Cold Regions Research and Engineering Laboratory
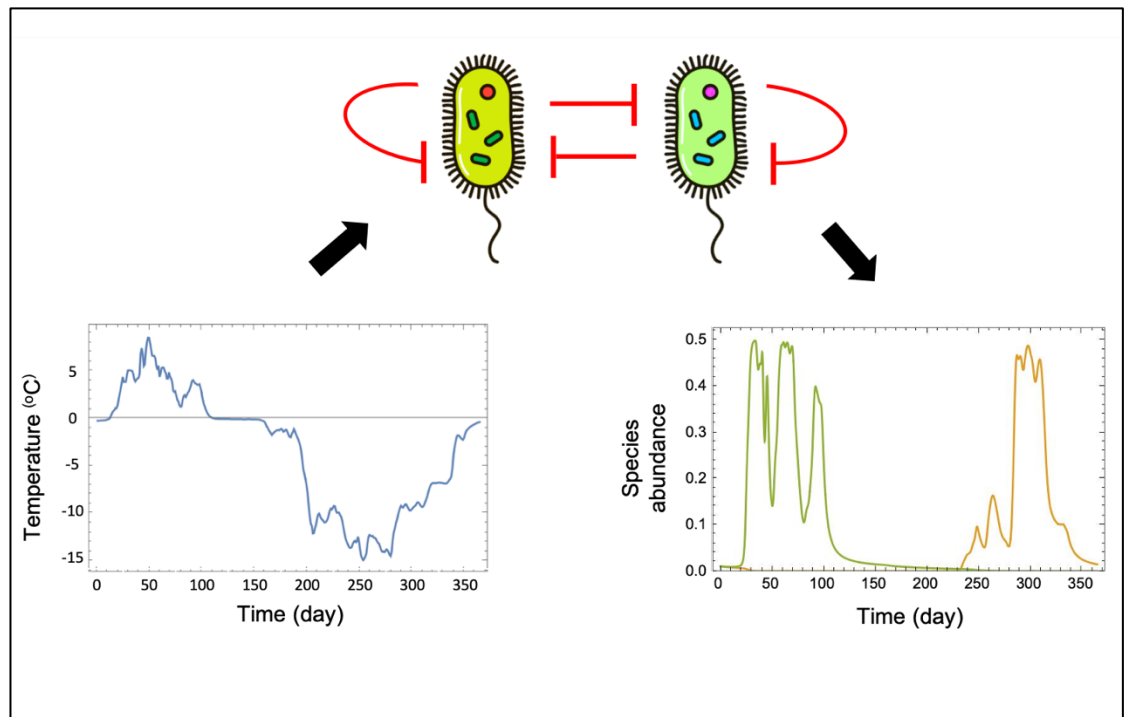
**US Army Corps of Engineers**
of Engineers®

U.S. ARMY

ERDC

# Ecological Modeling of Microbial Community Composition under Variable Temperatures

Logan M. Gonzalez, Christopher C. M. Baker, Stacey J. Doherty, and Robyn A. Barbato

February 2024

# Ecological Modeling of Microbial Community Composition under Variable Temperatures

Logan M. Gonzalez, Christopher C. M. Baker, Stacey J. Doherty, and Robyn A. Barbato

*US Army Engineer Research and Development Center (ERDC)*
*Cold Regions Research and Engineering Laboratory (CRREL)*
*72 Lyme Road*
*Hanover, NH 03755-1290*

Final Report

# Abstract

Soil microorganisms interact with one another within soil pores and respond to external conditions such as temperature. Data on microbial community composition and potential function are commonly generated in studies of soils. However, these data do not provide direct insight into the drivers of community composition and can be difficult to interpret outside the context of ecological theory. In this study, we explore the effect of abiotic environmental variation on microbial species diversity. Using a modified version of the Lotka-Volterra Competition Model with temperature-dependent growth rates, we show that environmentally relevant temperature variability may expand the set of temperature-tolerance phenotype pairs that can coexist as two-species communities compared to constant temperatures. These results highlight a potential role of temperature variation in influencing microbial diversity. This in turn suggests a need to incorporate temperature into predictive models of microbial communities in soil and other environments. We recommend future work to parameterize the model applied in this study with empirical data from environments of interest, and to validate the model predictions using field observations and experimental manipulations.

# Contents

# Figures and Tables

## Figures

## Tables

# Preface

# 1   Introduction

## 1.1   Background

The properties of soils depend heavily on microbial communities both at the surface and through the soil profile. These properties range from biogeochemical processes with global implications such as carbon (McGuire et al. 2009) and nitrogen cycling (Hayatsu et al. 2008), to local properties such as soil stabilization and pathogen emergence. Soil properties are valuable inputs to Army decisions regarding matters such as personnel and equipment mobility, location of forward operating bases, sensor placement and environmental threat mitigation (Barbato et al. 2018).

Soil microbial activity (e.g., respiration) varies with environmental conditions such as temperature, moisture (Moyano et al. 2013), and pH (Rousk et al. 2010; Ramoneda et al. 2023). This has led to the development of predictive models that attempt to elicit empirical relationships between environment conditions and soil activity. The Army's Dynamic Representation of Terrestrial Soil Predictions of Organisms' Response to the Environment (DRTSPORE) platform is an example of such modelling, in which remotely acquired temperature and moisture data are ingested to produce geospatial estimations of soil activity (Barbato et al. 2018).

Predictive models attempting to tackle the question of how microbial community composition is affected by environmental conditions are lacking. Community composition is an important determinant of soil microbial activity, as activity depends not only on the abundance of microorganisms, but also the species present and their metabolic capabilities (Waldrop et al. 2000). Our limited understanding of drivers of composition restricts the ability of predictive models to extrapolate soil activity beyond the range of the data, (e.g., to new climate scenarios or to regions where sampling is limited). It also hinders our ability to understand other properties of soil microbial communities, such as resilience to future disturbances.

Temperature is a well-known driver of microbial community activity, both by itself and in combination with other environmental parameters (Streit et al. 2014; Barbato et al. 2015; Doherty et al. 2018). Temperature may

affect microbial activity by inducing changes in metabolic rates (Brown et al. 2004). Different microbial species may be adapted to different temperature ranges; while mesophiles are best adapted to moderate temperatures, psychrophiles and thermophiles are better adapted to life in extreme cold or hot, respectively (Pikuta et al. 2007). Shifts in temperature regime through extreme weather events or warming climate are therefore also likely to influence microbial activity by causing changes in community composition, as species better adapted to the new conditions tend to outcompete those less well adapted (Hibbing et al. 2010).

Anthropogenic climate warming is likely to shift temperature regimes in a variety of ways, including increasing mean temperatures and increasing temperature variability (Bhutiyani et al. 2007). Such changes will influence life at all levels from cells to ecosystems. More research needs to be done to better understand how altered temperature regimes, especially elevated and more variable temperatures, will affect the biosphere given that nearly all ecosystems are connected through global biogeochemical cycles (Gounand et al. 2018).

## 1.2 Objective

The objective of this work was to incorporate temperature into a simple mechanistic model that can represent microbial communities, and use that model to analyze potential impacts of changing temperature regimes on community composition.

## 1.3 Approach

To explore potential impacts of temperature, we used a modified Lotka-Volterra Competition Model (LVCM) (Lotka 1924; Volterra 1931) to explore the effects of changing temperature regimes on microbial community composition. We first altered the standard LVCM by using temperature-dependent intrinsic growth rates in place of the usual constant values. We then compared model outcomes at different constant temperatures. Finally, we allowed temperature to vary with time, according to empirical data as well as a simple sine function, and compared results between the constant and variable temperature cases.

# 2 Ecological Community Models

We explored the potential impact of changing temperature regimes on microbial communities using a version of the LVCM (Lotka 1924; Volterra 1931) modified by making growth rates temperature-dependent as in Kremer and Klausmeier 2017. The LVCM has most commonly been used to study macro rather than microorganisms. These groups differ in important ways, for instance, microorganisms tend to have faster generation times and rates of evolution than macroorganisms (Prosser et al. 2007). Nonetheless, mechanistic models like the LVCM have proven invaluable for shedding light on drivers of ecological dynamics (Gavin et al. 2006; O'Sullivan et al. 2019; Shaw et al. 2016). By using temperature-dependent growth rates, the model allows us to make simple qualitative predictions about the effect of changing temperature regime, and shows how community composition may be affected by increases in mean temperature as well as variability when community members have different optimal growth temperatures.

## 2.1 The Lotka-Volterra Competition Model (LVCM)

The original LVCM describes a system of $k$ interacting species. Each species $i$ is assumed to be characterized by a single fixed growth rate parameter $r_i$, as well as $k$ interaction parameters $a_{1i} \ldots a_{ki}$ describing the effect of the $k$ species (including species $i$ itself) on species $i$.

In this model, the abundance of each species, $n_i$, changes over time according to its per capita growth rate

$$\frac{1}{n_i}\frac{dn_i}{dt} = r_i - \sum_{j=1}^{k} a_{ji}n_j, \tag{1}$$

where

$n_i$ = abundance of species $i$,
$r_i$ = intrinsic growth rate of species $i$, and
$a_{ji}$ = competition coefficient describing effect on species $i$ of competition with species $j$.

The LVCM thus considers only the intrinsic growth rate of each species, and interactions between and within species. These interactions are treated according to the law of mass action (Lund 1965) in which the rate of interaction is directly proportional to the product of the abundance of each species. The inclusion of species interactions in Equation (1) may be thought of as reflecting competition for some shared resource(s) or production of inhibitory molecules such as antibiotics, which are not explicitly modeled in the LVCM, but rather represented only through the interaction terms. We assume that the interaction parameters are positive to restrict attention to competition (and not, for example, mutualism or cooperation). Competition is thought to be the dominant ecological interaction in microbial communities (Palmer and Foster 2022). Competition may either be between members of the same species (intraspecific) or between different species (interspecific).

The basic LVCM does not attempt to model any population structure or any spatiotemporal environmental variation. Interactions are therefore modeled at the level of the entire population (rather than, for example, as interactions between individual pairs of organisms). The LVCM and its extensions have been previously applied to theoretical analysis of simplified communities (MacArthur and Levins 1967; Barabás and D'Andrea 2016; O'Sullivan et al. 2019; Kremer and Klausmeier 2017), and to model the dynamics of well controlled laboratory communities (Lax et al. 2020).

In the simplest case of a single species ($k = 1$) with positive competition coefficients, the model reduces to the logistic growth equation in which there is a finite carrying capacity (Tsoularis and Wallace 2002). The LVCM can therefore be thought of as an extension of the logistic model to multiple species.

## 2.2 Incorporating Environmental Conditions Into the LVCM

The simplicity and generality of the original LVCM has made it useful for studying broad outcomes in systems of interacting species (e.g., species coexistence, or the extinction of one or more species). However, modifications to the basic model may help better represent species or capture phenomena in real-world environments. For example, organisms generally experience spatiotemporal variability in environmental

conditions such as temperature, nutrients, and pH, which is not captured in the LVCM.

One way to accommodate spatiotemporal variation into the LVCM is to allow organismal traits (i.e., growth rates and competition coefficients) to vary as functions of some environmental variable. The model can then be analyzed while allowing the environmental variable to vary spatiotemporally (e.g., temperature in Kremer and Klausmeier [2017]). Such parameterization requires some *a priori* understanding of how organisms respond to the chosen environmental variable to make realistic predictions. Fortunately, organismal responses to environmental conditions such as temperature and nutrient concentration are well-studied both theoretically and empirically, and may be adequately modeled with simple functional forms parameterized according to the system of interest (Monod 1949; Sharpe and DeMichele 1977; Schoolfield et al. 1981).

## 2.3  Environmental Temperatures and Growth Rates

Relationships between temperature and organism growth rates are well studied, generally revealing a skewed, unimodal response of growth rates to temperature (Schulte et al. 2011; Sharpe and DeMichele 1977; Schoolfield et al. 1981). Low temperatures tend to result in slow growth rates according to the metabolic theory of ecology (Brown et al. 2004). Increasing temperature above some minimum temperature $T_{min}$ causes growth rates to increase exponentially, up to some optimum temperature $T_{opt}$, past which growth rates rapidly decline until a maximum temperature $T_{max}$ is reached above which the organism is incapable of growth (Schulte et al. 2011) (Figure 1). Different species may have different minimum, maximum and optimum temperatures, presumably reflecting selection by temperatures experienced over their evolutionary histories.

