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Climate variability disrupts microbial mutualism-driven population persistence

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Understanding how species interactions impact population dynamics and long-term persistence over broad temporal and spatial scales is crucial for predicting species distributions and responses to global change. Here we investigate how microbial mutualisms can promote long-term and range-wide population persistence of plants, particularly by ameliorating drought stress. We integrate range-wide field surveys of ~90 grass host populations spanning 13 years with demographic modelling based on 6-year common garden experiments conducted across the host range. We found that mutualistic fungal endophytes (genus *Epichloë*) promote population-level persistence and growth of their native host grass (*Bromus laevipes*) across its distribution, with non-mutualistic populations four times more likely to go locally extinct. However, endophyte prevalence declined eightfold more in historically mutualistic populations that experienced high climate variability. This demonstrates that mutualisms can underpin population persistence and buffer hosts against environmental stress but may themselves be vulnerable to global change, with concerning implications for long-term population viability and, ultimately, species distributions under an increasingly uncertain climate.

Under global change, many species are experiencing dramatic range shifts and local extinctions[1–3]. To predict long-term species viability, it is crucial to understand what drives the persistence of individual populations across large geographic scales. One potentially important determinant of population persistence is mutualism, or positive interspecific interactions, wherein partners provide reciprocal fitness benefits. Because mutualisms can ameliorate the impacts of both biotic and abiotic stressors[4,5], they may be especially important in the Anthropocene by enabling the persistence of organisms experiencing global change stress. However, empirical research scaling up the effects of mutualism to population persistence, especially across large spatial scales, has thus far been limited, with most studies focusing either on individual-level fitness[6,7], local-scale population outcomes[8] or correlated declines in occurrence records of mutualistic partners[9]. Here, we use a multifaceted approach directly linking mutualism to the long-term persistence and extinction dynamics of both natural and experimental populations in the context of increasing environmental stress and variability under global change. By doing so, we address two key questions: first, do microbial mutualisms promote population persistence and reduce extinction risk at large spatial and temporal scales, particularly in stressful or variable environments?; and second, which environmental factors promote or disrupt the prevalence of these crucial mutualistic relationships? Answering these questions will help us to understand and predict how species respond to global change.

Population persistence—a key component of both species viability and distributions—can be negatively impacted by abiotic forces such as drought and warming that are increasing in the Anthropocene[2,10], potentially leading to local population extinctions. By contrast, beneficial mutualistic interactions can positively affect population dynamics by ameliorating stressors such as drought and may thus enable population persistence and even range expansions under abiotic stress[11–14]. Mutualisms may also ameliorate complex aspects of global

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change, including climate variability and extreme events such as fire, which could in turn scale up to promote population growth and range expansion[15,16]. However, how these complex, long-term aspects of environmental stress such as climate variability and extreme events shape mutualism effects on populations is not well understood, especially in natural ecosystems.

Although mutualisms could be crucial for population persistence under increasing stress in the Anthropocene, they may themselves be disrupted by global change. The population-level benefits conferred by a mutualistic interaction are in part a product of its prevalence or the frequency with which it occurs[17–20]. Therefore, over time, declines in mutualism prevalence could impact population persistence, species ranges and, ultimately, species viability. As mutualism benefits can vary with factors such as aridity[13,21], the prevalence of mutualisms can depend on ecological context. For instance, the prevalence of mutualistic fungal endophytes is often higher under more arid conditions[22] and greater herbivory pressure[23], reflecting how they benefit hosts by ameliorating drought or herbivory stress[24–26]. Overall, mutualisms are expected to persist when the benefits they confer exceed the costs of maintaining them and decline in prevalence otherwise[27,28]. However, environmental change, both over time and space, could affect mutualism prevalence by shifting the balance of costs and benefits. In particular, global change could increase reliance on stress-ameliorating mutualisms or, alternatively, disrupt mutualistic interactions[29]. Global change could also reduce mutualism prevalence through means that are independent of costs and benefits, such as through creating phenological mismatches between partners[30]. Collectively, this emphasizes the importance of simultaneously tracking mutualism impacts on population outcomes and global change impacts on mutualism prevalence. Determining which environmental factors promote or disrupt the prevalence of mutualisms is crucial to predicting whether these beneficial interactions will continue to occur in a changing world and, in turn, underlie long-term population persistence.

Here, we explore how mutualism scales up to impact long-term population dynamics across species ranges, especially under environmental stress, and how global change has influenced the prevalence of these crucial mutualistic relationships. To do so, we perform (1) field surveys of ~90 widely distributed natural host populations 13 years apart to identify differential persistence of mutualistic and non-mutualistic populations as well as changes in mutualism prevalence, (2) two sets of 6-year common garden experiments spanning 92% of the host's climatic range to determine mutualist effects on host vital rates across space and time and (3) range-wide demographic modelling of mutualist-associated and non-associated populations to uncover the pathways through which mutualisms affect population trajectories. We conduct this research using the mutualism between the California-native grass *Bromus laevipes* and its symbiotic systemic foliar endophytic fungi[31]. In general, endophytic fungi are ubiquitous and occur in every major plant lineage[32], with vertically transmitted systemic fungal endophytes of the genus *Epichloë* (Clavicipitaceae) occurring in up to ~40% of species across cool-season grasses[33–36]. These widespread symbionts have also been shown to expand their host species range by conferring drought tolerance, although they may be costly to support in wetter habitats[13]. The endophytic fungi's established ability to ameliorate drought stress in our model grass species, combined with its natural variation in prevalence and a growing recognition of the importance and ubiquity of above-ground microorganisms, makes this system ideal for investigating how microbial mutualists influence plant population dynamics under global change.

Overall, we hypothesized that these microbial mutualists would provide range-wide benefits to host populations, especially in stressful or variable environments. We further hypothesized that mutualism prevalence would increase under those conditions where it was most beneficial. Our results revealed that microbial mutualisms promote population growth and persistence of their plant host across its distribution, yet climate variability—a key component of global change[37]—reduces mutualism prevalence, undermining the very interactions that support host resilience. These results uncover a critical paradox—that mutualisms that buffer plant populations against environmental stress may themselves be vulnerable to the destabilizing forces of global change.

