Modeling the effect of temperature on species coexistence

Serguei Saavedra[1,2,*], Yuguang Yang[1], José Ignacio Arroyo[2], and Chris P. Kempes[2]

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

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

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

Data and Code Availability. No new data were generted in this paper. The data is available in Gilpin et al. (1986). All code to generate simulations, compute feasibility measures, and reproduce the figures, together with the transcribed *Drosophila* competition outcomes from Gilpin et al. (1986), is openly available at `https://github.com/MITEcology/Temperature_Coexistence`.

Ethics Statement. This study involves no new experiments on animals or humans. Analyses are based on previously published laboratory data on *Drosophila* competition (Gilpin et al. 1986).

Competing Interests. The authors declare that no competing interests exist.

Acknowledgments. SS acknowledges the support by the National Science Foundation under Grant No. DEB-2436069. JIA acknowledges the support by the National Science Foundation under Grant No. 2133863, and Center for Mathematical Modeling (CMM), Grant FB210005, BASAL funds for Centers of Excellence from ANID-Chile.

Abstract

Empirical evidence shows that the energy expenditure—and thus the persistence—of organisms follows a unimodal relationship with temperature and a monotonic relationship with body size. However, most studies integrating these organismal properties into species competition have emphasized only the increasing phase of the thermal response. Understanding how performance declines beyond thermal optima is equally critical if we are to anticipate the impacts of global warming on community composition. Here, we provide a modeling framework to explore the conditions under which temperatures exceeding thermal optima hinder species coexistence. We contrast our theoretical predictions with publicly available experimental data on *Drosophila*. Our results show that warmer conditions reduce coexistence when species' preferred temperature ranges scale positively with body size and their maximum metabolic rates occur at optimal temperatures. When species share similar body size and thermal optima, coexistence probability peaks at the optimum but declines more sharply under warming than under cooling. Conversely, when species differ in thermal optima but have similar body size, coexistence probability is highest at temperatures closer to the lower optimum. Together, our work establishes a formal approach to understanding species losses and community reassembly under global warming.

Summary

Temperature affects how organisms perform and, in turn, how species compete and live together. We develop a simple way to connect these two levels. First, we describe how each species' consumption increases up to a thermal optimum and then declines as conditions become cooler or warmer. We then place these temperature- and size-dependent consumptions into a standard competition model and summarize coexistence by the size of the set of environmental conditions that allow all species to persist (the "feasibility domain"). Two clear outcomes emerge. When species have similar body sizes and share a thermal optimum, coexistence is highest near that optimum and declines on both sides, with a steeper drop under warming than under cooling. When species have different thermal optima but similar size, coexistence peaks at an intermediate temperature between the optima, closer to the lower one. We compare these patterns with classic laboratory data on pairwise competitions among *Drosophila* at 19°C and 25°C and find qualitative agreement. Our approach offers a transparent link between organismal thermal traits and community assembly, helping to explain when and why warming can reduce the range of conditions that support coexistence.

Introduction

Global warming is reshaping the distribution and abundance of species worldwide, driving shifts in community composition and altering ecosystem properties [1–3]. These changes can be understood as modifications to competition dynamics, where the arrival of new species and the loss of resident ones directly influence the structure, function, and stability of ecological communities [4, 5]. Yet, anticipating these competitive outcomes remains challenging because the consequences of species turnover are strongly context-dependent. They vary with local species pools, historical contingencies, and environmental conditions, which interact in complex ways to shape coexistence and community assembly [6, 7]. In this regard, theoretical ecology has played a central role in guiding the interpretation of ecological observations, identifying general principles across systems, and informing both experimental design and ecosystem management strategies [8–13]. Building on this tradition, it becomes essential to develop modeling strategies that explicitly account for the role of temperature in mediating species coexistence. Since temperature not only governs physiological performance [14, 15] but also drives the assembly and reassembly of ecological communities [16], understanding its effects is crucial to anticipating how global warming will reshape biodiversity and ecosystem functioning.

Empirical evidence shows that the energy expenditure—and thus the persistence—of organisms follows a unimodal relationship with temperature and a monotonic relationship with body size [15, 17–21]. However, understanding how performance declines beyond thermal optima is critical if we are to anticipate the impacts of global warming on community composition [22]. Yet, the complexity of thermal response curves has hindered the theoretical integration of coexistence and temperature [23, 24]. Despite the centrality of temperature in ecological theory, the consequences of conditions exceeding species' thermal optima remain underexplored in the context of coexistence. Supra-optimal temperatures often reduce metabolic performance, constrain reproductive success, and increase mortality [14, 15, 25], thereby altering the balance of competitive interactions. Such declines can disproportionately disadvantage certain species depending on their body size, thermal tolerance breadth, or position along the thermal niche axis [26–28]. As a result, warming beyond thermal optima has the potential to reconfigure community assembly, shifting the relative likelihood of persistence, exclusion, or replacement among competing species [29]. Yet, existing models of temperature-dependent competition have primarily emphasized conditions approaching the thermal optimum [30, 31], leaving a critical gap in our ability to assess the destabilizing impacts of global warming on biodiversity.

