

# Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity

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## 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.

## Data and Code Accessibility

Data will be made accessible as an Environmental Data Initiative package online  
**DOI:** [updated here when available](#). Code for all analysis is available through  
<https://github.com/joshuacfowler/Grass-Endophyte-Stochastic-Demography>

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**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 environmental extremes, microbial symbionts reduce hosts' demographic variance. We parameterized stochastic models using data from a 14-year symbiont-removal experiment including seven grass species that host *Epichloë* fungal endophytes. Endophytes reduced variance in fitness by > 10%, on average. Hosts with "fast" life history traits that lacked longevity as an intrinsic buffer benefited most from symbiont-mediated variance buffering. Under current climate conditions, contributions of variance buffering were modest compared to symbiont benefits to mean fitness. However, simulations of increased stochasticity amplified benefits of variance buffering and made it the more important pathway of host-symbiont mutualism than elevated mean fitness. Microbial-mediated variance buffering is likely an important, yet cryptic, mechanism of resilience in an increasingly variable world.

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139 **Introduction**

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141 Global climate change involves increases in environmental variability, including  
142 changes to precipitation patterns and the frequency of extreme weather events [1, 2].  
143 Yet, the ecological consequences of increased variability are less well understood than  
144 those of changing climate means, such as long-term warming or drying. Incorpor-  
145 rating environmental variability into forecasts of population dynamics can improve  
146 predictions of the future [3].

147 Classic theory predicts that long-term population growth rates (equivalently, pop-  
148 ulation mean fitness) will decline under increased environmental stochasticity because  
149 the costs of bad years outweigh the benefits of good years – a consequence of nonlinear  
150 averaging [4, 5]. For example, in unstructured populations, the long-term stochastic  
151 growth rate in a fluctuating environment ( $\lambda_s$ ) will always be lower than the average  
152 growth rate ( $\bar{\lambda}$ ) by an amount proportional to the environmental variance ( $\sigma^2$ ):

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$$\log(\lambda_s) \approx \log(\bar{\lambda}) - \frac{\sigma^2}{2\bar{\lambda}^2} \quad (1)$$
  
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157 Populations structured by size or stage similarly experience costs of variability [6, 7].  
158 There are accordingly two pathways to increase population viability in a variable  
159 environment: increase the mean growth rate and/or dampen temporal fluctuation in  
160 growth rates, also called “variance buffering”.

161 Both the inherent characteristics of species and the external properties of their envi-  
162 ronment can buffer demographic fluctuations. These inherent characteristics include  
163 life history traits [8, 9], negative correlations among vital rates [10], transient shifts in  
164 population structure [11]. For example, theory predicts that long-lived species, those  
165 on the slow end of the slow-fast life history continuum, will be less sensitive to environ-  
166 mental variability than short-lived species [12], a pattern which has empirical support  
167 across plants [13] and animals [9, 14]. Demographic variance is also determined by  
168 external abiotic factors, such as the magnitude of environmental variability [15] or  
169 the degree of environmental autocorrelation [16, 17]. These complex interplay of these  
170 factors determines the risks of extinction faced by populations [18] and underlies man-  
171 agement strategies promoting ecosystem resilience [19]. Yet little is known about how  
172 biotic interactions influence demographic variability or contribute to variance buffer-  
173 ing [20]. Intra-specific interactions, such as parental care, can reduce demographic  
174 variance in birds [21] and in primates [22]. While most research on inter-specific inter-  
175 actions focuses on their effects on mean demographic performance, species interactions  
176 also have the potential to influence demographic variance.