Figure 1. Typical relationship between organismal growth rate and temperature, based on the Sharpe-Schoolfield model. (Data for figure from Sharpe and DeMichele 1977 and Schoolfield et al. 1981.)
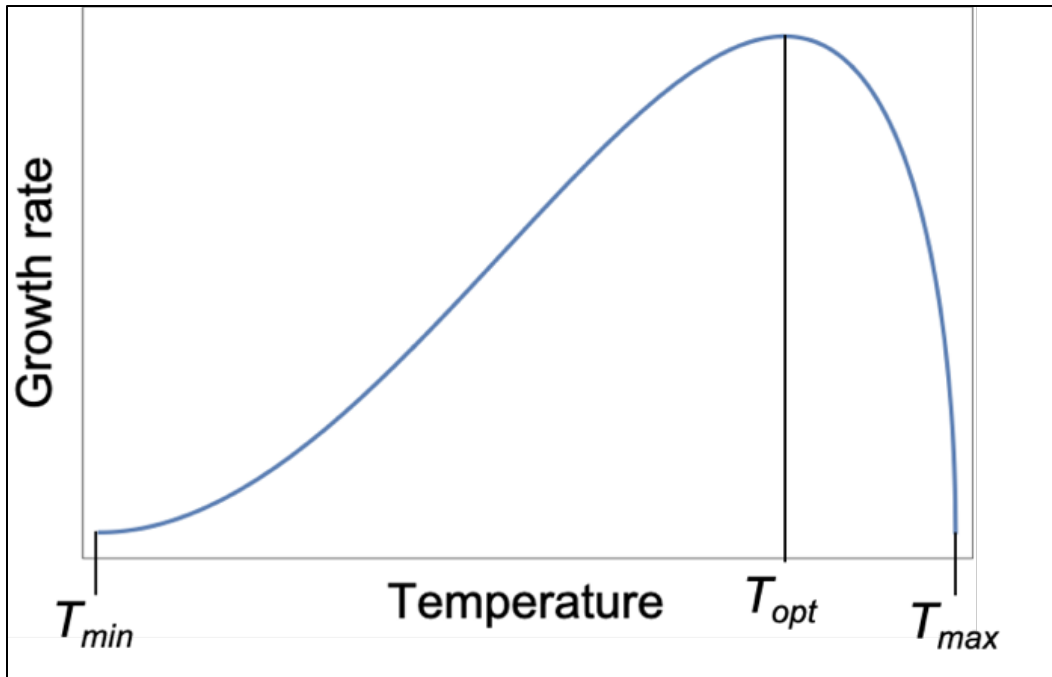
# 3   Methods

## 3.1   Extending the LVCM with Temperature-Dependent Growth

To explore potential effects of temperature on equilibrium outcomes in the LVCM, we focused on a two-species case of the general model shown in Equation (1), which we modified by replacing each species' constant growth-rate parameter $r_i$ with a temperature-dependent growth rate function $r_i(T)$. This function represents the intrinsic growth rate for species $i$ at temperature $T$ (i.e., ignoring any intra- or interspecific competition). Our modified model was thus given by the following system of equations:

$$\frac{1}{n_1}\frac{dn_1}{dt} = r_1(T) - a_{11}n_1 - a_{21}n_2, \tag{2}$$

$$\frac{1}{n_2}\frac{dn_2}{dt} = r_2(T) - a_{22}n_2 - a_{12}n_1, \tag{3}$$

where

$n_1, n_2$ = abundances of species 1 and 2,
$r_1(T), r_2(T)$ = intrinsic growth rates for species 1 and 2 at temperature $T$,
$a_{11}, a_{22}$ = intraspecific competition coefficients for species 1 and 2,
$a_{12}$ = interspecific competition coefficient for effect of species 1 on species 2, and
$a_{21}$ = interspecific competition coefficient for effect of species 2 on species 1.

In our analysis, the temperature-dependent intrinsic growth rate $r_i(T)$ was assumed to be a Gaussian function centered on species $i$'s optimal growth temperature $T_i^*$, following Kremer and Klausmeier (2017) (Figure 2):

$$r_i(T) = R_i . e^{-\left(\frac{T_i^* - T}{\sigma_i}\right)^2}, \tag{4}$$

where

$R_i$ = intrinsic growth rate constant for species $i$;

$T_i^*$ = optimal growth temperature of species $i$;

$T$ = environmental temperature; and

$\sigma_i$ = niche width of species $i$, governing the width of the growth rate reaction norm around the optimal temperature $T^*$ (i.e., larger values imply lower sensitivity to deviations of environmental temperature from $T^*$; see Figure 2 and refer Kremer and Klausmeier 2017).

In contrast to empirical growth responses to temperature, which are typically skewed (Figure 1; see Section 2.3), the Gaussian function that we used is symmetric around the organism's optimal growth temperature $T^*$. We chose to use the Gaussian function for analytical simplicity after Kremer and Klausmeier 2017 (whose approach to analyzing the LVCM we follow closely). We did not expect the presence or absence of skew to substantially alter the broad qualitative conclusions that were the goal of this study. However, it is likely that quantitative predictions would be affected, and this should be explored in future work.

Figure 2. Temperature-dependent growth rate $r(T)$ was assumed to be a symmetric, unimodal function of temperature $T$, with varying niche width $\sigma$, centered on the optimal temperature $T^*$, and spanning all real temperatures.
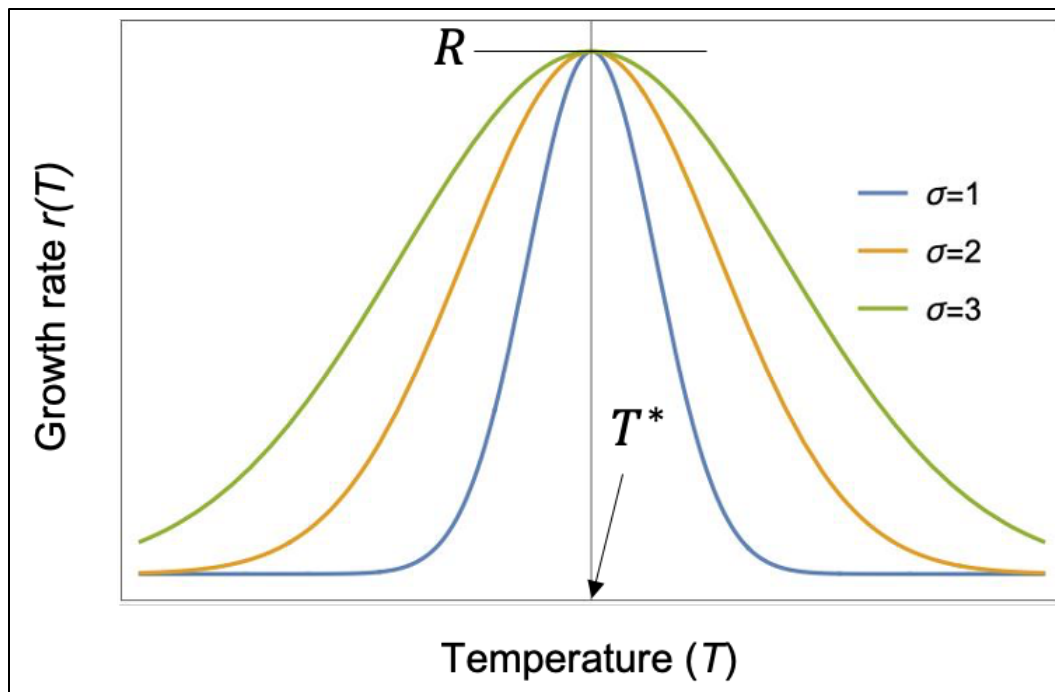
## 3.2 Equilibrium Outcomes of the Two-Species Modified LVCM

### 3.2.1 Equilibria of the Modified LVCM with Constant Temperatures

Our analyses of the modified LVCM (Equations [2] to [4]) focused extensively on equilibrium outcomes (i.e., the long-run behavior of species abundances). When temperature $T$ is constant, the two species' intrinsic growth rate functions $r_1(T)$ and $r_2(T)$ are simply constant values. In this case, an equilibrium consists of a set of fixed species abundances that the system converges on over infinite time. Equilibrium outcomes with constant temperatures are essentially the standard results for the original LVCM (in which intrinsic growth rates are constant by construction; Equation [1]) but with the slightly modified notation of Equations (2) to (4).

At any given temperature $T$, the model can have one of three qualitatively distinct equilibrium outcomes, depending on the relationship between the two species' growth rates ($r_1(T)$ and $r_2(T)$), the intraspecific competition coefficients ($a_{11}$ and $a_{22}$), and the interspecific competition coefficients ($a_{21}$ and $a_{12}$). When there is a sufficiently large difference between the growth rates, **single-species dominance** occurs in which the less competitive species is driven to extinction. This happens with species 1 being the sole survivor when

$$\frac{r_1(T)}{r_2(T)} > \frac{a_{21}}{a_{22}} \quad \text{and} \quad \frac{r_1(T)}{r_2(T)} > \frac{a_{11}}{a_{22}} \tag{5}$$

or with species 2 being the sole survivor when

$$\frac{r_2(T)}{r_1(T)} > \frac{a_{22}}{a_{21}} \quad \text{and} \quad \frac{r_2(T)}{r_1(T)} > \frac{a_{22}}{a_{11}}. \tag{6}$$

When growth rates are sufficiently similar, but interspecific competition is greater than intraspecific competition, the equilibrium outcomes is characterized by **founder control**. As with single-species dominance, only one species survives, with the other going extinct. However, under founder control, the identity of the surviving species is determined by the initial abundances of the two species. This happens when

$$\frac{a_{21}}{a_{22}} > \frac{r_1(T)}{r_2(T)} > \frac{a_{11}}{a_{12}}. \tag{7}$$

When growth rates are sufficiently similar, and intraspecific competition is greater than interspecific competition, **species coexistence** occurs, in which both species have positive abundances. This happens when

$$\frac{a_{11}}{a_{12}} > \frac{r_1(T)}{r_2(T)} > \frac{a_{21}}{a_{22}}. \tag{8}$$

Equations (5) through (8) are essentially standard results for the LVCM but with the modified notation of Equations (2) and (3). The results can be obtained by solving the invasibility conditions for the model. These conditions describe when a community consisting of only one species is able to be invaded by a small number of the other species. A derivation of the results using this approach is provided in the Appendix, Equations (A-1) through (A-6).

With the equilibrium outcome known, the species abundances at equilibrium can be solved analytically by setting Equations (2) and (3) to zero and solving for $n_1$ and $n_2$. When only species 1 is present at equilibrium, under either single species dominance or founder control, its abundance is

$$n_1^* = \frac{r_1(T)}{a_{11}}. \tag{9}$$

Likewise, when only species 2 is present at equilibrium, its abundance is

$$n_2^* = \frac{r_2(T)}{a_{22}}. \tag{10}$$

When both organisms are present at equilibrium, (i.e., under species coexistence), the abundances are

$$n_1^* = \frac{a_{21}r_2(T) - a_{22}r_1(T)}{a_{21}a_{12} - a_{11}a_{22}} \tag{11}$$

and

$$n_2^* = \frac{a_{12}r_1(T) - a_{11}r_2(T)}{a_{21}a_{12} - a_{11}a_{22}}. \tag{12}$$

A derivation of these results is provided in the Appendix, Equations (A-12) through (A-15).

### 3.2.2 Equilibria of the Modified LVCM with Variable Temperatures

Our analysis of variable temperatures in the modified LVCM focused on temperature variation with annual periodicity, motivated by data over the course of a year from one of our cold regions field sites. Section 3.3 provides information on this empirical data set, and Section 3.4.3 details our approach to analyzing the model with variable temperatures.

When environmental temperature $T$ changes with time, the intrinsic growth rates $r_i(T)$ also change, preventing species abundances from stabilizing as they do at equilibrium under constant temperatures (Section 3.2.1). Instead, when temperature varies periodically, an equilibrium of the modified LVCM consists of stable limit cycles, rather than fixed species abundances. A stable limit cycle is a closed trajectory in the model state space on which the system converges over infinite time. In other words, species abundances oscillate periodically in equilibrium.

Equilibrium outcomes can be categorized similarly to those under constant temperatures. **Single-species dominance** describes outcomes in which one particular species always goes extinct, and the other has positive (oscillating) abundance. **Founder control** likewise describes outcomes in which only one of the two species has positive (oscillating) abundance. However, founder control differs from single-species dominance in that the identity of the species that goes extinct is determined by initial conditions. **Species coexistence** describes outcomes in which both species have positive (oscillating) abundances in equilibrium.

To determine the conditions governing which of these equilibrium outcomes obtains, we made use of the invasibility conditions for the model (see Section 3.2.1 and the Appendix, Equations [A-1] through [A-6]). However, to allow for time-varying growth rates $r_i(T)$ and species abundances $n_i$, we averaged growth rates and abundances over the temperature variation period, that is, one year (Appendix, Equations [A-7] and [A-8]).

## 3.3 Field Temperature Data

We motivated and parameterized our model analyses using field temperature data relevant to our work on cold regions soils. Baker et al. (2023) examined spatiotemporal variation in permafrost and active-layer

microbial community composition at a site within the Imnavait Creek watershed on the North Slope of Alaska (latitude 68.61° longitude −149.32°). The site is located in the northern foothills of the Brooks Range, and overlies continuous permafrost 250 m–300 m deep (Osterkamp and Payne 1981).[*]

Baker et al. (2023) collected data on soil temperatures, pore water metal concentrations, and soil nutrients. To gather the temperature data, as part of a long-term monitoring effort in the watershed, HOBO U23 Pro v2 dual external temperature sensor thermistors were placed at depths of 20 cm, 40 cm, 60 cm, 80 cm, 100 cm, and 120 cm at a single location adjacent to the microbial community sampling pits. Soil temperature measurements were collected hourly from 6 June 2019 onwards.

