

# Variation in thermal sensitivity of ecological traits drives patterns of species richness across temperature gradients

Tom Clegg, Samraat Pawar

January 2021

## Abstract

...

## Introduction

The effect of temperature on biodiversity has long been a topic of interest in ecology (?), starting with the pioneering work of Alexander von Humboldt who in the 19th century identified temperature as a major environmental driver of plant richness along elevational gradients in the Andes (REF). Since then clear relationships between richness and temperature have been identified across different taxa and environments ranging from aquatic insects (REF) to terrestrial tree communities (?), with a number of mechanisms being suggested to explain these patterns (??). In particular the response of microbial diversity to temperature is of interest due to their status as both the most abundant and diverse organisms on earth (REF) and key players in the cycling of energy and nutrients through ecosystems (REF).

Previous studies looking at microbial diversity have generally found mixed responses to temperature, with the shape and direction of the relationship varying between the study system considered (REF). For example, whilst REF found that soil microbe diversity increased across a continental temperature gradient in North America others have found unimodal responses of diversity in tropical oceans (REF) and geothermal environments (REF), with richness peaking at intermediate temperatures. The presence of this variation in the temperature-diversity relationship was later quantified in a meta-analysis which showed that that large variation exists and that no single patterns dominates temperature responses in soil microbe communities.

The existence of such variation in the responses of diversity to temperature is unexplained by current models of biodiversity. • Many models predict single global thermal response • MTB predicts this • Also metabolic-niche hypothesis

One potential explanation for the variation in the response of is the variaion in thermal responses of microbes themselves • well demonstrated variation in E across microbe species • This in theory is likely to have significant effects on diversity through the emergent ecosystem dynamics • accounting for variation may allow us to predict variable responses.... • mismatches • non-linear thermal responses lead to non-linear richness responses

Although the assumption of a single temperature dependence has been successful in predicting broad scale macroecological patterns (??), this approach ignores the widespread variation in thermal sensitivity that has been observed across the tree of life. This variation has been documented in number of studies looking at thermal sensitivity both across different taxa and ecological processes (?) and has been highlighted as a potentially important factor in determining the response of ecological systems to temperature. For example “thermal mismatches”, the differences in the thermal responses between different species or

ecological processes, have been shown to be potentially important in a number of contexts such as consumer-resource (?) and virus-host systems (?). Furthermore, the non-linear nature of thermal responses mean that considering only the average thermal response (and thus ignoring all higher-order moments) is unlikely to be a good approximation if significant variation in thermal sensitivity exists (?). It follows then that variation in thermal responses should be important in driving patterns of species richness which are driven, at least in part, by processes sensitive to variation (e.g. interspecies interactions) and non-linear thermal responses.

Here we develop a general model

Unsurprisingly the existence of these patterns has resulted in various attempts to explain the how temperature drives species richness (?), invoking a range of mechanisms focused on the effects of temperature on both ecological (e.g. the effects of temperature on metabolism and population demography; (REF)) and evolutionary (e.g. the effects of temperature on mutation rate and generation time; (REF)) processes.

Only recently with advances in sequencing technology have we been able to explore these patterns in microbes, revealing diversity to temperature

One group whose response to temperature is of particular interest is microbial heterotrophs as they both make up a significant proportion of earth biomass (REF) and are a key part of the cycling of energy and nutrients thorough ecosystems. Exploring the responses of this group has only recently become possible with the advances in sequencing technology allowing explore patterns of their diversity.

Why we expect microbes to be temperature dependent explicitly

Explain the mechanistic explanations MTB

Most notably these were synthesised into a single framework in a series of papers as an extension of the metabolic theory of ecology (???) (hereafter referred to as the “metabolic theory of biodiversity” (MTB) (?)), which aimed to explain the effects of temperature on biodiversity through the link between individual metabolic rate and the various ecological and evolutionary processes that control species richness. One of the central predictions made by MTB is that species richness should follow an simple monotonic Arrhenius-type response with a single temperature sensitivity equal to the assumed universal value for metabolism ( $E = 0.65$ ; ?). This means that the natural log of species richness should follow a linear relationship with a slope of  $\sim 0.65$  when plotted against  $\frac{1}{kT}$ , where  $k$  is the boltzmann constant ( $8.617 \times 10^{-5}$  Ev) and  $T$  is temperature in Kelvin (?).

Despite the attractiveness of its simplicity and the apparent support of early tests with empirical data, MTB has received considerable criticism since its initial publication. Most of this has been focused on further tests of its central prediction, which revealed limited support for the single global temperature dependence of richness ((?)). In separate analyses across both latitudinal ((?)) and elevational (?) gradients species richness was observed to demonstrate thermal responses that both varied in shape, deviating from the predicted monotonic Boltzmann-Arrhenius form, and in magnitude, deviating from the predicted 0.65 slope. In response to this discrepancy ? proposed an extension to MTB, using a more general, trait-based eco-evolutionary framework. This framework provided a more “integrated” approach to MTB, explicitly including the temperature dependence of various ecological and evolutionary processes such as interactions between species, mortality and mutation rates, generating thermal response of species richness  $s$  that displayed similar variation to those seen in empirical data. One aspect that was not explored in this model however was variation in thermal sensitivity, with the authors assuming (like most work as part of the metabolic theory of ecology) that thermal sensitivity of different processes and populations took the single “universal” value of  $E = 0.65$ , an assumption based on the average thermal sensitivity of the respiratory complex (??).