177 Most multicellular organisms host symbiotic microbes that affect growth and per-  
178 formance [23, 24], and many of these are vertically transmitted from maternal hosts to  
179 offspring [25]. Vertical transmission links the fitness of hosts and symbionts in a feed-  
180 back loop that selects for mutual benefits [26]. Many vertically-transmitted microbes  
181 are mutualistic and protect hosts from stressful environmental conditions including  
182 drought, extreme temperatures, or natural enemies [27, 28]. Some of the best studied  
183 examples include bacterial symbionts of insects that provide their hosts with thermal  
184 tolerance through the production of heat-shock proteins [29], and fungal symbionts of

plants that produce anti-herbivore and drought-protective compounds [30–32]. However, these diverse protective symbioses are context-dependent: the magnitude of benefits depends on environmental conditions [33, 34] and thus will vary temporally in a stochastic environment [35]. We hypothesized that context-dependent benefits from symbionts may buffer hosts 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. Variance buffering is a previously unexplored mechanism by which symbionts may benefit their hosts instead of or in addition to elevating average fitness, the focus of most previous research.

To test the hypothesis that context-dependent benefits of symbiosis buffer hosts from the fitness costs of environmental stochasticity, we used a combination of long-term field experiments and stochastic demographic modeling. We used cool-season grasses and *Epichloë* fungal endophytes as 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 ~ 30% of  $C_3$  grass species [36]. These fungi are primarily transmitted vertically from maternal plants through seeds [37]. They produce a variety of alkaloids that can protect host plants from natural enemies [38] and drought stress [39].

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 stochastic population projection models in a hierarchical Bayesian framework. 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 contribution 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. The experiment focused on seven of these grasses (*Agrostis perennans*, *Elymus villosus*, *Elymus virginicus*, *Festuca subverticillata*, *Lolium arundinaceum*, *Poa alsodes*, and *Poa sylvestris*), each of which hosts a

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

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#### 234 **Endophyte removal, plant propagation, and field set-up**

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236 Seeds from naturally symbiotic populations of the seven focal host species were col-  
237 lected during summer-fall 2006 from Lilly-Dickey Woods and the nearby Bayles Road  
238 Teaching and Research Preserve (39.220167, -86.542683). To generate symbiotic (S+)  
239 and symbiont-free (S-) plants from the same genetic lineages, seeds from each species  
240 were disinfected with a heat treatment described in Table S1 or left untreated. The  
241 heat treatment created symbiont-free plants by warming seeds to temperatures at  
242 which the fungus becomes inviable but the host seeds can still germinate. Both heat-  
243 treated and untreated seeds were surface sterilized with bleach to remove epiphyllous  
244 microbes, cold stratified for up to 4 weeks, then germinated in a growth chamber before  
245 transfer to the greenhouse at Indiana University where they grew for ~ 8 weeks. We  
246 confirmed endophyte status by staining thin sections of inner leaf sheath with aniline  
247 blue and examining tissue for fungal hyphae at 200X magnification [40]. We estab-  
248 lished experimental populations with vegetatively propagated clones of similar sizes  
249 (plants ranging from one to six tillers across species). By starting the experiment with  
250 plants of similar sizes and the same number of unique genotypes, we aimed to limit  
251 any potential effects of heat treatments on initial plant growth [41].

252 During the fall of 2007 and spring of 2008, we established 10 3x3 m. plots for *A. perennans*, *E. villosus*, *E. virginicus*, *F. subverticillata*, and *L. arundinaceum* and 18  
253 plots for *P. alsodes* and *P. sylvestris*. Half of the plots were randomly assigned to be  
254 planted with either symbiotic (S+) or symbiont-free (S-) plants, and initiated with  
255 20 evenly spaced individuals labeled with aluminum tags. In spring 2008, we placed  
256 plastic deer net fencing around each plot to limit deer herbivory and disturbance;  
257 damaged fences were regularly replaced.

