

Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity

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Funding information

Division of Environmental Biology, Grant/Award Number: 1754468 and 2208857

Editor: Eelke Jongejans

Abstract

Species' persistence in increasingly variable climates will depend on resilience against the fitness costs of environmental stochasticity. Most organisms host microbiota that shield against stressors. Here, we test the hypothesis that, by limiting exposure to temporally variable stressors, microbial symbionts reduce hosts' demographic variance. We parameterized stochastic population models using data from a 14-year symbiont-removal experiment including seven grass species that host *Epichloë* fungal endophytes. Results provide novel evidence that symbiotic benefits arise not only through improved mean fitness, but also through dampened inter-annual variance. Hosts with "fast" life-history traits benefited most from symbiont-mediated demographic buffering. Under current climate conditions, contributions of demographic buffering were modest compared to benefits to mean fitness. However, simulations of increased stochasticity amplified benefits of demographic buffering and made it the more important pathway of host–symbiont mutualism. Microbial-mediated variance buffering is likely an important, yet cryptic, mechanism of resilience in an increasingly variable world.

KEY WORDS

environmental variability, *Epichloë*, life history, long-term data, mutualism, plant–microbe interactions, Poaceae, stochastic demography, symbiosis

INTRODUCTION

Global climate change involves heterogenous changes in environmental variability, including an increasing frequency of extreme weather events and of "whiplash events" that alternate between climate extremes (Bathiany et al., 2018; IPCC, 2021; Seneviratne et al., 2012; Swain et al., 2018). Yet, the ecological consequences of changing variability are less well understood than those of changing means, such as long-term warming or drying. Incorporating realistic variability into forecasts of population dynamics can improve predictive ability (Clark, 2005).

Classic theory predicts that long-term population growth rates (equivalently, population mean fitness) will decline under increased environmental stochasticity

because costs of bad years outweigh benefits of good years—a consequence of nonlinear averaging (Lewontin & Cohen, 1969; Tuljapurkar, 1982). For example, in unstructured populations, the long-term stochastic growth rate in a fluctuating environment (λ_S) will always be lower than the arithmetic mean of annual growth rates ($\bar{\lambda}_t$) by an amount proportional to the environmental variance (σ^2):

$$\log(\lambda_S) \approx \log(\bar{\lambda}_t) - \frac{\sigma^2}{2\bar{\lambda}_t^2}. \quad (1)$$

Populations structured by size or stage experience similar costs of temporal variability (Cohen, 1979; Tuljapurkar, 2013). There are accordingly two pathways

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to increase population viability in variable environments: increase the arithmetic mean growth rate and/or dampen temporal fluctuation in growth rates, also called “demographic buffering.”

Both inherent characteristics of species and their environments can buffer demographic fluctuations. Inherent characteristics include life-history traits (Pfister, 1998), trade-offs among vital rates (Compagnoni et al., 2016), and transient shifts in population structure (Ellis & Crone, 2013). For example, theory predicts long-lived species, those on the slow end of the slow-fast life-history continuum, to be less sensitive to environmental variability than short-lived species (Murphy, 1968), a pattern with empirical support across plants (Compagnoni et al., 2021; Davison et al., 2019) and animals (Le Coeur et al., 2022; Morris et al., 2008). Demographic variance is also determined by external abiotic factors, such as the magnitude of environmental variability (Rodríguez-Caro et al., 2021) or environmental autocorrelation (Fieberg & Ellner, 2001; Tuljapurkar & Orzack, 1980). The complex interplay of these factors determines populations' risk of extinction (Menges, 2000) and underlies management strategies promoting ecosystem resilience (Kuparinen et al., 2016). Yet, little is known about how inter-specific interactions contribute to demographic buffering (Hilde et al., 2020).

Most multicellular organisms host symbiotic microbes that affect growth and performance (McFall-Ngai et al., 2013; Rodriguez et al., 2009), many of which are vertically transmitted from maternal hosts to offspring (Funkhouser & Bordenstein, 2013). Vertical transmission links the fitness of hosts and symbionts in a feedback loop that selects for mutual benefits (Fine, 1975). These mutualistic microbes can protect hosts from stressful environmental conditions including drought, extreme temperatures, or natural enemies (Kivlin et al., 2013; Russell & Moran, 2006). Some well-studied examples include bacterial symbionts of insects that provide hosts with thermal tolerance through the production of heat-shock proteins (Dunbar et al., 2007), and fungal symbionts of plants that produce anti-herbivore and drought-protective compounds (Neyaz et al., 2022; Reyna et al., 2012; Saikkonen et al., 2013). However, these diverse protective symbioses are context-dependent: the magnitude of benefits depends on environmental conditions (Catford et al., 2022; Chamberlain et al., 2014) and thus will vary temporally in stochastic environments (Jordano, 1994). We hypothesized that context-dependent benefits from symbionts may buffer host populations against variability through strong benefits during harsh periods and neutral or even costly outcomes during benign periods, reducing the impacts of host exposure to extremes and dampening inter-annual variance relative to non-symbiotic hosts (Figure 1a). Variance buffering is a previously unexplored mechanism by which symbionts

may benefit their hosts instead of or in addition to elevating average fitness (Figure 1c), the focus of most previous research. To test the hypothesis that context-dependent benefits of symbiosis dampen inter-annual variance in host fitness, we used a combination of long-term field experiments and stochastic demographic modelling. We used cool-season grasses and *Epichloë* fungal endophytes, a tractable experimental model in which non-symbiotic plants can be derived from naturally symbiotic plants through heat treatment, providing a contrast of symbiont effects that controls for the confounding influence of host genetic background. *Epichloë* endophytes are specialized symbionts growing intercellularly in the aboveground tissue of ca. 30% of *C₃* grass species (Leuchtmann, 1992). These fungi are primarily transmitted vertically from maternal plants through seeds (Cheplick et al., 2009). They produce a variety of alkaloids that can protect host plants from natural enemies (Brem & Leuchtmann, 2001) and drought stress (Decunta et al., 2021). Over 14 years (2007–2021), we collected longitudinal demographic data on the survival, growth, reproduction, and recruitment of all plants within replicated endophyte-symbiotic and endophyte-free populations at our field site in southern Indiana, USA. Through taxonomic replication (seven host–symbiont species pairs), we aimed to understand whether host life-history traits could explain inter-specific variation in the magnitude of demographic buffering through symbiosis. We used this long-term data to parameterize Bayesian stochastic population projection models. Specifically, we (1) quantified the effect of symbiosis on the mean and variance of host vital rates (survival, growth, and reproduction) and fitness, (2) evaluated the relationship between host life-history traits and the magnitude of symbiont-mediated variance buffering, (3) determined the relative contributions of symbiont-mediated mean and variance effects to host fitness, and (4) projected how increased environmental stochasticity (expected under future climates) changes the importance of variance buffering as a pathway of host–symbiont mutualism.