In this paper we investigate the effects of variation in thermal sensitivity and its role in driving patterns of species richness over temperature gradients. Using a general model of ecosystem dynamics we first derive analytical results, explicitly linking realistic variation in thermal sensitivity to the number of species that can coexist within ecosystems. Then, using a newly-assembled dataset on bacterial growth rates, we show that variation in thermal sensitivity is indeed important in driving patterns of species richness across temperatures.

# Methods

## Theory

Our overall approach is to link the effects of a given distribution of key traits (i.e., growth rates and interaction strengths) to feasibility: the maximum number of species a single ecosystem can support without extinctions occurring. Feasibility is a necessary condition for stable species coexistence and therefore species richness and diversity (??). We subsequently use numerical simulations of assembly in complex, species-rich ecosystems to test whether our analytical results are robust to relaxation of two key assumptions.

## Model

In order to quantify the effects of temperature on feasibility and species richness, we use the generalised Lotka-Volterra model (GLVM) of an  $N$  species community, with the growth of the  $i$ th species given by

$$\frac{1}{x_i} \frac{dx_i}{dt} = r_i(T) - a_{ii}(T)x_i - \sum_{j \neq i}^N a_{ij}(T)x_j, \quad (1)$$

where  $x_i$  is its biomass density,  $r_i(T)$  it's intrinsic growth rate determining the rate at which new biomass is produced ( $\text{time}^{-1}$ ),  $a_{ij}(T)$  is the effect of interactions with the  $j$ th species' population, and  $a_{ii}(T)$  the effect of intraspecific interactions ( $\text{mass}^{-1} \cdot \text{time}^{-1}$ ). Note that all the parameters are expressed as functions of temperature ( $T$ ), the form of which will be addressed later. As such, these interaction coefficients are linear (Type I); later we show that incorporating Type II or III functional responses...

## Feasibility and Species Richness

To determine the number of species that can coexist in a given community, we need to derive an expression for its equilibrium biomass. Though it is not possible to derive an exact analytical solution for the GLVM (??), we use a mean-field approximation (??), which allows us to derive the average effect of interactions across the community as a whole (??) on equilibrium biomass ( $x_i^*$ ) of each species as:

$$x_i^* \approx K_i(T) - \bar{K}(T) \frac{(N-1)\bar{a}(T)}{1 + (N-1)\bar{a}(T)}. \quad (2)$$

Here,  $K_i = \frac{r_i(T)}{a_{ii}(T)}$  is its carrying capacity (the biomass this population would reach if grown in isolation, obtained by solving ?? with no interactions),  $(T)$  is ...,  $N$  is species richness, and  $\bar{a}(T)$  is the average pairwise, interspecific interaction strength. ?? is an intuitive expression for equilibrium biomasses; a population will reach the biomass that it would in isolation (first term,  $K_i(T)$ ) minus the effects of any interspecific interactions (second term). The strength of these interspecific interaction effects is determined by the average carrying capacity of all other species ( $\bar{K}(T)$ ) and a saturating function of the net interaction strength experienced by the focal species,  $(N-1)\bar{a}(T)$ . If interactions are overall competitive (i.e.,  $\bar{a}(T) > 0$ ) then equilibrium biomass will reduce relative to the individual carrying capacities, and if they are facilitatory (i.e., cooperative or mutualistic) ( $\bar{a}(T) < 0$ ), it will increase. This approximation (??) relies on the assumption that the system is large (large number of species) and that no individual pairwise interaction dominates. We test the sensitivity of our results to these key assumptions later using numerical simulations.

Next we use ?? to derive an expression for community feasibility in terms of the population demographic parameters (i.e. the  $r(T)$ 's and  $a(T)$ 's) which will then be used to determine the upper bound on species richness  $N$ . An ecosystem is feasible if all species have non-zero equilibrium biomasses (i.e.  $x_i^* > 0$ ), a condition that can be expressed as:

$$\kappa_i(T) > \frac{(N-1)\bar{a}(T)}{1 + (N-1)\bar{a}(T)} \quad \text{for all } i = 1 \dots N. \quad (3)$$

Here,  $\kappa_i = \frac{K_i(T)}{K(T)}$  is the mean-normalised carrying capacity of the  $i$ th species. ?? shows that an ecosystem is feasible as long as the effects of interspecific interactions on the each population (RHS) do not outweigh the growth rates and intraspecific interactions (LHS; because  $K_i = \frac{r_i(T)}{a_{ii}(T)}$ ). We can see that in the case of facilitatory interactions ( $\bar{a}(T) < 0$ ) the inequality will always hold and the system will be feasible. Only when interactions are on average competitive (i.e  $\bar{a}(T) > 0$ ) will the effects of interactions make the system unfeasible.