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#### 259 **Long-term demographic data collection**

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261 Each summer (2008–2021) we censused all individuals in each plot for survival,  
262 growth and reproduction, and added new recruits to the census. Plots contained 13.3  
263 individuals/m<sup>2</sup> on average over the course of the experiment. Each census year was a  
264 sample of inter-annual climatic variation (n = 14 years, comprising 13 demographic  
265 transition years). We censused each species during its peak fruiting stage (May: *Poa*  
266 *alsodes*, *Poa sylvestris*; June: *Festuca subverticillata*; July: *Elymus villosus*, *Elymus vir-*  
267 *ginicus*, *Lolium arundinaceum*; September: *Agrostis perennans*), such that the censuses  
268 were pre-breeding and new recruits came from the previous years' seed production.  
269 Leaf litter was cleared out of each plot prior to the census, to aid in locating plants.  
270 For each plant remaining from the previous year, we determined survival, measured  
271 its size as a count of tillers, and collected reproductive data as counts of reproductive  
272 tillers and seed-bearing spikelets on all reproductive tillers to a maximum of three. We  
273 also tagged all unmarked individuals that were recruits from the previous years' seed  
274 production and collected the same demographic data. New recruits typically had one  
275 tiller and were non-reproductive. In 2008 through 2010, we took additional counts of  
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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 the exotic *L. arundinaceum*, which had very high survival and low recruitment, and consequently very low variation across years. In total across 14 years, the dataset included demographic information for 16,789 individual host-plants and 31,216 transition-year observations.

We expected plots to maintain their endophyte status (symbiotic or symbiont-free) because these fungal symbionts are almost exclusively vertically transmitted, and plots were spaced a minimum of 5 m apart, limiting seed dispersal or horizontal transmission of the symbiont between plots. However, we regularly confirmed endophyte treatment throughout the lifetime of the experiment by opportunistically taking subsets of seeds from reproductive individuals and scoring them for their endophyte status with microscopy as above. Overall, these scores reflected 98% faithfulness of recruits to their expected endophyte status across species and plots (Fig. S23; Supplement data). Additionally, we have rarely observed fungal stromata, the fruiting bodies by which *Epichloë* are potentially transmitted horizontally, provided the fly vector is also present [42]. For *A. perennans*, *F. subverticillata*, *L. arundinaceum*, and *P. alsodes*, we never observed stromata. We observed stromata only infrequently for *E. villosus*, and even more rarely for *E. virginicus* and *P. sylvestris* (Table S2). For these species, stromata have only been observed irregularly across years on 35, 4, and 6 plants respectively, making up < 0.3% of all censused plants.

## Vital rate modeling

Equipped with these demographic data, we fit statistical models for survival, growth, flowering (yes or no), fertility of flowering plants (number of flowering tillers), 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 these vital rates as generalized linear mixed models in a hierarchical Bayesian framework using RStan [43] 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 the individual-level vital rates to population projection models [44]. All vital rate models included random plot and year effects, with separate estimates of year-to-year variance for symbiotic and symbiont-free plants, to quantify the effect of endophytes on inter-annual variance. All parameters were given vague priors [45]. We ran each vital rate model for 2500 warm-up and 2500 MCMC sampling iterations with three chains. We assessed model convergence with trace plots of posterior chains and checked for  $\hat{R}$  values less than 1.01, indicating low within- and between-chain variation [46, 47]. For those models that showed poor convergence, we extended the MCMC sampling to include 5000 warm-up and 5000 sampling iterations, which was only necessary for seedling growth. We graphically checked vital rate model fit with posterior predictive checks comparing simulated and observed data (Fig. S19-S20).

*Survival* - We modeled survival as a Bernoulli process, where the survival ( $S$ ) of an individual  $i$  in plot  $p$  and census year  $t$  was predicted by the plot-level endophyte

323 status ( $e$ ), host species ( $h$ ), size in the preceding census, and the plant's origin status  
324 (whether it was initially transplanted or naturally recruited into the plot).

