

# Context-dependent host-microbe interactions in stochastic environments

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This manuscript was compiled on October 13, 2021

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Classic ecological theory predicts that long-term population growth rates will be reduced by environmental variability (1, 2). Along with increases in average temperatures, global climate change is driving increases in the variability of precipitation events, temperature extremes, and droughts (3–5). In stochastic environments, populations can expect to experience good years and bad years. The long-term stochastic growth rate ( $\lambda_s$ ), which is the long-run geometric mean of annual growth rates, captures this variability; This geometric mean will always be less than expected from the mean growth rate alone.

$\lambda_s$  can be approximated as:

$$\log(\lambda_s) \approx \log(\bar{\lambda}) - \frac{\sigma^2}{2\bar{\lambda}^2}$$

Where  $\bar{\lambda}$  is the mean of annual population growth rates ( $\lambda_t$ ) and  $\sigma^2$  is the variance (1). Populations will increase over time if  $\lambda_s$  is greater than 1, and can be expected to decrease if  $\lambda_s$  is less than 1. Here, there are two pathways to influence  $\lambda_s$ : (1) increasing the mean growth rate, and/or (2) reducing the variance in growth rates. The demographic tradeoff between mean and variance has been important in shaping life-history theory (6) and population viability analysis (7). Anything that limits the negative effects of bad years, while being neutral or costly in good years has the potential to decrease the impact of interannual environmental variability on population dynamics because it would limit variance.

In nature, microbial symbionts provide protection from environmental stresses including drought, temperature, and enemies across a broad range of taxa (8). Commonly, the benefits from these symbioses are context-dependent where the magnitude of interaction benefit depends on environmental conditions (9). This can make it difficult to quantify the net effect of a given interaction, but it also allows for the possibility that interaction strength can vary through time (cite). Symbionts may provide benefits under harsh conditions when they are needed by their hosts, but be neutral or even costly under benign conditions (cite). Over time, this may lead symbiont-associated organisms to experience a reduction in variation in vital rates by reducing the frequency of extreme years (conceptual figure). Whether species interactions contribute to variance buffering is an underexplored question (10), and a novel mechanism by which symbionts can act as mutualists that may come to be of increasing importance in a more variable future.

Using long-term data from experimental grass-fungal endo-

phyte plots, we test the hypothesis that symbionts buffer hosts from the fitness consequences of environmental variability. Specifically, we ask first how fungal endophytes influence the mean and interannual variance of their hosts' vital rates; next, we ask if these vital rate effects buffer demographic variance, and, if so, what is the relative importance of demographic buffering vs. mean effects in the overall fitness impact of the symbiosis. With 13 years of demographic data, we employ structured, stochastic population models for seven species of cool-season grass hosts that are commonly infected with fungal endophytes (*Lolium arundinaceum*, *Festuca subverticillata*, *Elymus virginicus*, and *Elymus villosus*, *Poa alsodes* and *Poa sylvestris*). These long-term data, in which each annual census is a sample of environmental variation, allow us to construct a climate-explicit population models, which we use to evaluate the importance of buffering under simulated increases in mean and variance of climate drivers.

This paragraph is mostly talking off my head about results, but my idea is to include a brief statement of our results. Across species, we find that variance buffering by endophytes contributes (percentage) to population growth rates. While the effect is generally weaker than effects on the mean, we found that buffering was common in the most sensitive vital rates, and was most important for xxx species with xxx life history.

## Results

## Discussion

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**Table 1. Comparison of the fitted potential energy surfaces and ab initio benchmark electronic energy calculations**

Species	CBS	CV	G3
1. Acetaldehyde	0.0	0.0	0.0
2. Vinyl alcohol	9.1	9.6	13.5
3. Hydroxyethylidene	50.8	51.2	54.0

nomenclature for the TSs refers to the numbered species in the table.

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$$\begin{aligned}
 (x+y)^3 &= (x+y)(x+y)^2 \\
 &= (x+y)(x^2+2xy+y^2) \\
 &= x^3+3x^2y+3xy^2+y^3.
 \end{aligned}
 \tag{1}$$

## Materials and Methods

**Plant propagation and endophyte removal.** Seeds from naturally infected populations of seven species of cool-season grasses (*Agrostis perennans*, *Elymus villosus*, *Elymus virginicus*, *Festuca subverticillata*, *Lolium arundinaceum*, *Poa alsodes*, and *Poa sylvestris*) were collected in the Spring of 2006 from Lilly Dickie Woods (Lat,Lon) and Bayles Road (Lat,Lon) in Brown. Co. IN. Seeds with shared maternal ancestry were either experimentally disinfected by heat treatments or left naturally infected to reduce confounding genotype effects. Seeds were surface sterilized with XXXX and cold stratified for XXXX weeks, then germinated in a growth chamber for XXXX weeks. Seedlings were then transferred to the greenhouse at Indiana University and allowed to grow for XXXX weeks. We confirmed the endophyte status of these plants using leaf peels (cite), and vegetatively propagated clones of similar sizes from the plants. These clones were used to establish the experimental plots, and cloning reduces the potential for negative effects of heat treatments (cite).

