

Context-dependent host-microbe interactions in stochastic environments

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Microbial symbioses are ubiquitous in nature, yet our ability to predict how these interactions can affect species responses to climate change has been limited by interaction outcomes that vary with environmental context. Increased environmental variability is a key prediction of climate change. Here we present and test a novel hypothesis: microbial symbionts may buffer hosts from environmental variability by being beneficial in harsh years while being neutral or costly in good years.

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Along with increases in average temperatures, global climate change is driving increases in the variability of precipitation events, temperature extremes, and droughts (1–3). Thus discerning the effects of variability on population dynamics and species interactions is pivotal to forecasting the future of ecological systems. Classic ecological theory predicts that long-term population growth rates will decline under increased environmental variability (4, 5). This stochastic variability means that populations can expect to experience both good and bad years. The long-term stochastic growth rate (λ_s), which is the long-run geometric mean of annual growth rates, captures this variability; the geometric mean will always be less than expected from the mean growth rate alone.

Following Lewontin and Cohen (4), λ_s for unstructured populations can be approximated as:

$$\log(\lambda_s) \approx \log(\bar{\lambda}) - \frac{\sigma^2}{2\bar{\lambda}^2} \quad [1]$$

Where $\bar{\lambda}$ is the mean of annual population growth rates (λ_t) and σ^2 is the variance (4). 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. Here, there are two pathways to increase λ_s : (1) increasing the mean growth rate, and/or (2) reducing the variance in growth rates. All else equal, the negative effects of variability are expected to be similarly relevant to structured populations (6, 7). That both mean and variance are important in determining fitness underlies understanding of which aspects of a species' life history influence its success (8, 9) and has important implications for population viability analysis (10). Thus much attention has focused on the ways in which variation in vital rates (survival, growth and reproduction), correlations between vital rates (11), transient shifts in stage structure (12), and the degree of environmental autocorrelation (13, 14) can amplify or buffer environmental variation. The degree to which species interactions contribute to effects on the variance in growth rates is an underexplored question (15).

Microbial symbioses are ubiquitous in nature and are crucial determinants of host fitness (16, 17), and as yet, we know little about their potential influence on responses to climate change and environmental variation (18). Across a broad range of taxa, mutualistic host-associated microbes provide protection from environmental stresses including drought, extreme temperatures, and enemies (19–23). The role they play may be under-appreciated, and it can be difficult to quantify the net outcome of a given interaction because they are often viewed as being context-dependent where the magnitude of benefit depends on environmental conditions (24). Rather than considering context-dependence as some unexplainable intricacy of species interactions, environmental variation opens up the possibility for interaction strength to vary through time (25, 26) and to influence the variance of population growth rates.

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 would lead symbiotic hosts to experience a reduction in variation in vital rates by reducing the frequency of extreme years (conceptual figure). Incorporating context-dependence in this way, we propose a novel mechanism by which symbionts can act as mutualists that may come to be of increasing importance in a more variable future.

Using unique experimental data from long-term demography plots planted with seven grass species that are hosts of *Epichloë* fungal endophytes, we test the hypothesis that context-dependent benefits of microbial symbionts buffer hosts from the fitness consequences of environmental variability. These fungal endophytes are common among cool-season grasses and are primarily vertically transmitted from parent to seed (27). While they have been associated with contributing to drought tolerance for their hosts, these benefits are commonly context-dependent (28–30). And so, we ask first