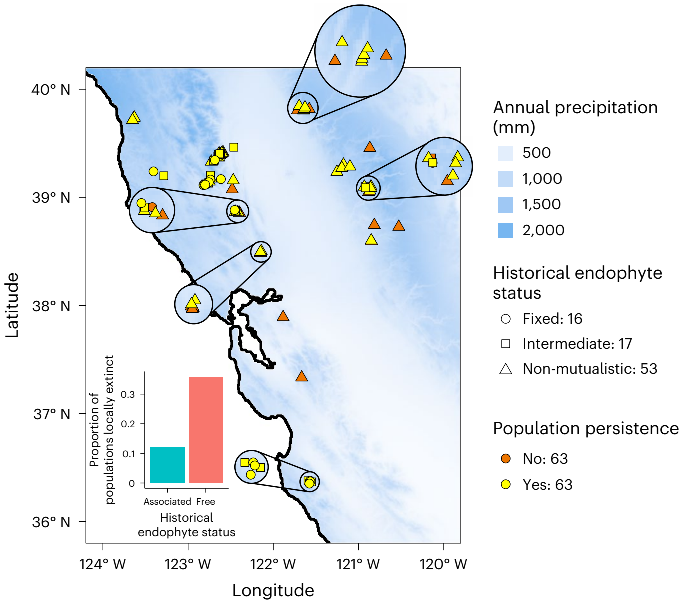

Fig. 1 | A map of surveyed *B. laevipes* populations. After 13 years, ~27% of monitored plant populations went locally extinct, with populations varying in persistence within and across regions of northern and central California (which spans much of this host's climatic range and geographic distribution; ~98% of *B. laevipes* population records are within the California floristic province, with the highest densities in northern and central California[13]). Map colours represent annual precipitation (mm; data from WorldClim). Each point represents one population surveyed in 2009–2010 and in 2022. Each point's colour corresponds to whether or not it persisted to 2022. Each point's shape corresponds to its historical (2009) endophyte status (fixed, prevalence ≥90%; intermediate, 10% < prevalence < 90%; non-mutualistic, prevalence ≤10%; cut-offs based on previous work[13]). Numbers following legend labels indicate how many populations fall under each category (for example, 63 populations persisted to resampling) (see also Supplementary Table 2 and Supplementary Fig. 4). Note that *B. laevipes* does not occur in the Central Valley (roughly 40° N, 123° W to 37° N, 120° W), which is dominated largely by invasive annual grasses, according to both our surveys and herbarium records. The inset bar plot depicts the proportion of endophyte-associated (prevalence >10%) and endophyte-free (prevalence ≤10%) populations that suffered local extinction from our surveys.

Results

Local extinction over 13 years was four times higher in non-mutualistic plant populations

To understand the importance of endophyte mutualism to host plant population persistence, we surveyed 86 natural populations of *B. laevipes* across its range in northern and central California in 2009–2010 and again 13 years later in 2022, evaluating persistence as well as endophyte prevalence at both timepoints for each population (>2,700 host plants evaluated; Fig. 1; Methods). After determining that ~27% of populations went locally extinct, we tested how host persistence across the 13 years and current endophyte prevalence (in 2022) of each population depended on historical endophyte prevalence (in 2009) and its interactions with environmental variables relevant to global change (mean climate, change in mean climate, climate variability and fire; climate was quantified using the standardized precipitation evaporation index (SPEI), a drought or aridity index accounting for temperature and precipitation, with lower values indicating greater

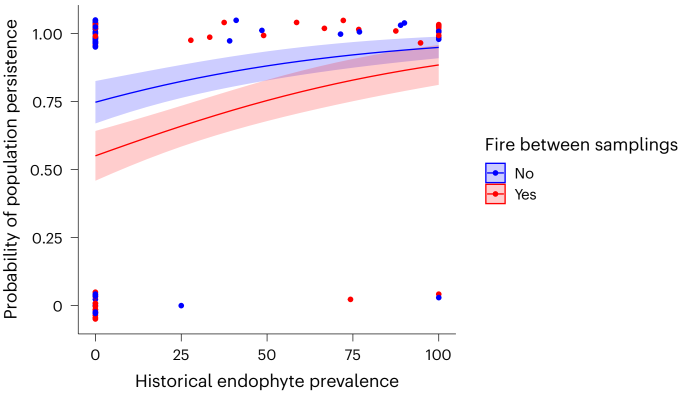

Fig. 2 | Plant population persistence increased with historical endophyte prevalence and decreased with fire occurrence. Plant population persistence was explained by historical endophyte prevalence (analysis of variance (ANOVA); $\chi^2_1 = 6.73$, $P = 0.0095$) and the occurrence of fire between surveys ($\chi^2_1 = 2.91$, $P = 0.088$) in our best supported statistical model, with probability of population persistence increasing with historical endophyte prevalence and decreasing with fire occurrence. Historical endophyte prevalence refers to the endophyte prevalence of a *B. laevipes* population in 2009 during the initial field surveys. Each point represents one *B. laevipes* population, with colour corresponding to whether or not fire had occurred between surveys. Points have been jittered for visualization purposes. The model is a logistic regression, with the red curve corresponding to predictions with fire occurrence and the blue curve corresponding to no fire occurrence; the shaded areas represent the standard error. Figure created with ggPredict[84].

drought[38]). Global model selection on candidate multiple logistic regression models identified that the best supported persistence model included two factors—historical endophyte prevalence and fire between surveys—important for predicting *B. laevipes* population persistence ($P = 0.012$), with no interaction effect between the two ($Z = 1.45$, $P = 0.15$). Interestingly, as historical endophyte prevalence within populations increased, populations were significantly more likely to persist ($\chi^2_1 = 6.73$, $P = 0.0095$; Fig. 2). Populations with no endophytes detected in 2009–2010 were roughly four times more likely to go locally extinct than populations with fixed (that is, 100%) endophyte mutualism in 2009–2010 (predicted probability of extinction of 45% for non-mutualistic populations versus 12% for fixed populations if fire occurred and 25% versus 5.1% if no fire occurred). We also found that plant populations were somewhat less likely to persist if fire had occurred between surveys ($\chi^2_1 = 2.91$, $P = 0.088$; Fig. 2). Overall, these results show that plant population persistence increased with endophyte prevalence, independent of whether fire has increased the probability of local extinction.

Mutualistic host populations had ~30% higher population growth rates driven by endophyte-enhanced fecundity

To assess the effect of endophyte mutualism on plant population dynamics, we performed two sets of common garden experiments involving 1,650 plants and 550 seeds from 11 populations, monitored for 6 years at five sites chosen to span the *B. laevipes* range and a wide ecological and climate gradient (northern to central California; ~420 km; ~450–1,750 mm average annual precipitation during the experiment years). We then measured and parameterized vital rates as functions of variables including endophyte association and climate and constructed a population projection matrix model from these vital rate functions. We used the population model to predict finite population growth rates (λ) for each population on the basis of their endophyte status and year-to-year climate. We tested how λ values depended on endophyte association and performed fixed-effect life table response experiments to assess whether endophytes impacted population dynamics through affecting host growth and survival or via host fecundity. Using our demographic model, we found that λ differed significantly between sampled populations, with endophyte-associated populations having 28.37% higher population growth rates on average than endophyte-free populations (pseudo-$P < 0.0001$; $\lambda = 1.67 \pm 0.021$ for endophyte-associated populations versus $\lambda = 1.30 \pm 0.025$ for endophyte-free populations; mean ± s.e.m.; Fig. 3a). Furthermore, our life table response experiment revealed that these endophyte benefits to population growth originated primarily through impacts on fecundity rather than on growth and survival (Wilcoxon signed-rank test; $V = 3{,}741$, $Z = 8.05$, $P < 0.0001$; mean ± s.e.m. contribution -0.045 ± 0.0055 through survival and growth and 0.35 ± 0.0058 through fecundity, with the difference between them being 0.39 ± 0.011; Fig. 3b). This life table response experiment was performed on demographic model predictions for each surveyed population to generalize across *B. laevipes*'s species range. Specifically, we tested how much endophyte association was predicted to increase λ for each population and partitioned that contribution to population growth between life class transitions and between host survival and growth and host fecundity.

