Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity

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J.C.F. contributed to data collection, data analysis, and led manuscript drafting. S.Z. contributed to data collection and manuscript revisions. K.D.W. contributed to research conception, data collection, and manuscript revisions. J.A.R. established transplant plots, contributed to research conception, data collection, and manuscript revisions. T.E.X.M. contributed to research conception, data collection, data analysis, and manuscript revisions.

Data and Code Accessibility

Data will be made accessible as an Environmental Data Initiative package online **DOI: updated here when available.** Code for all analysis is available through **add github repo**

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Abstract

Species' persistence in increasingly variable future climates will depend on resilience against environmental stochasticity, which typically reduces fitness. Most organisms host microbiota that shield against stressful conditions, but it remains unknown whether microbial symbioses buffer hosts against the fitness costs of stochasticity because experiments must span long-term environmental variability. We conducted a 14-year symbiont-removal experiment with seven host species to parameterize stochastic demographic models that predict both the mean and variance of host fitness. We used cool season grasses and *Epichloë* fungal endophytes as a model system. Symbiotic fungal endophytes reduced variance in the fitness of grass hosts by $> 10\%$ on average across species, with up to 50% reductions in fitness variance for some hosts. Hosts with "fast" life history traits that lacked longevity as an intrinsic buffer experienced the greatest benefits from symbiont-mediated buffering. The contributions of variance buffering to host-symbiont mutualism were modest under the current climate regime compared to symbiont benefits to mean fitness. However, simulations of increased environmental stochasticity amplified the benefits of variance buffering, which surpassed the symbionts' mean effects, which have dominated most prior research. These results establish microbial-mediated variance buffering as an important, yet cryptic, mechanism of resilience to increasing stochasticity under global change.

Introduction

Global climate change involves increases in environmental variability, including changes to precipitation patterns and the frequency of extreme weather events **??**. Yet, the ecological consequences of increased variability are less well understood than those of changing climate means, such as long-term warming or drying. Incorporating environmental variability into forecasts of population dynamics can improve predictions of the future.

Classic theory predicts that long-term population growth rates (equivalently, population mean fitness) will decline under increased environmental stochasticity because the costs of bad years outweigh the benefits of good years – a consequence of nonlinear averaging **??**. For example, in unstructured populations, the long-term stochastic growth rate in a fluctuating environment (λ_s) will always be lower than the average growth rate ($\overline{\lambda}$) by an amount proportional to the environmental variance (σ^2):

$$log(\lambda_s) \approx log(\overline{\lambda}) - \frac{\sigma^2}{2\overline{\lambda}^2} \tag{1}$$

Populations structured by size or stage similarly experience costs of variability **??**. There are accordingly two pathways to increase population viability in a variable environment: increase the mean growth rate and/or dampen temporal fluctuation in growth rates, also called "variance buffering".

Both the characteristics of species and the properties of their environment can buffer demographic fluctuations, including life history traits such as longevity **??**, correlations among vital rates **?**, transient shifts in population structure **?**, the magnitude of environmental variability **?**, or the degree of environmental autocorrelation **??**. These factors determine the risks of extinction faced by populations **?** and underlie management strategies promoting ecosystem resilience **?**. Yet little is known about how biotic interactions influence demographic