**Experimental design and data collection.** In 2007, we established 10 3x3 plots for *Lolium arundinaceum*, *Festuca subverticillata*, *Elymus virginicus*, and *Elymus villosus* and 18 plots for *Poa alsodes* and *Poa sylvestris*. For each species, an equal number of plots were randomly assigned to each endophyte status, E+ or E-, and was planted with only symbiotic or symbiont-free plants respectively. Each plot was planted with 25 evenly spaced individuals and each plant marked with aluminum tags.

In each Summer starting in 2007, we censused all original transplants and any recruits for survival, growth and reproduction. After clearing out leaf litter, for each plant alive in the previous year, we marked its survival. We measured the size of each plant as a count of the number of tillers. Further, we collected reproductive data by counting the number of reproductive tillers, and then counting the number of seed-bearing spikelets on up to three of those reproductive tillers. In XXXX year, we took additional counts of seeds per inflorescence (list of species) or seeds per spikelet (list of species). Together, we use these measurements to estimate seed production. In each plot, we also survey for and mark any unmarked individuals. New recruits are typically a size of one tiller and non-reproductive, but we also find and mark any individuals who may have been missed in previous censuses.

We typically expect plots of each endophyte status to maintain their status as the fungus is almost entirely vertically transmitted, and plots are spaced at least XX m apart, limiting the possibility for unwanted dispersal between plots or horizontal transmission of the fungus. Seeds from reproductive individuals are opportunistically taken and scored for their endophyte status. These scores reflect a XXXX% faithfulness of recruits to their expected endophyte status (Supplement data)

In sum, this individual-level demographic dataset covers 14 years and contains 30,XXXX individual transition-years.

**Demographic modeling.** Armed with this demographic data, we next constructed size-structured, stochastic population models. For each species

**Model description and estimation.**

**Model assessment.**

**Life table response experiment.**

**Estimating climate drivers of environmental context-dependence.**

**Climate data.**

**Climate-explicit Model description and estimation.**

**Climate-explicit Model assessment.**

**Forecasting under alternative climate forcings.** We used statistics

**ACKNOWLEDGMENTS.** Please include your acknowledgments here, set in a single paragraph. Please do not include any acknowledgments in the Supporting Information, or anywhere else in the manuscript.

1. R. C. Lewontin and D. Cohen. On Population Growth in a Randomly Varying Environment. *Proceedings of the National Academy of Sciences*, 62(4):1056–1060, April 1969. ISSN 0027-8424, 1091-6490. . URL <https://www.pnas.org/content/62/4/1056>. Publisher: National Academy of Sciences Section: Biological Sciences: Zoology.
2. Shripad D. Tuljapurkar. Population dynamics in variable environments. III. Evolutionary dynamics of r-selection. *Theoretical Population Biology*, 21(1):141–165, February 1982. ISSN 0040-5809. . URL <http://www.sciencedirect.com/science/article/pii/0040580982900107>.
3. IPCC (Intergovernmental Panel on Climate Change). *Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change. Special Report*. Cambridge University Press, 2012.
4. Sonia Seneviratne, Neville Nicholls, David Easterling, Clare Goodess, Shinjiro Kanae, James Kossin, Yali Luo, Jose Marengo, Kathleen McInnes, Mohammad Rahimi, et al. Changes in climate extremes and their impacts on the natural physical environment. 2012.
5. Thomas F Stocker, Dahe Qin, G-K Plattner, Lisa V Alexander, Simon K Allen, Nathaniel L Bindoff, F-M Br  n, John A Church, Ulrich Cubasch, Seita Emori, et al. Technical summary. In *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pages 33–115. Cambridge University Press, 2013.
6. Catherine A Pfister. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, 95(1):213–218, 1998.
7. Eric S Menges. Population viability analysis for an endangered plant. *Conservation biology*, 4(1):52–62, 1990.
8. Stephanie N Kivlin, Sarah M Emery, and Jennifer A Rudgers. Fungal symbionts alter plant responses to global change. *American Journal of Botany*, 100(7):1445–1457, 2013.
9. Scott A Chamberlain, Judith L Bronstein, and Jennifer A Rudgers. How context dependent are species interactions? *Ecology letters*, 17(7):881–890, 2014.
10. Christoffer H. Hilde, Marl  ne Gamelon, Bernt-Erik S  ther, Jean-Michel Gaillard, Nigel G. Yoccoz, and Christophe P  labon. The Demographic Buffering Hypothesis: Evidence and Challenges. *Trends in Ecology & Evolution*, 0(0), March 2020. ISSN 0169-5347. . URL [https://www.cell.com/trends/ecology-evolution/abstract/S0169-5347\(20\)30050-1](https://www.cell.com/trends/ecology-evolution/abstract/S0169-5347(20)30050-1). Publisher: Elsevier.