We used the 12 months of temperature data collected at the 20 cm depth and reported in Baker et al. (2023) (i.e., June 2019 through June 2020; Figure 3) as the basis of the constant- and variable temperature regime analyses described in section 3.4. This sampling depth is located in seasonally thawed active layer. It was the shallowest depth for which temperature data were collected in Baker et al. (2023), and was found to exhibit the most temperature variability of the depths surveyed. Temperatures varied from a maximum of +8.8°C in the summer to a minimum of −14.9°C in the winter, averaging $T_{avg}$ = −3.36°C over the year.

---

[*] For a full list of the spelled-out forms of the units of measure used in this document and their conversions, please refer to *US Government Publishing Office Style Manual*, 31st ed. (Washington, DC: US Government Publishing Office, 2016), 248–52 and 345–47, https://www.govinfo.gov/content/pkg/GPO-STYLEMANUAL-2016/pdf/GPO-STYLEMANUAL-2016.pdf.

Figure 3. Imnavait Creek soil temperatures at 20 cm depth, June 2019 through June 2020.
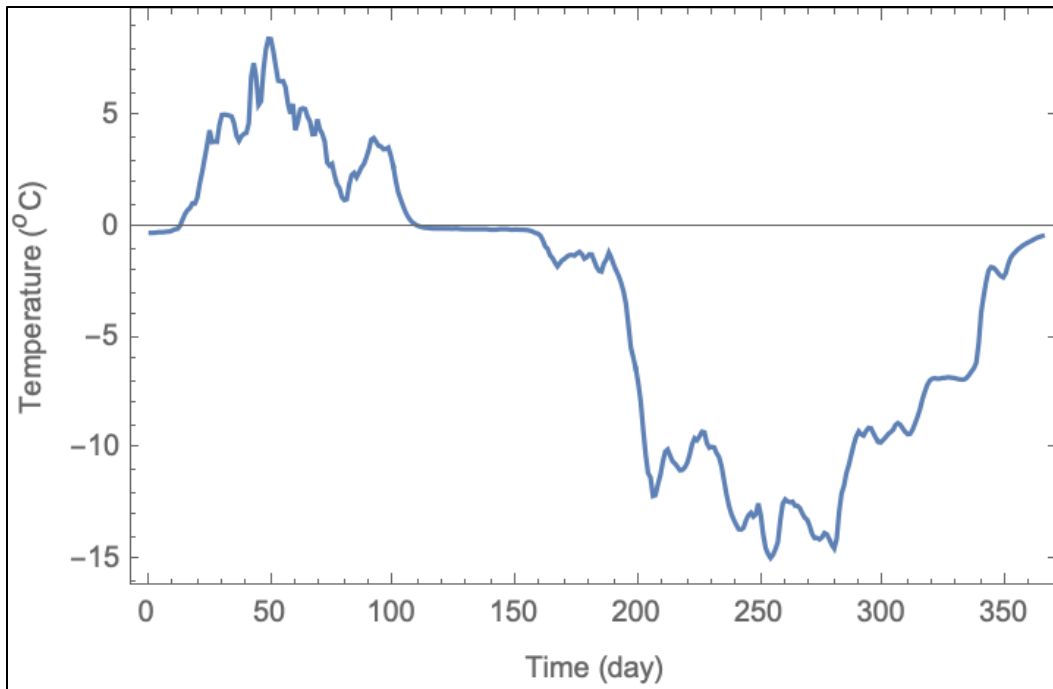


## 3.4  Analysis of the Modified LVCM

### 3.4.1  General Approach

To explore the effect of temperature on communities using our two-species temperature-dependent competition model (Equations [2]–[4]), we examined species dynamics and equilibrium outcomes under constant and variable temperature regimes. Evaluating the model at equilibrium allows species abundances to be analyzed over the long term, while species dynamics describe the movement of species abundances before reaching stability. See Section 3.2 for additional detail on the nature of equilibria in this model.

For our constant-temperature analyses, which we label Experiment 1, we looked at the effect of a step increase in the (otherwise constant) environmental temperature. For our variable-temperature analyses, which we label Experiment 2, we compared periodic environmental temperatures modelled on our field data (Section 3.3) to simple sinusoidal temperature variation and to constant temperatures. Sections 3.4.2 and 3.4.3 describe the analyses in detail.

Although we made use of field data on environmental temperatures, empirically derived parameter values for growth rate ($T_1^*$, $T_2^*$, $R_1$, $R_2$, $\sigma_1$, $\sigma_2$) and competition ($a_{11}$, $a_{12}$, $a_{21}$, $a_{22}$) are generally unavailable. This precluded making quantitative predictions with our model. Instead, we chose parameter values that would illustrate the possible equilibrium outcomes (Section 3.2), and show the potential for the equilibrium outcome to differ depending on the environmental temperature regime. Beyond these goals, our choices of growth rate and competition parameter values were mostly arbitrary. We generally used whole numbers for convenience, and took advantage of symmetry in the equations to minimize the calculations that needed to be performed (e.g., by swapping the values of the intra- and interspecific competition coefficients for certain comparisons). The parameter values used in our analyses are summarized in Table 1, and described in more detail in Sections 3.4.2 and 3.4.3.

Mathematica version 13.2 was used for all model analysis.[*] The EcoEvo package version 1.7.1 (https://github.com/cklausme/EcoEvo) was used to solve differential equations and generate time series and phase plane plots. The script used in this study is available at https://github.com/lg11235/LVCMwtemp.

---

[*] Wolfram Research, Inc. "Mathematica Version 13.2," Champaign, Il: Wolfram Research, Inc., 2022, https://support.wolfram.com/41360

Table 1. Summary of parameters used in our analyses.

| Symbol | Description | Experiment 1a: Constant Temperature | | | | Experiment 1b: Constant Temperature | | | | Experiment 2a: Variable Temperature | | Experiment 2b: Variable Temperature | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | — | | | | | | | | | | | | |
| Temperature Parameters | | | | | | | | | | | | | |
| $T$ | Environmental temperature | Scenario 1: constant −3.86°C; Scenario 2: constant −1.86°C | | | | Scenario 1: constant −3.86°C; Scenario 2: constant −1.86°C | | | | Scenario 3: constant −3.36°C; Scenario 4: sine function; Scenario 5: Fourier series | | Scenario 5: Fourier series | |
| $T^*_1$ | Optimum temperature, species 1 | −4.36°C | | | | −20°C to +10°C | | | | −20°C to +10°C | | −10°C, 0°C, +7°C, +1°C, −10°C | |
| $T^*_2$ | Optimum temperature, species 2 | −2.36°C | | | | −20°C to +10°C | | | | −20°C to +10°C | | +5°C, +3°C, 0°C, −5°C, −8°C | |
| $\sigma_i$ | Temperature niche breadth | 2.5 | | | | 2.5 | | | | 2.5 | | 2.5 | |
| Other Parameters | | | | | | | | | | | | | |
| | — | Case I | Case II | Case III | Case IV | Case I | Case II | Case III | Case IV | Case II | Case IV | Case II | Case IV |
| $R_i$ | Growth rate constant | 1 | | | | 1 | | | | 1 | | 1 | |
| $a_{11}$ | Intraspecific competition coefficient, species 1 | 1 | 2 | 3 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 1 |
| $a_{22}$ | Intraspecific competition coefficient, species 2 | 1 | 2 | 5 | 1 | 1 | 2 | 5 | 1 | 2 | 1 | 2 | 1 |
| $a_{12}$ | Interspecific competition coefficient, effect of species 1 on species 2 | 1 | 1 | 2.5 | 2 | 1 | 1 | 2.5 | 2 | 1 | 2 | 1 | 2 |
| $a_{21}$ | Interspecific competition coefficient, effect of species 2 on species 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 |
| | Key results figures | 4b–c | 4d–e | 4f–g | 4h–i | 5a | 5b | 5c | 5d | 7b–d (top); 8b (top) | 7b–d (bottom); 8b (bottom) | 8c, 8d | 8e |

This page intentionally left blank.

### 3.4.2 Experiment 1: Constant Temperature Regimes

With constant environmental temperature $T$, the temperature-dependent intrinsic growth rates $r_i(T)$ in the modified LVCM (Equations [2]–[4]) do not vary over time. Outcomes of our model may therefore be regarded as a special case of the basic LVCM (Equation [1]), in which each species has a fixed intrinsic growth rate $r_i$ by construction. The constant temperature case is useful; however, as a baseline for comparison with variable temperature regimes.

In Experiment 1a, we examined model outcomes under two constant temperature scenarios (see Table 1 for summary). We used the empirical average temperature $T_{avg}$ = −3.36°C from the Imnavait Creek data set (i.e., 20 cm depth, June 2019 through June 2020; Figure 3) to anchor the two scenarios as well as the species' temperature optima. The environmental temperature $T$ was set to $T_{avg}$ − 0.5°C = −3.86°C in Scenario 1, and $T_{avg}$ + 1.5°C = −1.86°C in Scenario 2. In both scenarios, we set the two species' optimal temperatures to $T_1^*$ = $T_{avg}$ −1°C = −4.36°C and $T_2^*$ = $T_{avg}$ +1°C = −2.36°C (see Section 4.1, Figure 4$a$). The same growth rate constant ($R_1$ = $R_2$ = 1) and temperature niche breadth parameter ($\sigma_1$ = $\sigma_2$ = 2.5) were assumed for the two species.

The values we used for $T$ and $T_i^*$ were chosen so that the environmental temperature was closer to species 1's optimum (i.e., $T_1^*$) in Scenario 1, and closer to species 2's optimum (i.e., $T_2^*$) in Scenario 2. We chose values that seemed reasonably close to $T_{avg}$ but were otherwise arbitrary. Note that although our parameters were anchored to empirical temperature measurements with the intention of generating realistic analyses, we do not have data for specific organisms found in the region where our temperature data were collected. Our results should therefore be interpreted as illustrating some possible qualitative outcomes given changing environmental temperatures, but not making quantitative predictions.

Given the environmental temperatures and growth parameters described above, we analyzed species dynamics and equilibrium outcomes under four sets of competition coefficients chosen to obtain outcomes that we wanted to illustrate. See Section 3.4.1 for discussion of our approach, and Section 3.2.1 for conditions determining the equilibrium outcomes.

- **Case I**—Setting all competition coefficients ($a_{11}$, $a_{12}$, $a_{21}$, $a_{22}$) to 1 led to single species dominance under both temperature Scenarios 1 and 2.

- **Case II**—Setting the intraspecies competition coefficients ($a_{11}$, $a_{22}$) to 2 and the intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 1 led to species coexistence under temperature Scenario 1, but single species dominance under temperature Scenario 2.
- **Case III**—With intraspecific competition greater than interspecific competition and with species 2 more affected by competition than species 1 ($a_{11}$=3, $a_{22}$=5, $a_{21}$=1, $a_{12}$=2.5), temperature Scenario 1 led to single-species dominance, while temperature Scenario 2 led to species coexistence.
- **Case IV**—Setting the intraspecies competition coefficients ($a_{11}$, $a_{22}$) to 1 and the intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 2 led to founder control under temperature Scenario 1, but single species dominance under temperature Scenario 2. Conveniently, swapping the intra- and interspecific competition coefficients from Case II allowed us to reduce the analytical work required for Case IV.

Our expectation, based on our understanding of the basic LVCM, was that the species with temperature optimum $T^*$ closest to the actual environmental temperature would dominate (i.e., achieve a higher overall abundance than the other species, and possibly drive the other species extinct).

To analyze our two temperature scenarios with each set of competition coefficients, the system of ordinary differential equations comprising Equations (2) and (3) was solved in Mathematica using the EcoEvo package, with time-dependent species abundances determined numerically. We first examined species dynamics and equilibrium outcome under temperature Scenario 1 using initial species abundances $n_1 = n_2 = 0.01$ to represent initial conditions in which both species are scarce. Then, starting from the calculated equilibrium abundances from that analysis, we examined species dynamics and equilibrium outcome following a switch from temperature Scenario 1 to temperature Scenario 2, (i.e., a step increase of 2°C). We visualized each of the two scenarios using phase plane plots.

If $n_1 = 0$ or $n_2 = 0$ in equilibrium under Scenario 1, we assumed that the switch between scenarios was accompanied by a small perturbation to the species abundances to avoid being trapped at an unstable equilibrium under Scenario 2. Although $n_1 = 0$ and $n_2 = 0$ are always absorbing states in our model, they are only reached at $t \rightarrow \infty$. Our small perturbation can therefore be interpreted as allowing the system to get arbitrarily close to

equilibrium under Scenario 1 but with $t < \infty$. Alternatively, it could be interpreted as representing an infinitesimal amount of dispersal into the system. In reality, finite population sizes do allow species to go extinct, but dispersal also allows species to rebound after being driven locally extinct.

In Experiment 1b, we generalized the Experiment 1a results to other values of the species' optimum temperatures $T_i^*$ (see Table 1 for summary). Instead of setting $T_1^* = -4.36°C$ and $T_1^* = -2.36°C$ and as we did in Experiment 1a, we allowed the $T_1^*$ to vary independently between $-20°C$ and $+10°C$, (i.e., $(T_1^*, T_2^*)$: $T_1^*, T_2^* \in [-20, 10]$). All other model parameters were kept the same as in Experiment 1a, including the environmental temperature scenarios ($T = -3.86°C$ in Scenario 1 and $T = -1.86°C$ in Scenario 2), growth rate constants ($R_1 = R_2 = 1$) and temperature niche breadth parameters ($\sigma_1 = \sigma_2 = 2.5$).