Despite extensive work on how temperature reshapes interaction strengths and whole food webs [5, 32–34], we still lack an explicit analysis of how temperature modifies the conditions that sustain species coexistence. Here we bridge organismal thermal physiology and coexistence theory, asking how sub- and supra-optimal temperatures tilt interaction symmetry and compress the set of environmental conditions that permit coexistence. Specifically, we develop a theoretical framework to model the effect of temperature on species coexistence. Our approach builds on metabolic scaling theory and the unimodal nature of thermal performance curves to identify the conditions under which sub- and supra-optimal temperatures reduce the likelihood of coexistence. We examine how body size, thermal niche breadth, and differences in thermal optima interact to shape the outcomes of competitive dynamics under cooling and warming scenarios. To illustrate the applicability of our framework, we contrast our theoretical predictions with publicly available experimental data on *Drosophila* [35]. By integrating organismal energetics with community-level processes, our work provides a guideline for understanding how global warming may drive species losses, replacements, and reassembly in ecological communities.

Methods

Our goal is to connect organismal thermal physiology with the likelihood that competing species can coexist as environments cool or warm beyond their thermal optima. To do so, we embed temperature- and size-dependent consumption into a generalized Lotka–Volterra (gLV) competition model, then evaluate coexistence using coexistence theory [24]. This approach lets us ask when (and why) warming or cooling compresses the set of environments that sustain all species, providing a direct link between thermal traits and coexistence probability. Figure 1 illustrates the theoretical model described below.

Consumption-based generalized Lotka–Volterra model

We study a community of S competitors with gLV dynamics in r/K form,

$$\frac{dN_i(t)}{dt} \;=\; \frac{r_i}{K_i}\Big(K_i - \sum_{j=1}^{S} a_{ij}\, N_j(t)\Big), \quad i = 1, \ldots, S, \tag{1}$$

where $N_i(t)$ is the biomass of species i, r_i its intrinsic growth rate, K_i its carrying capacity, and a_{ij} the per-capita effect of species j on species i (with $a_{ii} = 1$). Following the case of shared limiting resources, we parameterize interspecific competition via relative consumption [24],

$$a_{ij} \;\approx\; a_0\, \frac{C_j}{C_i}, \tag{2}$$

where C_i is the average resource consumption rate of species i and a_0 captures conversion/efficiency effects. We set intraspecific competition to unity, $a_{ii} = 1$. Biologically, Equation (2) implies that species that consume more of the common resources exert stronger suppressive effects on others, all else equal. We focus on competition-only communities throughout; all off-diagonal interaction coefficients satisfy $a_{ij} > 0$ for $i \neq j$.

The r/K gLV form separates environmental supply (K_i) from interaction strength (a_{ij}), so temperature can influence coexistence both by tilting competitive effects (through C_i) and by changing the effective environments that species experience (through K_i). This separation is crucial in our setting to diagnose whether warming reduces coexistence mainly via stronger asymmetric competition or via shrinking compatible environments. Moreover, Equation (2) makes the key link: interaction asymmetries depend on *relative* consumption (C_j/C_i). Thus, temperature will shape competition through its effects on each $C_i(T)$. We next specify how body size and temperature determine $C_i(T)$, which in turn determines the competition matrix ($\mathbf{A}$).

Linking consumption to temperature and body size

To make temperature dependence explicit, we follow work on metabolic scaling theory, which relates metabolic rates to body size and temperature [36]. At a given temperature, the metabolic rate b of an individual with body mass m is expected to scale as

$$b = b_0\, f(T)\, m^{3/4}, \tag{3}$$

where b_0 is a normalization constant and $f(T)$ is the temperature-dependent response. We use this relationship to link consumption with both body size and temperature, adopting the `flexTPC` formulation for $f(T)$, which allows unimodal responses with flexible skewness and breadth [37]. Accordingly,

$$C_i(T) = g_i(T)\, m_i^{3/4}, \tag{4}$$

with

$$g_i(T) = \begin{cases} g_{i,\max} \left(\dfrac{T - T_{i,\min}}{T_{i,\text{opt}} - T_{i,\min}} \right)^{\frac{\alpha_i}{1-\alpha_i}} \left(\dfrac{T_{i,\max} - T}{T_{i,\max} - T_{i,\text{opt}}} \right)^{\frac{1-\alpha_i}{\alpha_i}} \beta_i^{-2}, & T_{i,\min} < T < T_{i,\max}, \\ 0, & \text{otherwise}, \end{cases} \tag{5}$$

where $g_{i,\max}$ is the maximum trait performance (here, the maximum consumption rate), and $T_{i,\min}$ and $T_{i,\max}$ denote the lower and upper critical temperatures. The parameter $\alpha_i \in (0, 1)$

determines the location of the optimum temperature,

$$T_{i,\mathrm{opt}} = \alpha_i \, T_{i,\max} + (1 - \alpha_i) \, T_{i,\min}, \tag{6}$$

at which $g_i(T)$ attains its maximum value $g_{i,\max}$. We further assume a positive correlation between $g_{i,\max}$ and $T_{i,\mathrm{opt}}$. Note that we use *overall thermal breadth* for $T_{i,\max} - T_{i,\min}$ and *upper thermal breadth* for the right-hand width above $T_{i,\mathrm{opt}}$ (e.g., temperatures with $g_i(T) \geq \frac{1}{2} g_{i,\max}$), which is distinct from the upper limit $T_{i,\max}$.

In Equation (6), the parameter β_i controls the upper thermal breadth, and in our analysis we posit a scaling relationship between β_i and body mass m_i, given by $\beta_i = \beta_0 \, m_i^{3/4}$. We treat β_i as a dimensionless shape parameter that controls the right-hand breadth/skew of $g_i(T)$; the factor β_i^{-2} in Equation (5) ensures comparable scaling across species when breadth varies. In ecological terms, these expressions encode that species differ in their preferred temperatures, peak metabolic rates, and tolerance above the optimum; warming beyond $T_{i,\mathrm{opt}}$ depresses $g_i(T)$ and thus consumption. Empirically, thermal responses are unimodal but vary in skew and breadth across taxa and traits; a flexible curve avoids over-constraining these differences while remaining interpretable in terms of optima and tolerance. This choice aligns the organismal scale (thermal physiology) with community-level interaction strengths via Equation (2). These expressions define $C_i(T)$ and therefore $\mathbf{A}(T)$. With $\mathbf{A}(T)$ in hand, we now ask: for which environmental directions $\mathbf{K}$ does the community maintain a positive equilibrium, and how does that set shrink or expand with temperature?