Using ?? we next derive an expression for the probability of feasibility  $P_{feas}$ , the probability that a community is feasible given the distribution of species trait values ( $\kappa$ s and  $a$ s) and number of species ( $N$ ) in the system. To do so we take ?? and consider  $\kappa$  and  $a$  as random variables, each describing the distribution of the respective traits across the populations in the community (denoted by the loss of subscript). This allows us to consider  $\kappa$ 's cumulative density function (CDF), i.e., the probability that it is less than or equal to some value:  $F_\kappa(x, T) = P(\kappa \leq x)$ . As the condition for feasibility states that  $\kappa$  must be greater than the effect of interactions we can use this CDF and the condition in ?? to express  $P_{feas}$  as

$$P_{feas}(T) = P\left(\kappa(T) > \frac{(N-1)\bar{a}(T)}{1 + (N-1)\bar{a}(T)}\right)^N = \left[1 - F_\kappa\left(\frac{(N-1)\bar{a}(T)}{1 + (N-1)\bar{a}(T)}, T\right)\right]^N, \quad (4)$$

giving the probability of feasibility of an ecosystem as a function of the species traits. Note the expression is raised to the  $N^{\text{th}}$  power because the term in the brackets must hold for all  $N$  populations in a community for it to be feasible. ?? makes explicit the effect of species richness  $N$  on the probability of feasibility in a community, showing how  $P_{feas}$  will decline with increasing  $N$  through two mechanisms. Firstly it alters the strength of interactions experienced by individual populations via the  $(N-1)\bar{a}(T)$  term. A higher species richness means that the strength of interactions will be greater and if interactions are on average competitive ( $\bar{a}(T) < 0$ ) this will reduce the probability of feasibility. Secondly, the probability of feasibility will fall as the number of species increases as it becomes less likely that all  $N$  species meet the criteria in ?? as represented by the  $N$ th power term in ??.

Importantly, this decline in  $P_{feas}$  with increasing richness places an upper bound on species richness given a certain distribution of  $\kappa$  and  $a$  values within a community. If a system is too large then we expect that it will have a low probability of feasibility and thus be likely to experience population extinctions until the probability of feasibility becomes larger and extinctions become unlikely. Although ideally we would use ?? to determine this bound explicitly by solving for  $N$  this is not possible for most distributions of  $\kappa$  due to the complexity of their CDFs. We therefore use a numerical approach to determine the exact value of this upper bound on  $N$  (see ??). It is important to note that this does not preclude insights into the effects of variation in thermal sensitivity which we now address.

## Temperature responses of traits

Having defined the relationship between species richness and the distribution of species' traits across the community, we now turn to the effect of temperature. Broadly, our approach here is to consider how the distributions of the relevant species traits across populations change with temperature and thus  $P_{feas}$ , and the upper bound on  $N$ . We derive expressions for these trait distributions in terms of the distributions of their thermal sensitivity. This allows us to quantify the effect of variation in thermal sensitivity between species' populations as well as traits on the temperature-species richness relationship. Overall, this temperature dependence can be explained by the dependence of these processes on metabolic rate which determines the capacity of individuals to grow and interact with one another and is in turn affected by temperature through its effects on biochemical kinetics ??.

Following the metabolic theory of ecology ?? we use the Boltzmann-Arrhenius equation to represent the temperature dependence of  $\kappa$  and  $a$ :

$$B(T) = B_0 e^{-\frac{E}{k} \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right)}. \quad (5)$$

Here,  $B(T)$  is the relevant trait value,  $T$  is temperature in Kelvin,  $B_0$  is the normalisation constant, i.e., the trait value at some reference temperature ( $T_{ref}$ , also in Kelvin),  $E$  (eV) is the thermal sensitivity which

determines the change in trait value to a unit change in temperature, and  $k$  is the Boltzmann constant. Although empirically-measured thermal performance curves of single individuals or species are generally unimodal, the Boltzmann-Arrhenius equation adequately captures the the rising portion (before the temperature peak) of these curves, which is also the temperature range within which individuals and populations typically operate (or experience) (the “Operational Temperature Range”, or OTR) [?](#). Thus focusing on the Boltzmann-Arrhenius portion of thermal performance curves is relevant to the dynamics of real ecosystems, and also, conveniently, affords us analytic tractability .

Applying [??](#) allows us to characterise the distributions of parameters across species populations at different temperatures in terms of the distributions of the underlying parameters  $B_0$  and  $E$ . Assuming that the parameter values follow a log-normal distribution (a natural assumption given the exponential form of [??](#)), we obtain an expression for the temperature dependent distribution of  $B(T)$  (see [??](#)):

$$\log(B(T)) \sim \mathcal{N}(\mu_B(T), \sigma_B^2(T)) \quad \text{where} \quad \begin{aligned} \mu_B(T) &= \mu_{B_0} - \mu_E \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right) \\ \sigma_B(T)^2 &= \sigma_{B_0}^2 + \sigma_E^2 \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right)^2 . \end{aligned} \quad (6)$$