The four sets of competition coefficients used in Experiment 1a (labelled case I through case IV above) were also used in Experiment 1b. With the generalization of the species' optimum temperatures; however, these sets of coefficients no longer corresponded to a single equilibrium outcome in each temperature scenario, since the conditions determining the equilibrium outcome (Equations [5] through [8]) depend on the intrinsic growth rates $r_i(T)$, which in turn depend on the optimum temperatures (Equation [4]). Instead, for each temperature scenario, our Experiment 1b analysis effectively determined the equilibrium outcome for every possible combination of $T_1^*$ and $T_2^*$ within the limits that we set (i.e., each $T_1^*$ ranging from $-20°C$ to $+10°C$).

We used the RegionPlot function in Mathematica to visualize the equilibrium outcomes over the space of species temperature optima for each temperature scenario and for each set of competition coefficients. Used in this way, the RegionPlot function color-coded different regions of the $(T_1^*, T_2^*)$ parameter space based on the conditions determining the equilibrium outcome (Equations [5] through [8]). In contrast to Experiment 1a, it was infeasible to use phase plane plots to visualize outcomes in Experiment 1b, since every point in $(T_1^*, T_2^*)$ parameter space would correspond to a different phase plane diagram.

### 3.4.3  Experiment 2: variable Temperature Regimes

To help understand the implications of time-varying environmental temperatures in the modified LVCM, we examined model outcomes under

variable temperature regimes based on the Imnavait Creek field data (Baker et al. 2023; Section 3.3). As for Experiment 1, we made use of measurements from the 20 cm depth from June 2019 to June 2020 (Figure 3). This sampling depth, located in seasonally thawed active layer, showed the greatest variability out of the depths surveyed over the year.

Environmental variability is important to consider since no organisms exist in constant environments outside a laboratory setting. Organisms can actively influence their environment such as through the consumption of finite resources or the production of secondary metabolites that other organisms can interact with (Hibbing et al. 2010; O'Brien et al. 2011), or may be affected by abiotic variability in their environments such as temperature which cycles over multiple timescales (e.g., diurnally or seasonally). Taking such environmental variability into account in models may help to represent the behavior of organisms more accurately, allowing models to more closely approximate real-world environments.

In Experiment 2a, we examined model outcomes under three temperature scenarios (see Table 1 for summary). For clarity, we label these scenarios by continuing the numbering from Experiment 1. In Scenario 3, the environmental temperature $T$ was set to a constant −3.36°C, which was the average temperature $T_{avg}$ from the Imnavait Creek data set. In Scenario 4, $T$ was assumed to be a simple sine function with period 365 days fitted to the Imnavait Creek data using the Mathematica function NonlinearModelFit. In Scenario 5, $T$ was modelled as a Fourier series fitted to the Imnavait Creek data set as described below. This approach was intended to capture most of the temporal variation in the data. In effect, environmental temperatures in this scenario closely track the original data, repeating year after year.

For temperature Scenario 5, the Imnavait Creek data were converted from discrete observations to a continuous function for compatibility with the EcoEvo package in Mathematica. This was done by approximating the time series by fitting a Fourier series to the data. The empirical data were provided as input to the TrigFit function in Mathematica to generate a continuous function consisting of one hundred terms approximating the data. Residuals and root-mean-square-error (RMSE) between the Fourier series approximation and the original data were calculated to assess the goodness-of-fit.

We allowed the species' optimum temperatures $T_i^*$ to vary independently between −20°C and +10°C, (i.e., $(T_1^*, T_2^*): T_1^*, T_2^* \in [-20, 10]$, as we did in Experiment 1b). Growth rate constants were set to 1 (i.e., $R_1 = R_2 = 1$) and temperature niche breadth parameters to 2.5 (i.e., $\sigma_1 = \sigma_2 = 2.5$), as was the case throughout our study.

For brevity, we examined equilibrium outcomes under just two of the competition coefficient sets from Experiment 1:

- **Case II**—Intraspecies competition coefficients ($a_{11}$, $a_{22}$) were set to 2 and intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 1.
- **Case IV**—Intraspecies competition coefficients ($a_{11}$, $a_{22}$) were set to 1 and intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 2.

We selected these coefficients for comparison with Experiment 1, and because analyzing two cases in which the intra- and interspecific competition coefficients were simply swapped reduced the analytical work required due to symmetry in the equations.

Given these temperature scenarios and model parameters, we determined equilibrium outcomes for the modified LVCM (Section 3.2.2). For temperature Scenario 3, we used the conditions in Equations (5) through (8) for constant temperatures. For temperature Scenarios 4 and 5, the system of ordinary differential equations (Equations [2] and [3]) was modified to include the sine and Fourier time series respectively by replacing $T$ with $T(t)$ (Equation 4) and resolved. Temperature-dependent growth rates $r_i(T)$ and species abundances were averaged over the 365 day period of the variable environmental temperatures to determine equilibrium outcomes. See Section 3.2.2 and the Appendix, Equations (A-7) and (A-8) for additional detail on this approach.

As in Experiment 1b, the use of ranges rather than specific values for the species' optimum temperatures $T_i^*$ meant that these sets of competition coefficients did not correspond to a single equilibrium outcome in each temperature scenario. Instead, for each scenario, our analysis essentially determined the equilibrium outcome for every possible combination of $T_1^*$ and $T_2^*$ within the limits that we set (i.e., each $T_1^*$ ranging from −20°C to +10°C). We used the RegionPlot function in Mathematica to visualize these equilibrium outcomes over the space of species temperature optima for each temperature scenario and for each set of competition coefficients.

It was infeasible to visualize species dynamics using phase plane diagrams or plots of abundance versus time, since every point in ($T_1^*$, $T_2^*$) parameter space would correspond to a different trajectory.

In Experiment 2b, we investigated temperature Scenario 5 (i.e., the Fourier series approximating the Imnavait Creek data) in more detail (see Table 1 for summary). First, to help understand the RegionPlot results from Experiment 1a, we plotted the temperature probability distribution for the Imnavait Creek data set using Mathematica's SmoothHistogram function. This function draws a smooth kernel histogram for the probability density of the time series, helping identify the most common temperatures experienced over the time period. Second, to illustrate species dynamics and the potential for certain equilibrium outcomes under variable temperature regimes, we determined outcomes and plotted species abundance against time for selected parameter values.

- **Case II**—With intraspecies competition coefficients ($a_{11}$, $a_{22}$) set to 2 and intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 1, either species coexistence or single species dominance should be possible, depending on other parameter values. We first set $T_1^* = -10°C$ and $T_2^* = +5°C$, and then set $T_1^* = 0°C$ and $T_2^* = +3°C$, to obtain two different examples of species coexistence. Next, we illustrated single species dominance by first setting $T_1^* = +7°C$ and $T_2^* = 0°C$ for an example in which species 1 eventually goes extinct, and then setting $T_1^* = +1°C$ and $T_2^* = -5°C$ for an example in which species 2 eventually goes extinct.
- **Case IV**—With intraspecies competition coefficients ($a_{11}$, $a_{22}$) set to 1 and intraspecies competition coefficients ($a_{12}$, $a_{21}$) to 2, either founder control or species coexistence should be possible, depending on other parameter values. We examined two examples of founder control, both with $T_1^* = -10°C$ and $T_2^* = -8°C$. We first set initial species abundances to $n_1 = n_2 = 0.01$ for an example in which species 2 eventually goes extinct, and then set $n_1 = 0.02$ and $n_2 = 0.7$ for an example in which species 1 eventually goes extinct. We did not simulate species coexistence under case IV competition coefficients.

Growth rate constants were set to 1 (i.e., $R_1 = R_2 = 1$) and temperature niche breadth parameters to 2.5 (i.e., $\sigma_1 = \sigma_2 = 2.5$), as was the case throughout our study.

# 4 Results

## 4.1 Experiment 1: Constant Temperature Regimes

### 4.1.1 Experiment 1a

As expected, the rise in temperature from Scenario 1 to Scenario 2 (i.e., $T = -3.86°C$ to $T = -1.86°C$; Figure 4$a$) caused a change in the equilibrium outcome under each set of competition coefficients (Table 1 and Section 3.4.2). In general, the species whose optimal growth temperature $T^*$ was closest to the environmental temperature $T$ was favored, since this resulted in that species achieving a higher growth rate (although see case IV results below). This meant that Scenario 1 generally favored species 1 over species 2, since $T_1^*$ was closer to $T$ than was $T_2^*$. Under Scenario 2, the reverse was true: $T_2^*$ was closer to $T$ than was $T_1^*$, and species 2 was generally favored over species 1.

Phase plane plots in Figure 4 show zero net growth isoclines for species abundances in blue and yellow. Grey arrows depict trajectories that population abundances potentially follow through time before reaching equilibrium. As examples, the red arrows highlight approximate trajectories starting from species abundances $n_1 = n_2 = 0.01$ in Scenario 1, and from the Scenario 1 equilibrium in Scenario 2 (Figure 4$b$–$i$). Assuming other starting abundances would lead to other trajectories being highlighted. Stable and unstable equilibria are shown as closed and open circles, respectively.

Figure 4. Species' growth rate functions for Experiment 1a (*a*). Results for Experiment 1a with constant temperatures (*b–g*). Each panel shows a phase plane plot with species 1 and species 2 abundances as x- and y-axes. Cases I through IV for competition coefficients are shown with arrangement of panels into four columns. Top panels represent temperature Scenario 1 with example trajectory in *red* starting from initial abundances $n_1 = n_2 = 0.01$ Bottom panels represent temperature Scenario 2 with example trajectory starting from the Scenario 1 equilibrium to reflect a switch from Scenario 1 to Scenario 2 temperatures. The switch between scenarios is represented by *yellow arrows* connecting plots with the same competition coefficients.
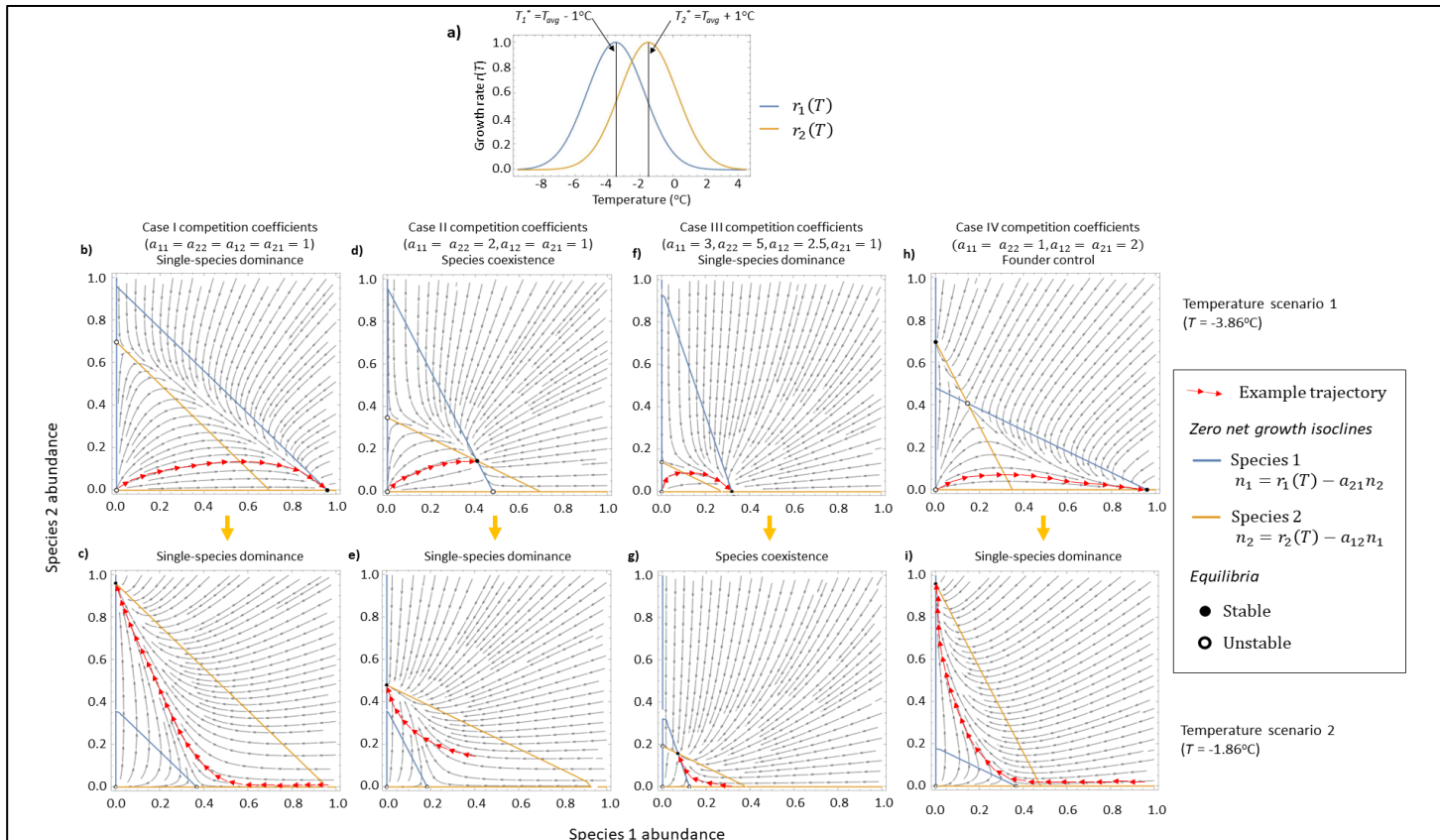
- Under case I for the competition coefficients, single-species dominance was the equilibrium outcome under both temperature scenarios. However, the change in temperatures led to a switch from species 1 to species 2 being the sole survivor in equilibrium (Figure 4$b$).
- Under case II, the system shifted from species coexistence in temperature Scenario 1, to single-species dominance under temperature Scenario 2 with species 2 the sole survivor.
- Case III illustrated the opposite shift to case II: temperature Scenario 1 led to single species dominance with species 1 the sole survivor, but the shift to temperature Scenario 2 allowed species coexistence to emerge.
- Case IV showed a shift from founder control with species 1 the sole survivor under Scenario 1 (given starting abundances of $n_1 = n_2 = 0.01$) to single species dominance with species 2 the sole survivor under Scenario 2. Different starting abundances in Scenario 1 would not have altered the equilibrium outcome (founder control) but could have allowed species 2 to be the sole surviving species, such that the switch to single species dominance under Scenario 2 would not have caused any change in the system.