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68	how fungal endophytes influence the mean and interannual	127
69	variance of their hosts' vital rates; next, we ask if these vital	128
70	rate effects buffer variance in fitness and, if so, what is the re-	129
71	lative contribution of variance buffering vs. mean effects to the	130
72	overall effect of the symbiosis on long-term growth rates. To	
73	answer these questions, we use data from experimental plots	
74	originally established in 2007 to build structured, stochastic	
75	population models for seven species of grass hosts (<i>Agrostis</i>	
76	<i>perennans</i> , <i>Elymus villosus</i> , <i>Elymus virginicus</i> , <i>Festuca subver-</i>	
77	<i>ticillata</i> , <i>Lolium arundinaceum</i> , <i>Poa alsodes</i> and <i>Poa sylvestris</i>).	
78	These long-term plots, which are censused annually, contain	
79	either naturally symbiotic plants (E+) or those which have	
80	had their symbionts experimentally removed (E-). Across	
81	14 years, the data contain 31,216 individual transition years.	
82	Each annual census is a sample of climatic variation. We ex-	
83	plore the consequences of variance buffering with simulations	
84	of increased variance and construct climate-explicit population	
85	models to evaluate the role of climate drivers as explanations	
86	for this buffering.	
87	We find that the symbiosis contributes positively to long-	
88	term population growth rates through both mean and variance	
89	buffering effects. Integrating across diverse effects on vital	
90	rates, contributions to long-term growth rates from effects on	
91	the mean are 4.17 times greater on average than contributions	
92	from variance buffering. However, these effects varied between	
93	species; for two species (<i>A. perennans</i> and <i>P. sylvestris</i>), contri-	
94	butions from variance buffering are greater than mean effects	
95	to long-term growth rates. Additionally, the effect of mutual-	
96	ism increases under simulations with increased variance driven	
97	by greater contributions of variance buffering. In the most	
98	extreme scenario, we find that variance buffering contributions	
99	across species are 1.5 times greater than effects on the mean on	
100	average, and that variance buffering contributions are greater	
101	than mean effects for five out of seven species.	
102	Results	
103	Endophyte effects on the mean and variance of vital rates.	
104	Our vital rate models reveal that the mean and variance effects	
105	of endophyte symbiosis vary across species and across vital	
106	rates. For example, endophytes provide a mean benefit for	
107	survival in SPECIES with only a negligible mean effect for	
108	SPECIES where we see stronger buffering. Similarly, vital	
109	rates that are typically more variable year-to-year (typically	
110	those associated with reproduction ()) show stronger buffering	
111	by endophytes, particularly for SPECIES.	
112	Endophyte effects on the mean and variance of population	
113	growth rates. The diverse effects of endophytes on the mean	
114	and variance of host vital rates warrants a demographic mod-	
115	eling approach to assess their total impact on host fitness. We	
116	find that, on average, Epichloë endophytes lead to a XXX%	
117	increase in the mean and a XXX% reduction in the standard	
118	deviation of annual growth rates across species (ref to Fig).	
119	This variance buffering affect is associated with uncertainty.	
120	There are contrasts across host species; Variance is reduced	
121	my as much as XXX% for some(<i>F. subverticillata</i>), while in	
122	others endophytes seem to have negligible () or even slightly	
123	elevated variance ().	
124	Contribution of mean and variance effects to long-term	
125	growth rates. We decomposed the overall effect of the symbio-	
126	sis to assess the contributions of mean and variance buffering	
	to long-term population growth rates. We found that variance	127
	buffering provided a small benefit overall (XXX%) (See fig-	128
	ure?) but note that even small changes in fitness can have	129
	profound effects over long time periods.	130
	Endophytes are buffering their hosts from environmental vari-	131
	ability. Symbiotic and non-symbiotic populations responded	132
	distinctly to environmental drivers. Our climate-explicit anal-	133
	ysis shows that on average, the population growth of non-	134
	endophytic plants was more sensitive to our drought index,	135
	SPEI, than endophytic populations (FIGURE). This pattern	136
	was particularly pronounced for species which showed strong	137
	buffering in our earlier analysis (SPECIES), suggesting that	138
	endophytes are buffering their hosts from this aspect of inter-	139
	annual variation, although a large amount of variation re-	140
	mained unexplained.	141
	Role of symbiotic buffering . In simulations with increased	142
	variance, we find that the cntribution of variance buffering	143
	increases.	144
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$$\begin{aligned}
 (x + y)^3 &= (x + y)(x + y)^2 \\
 &= (x + y)(x^2 + 2xy + y^2) \\
 &= x^3 + 3x^2y + 3xy^2 + x^3.
 \end{aligned}
 \tag{2}$$

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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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Materials and Methods

Natural history of grass-endophyte symbiosis. To study the effects of context-dependent microbial symbiosis, we focused on *Epichloë* fungal endophytes, which live in the aboveground tissue of many species of cool-season grasses and grow into their hosts' seeds where they can be transmitted vertically from mother to offspring plants. This vertical transmission couples host and symbiont fitness and leads to the expectation that the interaction be mutualistic, else the fungi cause their host to be selected out of the population (31–33). While there are demonstrated benefits against herbivory (34) and under drought stress (35) for some host species, these interactions outcomes are commonly context-dependent (28, 29).

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 during the 2006 growing season from Lilly Dickie Woods

(39.238533, -86.218150) and the Bayles Road Teaching and Research Preserve (39.220167, -86.542683) in Brown Co. IN. To reduce confounding genotype effects, seeds with shared maternal ancestry were disinfected with heat treatments (6d in a drying oven at 60° C for *E. villosus*, *E. virginicus*, *F. subverticillata*, and *L. arundinaceum*; 7d in a drying oven at 60° C for *P. alsodes*, and *P. sylvestris*; and 12 min. in a hot water bath at 60° C for *A. perennans*)* or left naturally infected. Seeds were surface sterilized with bleach and cold stratified for ??? weeks, then germinated in a growth chamber before being 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, where tissue from the leaf sheath is stained with aniline blue dye and examined for the presence of fungal hyphae (36). Then, we established the experimental plots with vegetatively propagated clones of similar sizes from the plants† to reduce the potential for negative side effects of heat treatments (37).

