Context-dependent host-microbe interactions in stochastic environments

Joshua C. Fowler^{a,1}, Shaun Ziegler^b, Kenneth D. Whitney^b, Jennifer A. Rudgers^b, and Tom E. X. Miller^a

^aRice University, Department of BioSciences, Houston, TX, 77005; ^bUniversity of New Mexico, Department of Biology, Albuquerque, NM, 87131

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C lassic ecological theory predicts that environmental variation will tend to have negative consequences for long-term population growth rates (1, 2). Long-term population growth rates (λ) incur a cost due to temporal variation. Our ability to explore the demographic consequences of environmental variation in nature relies on long-term observational studies and experiments that capture natural climatic 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 (3).

Long-term population growth rates, which are calculated as geometric means, incur a cost due to temporal variation (1, 2). A population will increase over time if the long term growth rate (λ) is >1, and can be expected to decrease if $\lambda < 1$. There are two pathways by which population growth can increase: mean λ can increase or variance can decrease (). include math somewhere here. 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 (4), the fitness consequences of species interactions may apply to both the mean and variance of vital rates. Whether variance buffering by species interactions occurs is an underexplored question, but it may come to be of increasing importance under climate change.

Climate projections indicate that environmental variability is expected to increase along with increases in mean climate conditions (5, 6). 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 (7). 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 (cite). Mutualistic symbioses in particular may have the potential to provide resilience to environmental variability (cite). I don't know about that last sentence, but I need some sort of transition to symbiosis.

In nature, microbial symbionts provide protection from environmental stresses across a broad range of taxa, including stress caused by drought, salinity, and temperature (cite). Commonly, the benefits from these symbioses are context-dependent where the magnitude of interaction benefit changes depending on environmental conditions (8). 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 events (conceptual figure). Variance buffering by symbionts is novel mechanism that may be common across many symbioses that

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 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).

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.

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 $^{^{1}\}text{To}$ whom correspondence should be addressed. E-mail: jcf3rice.edu

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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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$$(x+y)^3 = (x+y)(x+y)^2$$

= $(x+y)(x^2 + 2xy + y^2)$
= $x^3 + 3x^2y + 3xy^3 + x^3$. [1]

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Materials and Methods

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Plant propagation and endophyte treatment. 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. 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.

Data analysis. We used statistics

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- 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.
- Christoffer H. Hilde, Marlène Gamelon, Bernt-Erik Sæther, Jean-Michel Gaillard, Nigel G.
 Yoccoz, and Christophe Pélabon. 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.
 Publisher: Elsevier.
 - 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.
 - 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.
- 6. David T Iles, Robert F Rockwell, and David N Koons. Shifting vital rate correlations
 alter predicted population responses to increasingly variable environments. The American
 Naturalist, 193(3):E57–E64, 2019.
 - 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.

Scott A Chamberlain, Judith L Bronstein, and Jennifer A Rudgers. How context dependent are species interactions? Ecology letters, 17(7):881–890, 2014.

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