In sum, the results for Experiment 1a demonstrated the potential for a step increase in otherwise constant temperatures to produce changes either in the type of equilibrium outcome (single species dominance, species coexistence or founder control) or in the species abundances. With the assumed growth function and parameters, the temperature change was capable of causing species diversity to increase (case III), decrease (case II), or not to change at all (cases I and IV).

### 4.1.2 Experiment 1b

Experiment 1b expanded the results of Experiment 1a to other values for the temperature optima $T_i^*$. We focused on changes in the type of equilibrium outcome, that is, single species dominance, species coexistence or founder control. The conditions determining the equilibrium outcome (Equations [5] through [8]) depend on the species' growth rates $r_i(T)$. The growth rates in turn depend on the environmental temperature $T$, as evidence by the results of Experiment 1a, but also on the species temperature optima $T_i^*$ (see Equation [4]).

The region plots in Figure 5 therefore show how equilibrium outcomes depend on the species temperature optima under each temperature scenario for the four sets of competition coefficients that we examined

(Table 1). Temperature Scenarios 1 and 2 are shown in the top and bottom rows respectively. The effect of the temperature increase from Scenario 1 to Scenario 2 can therefore be discerned by comparing the region plots under the two scenarios. Any given pair of temperature optima is represented by single point in each region plot, so comparing the points under the different scenarios illuminates whether and how the equilibrium outcome changes for those temperature optima. As examples, the yellow crosses show the temperature optima values used in Experiment 1a.

- Under case I for the competition coefficients, only single-species dominance is possible (Figure 5*a*). This is evident from substituting $a_{11} = a_{12} = a_{21} = a_{22} = 1$ into Equations (7) and (8). The temperature change from Scenario 1 to Scenario 2 therefore never produces a change in the type of equilibrium outcome in this case. However, the identity of the surviving species may (as in Experiment 1a) or may not change.
- In cases II and III, the equilibrium outcome may be single species dominance or species coexistence, depending on the temperature optima (Figure 5*b* and 5*c*). Species coexistence is possible when the temperature optima are sufficiently similar (*blue x-shaped* region in plots; Equation [8]). The shift in temperatures may cause a change in equilibrium outcome either from coexistence to single species dominance or vice versa (as in Experiment 1a); or the type of equilibrium outcome may be unchanged.
- In case IV, the equilibrium outcome may be single species dominance or founder control, depending on the temperature optima (Figure 5*d*). Founder control is possible when the temperature optima are sufficiently similar (*red x-shaped* region in plots; Equation [7]). Because of our choice of competition coefficients, (i.e., exchanging the values for intra- and interspecific competition), the founder control region under case IV exactly matches the species coexistence region under case II (see the Appendix, Equations [A-7] to [A-9] for proof). The shift in temperatures may cause a change in equilibrium outcome either from founder control to single species dominance (as in Experiment 1a) or vice versa; or the type of equilibrium outcome may be unchanged.

Figure 5. Equilibrium outcomes for Experiment 1b. Each panel shows outcomes as a function of the two species' temperature optima $T^*_i$ Parameter values used in Figure 4 are shown with yellow crosses on each plot. Cases I through IV for competition coefficients are shown with arrangement of panels into four columns. Top panels represent temperature Scenario 1; bottom panels represent temperature Scenario 2. The switch between scenarios is represented by red arrows connecting plots with the same competition coefficients.
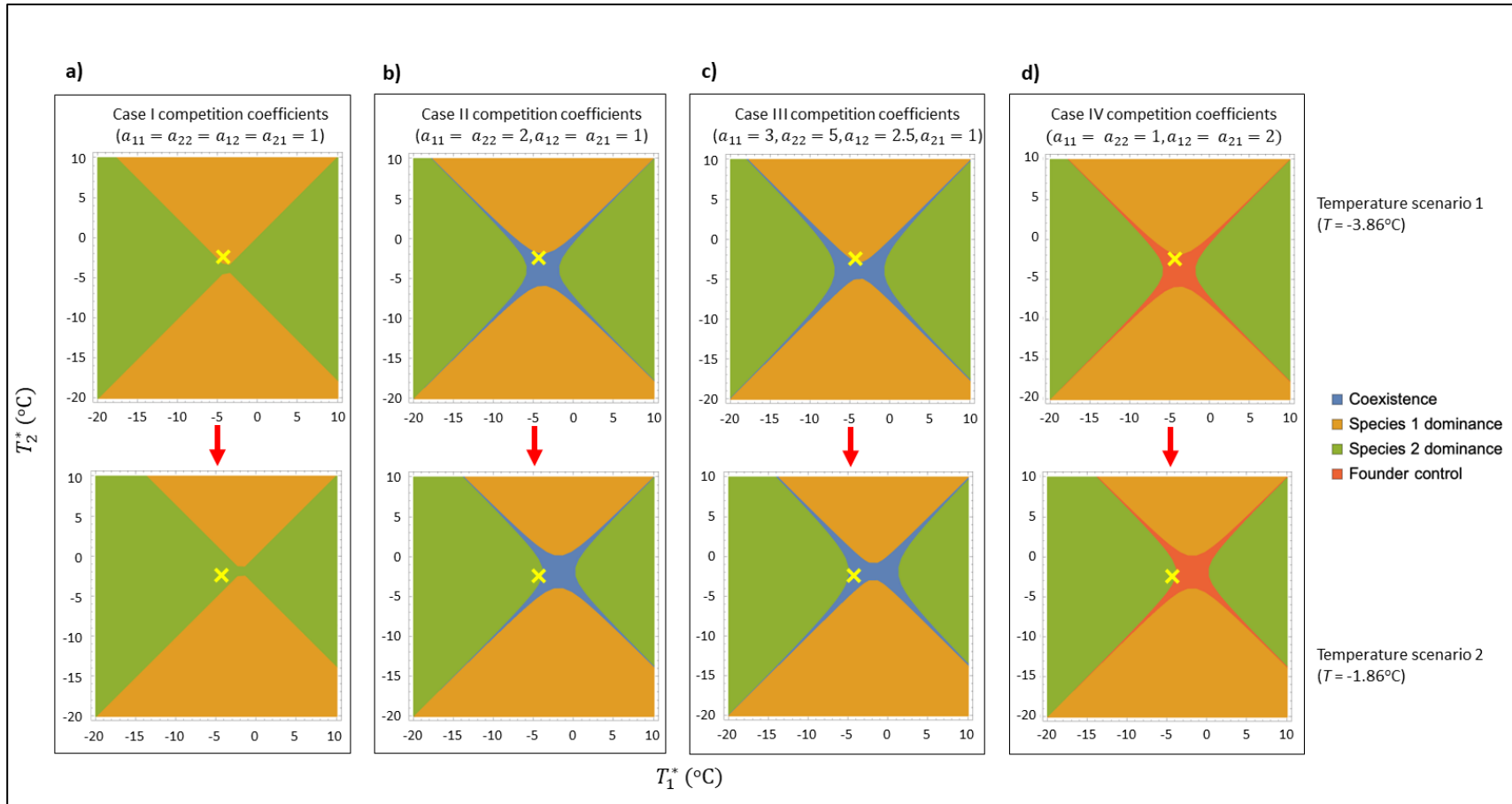
## 4.2  Experiment 2: Variable Temperature Regimes

### 4.2.1  Experiment 2a

Comparison of the Fourier series to the Imnavait Creek data set confirmed a good fit to the data, with an RMSE value of 0.201 (Figure 6). Some autocorrelation was evident in the data; however, this was not a concern as most of our analysis focused on conditions averaged over the time period.

Figure 6. Residual plot for the difference between predictions from the Fourier series fit and Imnavait Creek data set at each time point (root-mean-square-error [RMSE] = 0.201).
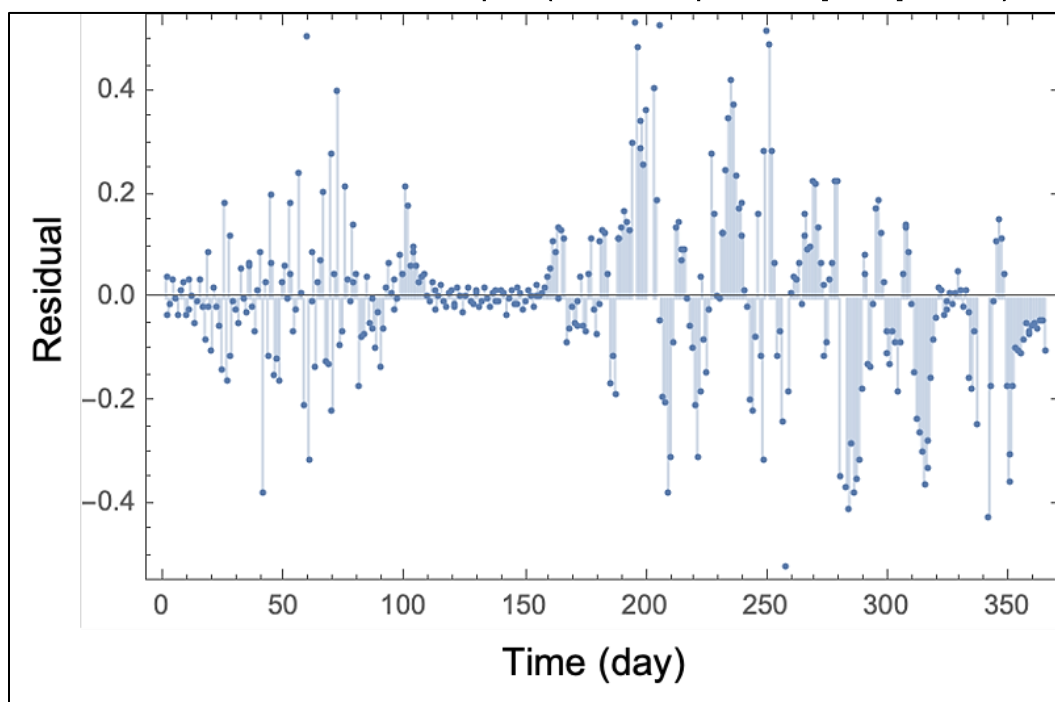


With constant temperatures under Scenario 3 ($T = -3.36$°C) and case II competition coefficients (interspecific competition greater than intraspecific competition), equilibrium outcomes were single species dominance or species coexistence depending on the species temperature optima (Figure 7b, *top panel*). With case IV competition coefficients (intraspecific competition greater than interspecific competition), equilibrium outcomes were single species dominance or founder control depending on the species temperature optima (Figure 7b, *bottom panel*). Species coexistence or founder control were only possible when the species temperature optima were very close to one another (*blue and red x-shaped regions in plots;* Equations [7] and [8]). These results closely resembled those from Experiment 2b (Figure 6b and 6d), differing only because of the different constant temperatures used. Our choice of competition

coefficients meant that the founder control region under case IV exactly matched the species coexistence region under case II (Appendix, Equations [A-7] to [A-9] for proof).

With variable temperatures under Scenario 4 (simple sine approximation), possible equilibrium outcomes resembled those under constant temperatures. that is, single species dominance or species coexistence were possible with case II competition coefficients (Figure 7*c*, *top panel*), and single species dominance or founder control were possible with case IV competition coefficients (Figure 7*c*, *bottom panel*) depending on the species optima. However, the two species' temperature optima did not need to be as close as they did under constant temperatures in order for species coexistence or founder control to emerge. This is evident from comparing the size of the blue and red regions in Figure 7*c* to the corresponding regions in Figure 7*b*. As before, our choice of competition coefficients meant that the founder control region under case IV exactly matched the species coexistence region under case II (Appendix, Equations [A-7] to [A-9]).