MATERIALS AND METHODS

Study site and species

This study was conducted at Indiana University's Lilly-Dickey Woods Research and Teaching Preserve (39.238533, -86.218150) in Brown County, Indiana, USA. This site is part of the Eastern broadleaf forests of southern Indiana, where the ranges of many understory cool-season grass species overlap. We focused on seven of these grasses (*Agrostis perennans*, *Elymus villosus*, *Elymus virginicus*, *Festuca subverticil-lata*, *Lolium arundinaceum*, *Poa alsodes*, and *Poa sylvestris*), each

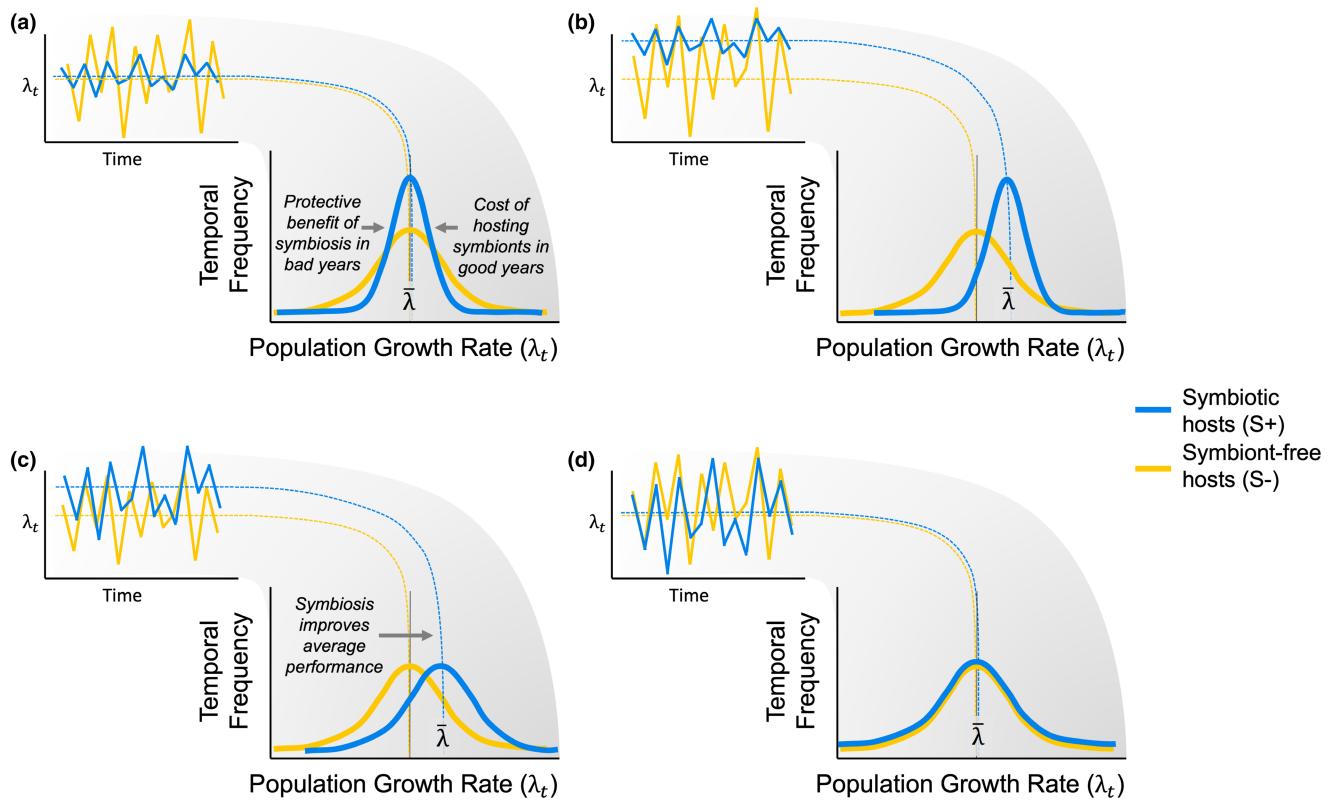


FIGURE 1 Hypothesized effects of symbiosis on the mean and variance of annual population growth rates. (a) Context-dependent symbiosis may provide benefits to hosts during harsh years while being neutral or costly during benign years. Temporal variance in populations' growth rates of symbiotic host populations (S+; blue lines) is expected to decrease relative to symbiont-free hosts (S-; yellow lines). (b) Symbiosis may improve average performance across years in addition to reducing temporal variance. (c) Consistent benefits of symbiosis could improve average performance across years with no influence on temporal variance. (d) Symbiosis may have an effectively neutral effect on population growth rates.

of which hosts a unique species of *Epichloë* endophyte (Table S1). All are native to eastern North America except the Eurasian species *L. arundinaceum*.

Seeds from local, naturally symbiotic populations of the seven focal host species were collected during summer–fall 2006. Seeds were disinfected with a heat treatment or left untreated to generate symbiont-free (S-) and symbiotic (S+) plants from the same genetic lineages. In fall of 2007 and spring of 2008, we established 10 3 × 3 m plots for *A. perennans*, *E. villosus*, *E. virginicus*, *F. subverticillata*, and *L. arundinaceum* and 18 and 20 plots for *P. alsodes* and *P. sylvestris* respectively. Each plot was randomly assigned to be planted with 20 evenly spaced symbiotic (S+) or symbiont-free (S-) plants. Full details of endophyte removal, plant propagation and field set-up are provided in Supplemental Methods and Table S1.