Coexistence analysis

Under the gLV equilibrium dynamics, coexistence of S species requires a positive equilibrium biomass vector [24]. In matrix form,

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

where $\mathbf{A} = [\mathbf{a}_1 \, \mathbf{a}_2 \, \ldots \, \mathbf{a}_S]$ is the interaction matrix with columns $\mathbf{a}_j$ and $\mathbf{K}$ is the carrying capacity vector. This *feasibility* condition implies that, for a given $\mathbf{A}$ (assumed invertible and normalized with $a_{ii} = 1$), the direction of $\mathbf{K}$ determines coexistence. The set of $\mathbf{K}$ yielding $\mathbf{N}^* > \mathbf{0}$ defines the feasibility domain

$$D_{\mathrm{F}}(\mathbf{A}) = \left\{ \mathbf{K}^* = \sum_{j=1}^{S} N_j^* \, \mathbf{a}_j : \; N_j^* \in \mathbb{R}_{>0} \right\} \subset \mathbb{R}^S. \tag{8}$$

We quantify the probability of coexistence by the normalized size of the feasibility domain [38],

$$\Omega(\mathbf{A}) = \frac{|\det(\mathbf{A})|}{\pi^{S/2}} \int_{\mathbb{R}^S_{\geq 0}} \exp\Big(-\mathbf{x}^\top \mathbf{A}^\top \mathbf{A}\, \mathbf{x}\Big)\, \mathrm{d}\mathbf{x}. \tag{9}$$

Although both r_i and K_i can vary with temperature, here we channel temperature effects primarily through $\mathbf{A}(T)$ via consumption asymmetries to isolate the role of interaction symmetry in shaping Ω.

In practice, we compute $\Omega(\mathbf{A}(T))$ across T to obtain temperature–coexistence curves. To build intuition for how asymmetries contract Ω, we perform an analytical analysis of the two-species case, where closed-form expressions clarify the roles of a_{12} and a_{21}. For a two-species competitive community, the gLV dynamics is given by

$$\begin{cases} \dfrac{\mathrm{d}N_1}{\mathrm{d}t} = \dfrac{r_1}{K_1}\left(K_1 - a_{11}N_1(t) - a_{12}N_2(t)\right), \\[2ex] \dfrac{\mathrm{d}N_2}{\mathrm{d}t} = \dfrac{r_2}{K_2}\left(K_2 - a_{21}N_1(t) - a_{22}N_2(t)\right), \end{cases} \tag{10}$$

where $a_{11} = a_{22} = 1$. The coexistence condition (i.e., system (10) admits a positive equilibrium solution) is

$$\begin{cases} K_1 - K_2 a_{12} > 0, \\ K_2 - K_1 a_{21} > 0, \end{cases} \tag{11}$$

which is equivalent to

$$a_{21} < \frac{K_2}{K_1} < \frac{1}{a_{12}}. \tag{12}$$

The corresponding feasibility domain size is

$$\Omega(\mathbf{A}) \;=\; \frac{1}{\pi}\,\arcsin\!\left(\frac{|\,1 - a_{12}a_{21}\,|}{\sqrt{1+a_{21}^2}\,\sqrt{1+a_{12}^2}}\right). \tag{13}$$

Suppose $a_{12} = \alpha a_0$ and $a_{21} = a_0/\alpha$ with $a_0 > 0$ and $\alpha \in (0, 1]$. Then the feasibility domain size becomes

$$\Omega(\mathbf{A}) \;=\; \frac{1}{\pi}\,\arcsin\!\left(\frac{|\,1 - a_0^2\,|}{\sqrt{1+\alpha^2 a_0^2}\,\sqrt{1+a_0^2/\alpha^2}}\right), \tag{14}$$

which increases monotonically with α. Therefore, $\Omega(\mathbf{A})$ reaches its maximum at $\alpha = 1$, i.e., when the two species exert equal competitive strengths on each other. For two-species case, we define θ_{F} as the angle between the column vectors $\mathbf{a}_1 = (1, a_{21})^\top$ and $\mathbf{a}_2 = (a_{12}, 1)^\top$ that span

the cone $D_{\mathrm{F}}(\mathbf{A})$. Hence

$$\cos\theta_{\mathrm{F}} = \frac{\mathbf{a}_1^\top \mathbf{a}_2}{\|\mathbf{a}_1\|\,\|\mathbf{a}_2\|}, \qquad \Omega = \theta_{\mathrm{F}}/\pi. \tag{15}$$

In higher dimensions Ω is the fraction of environmental directions that intersect the positive orthant.