With variable temperatures under Scenario 5 (Fourier series approximation), possible equilibrium outcomes again resembled those under constant temperatures. For example, single species dominance or species coexistence with case II competition coefficients (Figure 7*d*, *top panel*), and single species dominance or founder control with case IV competition coefficients (Figure 7*d*, *bottom panel*) depending on the species optima. As before, our choice of competition coefficients meant that the founder control region under case IV exactly matched the species coexistence region under case II (Appendix, Equations [A-7] to [A-9]). The two species' temperature optima did not need to be as close as they did under constant temperatures in order for species coexistence or founder control to occur, similarly to Scenario 4 (sine approximation). However, while Scenario 4 resulted in species coexistence or founder control for a continuous set of temperature optima centered around $T_{avg}$, under Scenario 5 there were small areas within the coexistence or founder control regions in which single-species dominance was the outcome.

Figure 7. Time series showing different time-dependent temperature functions used (*a*) and equilibrium outcomes for Experiment 2a (*b*–*d*). Each panel shows outcomes as a function of the two species' temperature optima $T^*_i$; (*b*) shows temperature Scenario 3 (constant temperature), (*c*) shows temperature Scenario 4 (sine function), and (*d*) shows temperature Scenario 5 (Fourier series approximation). Top panels represent case II for the competition coefficients; bottom panels represent case IV.
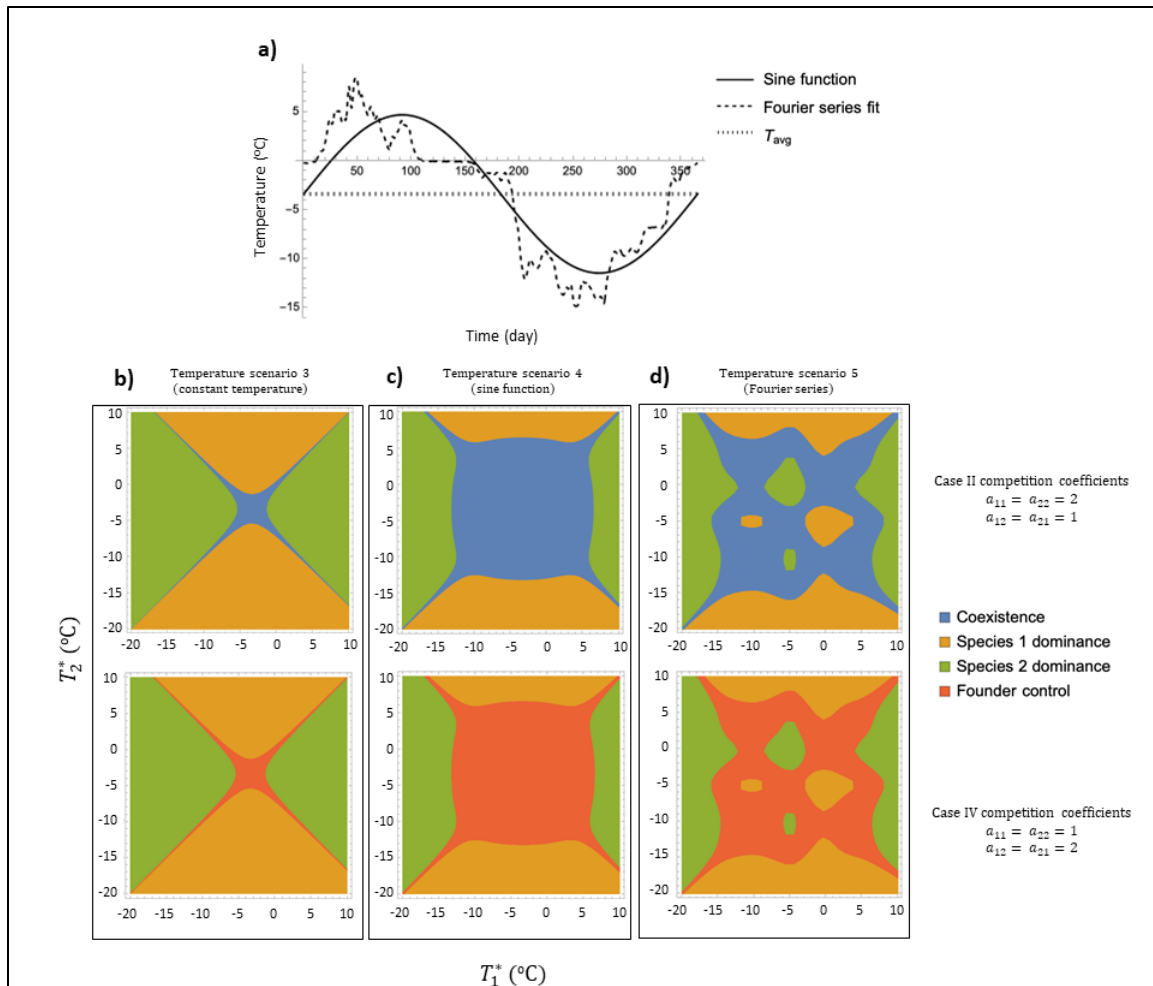


### 4.2.2  Experiment 2b

The probability distribution for the Imnavait Creek data set (Figure 8*a*) sheds light on the results for the Fourier series approximation (temperature Scenario 5) in Experiment 2a. The small areas of single species dominance within the regions of species coexistence or founder control (Figure 7*b*; redisplayed in Figure 8*b*) occur when one species has an optimal temperature $T^*_i$ close to a peak in the probability distribution while the other has an has an optimal temperature $T^*_i$ close to a trough. Peaks in the distribution identify temperatures that occur relatively frequently, while troughs identify those that are least likely. Such a

situation provides enough of a growth benefit to the species whose $T_i^*$ is close to a probability peak that that species may drive the other extinct.

Species dynamics for our selected model parameters (Table 1) with variable temperatures (Scenario 5, Fourier series approximation) are depicted over 1 year in Figure 8*c*–*e*. In all cases, species abundances appear to follow boom-bust-like dynamics, in which population abundances rapidly increase before crashing. These bursts of growth appear to be predominantly associated with periods of the annual temperature cycle when temperatures are close to the species' temperature optimum. For example, species 2 in the top panel of Figure 8*d* has temperature optimum $T_2^*$ = 0°C and exhibits strong growth around days 10, 100, and 350. These correspond to times of the year when environmental temperatures are around 0°C (see Fourier approximation in Figure 7*a*, and original Imnavait Creek data in Figure 3). These dynamics may continue indefinitely when model parameters permit species coexistence (Figure 8*c*), but eventually lead to the extinction of one species when parameters cause single-species dominance (Figure 8*d*) or founder control (Figure 8*e*) outcomes.

Figure 8. Probability distribution for Imnavait Creek temperature data (*a*) and experiment 2b equilibrium model outcomes under temperature Scenario 5 (*b*; Fourier series approximation). Note that (*b*) reproduces Figure 7*d* for convenience. Time series of species abundances under selected model conditions providing examples of species coexistence, single-species dominance and founder control respectively (*c*–*e*).
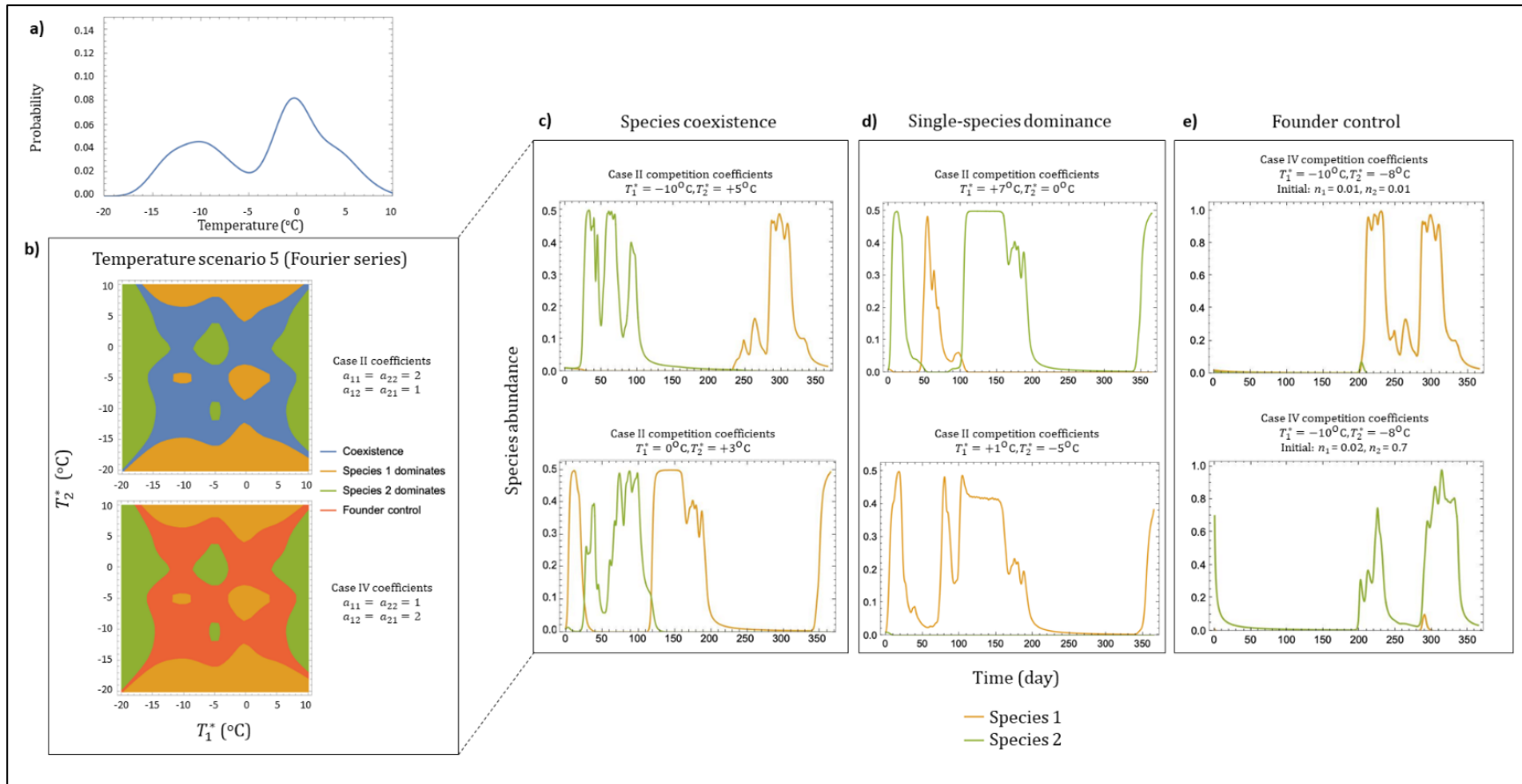
## 4.3   Discussion

Our results demonstrate that microbial community composition may be affected by a shift from one constant temperature to another. For any given temperature $T$, the outcome is a special case of the classic LVCM model (Equation [1]), because intrinsic growth rates $r_i(T)$ are simply constants when $T$ is fixed. The LVCM is analytically tractable, allowing for the thresholds between community outcomes to be exactly defined (Equations [5]–[8]). Specifically, outcomes are dependent solely on the relationship between growth rates of each species and competition coefficients. A change in the temperature $T$ causes a change in the intrinsic growth rates, which can alter competitive interactions through changes in the species abundances, potentially producing a different equilibrium outcome (Figure 4).

The constant temperature results highlight the varied outcomes of the Lotka-Volterra competition models. Even when organisms are assumed to compete, with interaction coefficients restricted to positive values, coexistence is a possible outcome, in addition to single-species dominance and founder control. Thus, even without considering environmental variability, ecological outcomes can be highly variable just based on the possibilities for biotic interactions and how they differ between different environments. These results have implications for environments that may experience abrupt shifts in conditions, such as might result from an extreme weather event (Glaspie et al. 2020), which may shift a system between two very different states.

Our results suggest that warming temperatures could allow warmer-adapted microbes to augment or replace existing cold-adapted microbes in environments such as cold-regions soils. In our model, multiple outcomes are possible depending on the specific parameter values of the organisms found in those environments. Therefore, to make more meaningful predictions about the responses of real-world environments, it is necessary to collect additional data with the goal of constraining the parameter values used.

We further showed that shifting from a constant temperature regime to a variable temperature regime may also alter microbial community composition. In particular, more species parameter combinations led to species coexistence in equilibrium under variable temperatures than under

constant temperatures. Furthermore, when temperature was modelled using a Fourier approximation rather than a simple sine function, the set of organisms capable of coexistence was no longer simply connected (Figure 7).

These results are in line with previous studies examining the effects of environmental variability on coexistence within generalized communities that found that temperature variability was related to the evolutionary stability of species with different $T^*$ values (Kremer and Klausmeier 2017). However, these studies have typically focused on simple variable temperature scenarios such as sinusoidal variation, unlikely to be experienced in nature. Our work demonstrates that predicted equilibrium outcomes can differ between simple variation scenarios and those more closely mimicking real-world data. This highlights the potential for details of environmental variation (e.g., shape of the probability density, not just mean and variance) to be important in determining outcomes. For example, if temperatures hover around particular values, then that is likely to select for organisms that operate well at those temperatures. It also seems likely that any skew in the distribution of temperatures or in the growth function may be important. This is worth considering in future modeling if real temperature growth functions are skewed such as that shown in Figure 1.