Experimental design and data collection. During the spring of 2007, we established 10 3x3 plots for *A. perennans*, *E. villosus*, *E. virginicus*, *F. subverticillata*, and *L. arundinaceum* and 18 plots for *P. alsodes* and *P. sylvestris*. For each species, an equal number of plots were randomly assigned to each endophyte status, E+ or E-. Each plot was planted with 20 evenly spaced symbiotic or symbiont-free individuals respectively and each plant marked with aluminum tags.

Each summer starting in 2007, we censused all individuals in each plot for survival, growth and reproduction, garnering a dataset covering 14 years that contains 31,216 individual transition years. After clearing out leaf litter, for each plant alive in the previous year, we marked its survival and measured its size 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 2009, we took additional counts of seeds per inflorescence. Together, we use these measurements to estimate seed production. In each plot, we also survey for and tag any unmarked individuals. New recruits typically have one tiller and are non-reproductive, but we also find and tag any individuals that may have been missed in previous censuses.

We typically expect plots of each endophyte status to maintain their status because the fungus is almost entirely vertically transmitted and plots are spaced at least 5 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. Overall, these scores reflect a 97.5% faithfulness of recruits to their expected endophyte status across species and plots (Supplement data).

Demographic modeling. Armed with this demographic data, we next constructed size-structured, stochastic population models. These models describe transitions between sizes (measured as a count of tillers) from one year to the next. For all species, we include a 1 year reproductive delay in the population model following the observation that these newly recruited plants are rarely observed flowering in their first year. Our population model can be expressed as:

$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t \quad [3]$$

where \mathbf{n}_{t+1} is a vector of abundances across sizes in year $t+1$ for each species and endophyte status.

$$\mathbf{n}_{t+1} = \begin{bmatrix} size^{sdlg} \\ size_i \\ \cdot \\ \cdot \\ \cdot \\ size_N \end{bmatrix} \quad [4]$$

* need to double check methods for temp, duration, etc.

† not sure this happened

and \mathbf{A} is expressed as a $N+1 \times N+1$ matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & F_i & \cdot & \cdot & F_N \\ T^{sdlg} & T_i & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ T^{sdlg} & \cdot & \cdot & \cdot & T_N \end{bmatrix} \quad [5]$$

in which T and F are size-transition (i.e. survival and growth) and reproduction kernels drawn from our vital rate estimates for each species and endophyte status.

Statistical analysis of vital rates. We modeled the effect of endophyte symbiosis on the mean and variance of vital rates by fitting generalized linear mixed models (GLMM) to the long-term data with year and plot random effects. We fit all vital rate models in a hierarchical Bayesian framework using Rstan (?), allowing us to propagate uncertainty from the vital rate estimates to our population model (38).

The probabilities of survival and flowering are recorded as successes or failures and consequently are modeled as Bernoulli processes. We modeled growth (measured as the number of tillers in year $t+1$), and the number of flowering tillers with the zero-truncated Poisson-Inverse Gaussian distribution, and the number of spikelets per inflorescence with the Negative Binomial distribution. Each of these size-dependent vital rates are modeled with the same structure of linear predictor (μ)

For example, growth ($G_{i,t+1}$) of a given individual (i) in year $t+1$ is modeled as:

$$G_{i,t+1} \sim P(IG(\mu_{s,e}, \lambda_{s,e})) \quad [6]$$

Similarly, survival $S_{i,t+1}$ in year $t+1$ is modeled as:

$$S_{i,t+1} \sim \text{Bernoulli}(\mu_{s,e}) \quad [7]$$

Where μ , for each species (s), is a linear function of the logarithm of plant size in year t (t), the plot level endophyte status (e), whether the plant was part of the initial transplanting or naturally recruited into the plot (r), along with random effects to account for plot(p), and year variation specific to each species and endophyte status. Thus μ can be written:

$$\begin{aligned} \mu_{s,e} &= \beta_s^1 + \beta_s^2 \log(size_t) + \beta_{s,e}^3 + \beta_r^4 \\ &\quad + \tau + \rho \\ \tau &\sim N(0, \sigma_{s,e}) \\ \rho &\sim N(0, \sigma_p) \end{aligned} \quad [8]$$