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327  $S_{i,p,e,h,t} \sim Bernoulli(\hat{S}_{i,p,e,h,t})$  (2a)

328  $\text{logit}(\hat{S}_{i,p,e,h,t}) = \beta_{0_h} + \beta_1 * \text{origin}_i$  (2b)

329  $+ \beta_{2_h} * \text{endo}_e + \beta_{3_h} * \text{size}_{i,t-1} + \tau_{e,h,t} + \rho_p$  (2c)

330  $\tau_{e,h,t} \sim \text{Normal}(0, \sigma_{\tau_{e,h}}^2)$  (2d)

331  $\rho_p \sim \text{Normal}(0, \sigma_\rho^2)$  (2e)

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334 Here,  $\hat{S}$  is the survival probability,  $\beta_{0_h}$  is an intercept specific to each host species,  
335  $\beta_1$  is the effect of the plant's recruitment origin,  $\beta_{2_h}$  is the endophyte effect,  $\beta_{3_h}$  is the  
336 size effect,  $\tau_{e,h,t}$  is a normally distributed year effect for each species and endophyte  
337 status with variance  $\sigma_{\tau_{e,h}}^2$ , and  $\rho_p$  is a normally distributed plot effect with variance  
338  $\sigma_\rho^2$  ( $p(e)$  indicates that plot identity is uniquely associated with an endophyte status).  
339 We assume that origin effect  $\beta_1$  and plot-to-plot variance  $\sigma_\rho^2$  are shared across host  
340 species, allowing us to "borrow strength" across the multi-species dataset; other model  
341 parameters are unique to host species. We separately modeled the survival of newly  
342 recruited seedlings with a similar model but omitting previous size dependence and  
343 origin status.

344 *Growth* - We modeled plant size in census year  $t$  ( $G$ ) with the same linear pre-  
345 dictor for the mean as described for survival. Because we measured size as positive  
346 integer-valued counts of tillers, we modeled it with a zero-truncated Poisson-inverse  
347 Gaussian distribution. This distribution includes a shape parameter  $\lambda_G$  to account for  
348 overdispersion in the data. We additionally modeled the growth of newly recruited  
349 seedlings separately with a Poisson-inverse Gaussian model omitting size structure  
350 and the plants' origin status as with seedling survival.

351 *Flowering* - We modeled whether or not a plant was flowering during the census ( $P$ )  
352 as a Bernoulli process, with the same linear predictor for the mean as described above  
353 for survival except that size dependence for reproductive vital rates was determined  
354 by the individual's size during the same census year as opposed to its size during the  
355 previous year.

356 *Fertility* - For a plant that was flowering during the census, its fertility was the  
357 number of reproductive tillers produced ( $F$ ), which we modeled as a function of size in  
358 the same census period with a zero-truncated Poisson-Inverse Gaussian distribution,  
359 with the same linear predictor for the mean as described above.

360 *Spikelets per Inflorescence* - Spikelet production ( $K$ ) was recorded as integer counts  
361 on up to three inflorescences per reproducing plant. We modeled these data with a neg-  
362 ative binomial distribution, with the same linear predictor for the mean as described  
363 above.

364 *Seed Production per Spikelet* - For individuals with recorded counts of seed pro-  
365 duction, we calculated the number of seeds per spikelet from our counts of seeds and  
366 spikelets per inflorescence, and then modeled seeds per spikelet ( $D$ ) as means of a  
367 Gaussian distribution for each species and endophyte status. Because we had less

detailed data across years and plants for seed production than for other reproductive vital rates, we omitted both plot and year random effects. 369  
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*Seedling Recruitment* - We used a binomial distribution to model the recruitment of new seedlings ( $R$ ) into the plots from seeds produced in the preceding year, assuming no long-lived seed bank. We included an intercept specific to each host and endophyte status and the same random effects structure as in other models. We estimated the number of seeds per plot in the preceding year by multiplying the total number of reproductive tillers per plant by the mean number of spikelets per inflorescence and mean number of seeds per spikelet ( $D$ ). For plants with missing fertility or spikelet data, we used the expected number of reproductive tillers ( $F$ ) or of spikelets per inflorescence from ( $K$ ), drawing from the full posteriors of our models. We rounded this value to get the estimated seed production for each individual, and finally summed across all reproductive plants in each year and plot to get the total number of seeds produced. 371  
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## Stochastic population model