While our analysis was necessarily limited to certain parameters (Table 1), alternative parameterizations will affect specific predictions. This may result in changes to the temperature shift required to change community outcomes, resulting in community dynamics becoming either more or less sensitive to temperature. However, qualitatively, the results of this analysis should be applicable to a variety of competitive interaction scenarios, with temperature variation leading to an overall increase in potential for coexistence or founder control compared to a constant temperature scenario. Future estimates of interaction parameters specific to organisms found in soil environments may help to make more meaningful predictions, for example through the use of laboratory-based competition experiments (Friedman et al. 2017)

While many studies focus on coexistence, founder control is an interesting case to consider, as it allows the dominant species to be determined in part by the abundances of species in the environment in addition to underlying environmental variability that may affect their physiology. Our results

show that temperature variability can not only promote coexistence, but also founder control. This is important to consider as dispersal is known to be an important process in structuring microbial communities (Ernakovich et al. 2022; Lennon et al. 1997). Thus, microbial communities in environments that experience founder control to a greater extent, as well as high dispersal rates for periods of time, may be particularly variable. This may be especially applicable to frozen soils that experience seasonal thawing in which large amounts of meltwater are produced, presumably allowing for a temporary increase in dispersal rates that may cause density-dependent shifts in the dominant species. Future modeling work should study the effect of dispersal on outcomes to better understand its role in determining communities under founder control.

# 5   Conclusions and Recommendations

## 5.1   Conclusions

In this study, our goal was to analyze the effects of temperature variability on the outcomes of the modified LVCM with temperature-dependent intrinsic growth. We first compared outcomes between different constant temperatures and showed that sufficiently large changes in temperature can change the type of equilibrium outcome as well as the equilibrium abundances or the identity of the dominant species. In the case of single-species dominance and founder control, temperature shifts resulted in a change to the surviving species at equilibrium. In the case of coexistence, the ratios of species abundances shifted between the different temperatures. In all cases, the organism with optimum temperature closer to the environmental temperature was favored.

When using variable temperatures derived from the Imnavait Creek data set, we found that the potential for coexistence and founder control increased compared to the scenario in which temperature was held constant (Figure 7). This meant that, given appropriate competition parameters, temperature variability could facilitate species coexistence or render the system vulnerable to initial conditions. Furthermore, we highlight the importance of incorporating empirical temperature data into ecological models rather than constant or simplified temperature functions, as the predicted outcomes differed among these scenarios.

## 5.2   Recommendations

There are multiple limitations to this study that point to the need for further research. One is that our study does not parameterize the model using data from organisms present in cold regions soils, thus limiting applicability to this specific environment. Another is that the number of microbial species present in soils is much higher than in the simple two-species communities we examined. The analysis presented here should be generalized to communities composed of arbitrarily large numbers of species.

The specific functional form used for temperature-dependent growth may also change results. We chose to use a Gaussian function, based on previous studies and for simplicity. The effect of using a more realistic

skewed function (e.g., Figure 1) was not considered here, but should be examined in future work.

In addition, while our analysis focused on the influence of temperature, other environmental factors such as moisture level and nutrient concentration may vary with time and are known to have significant effects on microbial activity. It may be valuable to consider environmental factors in addition to temperature in a future iteration of the model, both individually and in combination, since environmental variables in reality do not change in isolation.

Soils are heterogeneous environments and future iterations of the model would likely benefit from including a spatial component to account for this heterogeneity. Additionally, the Lotka-Volterra equations have most commonly been used to study macro rather than microorganisms and there are important differences between these types of organisms such as faster generation times and rates of evolution (Prosser et al. 2007). Incorporating these differences into future work will likely be beneficial for long-term predictions.

For these reasons, our current model is best viewed as an initial exploration of potential modelling approaches to capturing the effects of changing environments on microbial communities. Additional factors such as those described above should be considered in future work to improve ability to predict effects of environmental disturbances on microbial diversity in cold-regions soils. Using biological parameters collected from experimental or field data will also allow for model validation and refinement over time.

# Bibliography

Baker, C. C. M., A. J. Barker, T. A. Douglas, S. J. Doherty, and R. A. Barbato. 2023. "Seasonal Variation in Near-Surface Seasonally Thawed Active Layer and Permafrost Soil Microbial Communities." *Environmental Research Letters* 18 (5). https://doi.org/10.1088/1748-9326/acc542.

Barabás, G., and R. D'Andrea. 2016. "The Effect of Intraspecific Variation and Heritability on Community Pattern and Robustness." *Ecology Letters* 19 (8): 977–986. https://doi.org/10.1111/ele.12636.

Barbato, R. A., K. L. Foley, and C. M. Reynolds. 2015. *Soil Temperature and Moisture Effects on Soil Respiration and Microbial Community Abundance.* ERDC/CRREL TR-15-6. Hanover, NH: ERDC-CRREL. http://hdl.handle.net/11681/5549.

Barbato, R. A., L. Waldrop, K. Messan, R. Jones, S. J. Doherty, K. Foley, C. Felt, M. Morgan, and Y. Han. 2018. Dynamic Representation of Terrestrial Soil Predictions of Organisms' Response to the Environment. ERDC/CRREL TR-18-15. Hanover, NH: ERDC-CRREL. http://dx.doi.org/10.21079/11681/29349.

Bhutiyani, M. R., V. S. Kale, and N. J. Pawar. 2007. "Long-Term Trends in Maximum, Minimum and Mean Annual Air Temperatures Across the Northwestern Himalaya During the Twentieth Century." *Climatic Change* 85 (1): 159–177. http://dx.doi.org/10.1007/s10584-006-9196-1.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85 (7): 1771–1789. https://doi.org/10.1890/03-9000.

Doherty, S. J., S. L. LeGrand, K. L. Foley, S. A. Rosten, R. M. Jones, A. R. Fisher, M. Sikaroodi, P. Gillevet, and R. A. Barbato. 2018. *Heterotrophic Microbial Communities in Biological Soil Crusts: Responses to Temperature and Precipitation.* ERDC TR-18-11. Vicksburg, MS: USACE-ERDC. http://dx.doi.org/10.21079/11681/28491.

Ernakovich, J. G., R. A. Barbato, V. I. Rich, C. Schädel, R. E. Hewitt, S. J. Doherty, E. D. Whalen et al. 2022. "Microbiome Assembly in Thawing Permafrost and its Feedbacks to Climate." *Global Change Biology* 28 (17): 5007–5026. https://doi.org/10.1111/gcb.16231.

Friedman, J., L. M. Higgins, and J. Gore. 2017. "Community Structure Follows Simple Assembly Rules in Microbial Microcosms." *Nature Ecology and Evolution* 1 (5): 0109. https://doi.org/10.1038/s41559-017-0109.

Gavin, C., A. Pokrovskii, M. Prentice, and V. Sobolev. 2006 "Dynamics of a Lotka-Volterra Type Model with Applications to Marine Phage Population Dynamics." *Journal of Physics: Conference Series* 55 (1): 80. https://doi.org/10.1088/1742.

Glaspie, C. N., R. D. Seitz, and R. N. Lipcius. "Are Predator-Prey Model Predictions Supported by Empirical Data? Evidence for a Storm-Driven Shift to an Alternative Stable State in a Crab-Clam System." *Marine Ecology Progress Series* 645 (2020): 83–90. https://doi.org/10.1038/s41559-017-0109.

Gounand, I., C. J. Little, E. Harvey, and F. Altermatt. 2018. "Cross-Ecosystem Carbon Flows Connecting Ecosystems Worldwide." *Nature Communications* 9 (1): 4825. https://doi.org/10.1038/s41467-018-07238-2.

Hayatsu, M., K. Tago, and M. Saito. 2008. "Various Players in the Nitrogen Cycle: Diversity and Functions of the Microorganisms Involved in Nitrification and Denitrification." *Soil Science and Plant Nutrition* 54 (1): 33–45. https://doi.org/10.1111/j.1747-0765.2007.00195.x.

Hibbing, M. E., C. Fuqua, M. R. Parsek, and S. B. Peterson. 2010. "Bacterial Competition: Surviving and Thriving in the Microbial Jungle." *Nature Reviews Microbiology* 8 (1): 15–25. https://doi.org/10.1038%2Fnrmicro2259.

Kremer, C. T., and C. A. Klausmeier. 2017. "Species Packing in Eco-Evolutionary Models of Seasonally Fluctuating Environments." *Ecology Letters* 20 (9): 1158–1168. https://doi.org/10.1111/ele.12813.

Lax, S., C. I. Abreu, and J. Gore. 2020. "Higher Temperatures Generically Favour Slower-Growing Bacterial Species in Multispecies Communities." *Nature Ecology and Evolution* 4 (4): 560–567. https://doi.org/10.1038/s41559-020-1126-5.

Lennon, J. J., J. R. G. Turner, and D. Connell. 1997. "A Metapopulation Model of Species Boundaries." *Oikos* 78 (3): 486–502. https://doi.org/10.2307/3545610.

Lotka, A. J. 1924. *Elements of Mathematical Biology*. Mineola, NY: Dover Publications.

Lund, E. W. 1965. "Guldberg and Waage and the Law of Mass Action." *Journal of Chemical Education* 42 (10): 548–550. https://doi.org/10.1021/ed042p548.

MacArthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." The American Naturalist, 101 (921): 377–385. http://dx.doi.org/10.1086/282505.

McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. Guo, D. J. Hayes, et al. 2009 "Sensitivity of the Carbon Cycle in the Arctic to Climate Change." *Ecological Monographs* 79 (4): 523–555. https://doi.org/10.1890/08-2025.1.

Monod, J. 1949. "The Growth of Bacterial Cultures." *Annual Review of Microbiology* 3 (1): 371–394. https://doi.org/10.1146/annurev.mi.03.100149.002103.

Moyano, F. E., S. Manzoni, and C. Chenu. 2013. "Responses of Soil Heterotrophic Respiration to Moisture Availability: An Exploration of Processes and Models." *Soil Biology and Biochemistry* 59:72–85. https://doi.org/10.1016/j.soilbio.2013.01.002.

O'Brien, J., and G. D. Wright. 2011. "An Ecological Perspective of Microbial Secondary Metabolism." *Current Opinion in Biotechnology* 22 (4): 552–558. https://doi.org/10.1016/j.copbio.2011.03.010.

Osterkamp, T. E., and M. W. Payne. 1981. "Estimates of Permafrost Thickness from Well Logs in Northern Alaska." *Cold Regions Science and Technology* 5 (1): 13–27. https://doi.org/10.1016/0165-232X(81)90037-9.

O'Sullivan, J. D., R. J. Knell, and A. G. Rossberg. 2019. "Metacommunity-Scale Biodiversity Regulation and the Self-Organised Emergence of Macroecological Patterns." E*cology Letters* 22 (9): 1428–1438. https://doi.org/10.1111/ele.13294.

Palmer, J. D. and K. R. Foster. 2022. "Bacterial Species Rarely Work Together." *Science* 376 (6593): 581–582. https://doi.org/10.1126/science.abn5093.

Pikuta, E. V., R. B. Hoover, and J. Tang. 2007. "Microbial Extremophiles at the Limits of Life." *Critical Reviews in Microbiology* 33 (3): 183–209. https://doi.org/10.1080/10408410701451948.

Prosser, J. I., B. J. Bohannan, T. P. Curtis, R. J. Ellis, M. K. Firestone, R. P. Freckleton, J. L. Green, et al. 2007. "The Role of Ecological Theory in Microbial Ecology." *Nature Reviews Microbiology* 5 (5): 384–392. https://www.nature.com/articles/nrmicro1643.

Ramoneda, J., E. Stallard-Olivera, M. Hoffert, C. C. Winfrey, M. Stadler, J. P. Niño-García, and N. Fierer. 2023. "Building a Genome-Based Understanding of Bacterial pH Preferences." *Science advances* 9 (17). https://doi.org/10.1126/sciadv.adf8998.

Rousk, J., E. Bååth, P. C. Brookes, C. L. Lauber, C. Lozupone, J. G. Caporaso, R. Knight, and N. Fierer. 2010. "Soil Bacterial and Fungal Communities Across a pH Gradient in an Arable Soil." *The ISME Journal* 4 (10): 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. "Non-Linear Regression of Biological Temperature-Dependent Rate Models Based On Absolute Reaction-Rate Theory." *Journal of Theoretical Biology* 88 (4): 719–731. https://doi.org/10.1016/0022-5193(81)90246-0.

Schulte, P. M., T. M. Healy, and N. A. Fangue. 2011. "Thermal Performance Curves, Phenotypic Plasticity, and the Time Scales of Temperature Exposure." *Integrative and Comparative Biology* 51 (5): 691–702. https://doi.org/10.1093/icb/icr097.

Sharpe, P. J. H., and D. W. DeMichele. 1977. "Reaction Kinetics of Poikilotherm Development." *Journal of Theoretical Biology* 64 (4): 649–670. https://doi.org/10.1016/0022-5193(77)90265-x.

Shaw, G. T-W., Y-Y. Pao, and D. Wang. 2016. "MetaMIS: a Metagenomic Microbial Interaction Simulator Based On Microbial Community Profiles." *BMC Bioinformatics* 17 (1): 1–12. https://doi.org/10.1186/s12859-016-1359-0.

Streit, K., F. Hagedorn, D. Hiltbrunner, M. Portmann, M. Saurer, N. Buchmann, B. Wild, A. Richter, S. Wipf, and R. T. W. Siegwolf. 2014. "Soil Warming Alters Microbial Substrate Use in Alpine Soils." *Global Change Biology* 20 (4): 1327–1338. https://doi.org/10.1111/gcb.12396.

