J. F., Charnov, E. L., West, G. B., Savage, V. M., and Brown, J. H. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

Harte, J., Zillio, T., Conlisk, E., and Smith, A. B. 2008. Maximum entropy and the state-variable approach to macroecology. Ecology 89:2700–2711.

Hatton, I. A., Dobson, A. P., Storch, D., and Loreau, M. 2019. Linking scaling laws across eukaryotes. PNAS 116:21616–21622.

Hatton, I. A., Mazzarisi, O., Altieri, A., and Smerlak, M. 2024. Diversity begets stability: Sublinear growth and competitive coexistence across ecosystems. Science 383:1196.

Hofbauer, J. and Sigmund, K., 1998. Evolutionary games and population dynamics. Cambridge University Press.

Kempes, C. P., Dutkiewicz, S., and Follows, M. J. 2011. Growth, metabolic partitioning, and the size of microorganisms. PNAS 109:495–500.

Kleiber, M. 1932. Body size and metabolism. Hilgardia 6:315–353.

Logofet, D. O., 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

Lotka, A. J. 1920. Analytical note on certain rhythmic relations in organic systems. Proceedings of the National Academy of Sciences 6:410–415.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101:377–385.

Marquet, P. A., Labra, F. A., and Maurer, B. A. 2004. Metabolic ecology: linking individuals to ecosystems. Ecology 85:1794–1796.

Marquet, P. A., Navarrete, S. A., and Castilla, J. C. 1990. Scaling population density to body size in rocky intertidal communities. Science 250:1125–1127.

Marquet, P. A., Quiñones, R. A., Abades, S., Labra, F. A., Tognelli, M., Arim, M., and Rivadeneira, M. 2005. Scaling and power-laws in ecological systems. Journal of Experimental Biology 208:1749–1769.

Marshall, D. J., Cameron, H. E., and Loreau, M. 2023. Relationships between intrinsic population growth rate, carrying capacity and metabolism in microbial populations. The ISME Journal Pages 1–4.

Maurer, B. A. 1996. Relating human population growth to the loss of biodiversity. Biodiversity Letters 3:1–5.

McCann, K., Hastings, A., and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Medeiros, L. P., Boege, K., del Val, E., Zaldivar-Riverón, A., and Saavedra, S. 2021*a*. Observed ecological communities are formed by species combinations that are among the most likely to persist under changing environments. The American Naturalist 197:E17–E29.

Medeiros, L. P., Song, C., and Serguei, S. 2021*b*. Merging dynamical and structural indicators of resilience. J. of Animal Ecology 90:2027–2040.

Michaelian, K. 2005. Thermodynamic stability of ecosystems. Journal of Theoretical Biology 237:323 – 335.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Odum, E. P. and Barrett, G. W., 2005. Fundamentals of Ecology. Thomson, Brooks-Cole, Fifth Edition.

Rohr, R. P., Saavedra, S., Peralta, G., Frost, C. M., Bersier, L.-F., Bascompte, J., and Tylianakis, J. M. 2016. Persist or produce: a community trade-off tuned by species evenness. Am. Nat. 188:411–422.

Saavedra, S., Medeiros, L. P., and AlAdwani, M. 2020. Structural forecasting of species persistence under changing environments. Ecology Letters 23:1511–1521.

Saavedra, S., Rohr, R. P., Bascompte, J., Godoy, O., Kraft, N. J., and Levine, J. M. 2017. A structural approach for understanding multispecies coexistence. Ecological Monographs 87:470–486.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., and Charnov, E. L. 2004. Effects of body size and temperature on population growth. The American Naturalist 163:429–441.

Segura, A. M. and Perera, G. 2023. Metabolic constraints on the body size scaling of extreme population densities. Ecology Letts 26:919–928.

Song, C., Rohr, R. P., and Saavedra, S. 2018. A guideline to study the feasibility domain of multi-trophic and changing ecological communities. J. of Theoretical Biology 450:30–36.

Song, C. and Saavedra, S. 2018. Will a small randomly-assembled community be feasible and stable? Ecology 99:743–751.