Here,  $\log(B_0)$  and  $E$  are both normally distributed, with  $\mu$  and  $\sigma^2$  denoting their mean and variance respectively. [??](#) makes explicit the effect of the distribution of thermal sensitivity parameters on the distribution of  $B(T)$ . Specifically, it shows that the signs and magnitudes of (the distribution of) temperature responses of a trait across species is a linear function of temperature, with intercept and slope determined by the average normalization constant and thermal sensitivity ( $B_0$  and  $\mu_E$  respectively). It is important to note here that as  $B(T)$  is log-normally distributed, its moments are defined in terms of both the mean and variance ([??](#)), and thus both temperature dependent factors (the linear and quadratic parts) will contribute to the shape of the distribution. Therefore, the variance term  $\sigma_E$ , which introduces an additional quadratic term, creates an additional curvature in the thermal response. The distribution of the normalisation constant  $B_0$  are only present as a temperature-independent constant term in the expressions for both mean and variance, so do not affect the curvature of the emergent  $B(T)$  curves. Applying [??](#) to the distributions of  $\kappa$  and  $\bar{a}$  as defined in the [??](#) we obtain the expressions

$$\log(\kappa(T)) \sim \mathcal{N} \left( -\frac{\sigma_K^2(T)}{2}, \sigma_K^2(T) \right) \quad \text{and} \quad (7)$$

$$\bar{a}(T) = \exp \left( \mu_a(T) + \frac{\sigma_a^2(T)}{2} \right), \quad (8)$$

which show how the temperature responses of  $\kappa$  and  $\bar{a}$  are determined by the distributions of thermal response parameters. Importantly, we see that the variance terms are present in both expressions, meaning that the curvature introduced by the quadratic temperature term in [??](#) will be present in the emergent (mean) trait responses. Overall [??????](#) provide key qualitative insights into the effects of the distribution of thermal sensitivities on the shape of the response of species richness to temperature. Specifically, the average thermal sensitivity of  $a$  will control the direction and magnitude of the temperature response of species richness, whilst the mean  $K$  will have no effect (as the average does not affect the distribution of  $\kappa$  as seen in [??](#)). The variance in thermal sensitivity will, for both parameters, create curvature in the thermal response which will create a unimodal shape if strong enough.

## Calculating the thermal response curves of Species Richness

Finally, in order to obtain quantitative predictions of the effect of temperature on species richness, we substitute [??????](#) into the expression for  $P_{feas}$  ([??](#)), and numerically solve for  $N$ . To this end, we set a lower threshold value of  $P_{feas}$ ,  $\theta$ , as well as values for the parameters controlling the distributions of the thermal responses for both  $a$  and  $\kappa$ . We then use numerical optimisation to search for the maximum value of  $N$  with the given  $\theta$  value ([?](#)). Repeating this procedure at different temperatures gives the full temperature vs species richness curve for any given set of parameters. We calculated such species richness - Temperature

curves for different combinations of means and variances of thermal sensitivity of  $K$  and  $a$ . Holding one of the parameter’s distribution constant at a time, we calculated species richness curves in a fully factorial manner ( $\mu_E \in [-0.65, 0.0, 0.65]$  and  $\sigma_E \in [0.01, 0.05, 0.1]$ ). We did not vary the average thermal sensitivity of  $K$  as ?? shows the realised distribution of  $\kappa$  is independent of the average value.

## Community assembly simulations

In order to test the bound on species richness and the effects of temperature we simulate the assembly of communities using the full GLVM model in ?. This allows us to test the generality of the analytical predictions for the species richness by relaxing the assumptions made by the mean-field approximation about ecosystem dynamics. We use assembly here as a way to allow systems to reach the maximum species richness (i.e. the prediction generated by the model) given the distributions of thermal sensitivity parameters and temperature.

To simulate assembly we start with an empty system at a given temperature which we assemble into a community through sequential species invasions. Each invader has thermal performance traits ( $B_0$ s and  $E$ s) drawn from a global distribution which are used to calculate the actual trait values ( $\kappa$ s and  $a$ s) at that temperature. Following each invasion we simulate the system till it reaches steady state, remove extinct populations and record the species richness. We allow this process to continue for  $1 \times 10^5$  time steps to ensure that species richness is at quasi-equilibrium (approximate immigration-extinction balance) (REF). This process is then repeated at different temperatures and across different levels of variation in thermal sensitivity  $\sigma_E \in [0.01, 0.05, 0.1]$ , allowing us to examine the simulated temperature-species richness curves. All simulations were carried out using the Julia programming language and the DifferentialEquations.jl Package for numerical integration (?). To assess the fit of the analytical predictions we use the approach detailed in ?, calculating predicted species richness given the global thermal trait distributions by setting lower threshold probability of feasibility ( $\theta = 1 \times 10^{-10}$ ) and solving for the maximum richness permitted at this threshold.

## Data

To demonstrate the potential relevance of realistic variation in thermal sensitivity in ecological traits on community-level species richness, we compiled a novel data set of thermal performance parameters ( $B_0$ s and  $E$ s) of carrying capacity from a range of bacterial taxa. Using this data set we are able to estimate the distribution of thermal sensitivities across populations and assess whether variation is sufficient to affect the shape of the temperature species richness curve.