In sum, as shown in Figure 1, temperature reshapes the geometry of coexistence by modulating both pairwise interaction asymmetries and the range of compatible environmental conditions. Within the consumption-based generalized Lotka–Volterra framework, we summarize this geometry by the feasibility domain size, $\Omega(\mathbf{A}(T))$, equivalently captured by the feasibility angle θ_{F}. Both measures quantify the proportion of environments that yield positive equilibria for a temperature-dependent interaction matrix $\mathbf{A}(T)$. Across model realizations, $\Omega(\mathbf{A}(T))$ is maximized at intermediate temperatures and shrinks with either cooling or warming, reflecting how temperature tilts interaction strengths through relative consumption $C_j(T)/C_i(T)$ while simultaneously narrowing the set of compatible environments through $\mathbf{K}$. In the Results we hold the direction of $\mathbf{K}$ fixed and quantify temperature effects through $\mathbf{A}(T)$; sensitivity to $\mathbf{K}(T)$ is examined separately.

Empirical data

To corroborate our theoretical predictions, we analyzed the classic laboratory dataset on species competition in *Drosophila* compiled in Ref. [35]. This dataset reports pairwise coexistence outcomes under controlled laboratory conditions while systematically varying temperature and resource supply. Specifically, experiments were conducted in incubators using standard *Drosophila* culture medium. Environmental treatments included two distinct temperature regimes—19°C (representing temperate conditions) and 25°C (representing tropical conditions)—and different levels of food "thickness," which modulate per-capita resource availability. Each trial involved replicated pairwise competitions among several species combinations, resulting in either competitive exclusion or coexistence. Moreover, the dataset also presents the climate preference of each *Drosophila* species (i.e., a preference for tropical or temperate conditions). In our analysis, we interpret these climate preferences as proxies for thermal optima: species preferring tropical conditions are classified as having a thermal optimum of 25°C, whereas those preferring temperate conditions are classified as having a thermal optimum of 19°C. Taken together, these experimental features make the dataset particularly suitable for examining the role of temperature in shaping species coexistence.

We focused on the replicated *pairwise* competitions performed under "thick-food" conditions at

19°C and 25°C, because these conditions are most comparable to our model assumptions and were evaluated for the majority of species pairs (see Figs. 2.2A–E and associated text in the source). Species identities and their broad geographic distributions (temperate vs. tropical) are listed in Table 2.1 of the source. We assigned each species to a "temperate" or "tropical" group using that table's "Distribution" field and treated these groups as proxies for lower vs. higher thermal optima, respectively. For analyses we follow the source's indexing and treat IDs 1–10 as $T_{\text{opt}} = 19\,°\text{C}$ (temperate) and IDs 11–25 as $T_{\text{opt}} = 25\,°\text{C}$ (tropical).

From the pairwise competition matrices (Fig. 2.2 in the source), we transcribed, for each ordered pair and temperature, the reported long-term outcome: exclusion of species i by species j, exclusion of j by i, or coexistence. The matrices also mark trials with an asterisk when replicate outcomes contained a coexistence or a reversal relative to the modal result; in such cases we recorded both the modal outcome and a binary flag for "coexistence observed at least once" and performed sensitivity analyses under both interpretations. To minimize heterogeneity across media, we excluded "thin" and "augmented" food treatments and restricted to the standard thick-food serial-transfer protocol used by the authors for their main rank analyses.

Following the authors' usage, we defined pairwise coexistence as the persistent presence of both species after multiple serial transfers under a fixed environment, as recorded in the competition matrices and accompanying text. For analyses in Fig. 3, we used the "coexistence observed at least once" definition as the primary endpoint, and verified that results were qualitatively unchanged when using the modal outcome across replicates. To evaluate the predictions that (i) coexistence is maximized near species' thermal optima when optima are shared and (ii) the coexistence maximum lies between optima when they differ, we analyzed three categories of species pairs: (1) both temperate (shared low T_{opt} proxy), (2) both tropical (shared high T_{opt} proxy), and (3) mixed (different optima proxies). Within each category we computed the fraction of pairs coexisting at 19°C and at 25°C and compared these fractions across temperatures.

Results

Figure 2a–b shows that when competitors share similar body sizes and a common thermal optimum, T_{opt}, coexistence displays a clear unimodal response: $\Omega(\mathbf{A}(T))$ peaks at T_{opt} and declines on either side. Departures above the optimum curtail coexistence more sharply than comparable departures below it (Fig. 2a–b). Thus, communities composed of similarly adapted species are most likely to coexist at or near their shared optimum and are disproportionately vulnerable to warming beyond that point.

Instead, communities assembled from species with different thermal optima exhibit a distinct pattern. Displacing consumption peaks along the temperature axis shifts the coexistence maximum to an intermediate temperature between the optima, with the peak skewed toward the lower T_{opt} (Fig. 2c). That is, the temperature that maximizes coexistence lies between the minimum and maximum species optima and remains closer to the lower one, implying that assemblages spanning cool- and warm-adapted types achieve their greatest coexistence under relatively cooler conditions.

Empirical analyses of classic *Drosophila* competition experiments further support these theoretical predictions. Pairs of species with similar presumed optima—temperate (19°C) or tropical (25°C) preferences used as proxies—show enhanced coexistence near their preferred temperature and a steeper drop under warming than under cooling (Fig. 3a–b). For pairs with different presumed optima, coexistence is more frequent at 19°C than at 25°C, consistent with a coexistence maximum that lies between optima and closer to the lower one (Fig. 3c).

The common mechanism underlying these results is an increase in competitive asymmetries at supra-optimal temperatures. When thermal breadth increases with body size and peak consumption coincides with T_{opt}, warming amplifies $C_j(T)/C_i(T)$ imbalances and reduces $\Omega(\mathbf{A}(T))$ by tilting $\mathbf{A}(T)$ while simultaneously narrowing the set of compatible environments through $\mathbf{K}$. Sensitivity analyses spanning the parameter sets used in Fig. 2 (e.g., a_0, m_0, M_r, β_0) preserved these qualitative outcomes, indicating that the conclusions are robust to parameterization. Together, these findings paint a coherent picture: coexistence is highest at or near thermal optima for similarly adapted species; warming erodes coexistence more strongly than cooling in that setting; differing thermal optima shift the coexistence maximum to an intermediate temperature biased toward the lower optimum; and laboratory *Drosophila* competitions mirror these patterns across temperate and tropical regimes (Fig. 3).