For all species, we account for a reproductive delay by modeling seedling growth and survival separately from adult growth and survival. Seedlings are those plants that are recruited into the plot in a given year, and typically have only one tiller. So, for seedlings, growth ($G_{1,t+1}^{sdlg}$) is modelled as:

$$G_{1,t+1}^{sdlg} \sim P(IG(\mu_{s,e}^{sdlg}, \lambda_{s,e})) \quad [9]$$

Similarly, survival ($S_{i,t+1}^{sdlg}$) in year $t+1$ is modeled as:

$$S_{1,t+1}^{sdlg} \sim \text{Bernoulli}(\mu_{s,e}^{sdlg}) \quad [10]$$

Here, $\mu_{s,e}^{sdlg}$ is the linear function for these seedling specific vital rates. It does not include size-dependence or an effect to account for the initial benefits of greenhouse rearing.

$$\begin{aligned} \mu_{s,e}^{sdlg} &= \beta_s^1 + \beta_{s,e}^3 \\ &\quad + \tau + \rho \\ \tau &\sim N(0, \sigma_{s,e}) \\ \rho &\sim N(0, \sigma_p) \end{aligned} \quad [11]$$

The final element of fecundity comes from recruitment of plant into the plot. For this, we modeled the probability of germination as a proportion of seeds produced from the preceding year with a Binomial regression.

$$R_{1,t+1} \sim \text{Binomial}(\mu_{s,e}^{sdlg}) \quad [12]$$

$$\begin{aligned}\mu_{s,e}^{rec} &= \beta_s^1 + \beta_{s,e}^3 \\ &\quad + \tau + \rho \\ \tau &\sim N(0, \sigma_{s,e}) \\ \rho &\sim N(0, \sigma_p)\end{aligned}\quad [13]$$

We ran each vital rate model for 2500 warm-up and 2500 MCMC sampling iterations with three chains using rStan. We assessed model convergence with trace plots of posterior chains and checked for \hat{R} values less than 1.01, indicating low within and between chain variation (39, 40). For those models that show poor convergence, we extended the MCMC sampling to include 5000 warm-up and 5000 sampling iterations, which was only necessary for seedling growth. For each of these vital rate models, we graphically check model fit with posterior predictive checks comparing simulated data from 500 posterior draws with the observed data (See supplement?). These checks provide evidence that our models are accurately recreating size-specific growth, survival, and reproduction patterns in our data across endophyte treatments.

We calculate the effect of endophytes on mean and variance in population growth rates by assembling matrix models with and without endophyte symbiosis following equation [3]. To do this, we calculated annual population growth rates for 50 years drawn randomly from the joint posterior distribution of the year random effects, incorporating model uncertainty by sampling 500 posterior draws from our vital rate models. This 50 year sample allows for a robust estimate of the mean and variance of these annual growth rates for symbiotic and non-symbiotic populations.

Stochastic growth rate simulation experiment. We decomposed the contribution of endophyte symbiosis to long-term stochastic growth rates by calculating the geometric mean of 500 randomly sampled annual population growth rates, for simulated populations including mean-only, variance-only, and mean and variance endophyte effects compared to those without endophyte effects (13).can add better citations for this

$$\log(\lambda_s) E[\log(\Sigma(\mathbf{n}_{t+1})/\Sigma(\mathbf{n}_t))] \quad [14]$$

To explore the potential effects of future increased climate variability, we calculated the stochastic growth rates as above for simulations which sample the most extreme observed years more frequently. To do this, we randomly sampled the six annual population growth rates that were furthest from the mean growth rate across E+ and E- populations. Additionally, we tested the influence of temporal autocorrelation by sampling either alternating

Estimating climate drivers of environmental context-dependence. To ask whether the variance buffering effects of symbiosis are driven by environmental variation, and to forecast population dynamics under future climate change scenarios, we built climate-explicit population models. These models are built from vital rates as described above with the inclusion of a parameter describing the effect, for each endophyte status and species, of 12-month SPEI, a drought index intended to incorporate precipitation and evapotranspiration (). We calculated SPEI with weather station data from Bloomington, IN via the 'rnoaa' and 'spei' R packages (). This weather station has the most complete climate record over the study period and the historic record when compared to other nearby weather stations and is comparable to downscaled climate data (could include correlations) (See Supplement?). Preliminary model selection using the climwin package () with simpler vital rate models suggested that a 12-month SPEI would reasonably capture the relevant climate signal (see appendix?).

Forecasting under alternative climate forcings. We performed model experiments to explore the effect of altered mean and variance in climate as expected under climate change. First, we generated a 50 year climate time series by randomly drawing observed SPEI values,

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