Tabi, A., Gilarranz, L. J., Wood, S. A., Dunne, J. A., and Saavedra, S. 2023. Protection

from harvesting promotes energetically efficient structures in marine communities. PLoS Computational Biology 19:e1011742.

Tabi, A., Pennekamp, F., Altermatt, F., Alther, R., Fronhofer, E. A., Horgan, K., Machler, E., Pontarp, M., Petchey, O. L., and Saavedra, S. 2020. Species multidimensional effects explain idiosyncratic responses of communities to environmental change. Nature Ecology & Evolution 4:1036–1043.

Täuber, U. C. 2011. Stochastic population oscillations in spatial predator-prey models. Journal of Physics: Conference Series 319:012019.

Vandermeer, J. H. 1970. The community matrix and the number of species in a community. The American Naturalist 104:73–83.

Vandermeer, J. H. and Goldberg, D. E., 2013. Population ecology: first principles. Princeton University Press.

Vasseur, D. A. and McCann, K. S. 2005. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. Am. Nat. 166:184–198.

Vellend, M., 2016. The theory of ecological communities. Princeton University Press, NJ.

West, G. B., Brown, J. H., and Enquist, B. J. 1997. A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

Yeakel, J. D., Kempes, C. P., and Redner, S. 2018. Dynamics of starvation and recovery predict extinction risk and both Damuth's law and Cope's rule. Nature Communications 9:657.

Yodzis, P. and Innes, S. 1992. Body size and consumer-resource dynamics. The American Naturalist 132:1151–1175.

Zaoli, S., Giometto, A., Maritan, A., and Rinaldo, A. 2017. Covariations in ecological scaling laws fostered by community dynamics. Proceedings of the National Academy of Sciences 114:10672–10677.

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:

$$\begin{cases} \dfrac{\mathrm{d}R_1}{\mathrm{d}t} = r_{\mathrm{rsc}_1} R_1 \left[\left(\dfrac{k_1 - R_1}{k_1} \right) - c_{11} N_1 - c_{12} N_2 \right], \\ \dfrac{\mathrm{d}R_2}{\mathrm{d}t} = r_{\mathrm{rsc}_2} R_2 \left[\left(\dfrac{k_2 - R_2}{k_2} \right) - c_{21} N_1 - c_{22} N_2 \right], \end{cases} \tag{14}$$

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:

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1 \left(b_{11} R_1 + b_{12} R_2 - d_1 \right), \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2 \left(b_{21} R_1 + b_{22} R_2 - d_2 \right), \end{cases} \tag{15}$$

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. (14) to zero and solve for the equilibrium values R_1^* and R_2^* of the two resources:

$$\begin{aligned} R_1^* &= k_1(1 - c_{11} N_1 - c_{12} N_2), \\ R_2^* &= k_2(1 - c_{21} N_1 - c_{22} N_2). \end{aligned} \tag{16}$$

Then, we can substitute R_1 and R_2 in Eqs. (15) by R_1^* and R_2^*, respectively. That is,

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1 \left[b_{11} k_1 (1 - c_{11} N_1 - c_{12} N_2) + b_{12} k_2 (1 - c_{21} N_1 - c_{22} N_2) - d_1 \right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2 \left[b_{21} k_1 (1 - c_{11} N_1 - c_{12} N_2) + b_{22} k_2 (1 - c_{21} N_1 - c_{22} N_2) - d_2 \right], \end{cases} \tag{17}$$

which can also be written as

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = N_1\left[b_{11}k_1 + b_{12}k_2 - d_1 - (b_{11}k_1c_{11} + b_{12}k_2c_{21})N_1 - (b_{11}k_1c_{12} + b_{12}k_2c_{22})N_2\right], \\ \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = N_2\left[b_{21}k_1 + b_{22}k_2 - d_2 - (b_{21}k_1c_{11} + b_{22}k_2c_{21})N_1 - (b_{21}k_1c_{12} + b_{22}k_2c_{22})N_2\right]. \end{cases} \tag{18}$$

Multiplying and dividing the two equations in Eqs. (18) by

$$\begin{aligned} &b_{11}k_1 + b_{12}k_2 - d_1, \\ &b_{21}k_1 + b_{22}k_2 - d_2, \end{aligned} \tag{19}$$

respectively, we obtain

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

Again, dividing both the numerator and denominator of the fractions on the right sides of the two equations in Eqs. (20) by