Endophytes underlie host persistence in arid climates, but endophyte benefits decline under more variable climates

Using our demographic model, we calculated endophyte contribution to population growth rate (that is, how much endophytes would increase population growth rate) as the difference between predicted endophyte-associated and endophyte-free λ values for each of the 86 surveyed populations spanning the *B. laevipes* range. We found that broadly, as mean SPEI values across the four experimental years increased (that is, as sites became wetter), predicted λ values increased for both endophyte-associated and endophyte-free populations (Fig. 4a). Notably, in the driest of the sites occupied by *B. laevipes* populations, endophyte association allowed hosts to sustain positive population growth rates (that is, $\lambda \geq 1$) that were not achieved by endophyte-free populations, suggesting that in extremely dry conditions, endophyte mutualism is required for population persistence.

The endophyte contribution to population growth rate was positive across all sites, indicating that endophyte mutualism provided a range-wide demographic advantage to its host. Importantly, relative endophyte benefits to population growth rate had a unimodal relationship with mean SPEI across the experimental years, with the greatest endophyte contributions to population growth occurring in sites with intermediate to slightly dry conditions ($R^2 = 0.93$, $F_{2,83} = 584.3$, $P < 0.0001$; Fig. 4b). Furthermore, modelled endophyte contributions to population growth rates declined with increasing climatic variability across the experimental years ($R^2 = 0.042$, $F_{1,84} = 3.68$, $P = 0.058$; Fig. 4c). Overall, because of the difference in climatic optima for endophyte-associated and endophyte-free populations, the relative benefits of endophyte mutualism were the greatest in roughly average conditions and therefore declined with increasing climate variability (see 'The contribution of endophyte mutualism to population growth declines with increasing climatic variability' section in the Supplementary Discussion).

Endophyte prevalence declined in historically mutualistic host populations under high climate variability

Although results from both surveys of natural populations and demographic modelling indicate that endophytes were broadly beneficial, endophyte prevalence did not increase over time in surveyed field populations (see the 'Host populations maintained intrapopulation variation in mutualism rather than progressing towards endophyte fixation' section in the Supplementary Discussion). Thus, to understand the relationship between current and historical endophyte prevalence among all surveyed populations and what environmental factors promote or undermine endophyte prevalence, we conducted global model selection using the same candidate explanatory terms as in our population persistence model (Methods). Three factors—historical

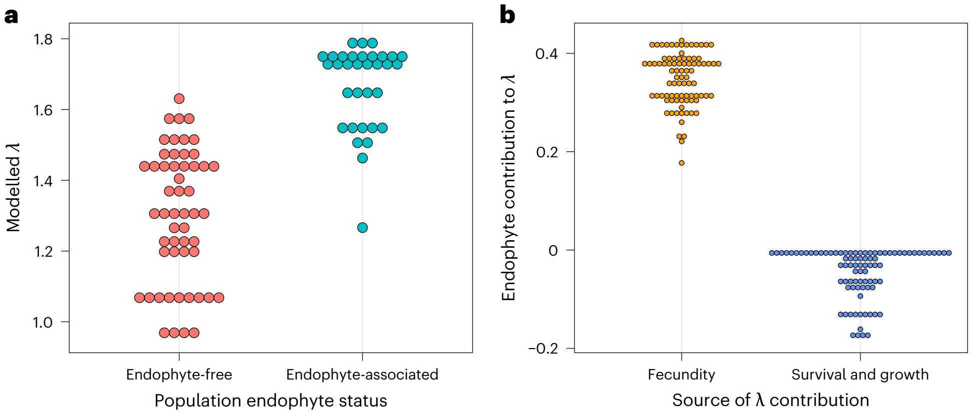

Fig. 3 | Endophytes enhanced population growth rates, largely through promoting host fecundity. a, Population growth rates of endophyte-associated populations were significantly greater (two-sided permutation two-sample *t*-test; pseudo-$P < 0.0001$) than those of endophyte-free populations on the basis of population growth rates projected for each of the 86 surveyed populations across the *B. laevipes* range (53 endophyte-free and 33 endophyte-associated). Endophyte-associated populations include both intermediate and 100% endophyte prevalence (fixed) populations. **b**, Modelled endophyte mutualism contributions to population growth rates were greater through fecundity than through survival and growth (two-sided Wilcoxon signed-rank test; $V = 3{,}741$, $Z = 8.05$, $P = 8.13 \times 10^{-16}$). Here, λ contribution refers to how much our model predicted endophytes would increase λ for each population (that is, predicted λ when endophyte-associated minus predicted λ when endophyte-free). Projections are based on a demographic model parameterized with data from our multi-site, multi-year common garden experiments. Although slight inflation of λ values may have resulted from germination data not including potential mortality of new recruits (see 'Field common garden experiments for demographic model construction' section in the Supplementary Methods for more details), simulations of increased recruit mortality resulted in more endophyte-free populations below the threshold for positive population growth, strengthening the result that endophyte mutualism can enable population persistence of host plants (Supplementary Fig. 16). Also see Supplementary Figs. 10 and 11 for additional details, such as bootstrapped confidence intervals, on population growth rates and endophyte contributions.

endophyte prevalence ($\chi^2_1 = 27.35$, $P < 0.0001$), variability in aridity (the standard deviation (s.d.) of SPEI; $\chi^2_1 = 10.52$, $P = 0.0012$) and aridity (mean SPEI; $\chi^2_1 = 3.31$, $P = 0.069$)—were important for current endophyte prevalence ($P < 0.0001$; Fig. 5). The interaction effect of the two significant explanatory terms, historical endophyte prevalence and s.d. of SPEI, was also significant ($Z = -2.93$, $P = 0.0017$; see the 'Historical endophyte prevalence, climate variability, and their interaction are important to current endophyte prevalence section' in the Supplementary Methods). As expected, we found that historical and current endophyte prevalence are strongly related (that is, populations with a historically higher endophyte prevalence continue to have a high endophyte prevalence and vice versa). Interestingly, under high climatic variability, historically highly mutualistic populations (90% endophyte prevalence) were predicted to lose their mutualists ~8× more on average compared with populations with historically low (10%) mutualism (historically high mutualism, 67.1% loss in prevalence versus historically low mutualism, 7.9% loss). Furthermore, the predicted loss of mutualists from high mutualism populations under high climatic variability (67.1% loss) was far greater than the gain in mutualists in low mutualism populations under low climatic variability (15.1% gain), suggesting differential responsiveness of endophyte prevalence to climate variability for high and low mutualism populations.