Long-term demographic data collection

Each summer (2008–2021), we censused all individuals in each plot for survival, growth, and reproduction. Plots contained 13.3 individuals/m² on average during the study. Each census year was a sample of

inter-annual variation ($n=14$ years, comprising 13 demographic transition years). We censused each species during its peak fruiting stage (May: *Poa alsodes*, *Poa sylvestris*; June: *Festuca subverticillata*; July: *Elymus villosus*, *Elymus virginicus*, *Lolium arundinaceum*; September: *Agrostis perennans*), such that censuses were pre-breeding and new recruits came from the previous years' seed production (Figure S1 shows a generalized life cycle diagram). Leaf litter was cleared out of each plot before the census, to aid in locating plants. For each tagged plant, we determined survival, measured size as a count of tillers, and collected reproductive data as counts of reproductive tillers and seed-bearing spikelets on up to three reproductive tillers. We also tagged all unmarked recruits from the previous years' seed production and collected the same demographic data. New recruits typically had one tiller and were non-reproductive. In 2008 through 2010, we took counts of seeds per inflorescence for all reproducing individuals in the plots to relate inflorescence and spikelet counts to seed production. In 2018, we stopped collecting data for *L. arundinaceum*, which had very high survival and low recruitment, and consequently low variation in population size across years. In total, the dataset included demographic information for

16,789 individual host-plants and 31,216 transition-year observations.

Vital rate modelling

Equipped with demographic data, we fit statistical models for adult survival, seedling survival, adult growth, seedling growth, reproductive status (flowering or vegetative), fertility of flowering plants (number of inflorescences), production of seed-bearing spikelets (number per inflorescence), the average number of seeds per spikelet, and the recruitment of seedlings from the preceding year's seed production. We fit vital rates as generalized linear mixed models in a hierarchical Bayesian framework using RStan (Stan Development Team, 2022) which allowed us to isolate endophyte effects on vital rate means and variances, borrow strength across species for some variance components, and propagate uncertainty from individual-level vital rates to population projection models (Elderd & Miller, 2016). All size-structured models included the same linear predictor, including two key parameters for each species: one which described the effect of endophyte symbiosis on the mean of that vital rate, and another which described inter-annual variance in the vital rate for symbiotic and symbiont-free plants, estimated using random year effects specific to each species and endophyte status. This species- and endophyte status-specific random year effect allowed us to quantify effects of endophytes on inter-annual variance for each vital rate. Other parameters accounted for size structure in the data (defined as the number of tillers) as well as differences between originally transplanted plants (started in a greenhouse) and those which recruited naturally into the plots. Each vital rate model included a random effect for plot variance shared across species. Full statistical analyses are detailed in Supplemental Methods.

Stochastic population model

We built stochastic matrix projection model for each host species. We parameterized the models using the fitted statistical vital rate models in a manner similar to continuous IPM models (Ellner et al., 2016), while accounting for the discrete data representing our focal species' growth (Ellner et al., 2022). Each matrix projection model included two state variables: r_t (the number of newly recruited individuals in year t which we assume to be non-reproductive), and \mathbf{n}_t (a vector including all non-seedling individuals of discrete sizes $x \in \{1, 2, \dots, U\}$ ranging from one to the maximum number of tillers U). We use these two state variables to avoid assuming demographic equivalence between seedling and non-seedling one-tiller plants. We used the same model

structure, corresponding to a pre-breeding census, for each species and endophyte status (not shown in model notation for readability; Figure S1).

The number of recruits in year $t+1$ is given by:

$$r_{\{t+1\}} = \sum_{\{x=1\}}^U P(x; \boldsymbol{\tau}_P) F(x; \boldsymbol{\tau}_F) K(x; \boldsymbol{\tau}_K) DR(\boldsymbol{\tau}_R) n_t^x. \quad (2)$$

The total number of seeds produced by a maternal plant of size x is the product of the size-specific probability of flowering P , the number of inflorescences conditional on flowering F , the number of spikelets per inflorescence K , and the number of seeds per spikelet D . Multiplying by the probability of transitioning from seed to seedling R gives a per-capita seedling production rate, which is multiplied by the number of plants of size x (\mathbf{n}_t^x , the x^{th} element of \mathbf{n}_t) and summed over all sizes. Each function also depends on species- and endophyte-specific year random effects for that vital rate ($\boldsymbol{\tau}$, a vector of year-specific values).

The number of y -sized plants in year $t+1$ is given by:

$$n_{\{t+1\}}^y = Z(y; \boldsymbol{\tau}_z) B(\boldsymbol{\tau}_B) r_t + \sum_{\{x=1\}}^U S(x; \boldsymbol{\tau}_S) G(x, y; \boldsymbol{\tau}_G) \mathbf{n}_t^x \quad (3)$$

where $n_{\{t+1\}}^y$ is the y^{th} element of vector \mathbf{n}_{t+1} . The first term on the right hand side of Equation 3 represents growth (Z) and survival (B) of seedling recruits. The second term includes survival of previously x -sized plants and the growth of survivors from size x to y , summed over all x . To avoid predictions of unrealistic growth outside of the observed size distribution, we capped the growth function for plants at the 97.5th percentile of observed sizes for each host species (Williams et al., 2012). We analysed projection models constructed from parameters representing the dynamics of naturally recruited plants.

Each vital rate function in Equations 2 and 3 has separate intercepts and year random effects for symbiotic and symbiont-free populations, allowing us to calculate the effect of endophyte symbiosis on the mean, variance, and coefficient of variation (CV) of λ_t , the dominant eigenvalue of the year- and endophyte-specific projection matrix. This model treats climate drivers implicitly through year-specific random effects. We also developed a climate-explicit version with additional parameters defining the relationship between either annual or growing season drought index and each vital rate (Supplemental Methods).

To calculate the stochastic population growth rates (λ_S) for each host species and endophyte status, we simulated population dynamics for 1000 years by randomly sampling from the 13 annual transition matrices, discarding the first 100 years to minimize the influence of initial conditions. Sampling observed transition matrices (rather than independently sampling regression coefficients) produces models that realistically capture inter-annual variation by preserving vital rate correlations (Metcalf et al., 2015).

We tallied total population size at each time step as $N_t = r_t + \sum_{\{x=1\}}^U n_t^x$ and calculated the stochastic growth

rate as $\log(\lambda_S) = E\left[\log\left(\frac{N_t}{N_{t+1}}\right)\right]$ (Caswell, 2001; Rees & Ellner, 2009). We calculated total effects of endophyte symbiosis as the difference in λ_S between S+ and S- populations. We propagated uncertainty from the vital rates to the calculation of λ_S using 500 draws from model posteriors.