We parameterized stochastic matrix projection models using the fitted statistical vital rate models. 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 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 having to assume demographic equivalence between seedling and non-seedling one-tiller plants. We used the same model structure for each species and endophyte status (not shown in model notation for readability). See Fig. S21 for a generalized life cycle graph. 399  
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The number of recruits in year  $t + 1$  is given by:

$$r_{t+1} = \sum_{x=1}^U P(x; \boldsymbol{\tau}_P) F(x; \boldsymbol{\tau}_F) K(x; \boldsymbol{\tau}_K) D R(\boldsymbol{\tau}_R) n_t^x \quad (3)$$

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 reproductive tillers  $F$ , 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 rate of seedling production, which is multiplied by the number of plants of size  $x$  ( $n_t^x$ , the  $x^{\text{th}}$  element of  $\mathbf{n}_t$ ) and summed over all sizes. Each function also depends on the species- and endophyte-specific year random effects for that vital rate ( $\boldsymbol{\tau}$ , a vector of year-specific values derived from the statistical models).

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

$$n_{t+1}^y = Z(y; \boldsymbol{\tau}_Z) B(\boldsymbol{\tau}_B) r_t + \sum_{x=1}^U S(x; \boldsymbol{\tau}_S) G(x, y; \boldsymbol{\tau}_G) n_t^x \quad (4)$$

where  $n_{t+1}^y$  is the  $y^{\text{th}}$  element of vector  $\mathbf{n}_{t+1}$ . The first term on the right hand side of Eqn. 4 represents growth ( $Z$ ) and survival ( $B$ ) of seedling recruits. The second term

415 includes the survival of previously  $x$ -sized plants and the growth of survivors from size  
 416  $x$  to  $y$ , summed over all  $x$ . To avoid predictions of unrealistic growth outside of the  
 417 observed size distribution, we set a ceiling on the growth function for plants at the  
 418 97.5<sup>th</sup> percentile of observed sizes for each host species [48].

419 Each of the vital rate functions in Eqns. 3 and 4 have separate intercepts and year  
 420 random effects for symbiotic and symbiont-free populations, allowing us to calculate  
 421 the effect of endophyte symbiosis on the mean, variance, and coefficient of variation  
 422 (CV) of  $\lambda$ , the dominant eigenvalue of the year- and endophyte-specific projection  
 423 matrix. This model treats climate drivers implicitly through year-specific random  
 424 effects. We also developed a climate-explicit version with the addition of parameters  
 425 defining the relationship between either annual or growing season drought index and  
 426 each vital rate. A full description of climate-explicit methods can be found in the  
 427 *Supporting Information Supplemental Methods*.

428

## 429 Life History Analysis

430

431 We collected metrics describing each host species' life history to test the relationship  
 432 between pace of life and variance buffering (Table S2). Using the Rage package [49],  
 433 we calculated  $R_0$ , longevity, and generation time from the mean transition matrix for  
 434 symbiont-free populations. We recorded seed size as the average lemma length from  
 435 the Flora of North America [50]. We also calculated the 99th percentile of maximum  
 436 observed age for symbiont-free plants from the census data for each species. Next, we  
 437 fit Bayesian phylogenetic mixed-effects models using the brms package [51] to test the  
 438 relationship between each life history trait and the effect of symbiosis on the CV of  $\lambda$   
 439 (a measure of variance buffering) while controlling for phylogenetic non-independence  
 440 between host and symbiont species. We pruned species-level phylogenies of plants  
 441 [52] and *Epichloë* fungi [53] to include the focal species. *Agrostis perennans* was not  
 442 included in the tree, and so we used the congener *A. hyemalis*. We defined separate  
 443 phylogenetic covariance matrices for each pruned tree. We propagated uncertainty in  
 444 the estimated variance buffering effect  $V$  with a measurement error model:

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$$V_{MEAN,h} \sim Normal(V_{EST,h}, V_{SD,h}) \quad (5a)$$