Discussion

Our analysis connects organismal thermal physiology to the geometry of coexistence in a way that is both mechanistic and predictive. By embedding temperature responses into a consumption-based generalized Lotka–Volterra framework and summarizing coexistence via the feasibility domain, we show that modest departures from thermal optima can cause large changes in the volume of environmental conditions that support positive equilibria. Two general principles emerge. First, when species share similar thermal optima, coexistence is maximized at or near that shared optimum and declines asymmetrically, with warming inflicting greater losses

than cooling. Second, when species differ in their optima, the coexistence maximum lies between them and is biased toward the lower optimum. These patterns—demonstrated analytically, in simulations, and in *Drosophila* competition experiments across 19°C and 25°C—offer a compact set of predictions for how warming will reconfigure communities.

The feasibility domain provides a geometric summary of coexistence that can be computed from the interaction matrix and environmental supply. Because temperature modulates relative consumption rates, $C_j(T)/C_i(T)$, it effectively tilts the interaction matrix and reshapes the domain. Increases in temperature beyond the optimum amplify asymmetries, especially when thermal breadth scales with body size, thereby contracting the domain more sharply under warming than under cooling. This mechanism reconciles observed asymmetries in empirical systems with a simple, interpretable axis of trait variation. Moreover, our results imply that the trajectory of warming, even when modest relative to species' thermal breadths, can have outsized impacts on diversity by pushing assemblages away from coexistence-maximizing temperatures. Communities composed of similarly adapted species should be most sensitive to warming beyond their shared optimum, while mixed communities spanning cool- and warm-adapted species may retain coexistence at relatively cooler temperatures but lose it rapidly as temperatures rise. Because the feasibility domain aggregates over many environmental directions, these conclusions do not depend on a single resource axis and generalize to multispecies assemblages.

Our framework complements the niche–neutral continuum by identifying a temperature-dependent axis that shifts the competitive balance [39–41]. At shared optima, temperature primarily acts via consumption symmetry, whereas departures create and magnify competitive asymmetries that reduce coexistence [15, 22, 27, 32, 36]. The bias of the coexistence maximum toward the lower optimum when species differ mirrors intuition from consumer–resource theory: cooler temperatures often diminish the advantage of fast consumers that would otherwise dominate at higher temperatures [14, 31, 33, 42]. A practical advantage of the feasibility approach is that it yields a single, comparable measure across parameter sets and community sizes, enabling robust sensitivity analyses. Our mapping from thermal traits to interaction coefficients clarifies when pairwise competition suffices to predict community-level changes and when higher-order effects are likely to matter [43]. Although we focused on competitive communities, the same pipeline could be extended to trophic systems by incorporating temperature dependence in attack rates and handling times [34].

Several assumptions delimit our inferences. We studied closed communities at ecological equilibrium, without explicit temporal environmental variability, migration, or evolutionary adap-

tation. Our parameterizations of thermal response curves and their scaling with body size, while grounded in empirical literature, remain simplifications of complex physiology. Finally, the empirical analysis uses temperature categories as proxies for optima; richer datasets with continuous temperature manipulations and trait measurements would sharpen tests of the theory. Yet, this framework yields testable predictions. In controlled microcosms or mesocosms, coexistence probability should be unimodal in temperature when species share optima, with a steeper decline under warming. For species with different optima, the coexistence maximum should lie between optima and closer to the lower one, with trait data on thermal breadth and body size improving quantitative forecasts. Future work could integrate temporal warming trajectories, dispersal, and eco-evolutionary feedbacks, and evaluate how cross-feeding or mutualism alter the geometry of coexistence under temperature change. Similarly, future studies could incorporate more mechanistic responses to temperature [21]. Moreover, extending and testing this framework to multi-species communities would enable exploration of how the interplay between network topology and temperature, as well as the influence of temperature on potential higher-order interactions, shapes coexistence. Notably, linking thermal physiology to coexistence geometry provides a tractable route to forecasting community responses to climate change.

References

[1] Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

[2] Walther GR, et al. (2002) Ecological responses to recent climate change. *Nature* 416:389–395.

[3] Pecl GT, et al. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355:eaai9214.

[4] Sala OE, et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.

[5] Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.

[6] Chase JM (2003) Community assembly: When should history matter? *Oecologia* 136:489–498.

[7] Fukami T (2015) Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23.

[8] May RM, McLean AR (2007) *Theoretical Ecology: Principles and Applications* (Oxford University Press).

[9] Pascual M, Dunne JA, eds (2006) *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Oxford University Press).

[10] Levin SA (2005) Self-organization and the emergence of complexity in ecological systems. *BioScience* 55:1075–1079.

[11] Case TJ (2000) *An Illustrated Guide to Theoretical Ecology* (Oxford University Press).

[12] Vellend M (2016) *The Theory of Ecological Communities* (Princeton University Press).

[13] Solé RV (2012) *Self-organization in Complex Ecosystems* (Princeton University Press).

[14] Angilletta MJ (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis* (Oxford University Press, Oxford, UK).

[15] Dell AI, Pawar S, Savage VM (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences* 108:10591–10596.