Life-history analysis

We collected metrics describing each host species' life history to test the relationship between pace of life and variance buffering (Table S2). We recorded seed size as the average lemma length from the Flora of North America (FoNAEC, 1993). We calculated the 99th percentile of maximum observed age for symbiont-free plants from the census data for each species. Using the Rage package (Jones et al., 2022), we calculated generation time, longevity, net reproductive rate R_0 , Keyfitz entropy (describing survivorship across lifespan), and Demetrius entropy (describing reproduction across lifespan) from the mean transition matrix for symbiont-free populations. Next, we fit Bayesian phylogenetic mixed-effects models using the brms package (Bürkner, 2017) to test the relationship between each life-history trait and the effect of symbiosis on the CV of λ_t (a measure of variance buffering) while controlling for phylogenetic non-independence. We pruned species-level phylogenies of plants (Zanne et al., 2014) and *Epichloë* fungi (Leuchtmann et al., 2014) to include the focal species (or a congener for one host), and defined separate phylogenetic covariance matrices from these pruned trees for host and symbiont species. We propagated uncertainty in the estimated variance buffering effect with a measurement error model, described in full in the Supplemental Methods.

Mean–variance decomposition

We decomposed total endophyte effects on λ_S into contributions from effects on vital rate means, and variances. Specifically, we repeated the calculation of S+ and S- λ_S described above for two additional “treatments”: (1) endophyte effects on mean vital rates only, with inter-annual variances shared between S+ and S- at the S- reference level for all vital rates, and (2) endophyte effects on vital rate variances only, with vital rate means shared between S+ and S- at the S- reference level. The combination of all four λ_S treatments (S+ vital rate means and variances, S- means and variances, S+ means with S- variances, and S- means with S+ variances) allowed us to quantify the extent that overall effects of symbiosis derive from changes in vital rates means, variances, and their interaction. The interaction occurs because the variance penalty to stochastic growth is proportional to the arithmetic mean of annual growth rates (as in Equation 1, for example) such that variance

is more detrimental for populations with lower average growth rates. To quantify how mean and variance effects of symbionts arise through effects on different vital rates, we performed an additional decomposition described in Supplemental Methods that isolates symbiont effects on growth and survival from effects on fertility and recruitment.

We simulated scenarios of increased variance relative to that observed during our study by sampling subsets of the 13 observed annual transition matrices. We created two scenarios of increased environmental variance by sampling the transition matrices associated with the set of either six or two most extreme λ_t values for S- populations. These extreme λ_t values represent the best and worst years experienced by symbiont-free populations. By sampling away from an average year in both directions, the 6- and 2-years scenarios increased standard deviation of annual host growth rates by 1.3 and 2.1 times, respectively, without changing mean growth rates (<2.1% difference in average λ_t between simulation treatments, Figure S80). We performed the same mean–variance decomposition for these scenarios as described above.

RESULTS

Symbionts buffer host demographic variance

Across 14 census years, endophytes reduced inter-annual variance for 66% (37/56) of host species-vital rate combinations (average Cohen's D for effects on vital rate standard deviation: -0.15) (Figure 2a; Figures S22–S29). Endophytes also increased mean vital rates for the majority (36/56) of host species-vital rate combinations (average Cohen's D for effects on vital rate mean: 0.15), and benefits were particularly strong for host survival, plant growth, and recruitment (Figure 2a; Figures S2–S11). The magnitude of mean and variance effects differed among hosts and vital rates. Symbiont effects on vital rate variance were as large and even exceeded mean effects for certain species. For example, endophytes modestly increased mean adult survival (Figure 2c) and strongly reduced variance in survival (Figure 2d) for *Festuca subverticillata*, while for *Poa alsodes*, variance buffering was more apparent in seedling growth and inflorescence production (Figure 2e). Additionally, some vital rates showed costs of symbiosis. Symbiotic individuals of *A. perennans* grew larger than symbiont-free hosts (Figure 2b), yet endophytes also reduced this species' mean recruitment (Figure 2a). Similarly, endophytes increased variance for certain species' vital rates, including seedling growth for *Elymus villosus* and *Festuca subverticillata* (Figure 2a).

Because not all vital rates contribute equally to fitness, we used stochastic matrix models to integrate diverse vital rate effects described above into comprehensive