Discussion

By combining large-scale common garden field experiments, demographic modelling, climate data and long-term population monitoring across the host species' range, our research provides two key insights. First, as hypothesized, microbial mutualists can underpin long-term plant population persistence across species ranges. Our demographic model predicted that facultative mutualistic microorganisms enhance host population growth across the range, consistent with significantly greater rates of persistence of mutualistic natural populations over 13 years from our surveys. Second, variability in a climate change-related stress (aridity) can select against a mutualism that ameliorates directional changes in the mean of the same stressor. Despite endophyte mutualism being broadly beneficial to host populations in this study, its prevalence did not increase and endophyte loss was the highest among natural populations experiencing greater temporal climate variability, potentially undermining the very interactions that support hosts in arid conditions. Our population model additionally revealed that endophytes promote host population growth primarily through enhancing fecundity. Furthermore, our demographic model showed that endophytes can underpin persistence in sites with the driest climates, which scales up our previous research showing that endophytes confer drought tolerance to individual plants and allow hosts to occupy the driest parts of their range[13]. However, we found no evidence that endophytes buffer hosts from climate variability or extreme events nor did we observe increases in endophyte prevalence, which was contrary to our second hypothesis. In fact, results from both our demographic predictions and surveys of natural populations support that more variable climates weaken endophyte benefits and reduce their prevalence, respectively, despite endophyte mutualism being broadly beneficial.

Our field surveys and demographic model showed endophyte mutualism positively impacts range-wide host population persistence and growth rates, respectively. Previous demographic modelling has also predicted that microbial mutualisms enhance plant population growth[11,16,39–41]. Our study complements predictions of increased population viability from demographic models with monitoring of natural populations and shows that in real-world field conditions, populations with microbial mutualists actually have significantly higher persistence across the species range. Consistent with endophyte association increasing predicted population growth rates, anecdotally, the largest natural populations tended to be endophyte-associated, and larger population sizes could reduce susceptibility to extinction. In fact, surveyed historically non-mutualistic populations were roughly four times more likely to suffer local extinction than their highly mutualistic counterparts—especially remarkable given that *B. laevipes* is a perennial grass and fewer than 15 years elapsed between surveys. Including tracking of natural population sizes would have provided an even more in-depth understanding of mutualism impacts on population dynamics and extinctions. Overall, the combination of the growing body of

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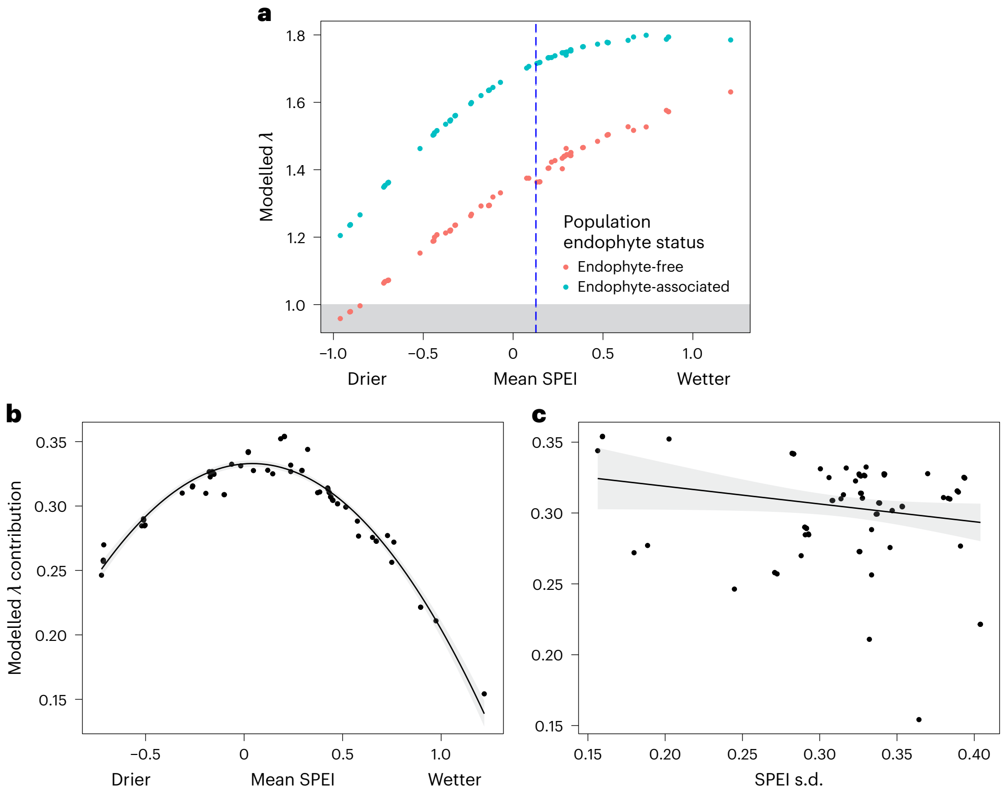

Fig. 4 | Positive endophyte contributions to population growth had a unimodal relationship with aridity and declined with increasing climate variability. a–**c**, Modelled population growth rates, both endophyte-free and endophyte-associated, for the 86 sites corresponding to our field survey populations across the *B. laevipes* range. As sites became wetter on average during the four experimental years, predicted λ values increased for both endophyte-associated and endophyte-free populations (**a**). Endophyte contributions to modelled population growth rates for the 86 sites (that is, the difference in modelled λ between endophyte-associated and endophyte-free populations) had a unimodal relationship with aridity (ANOVA; $R^2 = 0.93$, $F_{2,83} = 584.3$, $P < 2 \times 10^{-16}$) (**b**) and decreased marginally significantly with variability in aridity (ANOVA; $R^2 = 0.042$, $F_{1,84} = 3.68$, $P = 0.058$) (**c**). Each point represents one *B. laevipes* population, the line is the polynomial or linear regression and the shaded areas represent the standard error. Here, mean SPEI refers to the SPEI of each site in the *B. laevipes* range, averaged across the years of the common garden experiments. The dashed blue line represents the mean SPEI for all 86 surveyed sites of *B. laevipes* populations over the four experimental years; note that the mean is not centred at zero because the climate values from the four common garden experimental years represent only a subset of the climate data used to calculate SPEI values. SPEI s.d. refers to the s.d. of SPEI of each given site over the same years. Note that vital rate functions were parameterized using SPEI as a candidate term, which is, in turn, closely related to the mean SPEI across experimental years at each site. Thus, for **b** in particular, model predictions are strongly explained by site mean SPEI, with deviations from the unimodal curve largely due to year-to-year climate variability. Panel **b** therefore primarily shows that model predictions do indeed follow a unimodal curve.