[16] Tabi A, et al. (2020) Species multidimensional effects explain idiosyncratic responses of communities to environmental change. *Nature Ecology & Evolution* 4:1036–1043.

[17] West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.

[18] Gillooly JF, Brown JH, Allen AP, Savage VM, West GB (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.

[19] Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. *Nature* 417:70–73.

[20] Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.

[21] Arroyo JI, Díez B, Kempes CP, West GB, Marquet PA (2022) A general theory for temperature dependence in biology. *PNAS* 119:e2119872119.

[22] Clegg T, Pawar S (2024) Variation in thermal physiology can drive the temperature-dependence of microbial community richness. *eLife* 13:e84662.

[23] Kontopoulos DG, et al. (2024) No universal mathematical model for thermal performance curves across traits and taxonomic groups. *Nature Communications* 15:1–10.

[24] Saavedra S, Arroyo JI, Deng J, Marquet PA, Kempes CP (2025) Integrating metabolic scaling and coexistence theories. *Ecology* 106:e70173.

[25] Huey RB, Kingsolver JG (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4:131–135.

[26] Deutsch CA, et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668–6672.

[27] Vasseur DA, et al. (2014) Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences* 281:20132612.

[28] Sinclair BJ, et al. (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters* 19:1372–1385.

[29] Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species' responses to climate change. *Nature* 525:515–518.

[30] Amarasekare P, Savage VM (2012) A framework for elucidating the temperature dependence of fitness. *The American Naturalist* 179:178–191.

[31] Sunday JM, Bates AE, Dulvy NK (2019) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the National Academy of Sciences* 116:4094–4099.

[32] Rall BC, et al. (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B* 367:2923–2934.

[33] Vasseur DA, McCann KS (2005) A mechanistic approach for modeling temperature-dependent consumer–resource dynamics. *The American Naturalist* 166:184–198.

[34] Parain EC, Rohr RP, Gray SM, Bersier LF (2019) Increased temperature disrupts the biodiversity–ecosystem functioning relationship. *The American Naturalist* 193:227–239.

[35] Gilpin ME, Carpenter MP, Pomerantz MJ (1986) *The assembly of a laboratory community: multispecies competition in Drosophila*, eds Diamond JM, Case TJ (Harper and Row, New York), pp 23–40.

[36] Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL (2004) Effects of body size and temperature on population growth. *The American Naturalist* 163:429–441.

[37] Cruz-Loya M, Mordecai EA, Savage VM (2024) A flexible model for thermal performance curves. *bioRxiv* Preprint, Version 1.

[38] Saavedra S, et al. (2017) A structural approach for understanding multispecies coexistence. *Ecological Monographs* 87:470–486.

[39] Song C, Barabás G, Saavedra S (2019) On the consequences of the interdependence of stabilizing and equalizing mechanisms. *The American Naturalist* 194:627–639.

[40] Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399–409.

[41] Barabás G, D'Andrea R, Stump SM (2018) Chesson's coexistence theory. *Ecological Monographs* 88:277–303.

[42] Bernhardt JR, Sunday JM, O'Connor MI (2018) Metabolic theory and the temperature-size rule explain the temperature dependence of population carrying capacity. *The American Naturalist* 192:687–697.

[43] Song C, Saavedra S (2021) Bridging parametric and nonparametric measures of species interactions. *Oikos* 130:1027–1034.

