

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

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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 environmental variability (3–5). In stochastic environments, populations will have good years and bad years. The long-term stochastic growth rate (λ_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 λ_s is greater than 1, and can be expected to decrease if λ_s is less than 1.

λ_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 (λ_t) and σ^2 is the variance (1). Here, there are two pathways to influence λ_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).

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 symbionts 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*).

To explore how environmental variability drives symbionts' effects on demographic buffering we built climate-explicit population models (). We use these models to project how the relative importance of mean effects vs. variance buffering will affect populations under simulated increases in mean and variance relevant to future climate change.

Maybe need to mention vital rates more 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.

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73 Results

74 Across species, we find that variance buffering by endophytes
75 contributes (percentage) to population growth rates. While
76 the effect is generally weaker than effects on the mean, we
77 found that buffering was common in the most sensitive vital
78 rates, and was most important for xxx species with xxx life
79 history.

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

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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 from Indiana University field sites at Lilly Dickie Woods and Bayles Road in Brown County, 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 a 10% solution of NaOH and cold stratified for 6 weeks, then germinated in the XXXX weeks. They were then grown in the greenhouse at Indiana University for XXXX weeks.

We determined the endophyte status, either symbiotic (S+) or symbiont-free (S-), of reared plants using immunoblot assays and leaf peels.

It would also be nice if we could just say, see this other paper that describes our disinfection and germination protocol.

Experimental design and data collection. We established 87 3m x 3m plots in 2007 for each species by planting 25 individuals in a grid pattern. Overall, half of the plots were planted with known S+ individuals, and the other half with S- individuals, creating S+ and S- plots. 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. Each year, during their peak flowering time, we mark and census all individuals in the plots, including the original transplants and any seedlings that have recruited into the plots, recording their survival, size (measured as number of tillers), flowering status (measured as number of flowering tillers), and their seed production (measured as spikelets per inflorescence). Because endophytes are vertically transmitted, we expect that recruits will maintain the endophyte status of their parents in the plot. We opportunistically collect seeds from flowering individuals to confirm their endophyte status. Overall, plots have remained xxx% faithful to their original plot designations, indicating relatively low rates of imperfect transmission or dispersal between plots (see Supplementary Materials).

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

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