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$$V_{EST,h} \sim Normal(\mu_h, \sigma) \quad (5b)$$

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$$\mu = \alpha + \beta * trait + \pi_j \quad (5c)$$

450

$$\alpha \sim Normal(0, .5) \quad (5d)$$

451

$$\beta \sim Normal(0, .1) \quad (5e)$$

452

$$\sigma \sim Half-Normal(.04, .01) \quad (5f)$$

453

$$\pi_h \sim MVN(0, \sigma_\pi \mathbf{A}) \quad (5g)$$

454

$$\sigma_\pi \sim Half-Normal(0, .1) \quad (5h)$$

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457 Here,  $V_{EST}$  is the variance buffering effect for host species  $h$ , estimated from the  
 458 posterior mean ( $V_{MEAN}$ ) and standard deviation ( $V_{SD}$ ), propagating uncertainty asso-  
 459 ciated with the effect of symbiosis. The model includes an intercept ( $\alpha$ ) and a slope  
 460

( $\beta$ ) defining the relationship between the variance buffering effect and the life history trait. The residual standard deviation is given by ( $\sigma$ ). We used weakly informative priors to aid model convergence. Each prior was centered at zero, except for the residual standard deviation, which we centered at the standard deviation of the estimated variance buffering effect, .04. The phylogenetic random effect ( $\pi$ ), which is modeled as a multivariate normal distribution, has a between-species standard deviation ( $\sigma_\pi$ ) structured by the phylogenetic covariance matrix  $\mathbf{A}$ . We ran each MCMC sampling chain for 8000 warmup iterations and 2000 sampling iterations. We assessed model convergence as described for the vital rate models.

## Mean-variance decomposition

To calculate stochastic population growth rates ( $\lambda_s$ ) 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 produces models that realistically capture inter-annual variation by preserving correlations between vital rates [54]. We tallied the 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  $\log(\lambda_s) = E[\log(\frac{N_t}{N_{t+1}})]$  [55, 56]. We calculated the total effect of endophyte symbiosis as the difference in  $\lambda_s$  between S+ and S- populations. We propagated uncertainty from the vital rate models to the calculation of  $\lambda_s$  using 500 draws from the posterior distribution of model parameters.

We decomposed the total endophyte effect on  $\lambda_s$  into contributions from effects on vital rate means, variances, and their interaction. Specifically, we repeated the calculation of  $\lambda_s$  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  $\lambda_s$  treatments (S+ vital rate means and variances, S- means and variances, S+ means with S- variances, S- means with S+ variances) allowed us to quantify to what extent the overall effect of symbiosis derives 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 (see Eq. 1) such that variance is more detrimental for populations with lower average growth rates.

To create scenarios of increased variance relative to that observed during the study period, we repeated the stochastic growth rate decomposition, but sampling only 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  $\lambda$  values. These extreme  $\lambda$  values represent the best and worst years experienced by the plants, using the S- populations as the reference condition. By sampling away from an average year in both directions, the six- and two- years scenarios increased the standard deviation of yearly host growth rates by 1.3 and 2.1 times, respectively, without changing mean growth rates (< 2.3% difference in  $\bar{\lambda}$  between simulation treatments, Fig. S22). We performed the same

507 mean-variance decomposition for these scenarios as for the ambient conditions (all 13  
508 years sampled) for all host species described above.