demographic modelling research predicting that microbial mutualists increase population growth[11,16,39–41] and our new work validating that mutualistic populations do, in fact, have greater persistence through time and across space suggests microbial mutualist impacts on population persistence are widespread. Furthermore, this study demonstrates that demographic model predictions based on experimental populations align with population outcomes in real communities. The life table response experiment revealed that biologically, endophytes provide these demographic benefits largely through enhancing host fecundity, in line with dynamics in other grass–endophyte systems[42,43]. While this mutualism was overall beneficial for host population growth, the negligible or even negative effects of endophytes on particular vital rates related to host growth and survival may hint at subtle partner conflict (discussed in 'Endophyte effects on host vital rates suggest possibilities for host–mutualist conflict' section of the Supplementary Discussion).

Importantly, the effects of mutualism on populations could ultimately impact host species ranges. By enhancing fitness and modifying niches through abiotic stress amelioration, mutualisms can expand the set of environmental conditions and thus the geographic ranges wherein species persist[44]. Previous empirical research has linked low mutualist prevalence outside a species' established range to reduced individual fitness, highlighting how mutualisms can help set range limits[6,18,20,45–47]. Here, we demonstrated that low mutualist prevalence can also explain local extirpations within species ranges, which, if not compensated for by dispersal, could manifest in range contractions over long timescales. Our demographic model predictions also provide experimental insight into how microbial mutualists can expand species ranges through abiotic stress amelioration. Endophyte mutualisms can enhance host drought tolerance[26], and our original study[13] demonstrated how endophyte-conferred drought amelioration allows *B. laevipes* to expand its range into drier habitats. Supporting this, here, our demographic model showed that endophyte association was necessary for host populations to achieve positive population growth rates in the driest parts of their range. Therefore, by ameliorating aridity stress, endophyte mutualism enables *B. laevipes* populations to inhabit regions that are otherwise overly stressful[4]. In the context of global change, moisture deficit across *B. laevipes*'s range is projected to increase by >40% in some areas[48]. As mean climate becomes more arid, our demographic model predicts that endophytes may become indispensable to the persistence of *B. laevipes* and potentially other hosts.

However, multiple lines of evidence implicated climate variability as a disruptor of endophyte mutualism. First, although our

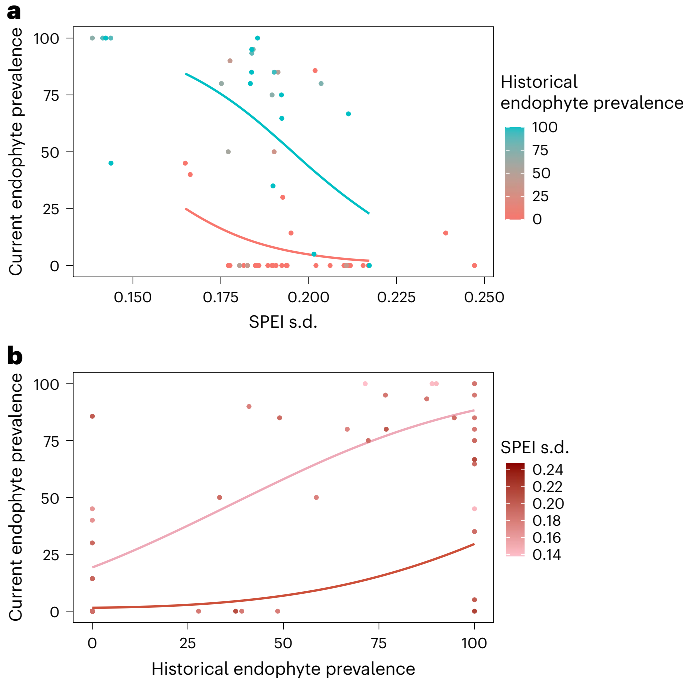

Fig. 5 | Current endophyte prevalence has declined with increasing climate variability. a,**b**, Current endophyte prevalence in 2022 resurveys plotted against the s.d. of SPEI (**a**) and historical endophyte prevalence (**b**) in the original 2009 surveys. Current endophyte prevalence was generally positively related to historical endophyte prevalence, but endophyte prevalence has declined over time in historically highly mutualistic populations with higher climate variability. Points represent *B. laevipes* populations and their colours represent their historical endophyte prevalence (**a**) and climate variability experienced (**b**). The curves are the regression model plotted for both high (90%) and low (10%) levels of historical endophyte prevalence (**a**) and both high (0.22) and low (0.16) levels of climate variability (**b**). The regression model shows that current endophyte prevalence is a function of historical endophyte prevalence (ANOVA; $\chi_1^2 = 27.35$, $P = 1.70 \times 10^{-7}$), interannual variation in aridity (that is, s.d. of SPEI; $\chi_1^2 = 10.52$, $P = 0.0012$) and mean aridity ($\chi_1^2 = 3.31$, $P = 0.069$); the interaction effect between current endophyte prevalence and variation in aridity was also significant (two-sided *Z*-test; $Z = -2.93$, $P = 0.0017$).

demographic model predicted consistently positive endophyte effects on population growth rates and that endophytes are crucial in highly arid conditions, endophyte contributions to population growth rate declined with increasing climate variability. Specifically, predicted endophyte contributions were 10.56% higher in the least variable site compared with the most variable one. This was due to endophyte-associated and non-associated populations having different climatic optima, leading to the relative benefit of endophyte mutualism to population growth from our demographic model being the greatest in intermediate to slightly dry climates. As variable climates inherently include more climatically extreme years, and in both directions (extreme dry and wet) the relative benefit of endophyte mutualism is diminished, climate variability weakens positive selection for endophyte mutualism.

Second, rather than increasing through time was we predicted, endophyte prevalence within natural host populations declined most strongly in populations with greater climate variability and historically high mutualism prevalence. Historical endophyte prevalence was also likely negatively shaped by pre-survey (that is, before 2009) climate variability. However, climate variability has substantially increased across *B. laevipes*'s range in recent years and has therefore probably only become more important in structuring mutualism within these populations (see 'Climate variability structures endophyte prevalence' section in the Supplementary Discussion). Interestingly, while historically highly mutualistic populations declined in prevalence under high climatic variability, historically non-mutualistic populations did not see equivalent prevalence increases under low climatic variability. This asymmetry may result from the ability of mutualistic populations to lose mutualists more readily (for example, via imperfect vertical transmission within mutualistic populations[49]) than non-mutualistic populations gain mutualists (for example, via migration of infected individuals into a population). Taken in conjunction with evidence from studies of other important mutualisms (for example, arbuscular mycorrhizal fungi colonization[50]), our work suggests that climate variability may commonly impact mutualism prevalence. Importantly, our study further revealed that variability in a climate change-related stress (that is, aridity) can select against a microbial mutualism that ameliorates the same stressor. This negative selection occurred despite clear evidence that this mutualist increases host tolerance to drought in field and greenhouse experiments[13] and, in this study, increases population growth above a critical threshold for maintaining persistence under severe aridity. Therefore, researchers should exercise caution when concluding that stress-ameliorating mutualisms should be selected for by global change because mutualisms providing benefits under one parameter of a stressor (that is, mean aridity) may simultaneously be weakened by another parameter in the same stressor (that is, variability in aridity).