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

respectively, gives us

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

Essentially, Eqs. (22) are the Lotka-Volterra competition dynamics, which can be easily recognized if we make the following substitutions

$$\begin{aligned} r_1 &\triangleq b_{11}k_1 + b_{12}k_2 - d_1, \\ r_2 &\triangleq b_{21}k_1 + b_{22}k_2 - d_2, \\ K_1 &\triangleq \frac{b_{11}k_1 + b_{12}k_2 - d_1}{b_{11}k_1c_{11} + b_{12}k_2c_{21}}, \\ K_2 &\triangleq \frac{b_{21}k_1 + b_{22}k_2 - d_2}{b_{21}k_1c_{12} + b_{22}k_2c_{22}}, \end{aligned} \tag{23}$$

and

$$
\begin{aligned}
a_{12} &\triangleq \frac{b_{11}k_1c_{12}+b_{12}k_2c_{22}}{b_{11}k_1c_{11}+b_{12}k_2c_{21}} = \frac{C_2(b_{11}k_1n_{12}+b_{12}k_2n_{22})}{C_1(b_{11}k_1n_{11}+b_{12}k_2n_{21})} = \frac{C_2}{C_1}\cdot \text{normalization constant},\\
a_{21} &\triangleq \frac{b_{21}k_1c_{11}+b_{22}k_2c_{21}}{b_{21}k_1c_{12}+b_{22}k_2c_{22}} = \frac{C_1(b_{21}k_1n_{11}+b_{22}k_2n_{21})}{C_2(b_{21}k_1n_{12}+b_{22}k_2n_{22})} = \frac{C_1}{C_2}\cdot \text{normalization constant},
\end{aligned}
\tag{24}
$$

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, $C_j = \frac{c_{ij}}{n_{ij}}$ is the average rate at which consumer i consumes resources, where n_{ij} is a normalization constant. 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. (24), 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

$$
a_{ij} = a_0' \left(\frac{C_j}{C_i}\right), \tag{25}
$$

where a_0' is a normalization constant.

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

$$
\frac{\mathrm{d}R}{\mathrm{d}t} = rR\left[\left(\frac{k-R}{k}\right) - cN\right], \tag{26}
$$

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

$$
\frac{\mathrm{d}N}{\mathrm{d}t} = (bR-d)N, \tag{27}
$$

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:

$$R^* = k(1 - CN), \tag{28}$$

and then substitute R^* in place of R in the consumer equation Eq. (27). We obtain

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [bk(1 - CN) - d]N, \tag{29}$$

which can also be written as

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(bk - d - bkCN). \tag{30}$$

Multiplying and dividing Eq. (30) by $(bk - m)$ gives us

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (bk - d)N\left(\frac{bk - d - bkCN}{bk - d}\right). \tag{31}$$

Next, dividing both the numerator and the denominator of the fraction on the right side of the Eq. (31) by bkC, we have

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (bk - m)N\left(\frac{\frac{bk-d}{bkC} - N}{\frac{bk-d}{bkC}}\right). \tag{32}$$

If we denote

$$\begin{aligned} r &\triangleq bk - d, \\ K &\triangleq \frac{bk - d}{bkC}, \end{aligned} \tag{33}$$

then Eq. (32) can be written as the classic population model with logistic growth:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{K - N}{K}\right), \tag{34}$$

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. (33) 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 $(r + m)$ from the first equation into the second equation, we obtain

$$C = \frac{1}{K\left(1 + \frac{d}{r}\right)}. \tag{35}$$

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 avereage 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). Thus, Eq. (35) can be expressed as:

$$C_i = a_0'' \cdot e^{\frac{-E_i}{k \cdot T}} \cdot M_i^{3/4}. \tag{36}$$

Eventually, by combining Eq. (25) with Eq. (36), we can derive an estimation of competitive interaction strength a_{ij}:

$$a_{ij} = a_0 \cdot e^{E_i - E_j} \cdot (M_j/M_i)^{3/4}, \tag{37}$$

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.