We compiled a data set of bacterial population growth curves across different temperatures, collecting experimental measurements of full population growth curves (i.e. some measure of abundance or biomass over time) for bacterial strains across multiple temperatures from the literature. We then used this data set, comprising of 105 strains over 21 studies, to get estimates of growth rates  $r$  and carrying capacities  $K$  by fitting the logistic growth model to each growth curve using non-linear least squares fitting. After filtering curves that did not converge or had poor fits, we were left with 74 and 95 sets of measurements for  $r$  and  $K$  across temperature respectively. We then fit both the Boltzmann-Arrhenius and Sharpe-Schoolfield (?) to each of set of measurements, selecting the best fitting model for each TPC using AIC. As we need only estimates of  $\kappa$  to calculate the thermal response of species richness (not  $r$ ) we considered only the TPC fits for  $K$ . After removing measurements for which no model converged we were left with 74 estimates of TPC parameters for  $K$ . From these data we obtained the mean and variance for the normalisation constant  $\log(K_0)$  and thermal sensitivity  $E_K$  by fitting a normal distribution using maximum-likelihood estimation (MLE) (REF). Using this distribution for  $K$ , we then parameterised ?? and calculated the maximum species richness using the method outlined in ?. We repeated this process to get predictions of species richness over temperature setting distributions of thermal sensitivity for the interaction parameter to ( $\mu_{E_a} = -1$  and  $\sigma_{E_a} = 1$ ). We compared this to a null model where we set the  $\mu_E$  and  $\sigma_E$  to 0.65 and 0.0 for both  $K$  and  $a$  with zero variation.

## Results

### The distribution of thermal sensitivities determines the thermal response of species richness

We first examined the effect of the distribution of thermal sensitivities across populations on the temperature response of species richness. As expected from the expressions for the distributions of traits across temperature in ????, both the mean and variance of thermal sensitivity of  $a$  contributed to the shape of the species richness temperature response (??) whilst for  $K$  only variance in thermal sensitivity mattered (??). Broadly, the mean and variance in thermal sensitivities had the same effect to that seen in the distributions of traits in ??. The average thermal sensitivity for interactions determined the overall direction and magnitude of the species richness response (??), when positive (i.e. interactions become stronger with increasing temperature) this resulted in a negative response of species richness and vice versa. The degree of variance in thermal sensitivity had the same effect for both  $K$  and  $a$  (????), increasing the curvature in the thermal response of richness and, when strong enough, creating a unimodal shape.

### Empirical estimates of thermal sensitivity show variation in $E$ is relevant for community level thermal responses

Our empirical dataset on the thermal performance of microbial growth showed significant variation in the thermal sensitivity of  $K$  (??). Normal distribution fits using MLE yielded estimates of  $\log(K_0) \sim \mathcal{N}(-0.14, 0.58)$  and  $E_K \sim \mathcal{N}(0.06, 0.29)$  for the normalisation constant and sensitivity respectively (??a-b). As expected, this variation in the thermal sensitivity resulted in unimodality in the thermal response of species richness in comparison to a monotonic response predicted by the no-variation scenario (??c).

### The distribution of thermal sensitivities predicts the species richness of randomly assembled communities

Our analytical result ?? was able to predict species richness patterns in randomly assembled communities across temperatures remarkably well (??). Across the randomly assembled communities, species richness followed the qualitative patterns expected from the analytical predictions, with the thermal response of richness exhibiting an increasingly unimodal shape with an increase in the variation in thermal sensitivity. The actual species richness reached by assembling communities matched the analytical predictions well, though the actual species richness reached by simulated communities deviated at the lower and higher ends of the temperature scale.

## Discussion

Understanding how variation in thermal responses between different processes and taxa affects ecological communities is an important problem in ecology, especially given current rates of warming (REF). Here we show that through its effects on the distributions of key species traits, this variation affects the feasibility of ecosystems and thus the total species richness they can support. Furthermore, we have shown that the level of variation seen in a specific taxonomic group (bacteria) is sufficient to significantly affect this relationship and that the predictions of our analytical theory are robust to relaxation of key assumptions.

Our analytical approach provides novel insights into the effects of the shape of the distribution of thermal sensitivity.

- Clearly our work shows the effect of altering the first two moments of this distribution