Tripathi, B. M., H. M. Kim, J. Y. Jung, S. Nam, H. T. Ju, M. Kim, and Y. K. Lee. 2019. "Distinct Taxonomic and Functional Profiles of the Microbiome Associated with Different Soil Horizons of a Moist Tussock Tundra in Alaska." *Frontiers in Microbiology* 10:1442. https://doi.org/10.3389/fmicb.2019.01442.

Tsoularis, A., and J. Wallace. 2002. "Analysis of Logistic Growth Models." *Mathematical Biosciences* 179 (1): 21–55. https://doi.org/10.1016/S0025-5564(02)00096-2.

Volterra, V. 1931. *Leçons sur la Theorie Mathématique de la Lutte pour la Vie*. Paris: Goutliers-Vallars. http://catalogue.bnf.fr/ark:/12148/cb35067585k.

Waldrop, M. P., T. C. Balser, and M. K. Firestone. 2000. "Linking Microbial Community Composition to Function in a Tropical Soil." *Soil Biology and Biochemistry* 32 (13): 1837–1846. https://doi.org/10.1016/S0038-0717(00)00157-7.

# Appendix: Analytical Results for the Lotka-Volterra Competition (LVCM)

## A.1 Invasibility Conditions for the Temperature Dependent LVCM

We start by considering communities consisting of either species 1 or species 2 at equilibrium and derive the invasion fitnesses for the absent species. These determine the possible outcomes of the model: single-species dominance, coexistence, or founder control. From Equations (2) and (3), the equilibrium abundances are $\frac{r_1(T)}{a_{11}}$ and $\frac{r_2(T)}{a_{22}}$ in these two communities. Using these abundances in Equations (2) and (3), we can define the per capita growth rate of the absent species when it is introduced.

$$\frac{1}{n_1}\frac{dn_1}{dt}\Big|_{n_2=\frac{r_2(T)}{a_{22}}} \equiv \lambda_1 = r_1(T) - a_{11}n_1 - a_{21}\frac{r_2(T)}{a_{22}} \tag{A-1}$$

and

$$\frac{1}{n_2}\frac{dn_2}{dt}\Big|_{n_1=\frac{r_1(T)}{a_{11}}} \equiv \lambda_2 = r_2(T) - a_{22}n_2 - a_{12}\frac{r_1(T)}{a_{11}}, \tag{A-2}$$

where $\lambda_1$ and $\lambda_2$ are termed the invasion fitnesses for species 1 and 2, respectively. Assuming that the invading species is initially so rare that it has no effect on the per capita growth rate ($n_1 \sim 0$ for Equation [A-1] and $n_2 \sim 0$ for Equation [A-2]), these equations become

$$\lambda_1 = r_1(T) - a_{21}\frac{r_2(T)}{a_{22}} \tag{A-3}$$

and

$$\lambda_2 = r_2(T) - a_{12}\frac{r_1(T)}{a_{11}}. \tag{A-4}$$

These equations are equivalent to one of the eigenvalues of the single-species equilibria for each organism; (A-3) represents one of the eigenvalues for the species 2 single-species equilibrium, while (A-4) represents one of the eigenvalues for the species 1 single-species equilibrium. The second eigenvalue will always be negative for positive growth rates according to the Jacobian matrix for the system of equations

consisting of Equations (1) and (2) at the single-species equilibria for species 1 and 2:

$$\text{Species 1:} \begin{pmatrix} \frac{\partial \frac{dn_1}{dt}}{\partial n_1} & \frac{\partial \frac{dn_1}{dt}}{\partial n_2} \\ \frac{\partial \frac{dn_2}{dt}}{\partial n_1} & \frac{\partial \frac{dn_2}{dt}}{\partial n_2} \end{pmatrix}_{\Big|(n_1=\frac{r_1(T)}{a_{11}},\, n_2=0)} = \begin{pmatrix} -r_1(T) & \frac{-a_{21}r_1(T)}{a_{11}} \\ 0 & r_2 - \frac{a_{12}r_1(T)}{a_{11}} \end{pmatrix} \quad \text{(A-5)}$$

and

$$\text{Species 2:} \begin{pmatrix} \frac{\partial \frac{dn_1}{dt}}{\partial n_1} & \frac{\partial \frac{dn_1}{dt}}{\partial n_2} \\ \frac{\partial \frac{dn_2}{dt}}{\partial n_1} & \frac{\partial \frac{dn_2}{dt}}{\partial n_2} \end{pmatrix}_{\Big|(n_1=0,\, n_2=\frac{r_2(T)}{a_{22}})} = \begin{pmatrix} r_1 - \frac{a_{21}r_2(T)}{a_{22}} & 0 \\ \frac{-a_{12}r_2(T)}{a_{22}} & -r_2(T) \end{pmatrix}, \quad \text{(A-6)}$$

where $-r_1(T)$ and $r_2(T) - \frac{a_{12}r_1(T)}{a_{11}}$ from (A-5) are the eigenvalues for the single-species equilibrium for species 1, and $-r_2(T)$ and $r_2 - \frac{a_{21}r_2(T)}{a_{22}}$ from (A-6) are the eigenvalues for the single-species equilibrium for species 2 respectively.

The equilibrium outcome is therefore determined by the sign on the invasion fitnesses. When $\lambda_1 > 0$ and $\lambda_2 > 0$, single-species dominance is unstable and each species can invade the other when rare, implying that the species can coexist indefinitely. When $\lambda_1 > 0$ and $\lambda_2 < 0$, or $\lambda_1 < 0$ and $\lambda_2 > 0$, the system is semistable and only the species with positive invasion fitness can invade the other when rare, so the outcome is single-species dominance. Finally, when $\lambda_1 < 0$ and $\lambda_2 < 0$, single-species dominance for both species is stable and neither species is invasible at equilibrium. The result therefore depends on the species that reached equilibrium first. In this case, the outcome is founder control. The conditions governing equilibrium outcomes shown in Equations (5)–(8) result directly from setting the signs on the invasion fitnesses in Equations (A-3) and (A-4) and rearranging. Assuming that initial species abundances are not necessarily rare, these results still hold, since growth rate decreases with species abundance as shown in Equations (A-1) and (A-2). Therefore, growth rate is highest when the abundance of an invading species approaches zero and these results generalize for larger population sizes.

For variable temperature conditions, since abundance and intrinsic growth rate $r(T)$ are not constant over time, species abundances and

intrinsic growth rates under single-species dominance were averaged over the period of the timeseries (i.e., one year) and used in Equations (A-1) and (A-2) instead of the theoretical equilibrium abundances, in which case the Equations (A-3) and (A-4) become

$$\lambda_1 \equiv \frac{1}{365} \int_0^{365} (r_1(T(t)) - a_{21}n_2(t))dt = \overline{r_1(T)} - a_{21}.\overline{n_2} \qquad \text{(A-7)}$$

and

$$\lambda_2 \equiv \frac{1}{365} \int_0^{365} (r_2(T(t)) - a_{12}n_1(t))dt = \overline{r_2(T)} - a_{12}.\overline{n_1}, \qquad \text{(A-8)}$$

where

$\overline{r_i(T)}$ = average intrinsic growth rate for species $i$ and
$\overline{n_i}$ = average abundance for species $i$.

## A.2 Equivalence of the Regions of Coexistence and Founder Control When Coefficients are Swapped

From Equations (5)—(8), coexistence conditions are met when

$$\frac{a_{11}}{a_{12}} > \frac{r_1}{r_2} > \frac{a_{21}}{a_{22}}, \qquad \text{(A-9)}$$

whereas founder control conditions are met when

$$\frac{a_{21}}{a_{22}} > \frac{r_1}{r_2} > \frac{a_{11}}{a_{12}}. \qquad \text{(A-10)}$$

Here, we describe the special case resulting from using intraspecific competition coefficients that are double that of the interspecific competition coefficients and vice-versa, in which the set of two species combinations with different $T^*$ values resulting in either coexistence or founder control are equivalent. Under coexistence conditions, we chose competition coefficients such that $a_{11}=2a_{12}$ and $a_{22}=2a_{21}$ (Table 1). Substituting this into Equation (A-10) gives

$$2 > \frac{r_1}{r_2} > \frac{1}{2}. \qquad \text{(A-11)}$$

To represent founder control conditions, competition coefficients were swapped such that $2a_{11}= a_{12}$ and $2a_{22}= a_{21}$. Substituting this into

Equation (A-10) gives $2 > \frac{r_1}{r_2} > \frac{1}{2}$, which is equivalent to Equation (A-11), therefore showing that the values of $r_1$ and $r_2$ satisfying conditions for coexistence and founder control are equivalent when values are swapped between the two conditions.

## A.3 Solving for equilibrium outcomes

Setting Equations (2) and (3) equal to zero, we can solve for $n_1^*$ and $n_2^*$, the equilibrium abundances of species 1 and species 2 respectively as

$$n_1^* = \frac{r_1 - a_{21} n_2^*}{a_{11}}$$

(A-12)

and

$$n_2^* = \frac{r_2 - a_{12} n_1^*}{a_{22}}.$$

(A-13)

When the equilibrium abundance of the alternate species is zero, these equations simplify to the following:

$$n_1^* = \frac{r_1}{a_{11}}$$

(A-14)

and

$$n_2^* = \frac{r_2}{a_{22}}.$$

(A-15)

In the case where abundances of both species are nonzero, we can further simplify this by eliminating one of the population abundance variables in each equation to give

$$n_1^* = \frac{a_{12} r_2 - a_{22} r_1}{a_{12} a_{21} - a_{11} a_{22}}$$

(A-16)

and

$$n_2^* = \frac{a_{21} r_1 - a_{11} r_2}{a_{12} a_{21} - a_{11} a_{22}}.$$

(A-17)

# Abbreviations

| | |
|---|---|
| DRTSPORE | Dynamic Representation of Terrestrial Soil Predictions of Organisms' Response to the Environment |
| LVCM | Lotka-Volterra Competition Model |
| RMSE | Root-mean-square-error |

# REPORT DOCUMENTATION PAGE

| 1. REPORT DATE February 2024 | 2. REPORT TYPE Final Report | 3. DATES COVERED | |
|---|---|---|---|
| | | START DATE FY21 | END DATE FY22 |

**4. TITLE AND SUBTITLE**
Ecological Modeling of Microbial Community Composition under Variable Temperatures

| 5a. CONTRACT NUMBER | 5b. GRANT NUMBER | 5c. PROGRAM ELEMENT 0622144A |
|---|---|---|
| 5d. PROJECT NUMBER BN8 | 5e. TASK NUMBER | 5f. WORK UNIT NUMBER |

**6. AUTHOR(S)**
Logan M. Gonzalez, Christopher C. M. Baker, Stacey J. Doherty, and Robyn A. Barbato

| 7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) US Army Engineer Research and Development Center (ERDC) Cold Regions Research and Engineering Laboratory (CRREL) 72 Lyme Road Hanover, NH 03755-1290 | 8. PERFORMING ORGANIZATION REPORT NUMBER ERDC/CRREL TR-24-2 |
|---|---|

| 9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) Headquarters, US Army Corps of Engineers Washington, DC 20314-1000 | 10. SPONSOR/MONITOR'S ACRONYM(S) | 11. SPONSOR/MONITOR'S REPORT NUMBER(S) |
|---|---|---|

**12. DISTRIBUTION/AVAILABILITY STATEMENT**
Distribution Statement A. Approved for public release: distribution is unlimited.

**13. SUPPLEMENTARY NOTES**
Congressional Ad Program Defense Resiliency Platform Against Extreme Cold Weather

**14. ABSTRACT**
Soil microorganisms interact with one another within soil pores and respond to external conditions such as temperature. Data on microbial community composition and potential function are commonly generated in studies of soils. However, these data do not provide direct insight into the drivers of community composition and can be difficult to interpret outside the context of ecological theory. In this study, we explore the effect of abiotic environmental variation on microbial species diversity. Using a modified version of the Lotka-Volterra Competition Model with temperature-dependent growth rates, we show that environmentally relevant temperature variability may increase the range of two-species communities that can persist compared to constant temperatures. These results highlight a potential role of temperature variation in influencing microbial diversity. This in turn suggests a need to incorporate temperature into predictive models of microbial communities in soil and other environments. We recommend future work to parameterize the model applied in this study with empirical data from environments of interest, and to validate the model predictions using field observations and experimental manipulations.

**15. SUBJECT TERMS**
Biodiversity-Climatic-factors; Biological-systems-Mathematical-models; Microbial ecology; Psychrotrophic organisms

| 16. SECURITY CLASSIFICATION OF: | | | 17. LIMITATION OF ABSTRACT SAR | 18. NUMBER OF PAGES 55 |
|---|---|---|---|---|
| a. REPORT Unclassified | b. ABSTRACT Unclassified | C. THIS PAGE Unclassified | | |

| 19a. NAME OF RESPONSIBLE PERSON | 19b. TELEPHONE NUMBER (include area code) |
|---|---|

**STANDARD FORM 298 (REV. 5/2020)**

PREVIOUS EDITION IS OBSOLETE.

*Prescribed by ANSI Std. Z39.18*