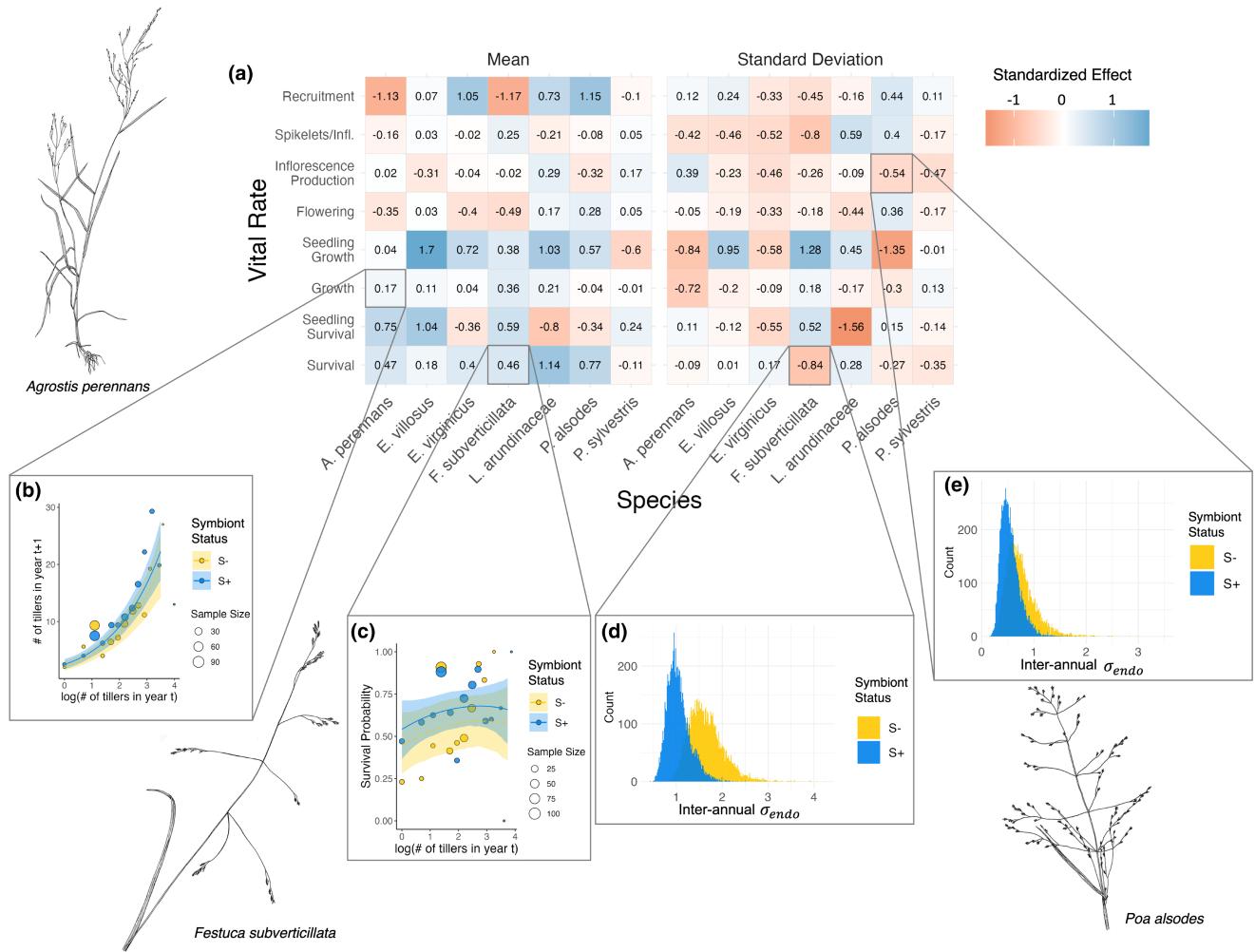


FIGURE 2 Endophyte symbiosis altered host vital rates. (a) Shading represents the posterior mean 1002 standardized effect size (Cohen's D) of endophyte symbiosis on mean or standard deviation of host ¹⁰⁰³ vital rates (blue indicates that symbiosis increased the mean or standard deviation and red indicates a reduction). Endophytes' diverse vital rate effects include increased (b) mean growth of *A. perennans* and (c) mean survival probability of *F. subverticillata*. Endophyte presence also reduced inter-annual standard deviation in (d) the survival of *F. subverticillata* and (e) the fertility of *P. alsodes*. In panels b, c, expected mean vital rates that average across years and plots are shown with 80% credible intervals along with points representing data binned by size for symbiotic (S+) and symbiont-free (S-) plants. Panels d, e show estimated posterior distributions of endophyte-status specific inter-annual standard deviation (σ^2) for each vital rate for S+ (blue) and S- (beige) populations. Organism te,h silhouettes modified from “*Festuca subverticillata*” by Cindy Roché and “*Agrostis hyemalis*” and “*Poa alsodes*” by Sandy Long ©Utah State University.

measures for the arithmetic mean and variance of year-to-year fitness (λ_t). On average across host species, mean fitness of S+ populations increased by more than 10% (>92% confidence that endophytes increased λ_t) and inter-annual variability in fitness was 26% lower (>86% confidence that endophytes decreased the coefficient of variation of λ_t) than S- populations (Figure 3). For some host species, the CV of λ_t declined by more than 62% (*P. alsodes*, *F. subverticillata*), while for others, endophyte effects on variance were substantially smaller (5% lower for *E. villosus*, 13% lower for *A. perennans*), or even positive (37% increase for *E. virginicus*). Considering mean and variance effects together, none of the host–symbiont pairings were antagonistic (i.e., with endophytes that both decreased mean fitness and increased variance; Figure 3c).

Faster life histories predict stronger symbiont-mediated variance buffering

Hosts with slow life-history trait values experienced weaker variance buffering from endophytes than those with fast life histories (Figure 4). Variance buffering was stronger for host species with shorter lifespan (Figure 4a; 67% probability of positive relationship with empirically observed maximum plant age) and smaller seeds (Figure 4b; 65% probability of positive relationship with seed length). Other life-history traits similarly had weak, positive support for the prediction that faster life-history traits correlate with stronger variance buffering (Figures S83–S85). Models indicate moderate phylogenetic signal in the effect of variance buffering (average Pagel's λ of 0.22 (90% CI: 0–0.8) and of 0.56 (90% CI:

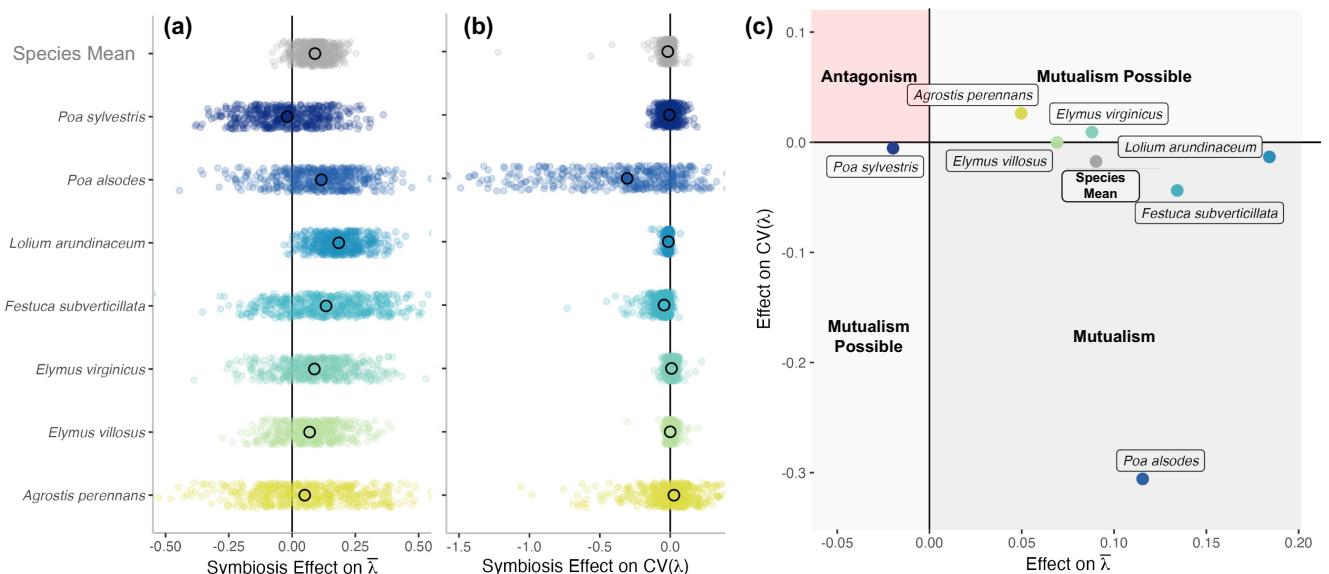


FIGURE 3 Mean and variance-buffering effects on fitness. Black circles indicate the posterior median effect of endophytes along with 500 posterior draws (smaller coloured circles) on the (a) mean and (b) coefficient of variation in λ_t for each host species as well as a cross species mean. (c) For all hosts, endophytes either reduce variance, increase the mean, or both, and consequently when considering stochastic environments, the interactions are always at least potentially mutualistic.

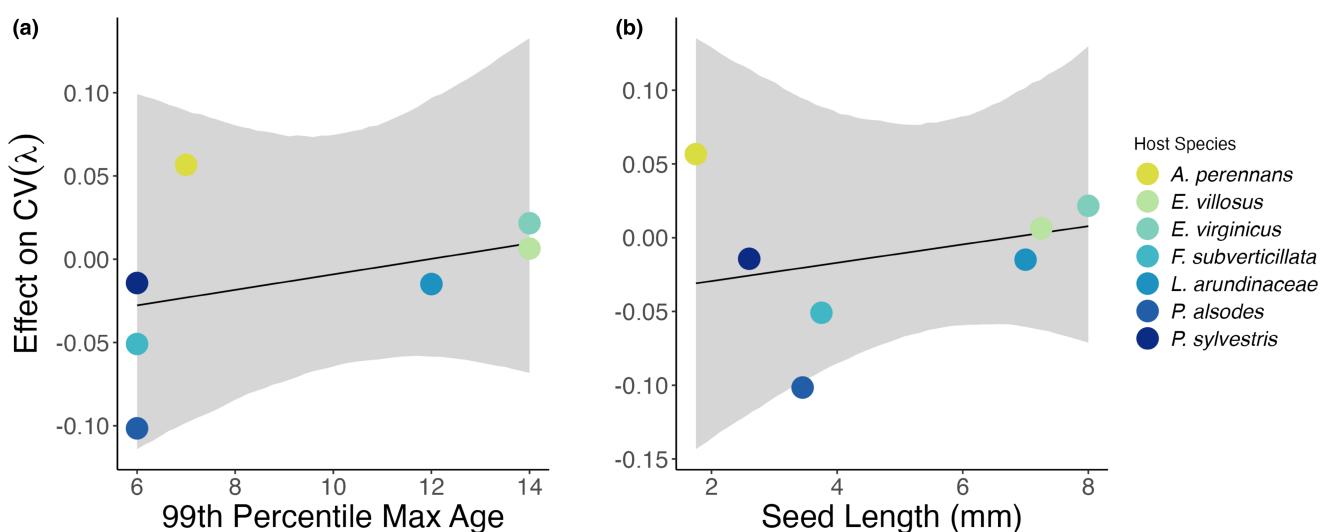


FIGURE 4 Host species with faster life-history traits experience stronger effects of symbiont-mediated variance buffering. Regressions between life-history traits describing the fast-slow life-history continuum ((a) 99th percentile maximum age observed during long term censuses in years; (b) Seed size) and the effect of endophyte symbiosis on the co-efficient of variation in annual population growth rate (λ_t). Each panel shows the fitted mean relationship (line) along with the 95% credible interval.

0–0.9) from models including host and symbiont phylogeny, respectively (Table S2).

Contributions from variance buffering are weak relative to mean effects

To evaluate the relative importance of mean fitness benefits and variance buffering as alternative pathways of mutualism, we decomposed the overall effect of the symbiosis

on stochastic growth rates λ_S using simulations including either the full symbiosis effect (both mean and variance effects), mean effects alone, variance effects alone, or neither mean nor variance effects. Overall, the full effect of symbiosis on λ_S , averaged across host species, provided strong evidence of grass–endophyte mutualism (99% certainty of a positive total effect on λ_S ; Figure 5; see Figure S81 for individual host species). Contributions to this full effect derived from both mean and variance buffering effects, as well as a slightly negative interaction (i.e., the combined

influence of mean and variance effects was smaller than the sum of their individual effects). Endophytes' contributions to λ_S from mean effects were four times greater, averaged across species, than contributions from variance buffering (Figure 5), suggesting that, under the regime of environmental variability represented by our 14-year study, damped fluctuations in fitness via variance buffering was a less important element of symbiont benefits than increased mean fitness. Decomposing this result further into contributions through different vital rates demonstrated that demographic buffering arose primarily from symbionts' effects on host survival and growth, rather than from effects on reproduction (Figure S82). Results for individual host species were largely consistent with cross-species trends (Figure S81). The full effect of symbiosis on λ_S was positive for five out of seven host species, with statistical confidence ranging from 78% to >99% certainty. The exceptions were *P. sylvestris* and *A. perennans*, for which our analysis indicated effectively neutral symbionts in their overall fitness effect (42% and 57% posterior probability of positive effects, respectively; Figure S81).

Variance buffering strengthens under increased environmental variability

To simulate increased variability, we repeated the decomposition of λ_S for two alternative scenarios,

randomly sampling transition matrices that represented either the six or two most extreme years, subsets of the 13 transition matrices across the 14-year study period. Increased variability elicited stronger mutualistic benefits of endophyte symbiosis than ambient variability (Figure 5; overall effect of the symbiosis increased by ca. two fold). This increase was driven by increased contributions from variance buffering (from a 16% contribution in the ambient scenario to a 54% contribution in the most variable scenario) rather than from greater mean effects. In the most variable scenario, the relative importance of mean and variance effects reversed, with variance buffering contributions that were 1.2 times greater than mean contributions, averaged across species (Figure 5).