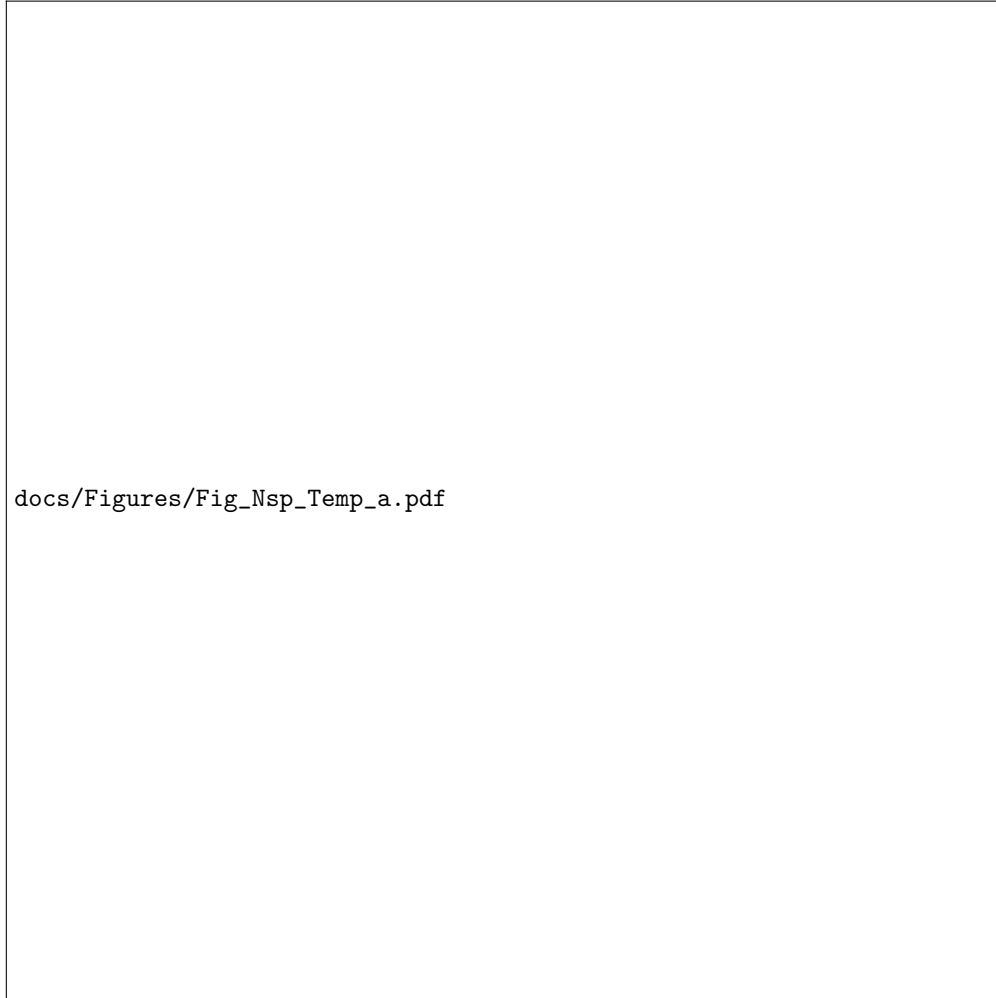


Figure 1: **The thermal response of species richness varies with the distribution of thermal sensitivities of interactions** a-c) The shape of the relationship between species richness and temperature changes depending on the exact shape of the distribution of thermal sensitivities of interactions  $E_a$ . As predicted by ?? the average thermal sensitivity determines the overall direction of the thermal response with species richness responding in the opposite direction as seen moving from a-c (positive temperature dependence means stronger interactions at higher temperatures and thus lower probability of feasibility). Increasing the variance in thermal sensitivity (coloured lines, see legend) introduces additional curvature to the species richness curve. Curves were generated using the approach outlined in ?? with parameters  $\sigma \log(K_0) = 0.5$ ,  $\sigma_{E_K} = 0.2$ ,  $\mu_{a_0} = \log(0.01)$  and  $\sigma_{a_0} = 0.5$



docs/Figures/Fig\_Nsp\_Temp\_K.pdf

Figure 2: **Variation in the thermal sensitivity of carrying capacity alters the Species richness Temperature relationship.** As expected increasing variance in thermal sensitivity of carrying capacity  $K$ , represented by the coloured lines, results in greater curvature in the species richness thermal response as seen between the colored lines. Curves were generated using the method outlined in ?? with parameters  $\sigma \log(K_0) = 0.5$ ,  $\mu_{a_0} = \log(0.01)$ ,  $\sigma_{a_0} = 0.5$ ,  $\mu_{E_a} = 0.65$  and  $\sigma_{E_a} = 0.2$

- Our approach also makes this relationship explicit, avoiding the problem with simulation based methods such as ? whose simulations are hard to gain general insight from

We use feasibility as a mechanism to determine species richness

- This is one (important) ecosystem dynamics property which in and of itself does not guarantee a system will persist

- future work could extend the approach here with other properties such as stability (though it is worth noting that feasibility implies stability in the GLVM) and the newly developed extinction boundary (VAN's paper).

Our results are robust to relaxations of the assumptions of the mean-field system

- when we assemble communities randomly their behaviour is relatively well predicted
- demonstrates that the analytical expectations should be applicable in a variety of contexts
- Other models of ecosystem dynamics are possible, which may allow other types of systems to be explored in more detail (consumer resource, mutualisms?)

Our analysis of data on variation in thermal sensitivity shows that it is sufficient to affect the response of species richness curves.

- given that variation appears ubiquitous in nature this would imply that curved responses of richness with temperature should be more common

- Is in alignment with empirical data which shows the Temperature-Richness relationship is very variable

This work supports (growing?) focus on variation in thermal sensitivity as opposed to the use of a single universal value

- important for other applications such as climate models?