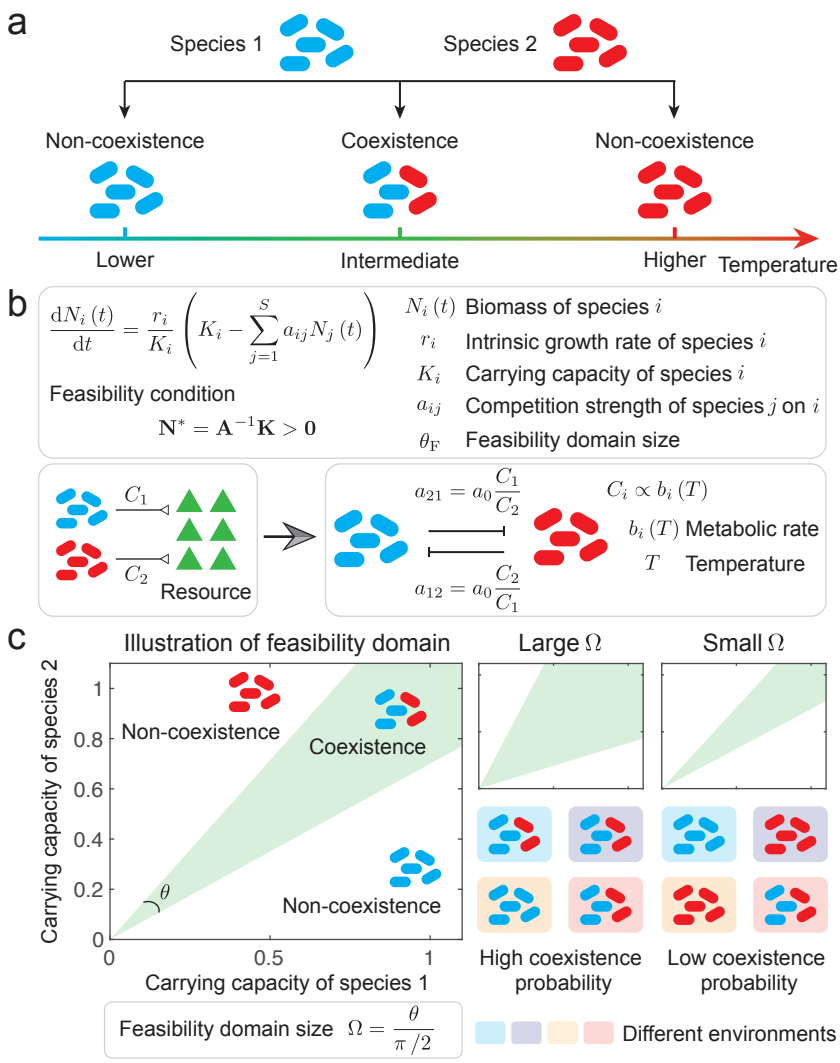

Figure 1: **Temperature effects on species coexistence.** **a**, Conceptual illustration of temperature-dependent coexistence. Species 1 (blue rods), adapted to lower temperatures, and species 2 (red rods), adapted to higher temperatures, can coexist under intermediate environmental conditions, but fail to coexist under either lower or higher temperatures. **b**, Incorporating temperature effects into ecological dynamics. Temperature dependence is introduced by linking the generalized Lotka–Volterra (gLV) competition model with metabolic scaling theory. In the gLV framework, coexistence requires the feasibility condition—the existence of a positive equilibrium solution ($\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K} > 0$). Here, the competition coefficients are parameterized by the relative consumption rates of shared resources, which in turn depend on the species' metabolic rates. Because metabolic rates scale with temperature, the influence of temperature propagates into the effective interaction strengths between species. **c**, Coexistence theory. The feasibility of coexistence depends on the combination of species' carrying capacities ($\mathbf{K}$). The set of carrying capacities that yield positive equilibria defines the *feasibility domain* (green region). The size of this domain (Ω) quantifies the probability of coexistence across environments: a larger Ω corresponds to a higher coexistence probability, where species can coexist under a broader range of environmental conditions (illustrated by different colored boxes), whereas a smaller Ω indicates a lower likelihood of coexistence.

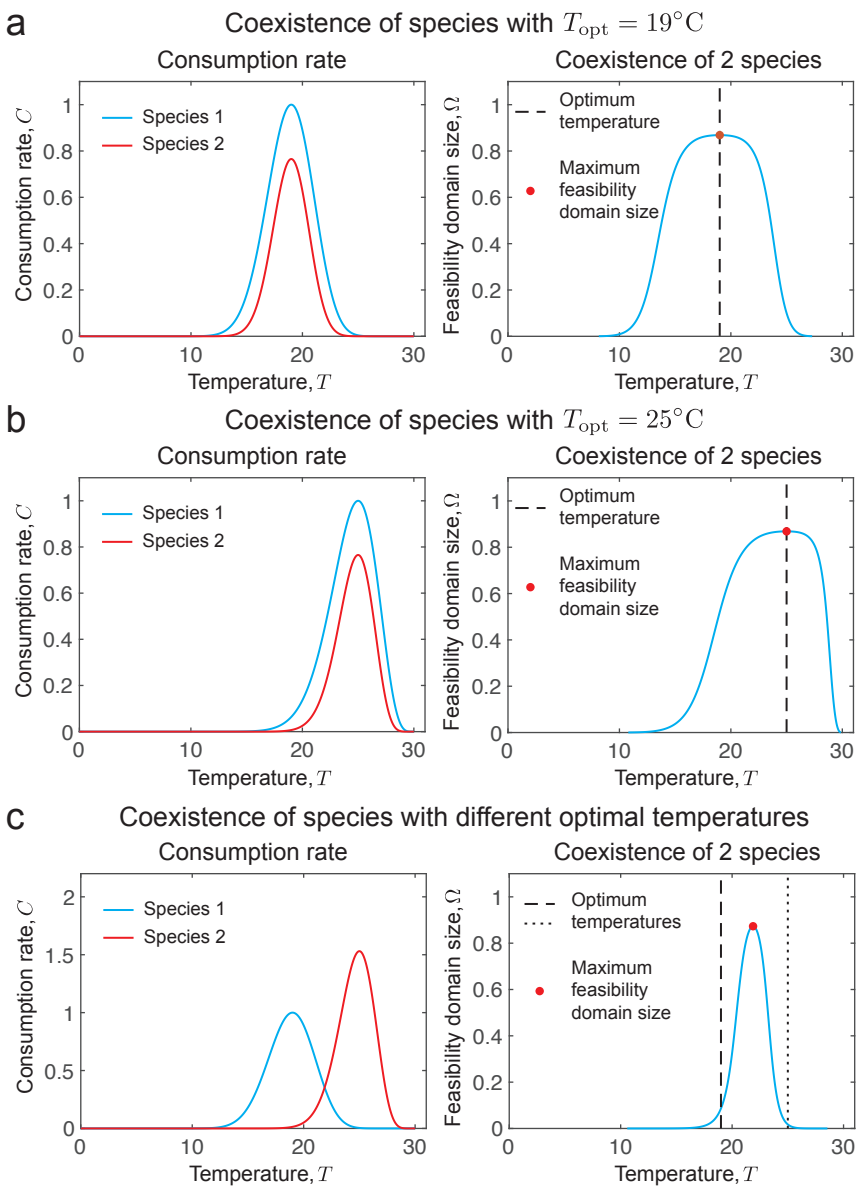

Figure 2: **Theoretical predictions of temperature effects on species coexistence.** Coexistence outcomes are shown for two species sharing the same optimal temperature (**a**, **b**) and for two species with distinct optimal temperatures (**c**). In each panel, the left subplots depict the temperature-dependent consumption rates of the two species, while the right subplots show the corresponding coexistence probabilities. When species share the same optimal temperature (dashed black lines in **a** and **b**), coexistence probability peaks at this shared optimum (red dots in **a** and **b**), indicating that coexistence is most likely near this point. Moreover, increasing temperature beyond the optimum reduces coexistence probability more strongly than decreasing temperature below it. When species have different optimal temperatures (**c**), the coexistence probability peaks (red dot in **c**) at an intermediate temperature between the two optima (dashed and dotted lines in **c**), closer to the lower optimum. In addition, coexistence probability at the lower optimum exceeds that at the higher optimum. Model parameters: $a_0 = 0.1$, $m_0 = 1$, $M_{\mathrm{r}} = 2$, and $\beta_0 = 0.07$, with species body mass given by $m_i = m_0\, M_{\mathrm{r}}^{i-1}$.