DISCUSSION

Across seven host species, eight vital rates, 14 years, and 16,789 individuals, our analysis provided the first empirical evidence, to our knowledge, of demographic buffering conferred by microbial symbionts. Our taxonomically replicated, long-term field experiments that manipulated the presence/absence of fungal symbionts in plants revealed that heritable microbes can commonly benefit hosts not only through improved mean fitness—the focus of most previous

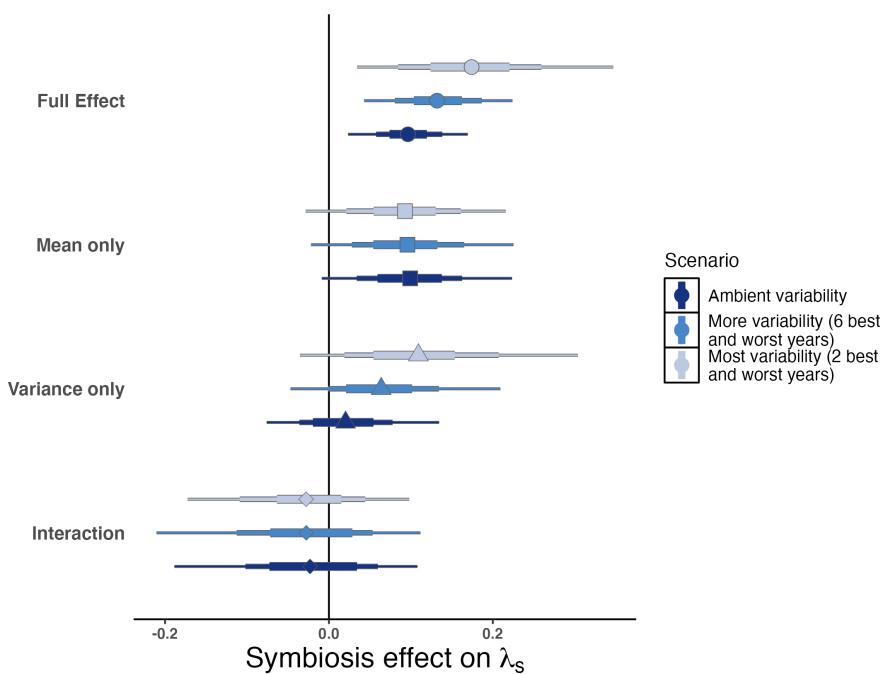


FIGURE 5 Cross-species average endophyte contributions to stochastic growth rates under observed and ¹⁰⁹⁵ elevated variance. Endophyte symbiosis contributes to the total effect of mutualism on λ_S through benefits to mean growth rates and through variance buffering as well as the interaction between mean and variance effects. Shapes indicate the posterior mean of each contribution averaged across the seven focal symbionts, along with bars for the 50, 75, and 95% credible intervals. The full effect of the symbiosis (circles) becomes more mutualistic under scenarios of increased variance (represented by colour shading). Relative to the ambient scenario sampling transition matrices for all 13 transition years during the study period, simulations increased variance by sampling the most extreme 6 or 2 years, leading to increased contributions from variance buffering effects (triangles) and a constant contribution from mean effects (squares).

research—but also through buffering against environmental variance (Figure 1). Benefits to mean fitness dominated the overall fitness advantage of endophyte symbiosis under observed environmental variability. However, the strongest symbiotic benefits derived from the combination of both mean effects and variance buffering (Figure 1b), and simulation experiments point to an increasing role for demographic buffering under increased temporal environmental stochasticity (Figure 5; Figures S81 and S82). There is growing interest in demographic buffering as a potential source of resilience against increased stochasticity under global change (Hilde et al., 2020). Our results suggest that biotic interactions, and microbial mutualisms in particular, may be an under-appreciated mechanism of demographic buffering. In fact, any interaction that is subject to context-dependence—where magnitudes of cost or benefit depends on harshness of the environment—holds potential to modify demographic variance across years. However, long-term experimental data required to detect such an influence are rarely available.

Taxonomic replication of host–symbiont pairs enabled us to generalize beyond the focal taxa and facilitated inference about the *types* of species in which demographic buffering may be more or less likely. Because host taxa with “slow” life-history traits, such as long lifespan, may be intrinsically buffered from environmental variability (Moles & Westoby, 2004; Morris et al., 2008; Rees, 1996), we predicted that buffering effects of endophyte symbiosis would be stronger in hosts with faster pace of life. Supporting this prediction, we found that shorter lived and smaller seeded host species experienced stronger reductions in demographic variance through endophyte symbiosis. Thus, microbial symbiosis may compensate for the lack of intrinsic tolerance of variability conferred by slow life-history traits. Future studies may consider fungal life-history traits, such as diversity in biologically active alkaloids, or the production of stromata-fruiting bodies capable of horizontal (contagious) transmission. The host species for which the net mutualism benefit was greatest (*F. subverticillata* and *L. arundinaceum*; Figure S79) were among those never observed to produce fungal stromata (Table S2), supporting theoretical expectations that strict vertical transmission drives evolution of strong host–symbiont mutualism (Afkhami & Rudgers, 2008; Fine, 1975). We caution that inferences on trait correlates of demographic buffering were subject to large uncertainties (Figure S85), reflecting relatively narrow taxonomic breadth (closely related grass species in the sub-family Pooideae and their co-evolving symbionts). Understanding of how life-history variation modulates fitness consequences of microbial symbiosis would profit from tests across a wider span of plant and animal groups (Jeschke & Kokko, 2009). We also found relatively consistent, positive effects of endophyte symbiosis on stochastic fitness (Figures S78 and S79), suggesting

that variation across host species and vital rates in mean and variance effects (Figure 3c) may reflect alternative strategies that yield similar net benefits.