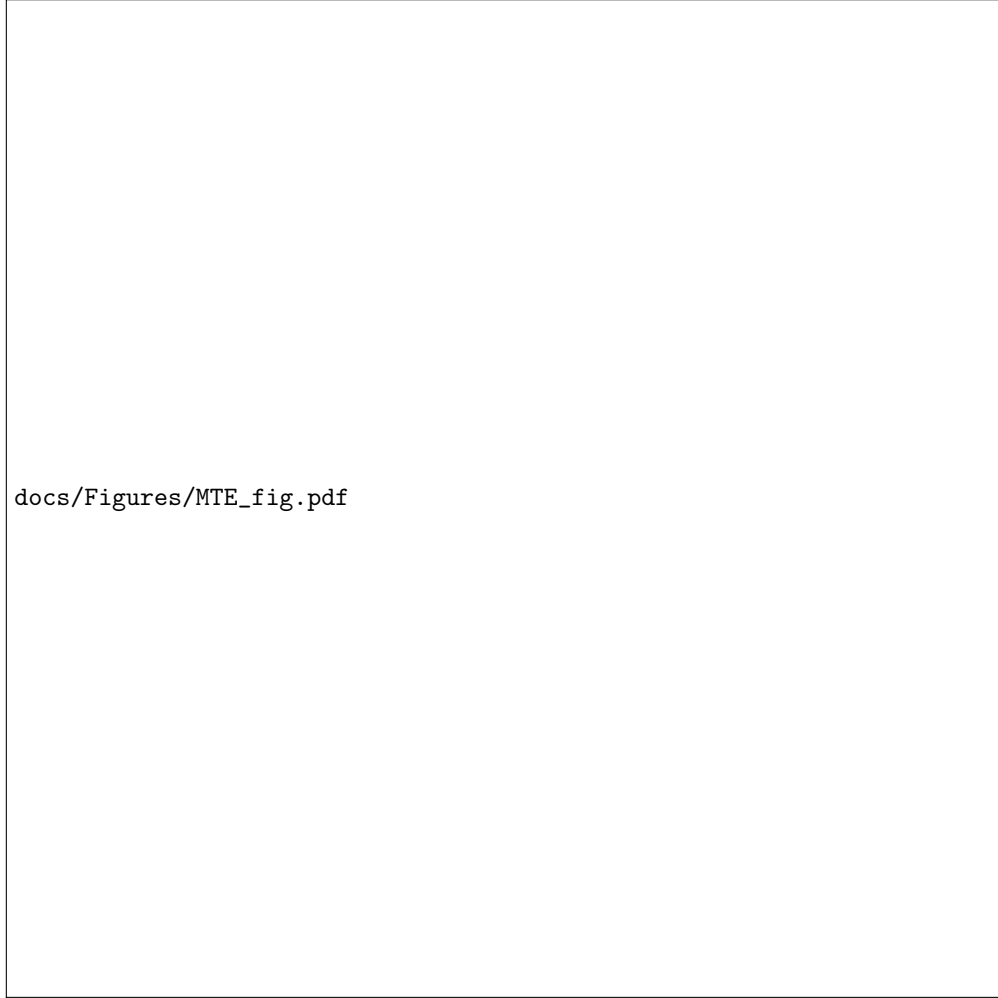


Figure 3: **Empirical variation in thermal sensitivity shifts the thermal response of species richness**. a-b) Distributions of empirical estimates of a)  $\log(K_0)$  and b)  $E_K$ . Colored density plots are the actual empirical distributions of the parameters with the solid black line showing the fitted normal distribution. The distribution of thermal sensitivity (b) shows variation in the thermal response ( $\sigma_{E_K} = 0.29$ ). c) Prediction of species richness thermal response using the empirical distributions. The blue and red lines represent the estimates with and without variance in thermal sensitivity, showing how the observed variance creates a unimodal response of species richness to temperature.

docs/Figures/Fig\_4.pdf

Figure 4: The assembly of ecosystems at different temperatures is predicted by the analytical feasibility condition. A) Trajectories of species richness over assembly across temperature at a single level of variation in  $E$  ( $\sigma_a = 0.01$ ). Each line is the average species richness over time at a given temperature. Species richness is seen to saturate over time, with systems assembling at higher temperatures having lower species richness. B) The observed final species richness reached by the assembly simulations plotted against the analytical predictions of  $??$ . Each point is the average species richness across the 5 replicates with error bars showing the standard deviation. The blue line and shaded region represent the 1:1 line of predictions and observations, representing a probability threshold of  $1 \times 10^{-10}$ , with the shaded region corresponding to the richness predicted by thresholds between  $1 \times 10^{-8} - 1 \times 10^{-12}$ . Overall the predictions and observations of species richness match well, with most of the points variation falling within the predicted bounds, though there is a tendency for the actual species richness to be above and below the predictions at low and high species richness respectively. C-E) The species richness - temperature relationship at 3 levels of variation in  $E$ . Each points represents the species richness reached by a single assembly simulation with the red line and shaded area representing the predicted species richness at a threshold of  $1 \times 10^{-10}$  and within the bounds  $1 \times 10^{-8} - 1 \times 10^{-12}$ . Overall the observed species richness and predictions match well with most observations falling within the prediction bounds. Only at the extremes of temperature (e.g. at 280K in (C)) do the observations significantly fall outside the prediction bounds.