Variability selecting against mutualism was surprising. Given that recent modelling research predicted endophytes provide demographic buffering that protects against environmental stochasticity[16], we expected their prevalence to increase under more variable climates. However, not only did we detect that endophyte prevalence declined in surveyed natural populations under high climate variability but our demographic model also predicted decreasing benefits of endophyte mutualism with increasing climatic variability. Mutualisms can be environmentally context dependent[51], and in variable environments, where the costs and benefits of a microbial symbiont can change over time, models suggest that the ability to lose microbial symbionts when they are costly improves host fitness[52]. Collectively, this suggests climate variability reduces the benefits of endophytes relative to their costs, leading to declining prevalence.

Climate variability could also select against endophyte prevalence through several additional pathways. First, climate variability could directly reduce transmission frequencies, which for vertically transmitted mutualists is linked to prevalence[53]. For instance, endophytes can confer thermal tolerance for their hosts, but higher temperatures have been associated with lower transmission frequencies in some grasses[7,54–57]. In cases where endophyte-infected hosts are favoured but endophyte transmission is reduced in hotter years that occur in more variable climates, mutualism effects could become unlinked from transmission and therefore prevalence. Alternatively, climate variability could promote coexistence between mutualistic and non-mutualistic individuals within populations if they exhibit niche differentiation[58]. Context dependency in mutualisms can result in niche differentiation between mutualistic and non-mutualistic hosts, which temporal environmental variability can then act upon to promote coexistence of host types[58,59]. Previous research and our demographic modelling here suggest that endophyte-associated and endophyte-free *B. laevipes* populations occupy different climatic niches, with mutualistic populations occupying drier climates and vice versa[13]. When niche differences exist between mutualistic and non-mutualistic host individuals, a more heterogeneous environment through time may allow for coexistence, resulting in selection against mutualism in populations with a relatively high prevalence and thus populations that are stable at intermediate rather than near-fixed levels of mutualism[60]. These scenarios demonstrate how a mutualism being broadly beneficial does not necessitate increases in its prevalence under increased climate variability.

Taken together, our study demonstrates facultative microbial mutualisms can have outsized importance for the persistence of host plant populations across range-wide and decadal scales. However, the benefits of mutualism are not necessarily accompanied by increases in mutualism prevalence; in fact, we found that mutualism prevalence declined in populations experiencing more variable climates. Moving forward, many regions, including the range of *B. laevipes*, are anticipated to experience mean shifts in climate but also more variable climates[37,48]. Our findings demonstrate that even when mutualisms are beneficial under anticipated shifts in mean conditions—for example, towards drier climates—selection for increased mutualism prevalence could be outweighed by increases in climate variability (for example, in precipitation). This may ultimately be detrimental to long-term host population viability if mutualisms decline or are lost. Given the importance of mutualisms for biodiversity[61] and ecosystem function[62,63] and agriculture[64,65], as well as how mutualisms ameliorate stress from environmental change[66–69], this possibility is alarming. Therefore, we advocate for research investment by the scientific community into the combined and interactive effects of mean and variability in climate on mutualisms spanning the tree of life. These efforts are vital for not only predicting how complex global change scenarios will affect the stability of these important stress-ameliorating interactions and the persistence of partnering organisms but also for developing management strategies to protect the critical ecosystem services that mutualisms underpin.

Methods

Study system

Endophytic fungi are ubiquitous, occurring in every major plant lineage[32], with clavicipitaceous endophytes living as endosymbionts in the foliar tissue of an estimated 20–30% of the over 10,000 grass species (Poaceae)[70]. Occurrence estimates of systemic fungal endophytes of the genus *Epichloë* (Clavicipitaceae) in groups of cool-season grasses have ranged from 7.5% to 42.5% (refs. 33–35). *Epichloë* endophytes are often mutualistic, conferring drought tolerance, resistance to herbivory and pathogens and enhanced nutrient uptake to their hosts in exchange for photosynthetic carbon[24–26,71]. However, the costs and benefits of endophyte mutualism can vary through time and with environmental conditions[72]. This mutualism is facultative from the perspective of the plant and obligate from the perspective of the endophyte in that endophytes are not free living and often depend on their hosts for transmission through the maternal lineage[32].

Bromus laevipes (Shear) (Chinook brome) is a perennial C_3 bunchgrass that occurs in small, patchy populations across the California floristic province[73]. *B. laevipes* commonly associates with vertically transmitted systemic fungal endophytes[36]. Previous research combining range-wide field surveys across 92 populations, species distribution modelling, field common garden experiments and greenhouse experiments demonstrated that the presence of these endophytes was associated with the expansion of the geographic range of *B. laevipes* by thousands of square kilometres into drier habitats[13]. Furthermore, while endophytes confer drought tolerance, which is beneficial in drier environments, they probably also result in a net cost in wetter habitats, where carbon costs of supporting endophytes outweigh their drought-amelioration benefits[13].

Population surveys

In 2009–2010, we surveyed endophyte prevalence in 92 natural populations of *B. laevipes* across northern and central California (19.81 ± 1.20 plants per population, mean ± s.e.m.). Sites were selected on the basis of herbarium records and accessibility (Consortium of California Herbaria, https://ucjeps.berkeley.edu/consortium; see previous work[13] for details on initial survey procedures). In 2022, we resurveyed ~95% of the original 92 populations (15.94 ± 0.67 plants per population, mean ± s.e.m., >1,000 total; six sites not resurveyed owing to inaccessibility; Fig. 1), evaluating persistence of each population and quantifying endophyte prevalence (mutualism interaction frequency). Note that *B. laevipes* is a short-lived perennial, with turnover of individuals expected between initial surveys and resurveys. To match previous survey methods for endophyte prevalence, each plant from a given population was evaluated for fungal hyphae by staining with aniline blue lactic acid dye under a compound microscope (Supplementary Fig. 1), which yields similar results to immunoblot assay or PCR detection methods[74,75] (see 'Seed staining for endophyte detection' section in the Supplementary Methods). Population-level endophyte prevalence was then quantified as the percentage of individuals sampled from each host population in which endophyte was detected.