While our results highlight symbiont-mediated demographic buffering as a potential source of resilience against increased environmental stochasticity, much work remains to connect symbiont effects on mean and variance to quantitative forecasts of host–symbiont dynamics under global change. Like most temporally stochastic population projection models, our approach quantified demographic variance across years (and simulated increasing variance) without attributing its cause(s). Realistic forecasts for host–symbiont dynamics under environmental change will require explicit connections between driver variables and demographic responses. Reduced sensitivity to drought, as is common in *Epichloë* symbioses (Decunta et al., 2021; Neyaz et al., 2022; Reyna et al., 2012; Saikkonen et al., 2013), is a candidate mechanism that could generate a signature of variance buffering: drought conditions may be less costly for S+ hosts, dampening the effects of drought years and reducing fluctuations in fitness through time (Figure 1). Preliminary climate-explicit analyses indicated that symbionts reduced sensitivity to drought indices for five of seven host taxa (Figures S88 and S89; Table S3). However, we did not find a strong relationship between magnitude of variance buffering and relative drought sensitivities, suggesting that other climatic factors or temporally varying aspects of the environment may elicit benefits of symbiosis, including documented resistance to herbivory for six of these host taxa (Crawford et al., 2010; Rudgers & Clay, 2008). Identifying the type and timescale of relevant drivers would allow more direct connections between demographic models and outputs from global climate models. Symbiont-mediated demographic buffering is a potential target of selection for improved holobiont fitness (Vandenkoornhuyse et al., 2015) and carries implications for the evolution of bet-hedging strategies in variable environments. Demographic buffering may be considered a bet-hedging strategy if reduced temporal variance comes at the cost of arithmetic mean fitness (Childs et al., 2010). This may be unlikely in this system, where most host species exhibited both reduced variance and elevated mean fitness through symbiosis (Figure 3c). However, the context-dependent fitness effects that underlie demographic buffering may favour other forms of evolutionary bet-hedging. Theory suggests that imperfect transmission (the production of S− offspring from S+ parent) may be an adaptive host strategy in spatially or temporally varying environments when fitness effects of symbionts are environment-dependent by extending phenotypic variance of offspring and improving the odds of some having the optimal symbiont status for their environment (Brown & Akçay, 2019; Bruijning et al., 2022; Lange et al., 2023). Imperfect vertical transmission is well-documented in grass–endophyte

symbioses (Afkhami & Rudgers, 2008), including our focal taxa (Table S2), and could be incorporated into our model by dynamically linking S+ and S- populations (Chung et al., 2015; Yule et al., 2013). A further step could incorporate diverse symbiont partners (e.g. different strains of *Epichloë* fungi or multiple species within the microbiome) to understand how microbial diversity contributes to host genotypic and phenotypic variance (Henry et al., 2021). Several limiting features of our study point to new directions and valuable next steps. We focused explicitly on temporal variation and intentionally averaged over spatial heterogeneity. Endophytes may dampen spatial heterogeneity in host fitness in ways that parallel their effects on temporal variance, and this hypothesis could be explored by leveraging the plot replication in our experiment. At larger spatial scales, buffering effects of symbionts may vary across the broad geographic distributions of these eastern North American grass species, especially since historical and projected 552 trends in climate variability are geographically heterogeneous (Bathiany et al., 2018). Finally, our demographic modelling framework could be further “unpacked” to explore other elements of fitness in stochastic environments. We identified damping variance in survival and growth as the key avenue by which symbionts' variance effects contributed to host fitness (Figure S82). Elasticity analyses could explore the selection that drives diverse symbiont effects across host vital rates. Small changes in variance of vital rates that are highly important to population growth (i.e. those with high elasticities) may be more strongly selected for than larger changes in less important vital rates (Doak et al., 2005), and symbionts may even provide an adaptive advantage by increasing temporal variance in certain vital rates (i.e. demographic lability; Koons et al., 2009). Further, our simulations assumed an independently distributed environmental distribution through time, but environmental auto-correlation can be an important component of stochastic population projections (Tuljapurkar & Haridas, 2006) and might modify the fitness consequences of symbiont-mediated variance buffering. Similarly, correlated responses of multiple vital rates could amplify or dampen demographic variance (Compagnoni et al., 2016; Davison et al., 2013; Tuljapurkar, 2013). Our “matrix sampling” approach accounted for vital rate correlations implicitly (Metcalf et al., 2015) but exploring whether and how endophyte symbiosis alters the correlation structure of host vital rates could add nuance to understanding of symbionts' contributions to variance buffering.

CONCLUSION

Ecologists increasingly recognize the importance of symbiotic microbes for host organisms and the populations, communities, and ecosystems in which their hosts reside

(Afkhami & Strauss, 2016; Dallas & Warne, 2022; Smith et al., 2017; Wu et al., 2022). Despite awareness of these ubiquitous interactions, long-term studies of microbial symbiosis are rare. Our results provide an important advance to improve forecasts of the responses of populations (and symbiota) to increasing environmental stochasticity under global change. We found that, relative to mean fitness benefits, symbiont-mediated variance buffering made weak contributions to host–symbiont mutualism under observed environmental variability. However, demographic buffering is likely to become the dominant benefit that fungal endophytes confer to grass hosts in more variable future environments. Thus, demographic buffering—a cryptic microbial influence that manifests only over long time scales—is poised to become the dominant benefit of symbiosis. This result emerges from the context-dependent nature of grass–endophyte interactions, combined with the observation that environmental stochasticity generates fluctuation in context. These key ingredients, and thus the potential for symbiont-mediated variance buffering, similarly apply to the diverse host–microbe symbioses across the tree of life.

AUTHOR CONTRIBUTIONS

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.

ACKNOWLEDGEMENTS

We thank Mark Sheehan, Ali Campbell, Kyle Dickens, Blaise Willis, and Sar Lindner for contributions to field data collection. We also thank Volker Rudolf, Daniel Kowal, Lydia Beaudrot and Judie Bronstein for helpful comments on and discussion of this project. This research was supported by the National Science Foundation (grants 1754468 and 2208857).

FUNDING INFORMATION

Division of Environmental Biology, Grant/Award Number: 1754468, 2208857.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14438>.

DATA AVAILABILITY STATEMENT

Data is accessible as an Environmental Data Initiative package online DOI: <https://doi.org/10.6073/pasta/ea7db07a578fb030a173f37f76596b62>. Code for all analysis is available through <https://github.com/joshuacfowler/Grass-Endophyte-Stochastic-Demography>.

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SUPPORTING INFORMATION

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How to cite this article: Fowler, J.C., Ziegler, S., Whitney, K.D., Rudgers, J.A. & Miller, T.E.X. (2024) Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity. *Ecology Letters*, 27, e14438. Available from: <https://doi.org/10.1111/ele.14438>