# Supplementary Materials

## S0.1 Mean-field approximation

In this section we show the derivation of the mean-field approximation and equilibrium solution. Broadly the mean-field approximation works by considering interactions through their average effect on species populations, not through their individual pairwise effects. In doing so we are able to consider the properties of the system's equilibrium state. To do this we consider the interaction term from ??, which we can rewrite as:

$$\sum_{i \neq j}^N a_{ij}x_j = (N-1)\bar{a}\bar{x} = (N-1)\bar{a}\bar{x} + (N-1)\text{cov}(a, c), \quad (9)$$

where the bar notation,  $\bar{\cdot}$ , represents the average of that quantity over all  $N$  species in the system. ?? partitions the effects of interactions on the  $i$ th species into the average effect across the system,  $\bar{a}\bar{x}$ , and the covariance between heterospecific's biomass and the strength of interactions,  $\text{cov}(a, x)$ . The mean-field approximation assumes that this second term is negligible, which is equivalent to saying that any individual interaction between the focal species and another species population has little effect on that heterospecific's biomass. We also assume here that the system we consider is large ( $N \gg 0$ ), meaning that the difference between the average biomass across the system and that of heterospecifics is small (as it is in the order  $N^{-1}$ ) and can thus be ignored. Finally we assume that intraspecific interactions are constant across populations with value of 1. Combining ???? we can then express population dynamics in terms the average interaction strength, giving the full mean-field model:

$$\frac{1}{x_i} \frac{dx_i}{dt} \approx r_i - x_i - (N-1)\bar{a}(T)\bar{x}. \quad (10)$$

Next, we obtain an expression for equilibrium by setting ?? equal to zero and solving for  $x_i$  giving:

$$x_i^* = r_i(T) - (N-1)\bar{a}(T)\bar{x}^*. \quad (11)$$

Then, taking the average across the  $N$  populations and rearranging we obtain an expression for the average biomass in the community:

$$\bar{x}^* = \frac{\bar{r}(T)}{1 + (N-1)\bar{a}(T)},$$

which we can then substitute into ?? to get equilibrium biomass:

$$x_i^* = r_i(T) - \bar{r}(T) \frac{(N-1)\bar{a}}{1 + (N-1)\bar{a}}.$$

Next we can see that in the case of no interspecific interactions ( $\bar{a} = 0$ ) ?? gives the carrying capacity, the biomass a species would reach if grown in isolation  $x_i^* = r_i(T) = K_i(T)$  which gives us the final mean-field biomass expression:

$$x_i^* = K_i(T) - K(T) \frac{(N-1)\bar{a}}{1 + (N-1)\bar{a}}$$

which is equivalent to ?? in the main text.

## Derivation of thermal response distributions

In order to derive the distribution of some trait value  $B(T)$  from the distribution of its thermal sensitivity parameters  $B_0$ s and  $E$ s we start with the Boltzmann-Arrhenius as detailed in the main text ??:

$$B(T) = B_0 e^{-\frac{E}{k} \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right)},$$

which taking the natural log gives:

$$\log(B(T)) = \log(B_0) - \frac{E}{k} \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right). \quad (12)$$

Next we assume that both  $\log(B_0)$  and  $E$  are normally distributed such that:

$$\log(B_0) \sim \mathcal{N}(\mu_{B_0}, \sigma_{B_0}),$$

$$\log(E) \sim \mathcal{N}(\mu_E, \sigma_E),$$

where  $\mu_{B_0}$  and  $\mu_E$  are the mean and  $\sigma_{B_0}^2$  and  $\sigma_E^2$  are the variances of the normalisation constant and thermal sensitivity respectively. This assumption is backed for  $B_0$  by the distributions of actual values observed in our meta-analysis of bacterial population traits (see SEC). Whilst distributions of  $E$  tend to be more skewed in reality (as seen in both our data and previous work) we use the normal distribution here as it remains a good approximation, and a way to account for variance in thermal sensitivity values. Now, considering ?? as a linear function of two normally distributed variables we can see that  $\log(B(T))$  will itself be normally distributed as:

$$\log(B(T)) \sim \mathcal{N}(\mu_B(T), \sigma_B^2(T)) \quad \text{where} \quad \begin{aligned} \mu_B(T) &= \mu_{B_0} - \mu_E \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right) \\ \sigma_B(T)^2 &= \sigma_{B_0}^2 + \sigma_E^2 \left( \frac{1}{kT} - \frac{1}{kT_{ref}} \right)^2 \end{aligned}$$

which is the same as ?? in the maintext.

## Distribution of $\kappa$ and $\bar{a}$

Next we apply the expression for the distribution of a trait across populations at a given temperature to the distribution of  $\kappa$  and the value of  $\bar{a}$  which determines feasibility in ??.

We start with  $\kappa$  by recalling that as the mean-normalised carrying capacity  $\kappa$  is defined as:

$$\kappa(T) = \frac{K(T)}{\bar{K}(T)}.$$

Assuming that  $K$ 's temperature dependence follows an Arrhenius-type form and that its thermal sensitivity parameters are distributed as described in ?? we can see that:

$$\bar{K}(T) = e^{\mu_K(T) + \frac{\sigma_K(T)^2}{2}}$$

which applying to the equation above and taking the natural log gives:

$$\log(\kappa(T)) = \log(K(T)) - \mu_K(T) - \frac{\sigma_K(T)^2}{2}.$$

Thus,  $\log(\kappa)$  is normally distributed as:

$$\log(\kappa(T)) \sim \mathcal{N}\left(-\frac{\sigma_K(T)^2}{2}, \sigma_K(T)\right).$$

The thermal dependence of  $\bar{a}$  is obtained by simply considering  $a(T)$  which, assuming it follows a Arrhenius-type response with temperature and again its thermal sensitivity parameters are distributed as described in ?? has an average given by:

$$\bar{a}(T) = e^{\mu_a(T) + \frac{\sigma_a(T)^2}{2}}.$$

## Bacterial Growth Meta-analysis

### Feasibility simulations