

# Demographic buffering by context-dependent host-microbe interactions in stochastic environments

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This manuscript was compiled on August 3, 2021

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Keyword 1 | Keyword 2 | Keyword 3 | ...

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 environmental variability (3–5). In stochastic environments, populations will have good years and bad years. The long-term stochastic growth rate ( $\lambda_s$ ) is the long-run geometric mean of annual growth rates; This geometric mean will always be less than expected from the mean growth rate alone. 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.

$\lambda_s$  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). Here, there are two pathways to influence  $\lambda_s$ : increasing the mean growth rate, and reducing the variance in growth rates. 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. The demographic tradeoff between mean and variance has been important in shaping life-history theory (6) and population viability analysis (7).

Maybe need to mention vital rates in introduction? not sure how much that will be part of our paper? It's kind of question 1, but also, not necessarily the main result.

Across the tree of life, microbial symbionts provide protection from environmental stresses including drought, temperature, and enemies (8). By affecting demographic vital rates such as survival, growth and reproduction, these symbioses range from facultative to obligate that determine their partners fitness (). Commonly, the costs and benefits from symbioses depend on environmental conditions (9). This can make it difficult to quantify the net effect of a given interaction, but it also allows for interactions to be dynamic 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 by reducing the frequency of extreme years (conceptual figure).

Variance buffering is a novel mechanism by which sym-

bionts can act as mutualists that may come to be of increasing importance under a more variable future climate. Contributions from demographic buffering in natural populations may become more important under this scenario and will be important for projecting species' responses to climate change (10). In particular, it is unclear how commonly demographic buffering plays an important role in population dynamics in general, and how species interactions may contribute to demographic buffering (11). Our ability to explore the demographic consequences of environmental variation in nature relies on long-term observational studies and experiments that sample from the distribution of natural climatic variation ().

Using long-term data from experimental grass-fungal endophyte plots, we test the hypothesis that symbionts buffer hosts from the fitness consequences of environmental variability. Specifically, we ask if fungal endophytes buffer demographic variance in their grass hosts, and, if so, what is the relative importance of demographic buffering vs. mean effects in the overall fitness impact of the symbiosis. With 14 years of demographic data, we employ structured, stochastic population models for seven species of cool-season grass hosts that are common hosts of vertically-transmitted fungal endophytes (*Lolium arundinaceum*, *Festuca subverticillata*, *Elymus virginicus*, and *Elymus villosus*, *Poa alsodes* and *Poa sylvestris*).

As in the demographic buffering hypothesis, where the fitness consequences of environmental variability may select for buffering in the vital rates that are most consequential for population growth (6), the fitness consequences of species interactions may apply to both the mean and variance of vital rates.

Our ability to explore the demographic consequences of environmental variation in nature relies on long-term observational studies and experiments that capture natural climatic

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variation (cite) plus maybe examples of other studies looking at demographic buffering. While there is appreciation for long-term studies and recognition of the importance of studying both climate mean and variance in ecology, demographic studies that examine demographic buffering are limited due to the need for long term data and the need to account for multiple sources of variation within data (11).

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

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## 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????? for Lilly Dickie Woods and Bayles Road 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 the XXXX for XXXX weeks. They were then grown in the greenhouse at Indiana University for XXXX weeks.

**Experimental design and data collection.** We collected long-term demographic data from experimental plots established in 2007. We established 10 plots for *Lolium arundinaceum*, *Festuca subverticillata*, *Elymus virginicus*, and *Elymus villosus* and 18 plots for *Poa alsodes* and *Poa sylvestris* with 25? individuals.

**Demographic modeling.**

**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.

- 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.
- 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>.
- 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.
- 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.
- 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.
- 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.
- Eric S Menges. Population viability analysis for an endangered plant. *Conservation biology*, 4(1):52–62, 1990.
- 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.
- Scott A Chamberlain, Judith L Bronstein, and Jennifer A Rudgers. How context dependent are species interactions? *Ecology letters*, 17(7):881–890, 2014.
- Daniel F Doak, William F Morris, Cathy Pfister, Bruce E Kendall, and Emilio M Bruna. Correctly estimating how environmental stochasticity influences fitness and population growth. *The American Naturalist*, 166(1):E14–E21, 2005.
- 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.