Environmental data

To gain insight into the relationship between changing climates and both plant population persistence and mutualism interaction prevalence, we obtained data on two major environmental factors often shaped by climate change—aridity and fire history—for all surveyed grass population sites. For aridity and drought, downscaled climate data were obtained from the PRISM Climate Group for the period between the plant–endophyte surveys in 2009 and 2022. Then, potential evapotranspiration was calculated at each site using the hargreaves function, and the SPEI was calculated for each site using the spei function[76]. SPEI is a standardized drought index quantifying relative aridity of a site, with more negative values indicating more extreme drought and more positive values indicating wetter conditions[38]. We calculated three aspects of SPEI for each site over the period between surveys: mean SPEI (mean of the annual mean SPEIs), interannual variation in SPEI (s.d. of the annual mean SPEIs) and the rate of change in SPEI across those years (that is, the regression coefficient between annual mean SPEI and time). For fire history, fire data were obtained from the California State Geoportal, and sites were scored dichotomously (1 or 0) on the basis of whether a fire had occurred during the period between the plant–endophyte surveys in 2009 and 2022. Data preparation and all statistical analyses were performed within R version 4.3.1 (R Core Team, 2023).

Statistical analyses of long-term population persistence and changes in mutualism prevalence in natural host populations

To determine if historical mutualism prevalence predicts plant population persistence and whether this is moderated by environmental factors, we first used global model selection to identify the best-supported multiple logistic regression model using the glm function. *B. laevipes* population persistence was the binary response variable. The candidate explanatory variables were historical endophyte prevalence (in 2009), mean SPEI, interannual variation in SPEI, rate of change in SPEI and occurrence of fire between surveys, as well as the two-way interactions between historical endophyte prevalence and each environmental variable. Collinearities were checked using the cor function for pairs of continuous variables and by calculating an R^2 value for pairs of continuous and categorical variables, with cut-offs of 0.7 and 0.49, respectively. We did not detect collinearities between candidate explanatory terms. Subsequent global model selection based on the corrected Akaike information criterion (AIC_c) was conducted using the dredge function in R[77] (Supplementary Table 4). The best supported model had two explanatory variables—historical endophyte prevalence and fire occurrence. We further tested for an interaction effect in our best model (see 'Testing for interaction effects in the population persistence model' section in the Supplementary Methods).

To determine which environmental factors promote or disrupt endophyte mutualism, we first evaluated whether host populations had shifted towards increased endophyte prevalence between surveys. Upon finding that they did not (see 'Host populations maintained intrapopulation variation in mutualism rather than progressing towards endophyte fixation' section in the Supplementary Discussion), we analysed how endophyte prevalence shifted over time within populations with different environmental conditions and mutualism backgrounds. Specifically, we first constructed a multiple beta regression model using the betareg function[78] with a response variable of current endophyte prevalence as a proportion (frequency in 2022) and candidate explanatory variables of historical endophyte prevalence, fire occurrence and mean, variation and rate of change in SPEI as well as the interactions between historical endophyte prevalence and each environmental variable. This was followed by global model selection (Supplementary Table 6).

Residuals from all best models were checked for spatial autocorrelation using the moran.test function or 9999 permutations and the moran.mc function to conduct a permutation test for Moran's I, depending on normality of residuals[79]. None of our statistical models exhibited significant spatial autocorrelation (P or pseudo-$P > 0.05$ for Moran's I of all models).

Demographic modelling to evaluate endophyte effects on predicted population persistence

To further assess and predict the effects of endophytes on plant population dynamics, we constructed a demographic model for *B. laevipes* parameterized with independent data from several multi-year, multi-site common garden experiments manipulating endophyte mutualism and measuring its effects on host plant recruitment, survival and growth. We tested the predictions of our model against actual persistence of populations from our resurveys. Then, we evaluated our model across a set of abiotic conditions spanning the *B. laevipes* range and conducted life table response experiments to gain mechanistic understanding into how (that is, through enhancing which vital rates) and under what conditions endophytes provide demographic benefits.

As they predict population growth rates (λ), demographic model outputs are highly relevant to population persistence. To construct a population model, we first performed a set of common garden experiments tracking individual plants from 2010 to 2015. These experiments involved 1,650 plants and 550 seeds, which were monitored for 6 years at five sites chosen to span a large part of the *B. laevipes* range[80] (northern to central California; ~420 km; Supplementary Table 7), including a wide ecological and climatic gradient (for example, ~450–1,750 mm average annual precipitation during experiment years, which includes 92% of the range of average annual precipitation experienced by this species during these years). To allow assessment of endophyte effects on host demography, fungal endophyte manipulation was achieved in two ways: first, by selecting plants and seeds from 11 populations with different endophyte mutualism statuses (that is, naturally mutualistic and non-mutualistic populations) and second, through experimental fungicide application to allow assessment of endophyte demographic effects (that is, experimental reduction of endophyte mutualism) (see 'Field common garden experiments for demographic model construction' section in the Supplementary Methods for more details). Using data from our experiments and from the PRISM database, we modelled vital rates (for example, survival, growth and flower number) in relation to plant size and age, endophyte status, site and year-specific SPEI and other factors (see 'Vital rate parametrizations' section in the Supplementary Methods). We then used the vital rate models to parameterize a demographic model (see 'Population projection matrix model construction' section in the Supplementary Methods). This model allowed us to predict the growth rate for each host population site using its endophyte status and its yearly climate across the experimental years as inputs. For each population, we further predicted by how much the growth rate would increase if it was endophyte-associated compared with if it was endophyte-free, allowing us to relate endophyte population benefits to climatic factors. Although slight inflation of λ values may have resulted from germination data not including potential mortality of new recruits (see 'Field common garden experiments for demographic model construction' section in the Supplementary Methods for more details), simulations of increased recruit mortality resulted in more endophyte-free populations below the threshold for positive population growth, strengthening the result that endophyte mutualism can enable population persistence of host plants (Supplementary Fig. 16).

Across the 86 natural populations that we surveyed, we evaluated whether endophyte association was related to higher predicted population growth rates using 9999 permutations and the function perm.t.test[81]. We also performed fixed-effect life table response experiments to quantify class-dependent contribution of endophyte mutualism to the population growth rate[82] (see the 'Life table response experiment' section in the Supplementary Methods). A life table response experiment calculates the contribution to population growth rate (that is, the difference in λ) of a fixed effect (here, endophyte mutualism) through all possible transitions between classes (Supplementary Fig. 12). We tested whether endophyte effects on population growth were greater via growth and survival or fecundity using a Wilcoxon signed-rank test (wilcox.test function). Finally, we evaluated how endophyte effects varied with climate conditions across our 86 field sites. For each site, we calculated the difference in λ between hypothetical endophyte-associated and endophyte-free populations, which represented the contribution of endophytes to population growth rates (that is, the relative benefit of endophyte mutualism). We then ran a polynomial regression and a linear regression between this difference in modelled λ and the mean SPEI or variation in SPEI of each site across the experimental years, respectively, to determine whether endophyte mutualism effects on population growth rates varied by site climate.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All datasets involved are available via Zenodo at https://doi.org/10.5281/zenodo.17379577 (ref. 83). Raw climate data are available from the PRISM Group (https://prism.oregonstate.edu/).