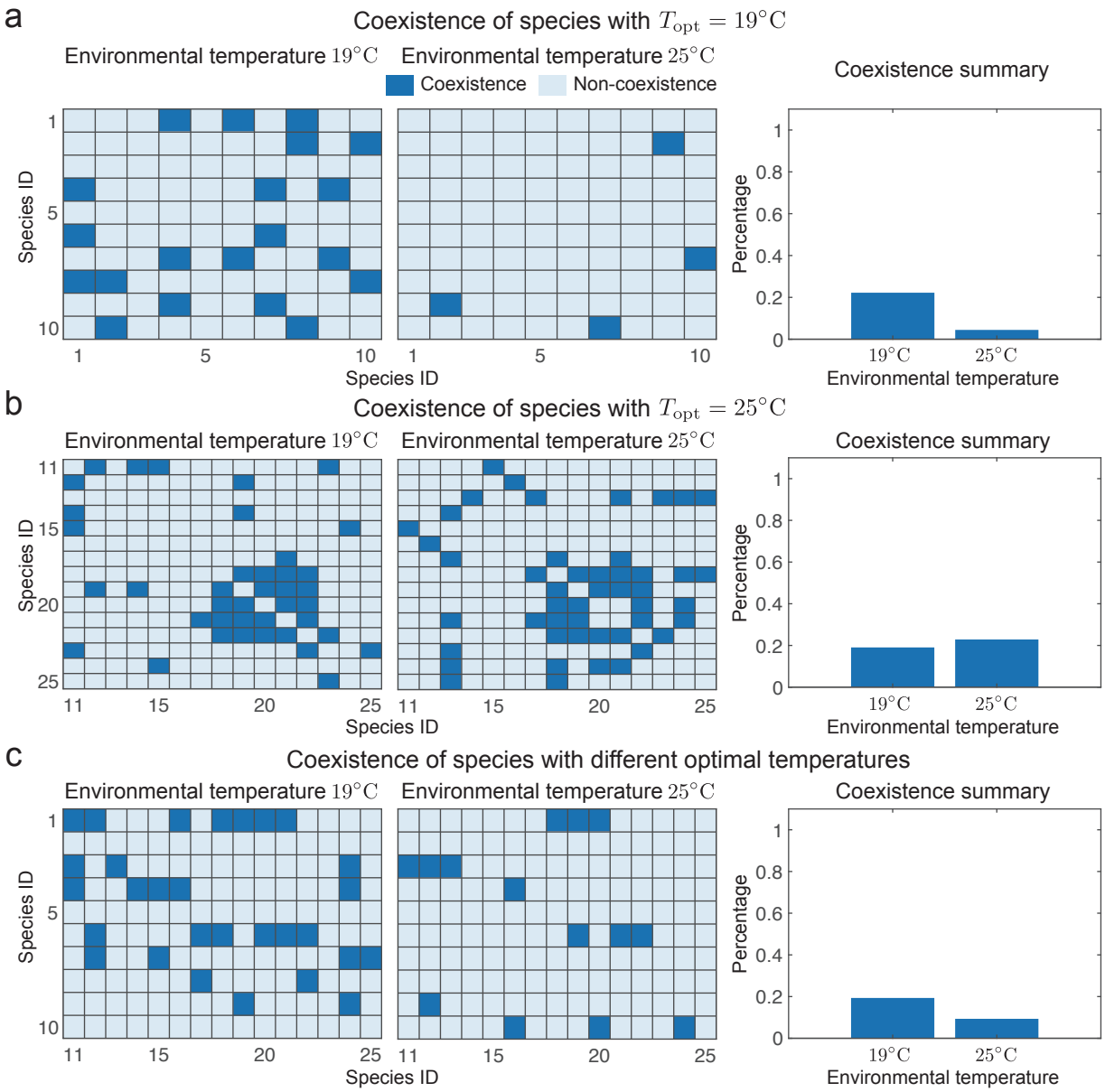

Figure 3: **Empirical analysis of temperature-dependent coexistence among *Drosophila* species.** Coexistence patterns of *Drosophila* species with similar (panels (**a**), (**b**)) and different (panel (**c**)) thermal optima. Species with IDs 1-10 have an optimal temperature of 19°C, and species with IDs 11-25 have an optimal temperature of 25°C. The left subplots show the coexistence matrices under different environmental temperatures, where dark blue squares represent coexistence and light blue squares represent non-coexistence. The right subplots show the corresponding proportions of coexisting species pairs under each temperature. Consistent with theoretical predictions, species sharing similar optimal temperatures tend to exhibit a higher probability of coexistence near their optima, and increasing environmental temperature from the optimum reduces coexistence more strongly than decreasing temperature. On the other hand, species with different optimal temperatures show a higher probability of coexistence at lower temperatures.