Code availability

Code to replicate our analyses and associated datasets are available via Zenodo at https://doi.org/10.5281/zenodo.17379577 (ref. 83).

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Author contributions

V.W.L. collected field survey data, performed data analysis and demographic modelling and wrote the manuscript. J.C.F. contributed to demographic model construction and manuscript revisions. A.S.D. contributed to building and writing methods for the demographic model and manuscript revisions. S.Y.S. contributed to the conceptualization and design of the common garden experiments as well as the manuscript revisions and student supervision. C.A.S. contributed to survey data collection, manuscript revisions and feedback on modelling and statistical analyses. M.E.A. led overall project conception and contributed to data collection for field surveys and common gardens, common garden experimental design and establishment, feedback on analyses, manuscript revisions and student supervision.

Competing interests

The authors declare no competing interests.

Additional information

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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software used
Data analysis	R Version 4.3.1 was used for all analyses. Scripts were written by the authors and have been uploaded to Zenodo (https://doi.org/10.5281/zenodo.17379577).

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Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

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Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study involved two components. The first was field monitoring of 86 natural populations of the host plant Bromus laevipes across much of its range. These populations were surveyed twice, 13 years apart. For each survey, prevalence of a microbial symbiont (Epichloe systemic fungal foliar endophytes) were quantified using established methods. The other component consisted of two sets of five common garden experiments. The first set of experiments were seedling transplant experiments, and the other set consisted of germination experiments. The five garden locations were chosen to span the host's climatic gradient and geographic range and were crossed factorially with 11 source populations (of varying endophyte symbiosis status), as well as experimentally-manipulated endophyte level for the transplant experiments. These data were used to generate demographic models to predict population growth rates/persistence of host populations across the species range.
Research sample	For the field surveys of natural populations, at least 20 individuals of the host species Bromus laevipes were sampled from each population when possible. The 86 natural populations used in this study were chosen based on herbarium occurrence data and accessibility and span most of the host's range. The host species Bromus laevipes was chosen because it is known to form associations with vertically transmitted systemic fungal endophytes of the genus Epichloe. Furthermore, previous research has shown these endophytes expand the host's range into drier environments but may represent a cost in wetter environments. For the common garden experiments, 11 source populations for plants were chosen to provide a range of endophyte statuses, with some populations naturally forming associations with endophytes and others being endophyte-free. The five gardens were chosen to span most of the host's climatic and geographic range.
Sampling strategy	For the field surveys, 86 host plant populations were selected based on herbarium occurrence records and accessibility. At least 20 individuals from each population were surveyed when possible following methods in Afkhami et al. (2014). For the common garden experiments, 15 and 10 replicates for each treatment combination were used for the seedling transplant and seed germination experiments, respectively.
Data collection	Author MEA performed the data collection for the initial surveys as well as the common garden experiments. Authors MEA and CAS performed the field resurveys 13 years later, for which MEA and VWL performed the endophyte detection staining. Endophyte detection was performed using a compound microscope and aniline blue lactic acid staining, following established methods (Bacon & White, 1994) commonly used to detect Epichloe in host grasses. MEA visited field sites annually to collect data on survival, size (leaves & tiller counts), flowering (occurance and number), and germination of experimental plants as well as estimate herbivore damage for each plant.
Timing and spatial scale	The original surveys were conducted between 2009-10, and the resurveys were conducted in 2022. The 86 populations span most of northern and central California, which contains most occurrence records for the host plant Bromus laevipes. For the common garden experiments, the seedling transplant experiments ran from 2010-2016, with data collection occurring each year starting in 2011. The germination experiments ran from 2010-2012 and were also monitored each year, starting in 2010. The five common gardens were established across northern and central California to span most of Bromus laevipes's climate and geographic range.
Data exclusions	The final two years of our common garden experiments were not included in our demographic model predictions because it was not

Data exclusions	possible to distinguish between truly dead and merely dormant individuals in the final years of the experiments, which is an important distinction for demographic modeling. However, analysis of endophyte effects on plant performance metrics in those years showed similar effects to earlier years.
Reproducibility	All raw data is publicly accessible through Zenodo (https://doi.org/10.5281/zenodo.17379577).
Randomization	For the common garden transplant experiments, within each garden, seedlings from each treatment combination (source population x endophyte treatment) were transplanted into randomly assigned locations in the common garden grid. For the germination experiments, within each garden, seeds were placed in random locations within field garden arrays.
Blinding	No human participants were involved in this study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	This study was conducted in the California Floristic Province across Northern and Central California. The population surveyed and field experiment sites have Mediterranean climates and in some case Continental climates and typically occur in the foothills of mountain ranges like the Sierra Nevada and the Coast Range. The plants grow at the edge of forests (or near shrubs on serpentine soils) where they typically experience partial shade and partial sun conditions.
Location	The 86 populations and 5 common garden experiment sites span most of northern and central California, which include most occurrences of the host plant Bromus laevipes. The latitude and longitude are provided for each in the Supplementary Information (Tables S1 and S3).
Access & import/export	This research was all conducted within the US, and samples were collected with appropriate permitting or permissions (e.g., permission from University of California Reserve System and permits from Mendocino National Forest). All common gardens occurred with permission on University of California Reserves (Quail Ridge, McLaughlin, Hastings, and Angelo).
Disturbance	For surveys, we were careful to minimize disturbance to the population by just sampling needed tissue rather than whole plant removal, such that plants could continue to grow at the sites. To minimize disturbance in the seedling common garden experiments, we planted seedlings into the existing matrix of the plant community--which is typically sparse in B. laevipes preferred habitat--with minimal soil disturbance during initial planting (~5cm depth) in year 1. Plant tags were attached at soil level, and no other changes were made to the area. Disturbance in seed common garden experiments was very minimal -- we placed seeds marked with toothpick into the natural, undisturbed plant community already at the sites. Because seeds germinate near the soil surface for this species, there was very little change to the habitat with soil disturbance limited to toothpicks penetrating 0.5cm into soil.

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We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern
☐	☒	Plants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
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Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

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☒ ☐ Enable evasion of diagnostic/detection modalities
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☒ ☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	Seeds were collected from 11 natural populations the growing season prior to the experiments (all populations used in experiments are listed in with gps locations in the supplement) and seeds were stored at 2oC until use in experiments.
Novel plant genotypes	N/A
Authentication	N/A