509

## 510 **Results**

511

### 512 **Symbionts buffer host demographic variance**

513

514 Across the 14 census years, endophytes reduced inter-annual variance for 66% (37/56)  
515 of host species-vital rate combinations (average Cohen's D for effects on vital rate stan-  
516 dard deviation: -0.15) (Fig 1A; Fig. S6 - Fig. S18). Endophytes also increased mean  
517 vital rates for the majority (36/56) of host species-vital rate combinations (average  
518 Cohen's D for effects on vital rate mean: 0.15), and benefits were particularly strong  
519 for host survival, plant growth and recruitment (Fig. 1A; Fig. S1 - Fig. S5). The magni-  
520 tude of mean and variance effects differed among host species and vital rates. Symbiont  
521 effects on vital rate variance are as large and even exceed effects on vital rate means  
522 for certain species. For example, endophytes modestly increased mean adult survival  
523 (Fig. 1C) and strongly reduced variance in survival (Fig. 1D) for *Festuca subverticil-  
524 lata*, while for *Poa alsodes*, variance buffering was more apparent in seedling growth  
525 and inflorescence production (Fig 1E). Interestingly, certain vital rates showed costs  
526 of endophyte symbiosis. Symbiotic individuals of *A. perennans* grew larger than those  
527 without endophytes (Fig. 1B), yet endophytes also reduced this species' mean recruit-  
528 ment rates (Fig. 1A). Similarly, variance was increased for certain species' vital rates,  
529 such as in seedling growth for *Elymus villosus* and *Festuca subverticillata* (Fig. 1A).

530

531 Because not all vital rates contribute equally to fitness, we used stochastic matrix  
532 models to integrate the diverse effects on vital rates described above into comprehen-  
533 sive measures for the mean and variance of year-to-year fitness ( $\lambda_t$ ) and the long-run  
534 stochastic fitness that integrates both mean and variance ( $\lambda_S$ ). On average across host  
535 species, S+ populations had greater mean fitness (> 92% confidence that endophytes  
536 increased  $\bar{\lambda}$ ) and lower inter-annual variability in fitness (> 86% confidence that endo-  
537 phytes decreased the coefficient of variation of  $\lambda_t$ ) than S- populations (Fig. 2). For  
538 some host species, the CV of  $\lambda_t$  declined by as much as 170% (*P. alsodes*, *F. subverti-  
539 cillata*), while for others, endophyte effects on variance were substantially smaller (6%  
540 lower for *E. villosus*, 16% lower for *A. perennans*), or even positive (27% increase for  
*E. virginicus*).  
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542

### 543 **Faster life histories predict stronger symbiont-mediated variance buffering**

544

545 Maybe need to bring up the "prediction" here or in introduction, but I moved it to  
the discussion<sup>1</sup>

546

547 In support of the prediction that hosts with long lifespans, which are intrinsically  
548 buffered from environmental variability, should benefit less from symbiont-mediated  
549 variance buffering, we found that hosts with trait values representing faster life history  
550 strategies experienced greater variance buffering from endophytes than those with  
551 slow life histories (Fig. 3). Bayesian phylogenetic mixed-effects models, controlling for  
552

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1

species' relatedness, indicated that variance buffering was stronger for host species with shorter lifespan (Fig. 3A; 75% probability of positive relationship with empirically observed maximum plant age) and smaller seeds (Fig. 3B; 73% probability of positive relationship with seed length). Other life history traits similarly had positive, but weaker, support for the prediction that faster life history traits correlate with stronger variance buffering (Fig. S26-S28).

## 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 the stochastic growth rate  $\lambda_S$  using simulations from the population models in four configurations<sup>2</sup>. These included either the full symbiosis effect (both mean and variance buffering effects), mean effects alone, variance effects alone, or neither mean nor variance effects. Overall, the full effect of symbiosis on  $\lambda_S$ , averaged across host species, provided strong evidence of grass-endophyte mutualism (99% certainty of a positive total effect on  $\lambda_S$ ) (Fig. 4; see Fig. S22 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  $\lambda_S$  from mean effects were four times greater, averaged across species, than contributions from variance buffering (Fig. 4), suggesting that, under the regime of environmental variability represented by our 14-year study, damped fluctuations in fitness via variance buffering was a far less important element of the benefits of symbiosis than increased mean fitness. Results for individual host species were largely consistent with the cross-species trends (Fig S22). The full effect of symbiosis on  $\lambda_S$  was positive for seven out of eight host species, with statistical confidence ranging from 66% to > 99% certainty. The one exception was the host species *P. sylvestris*, for which our analysis indicated that fungal endophytes were effectively neutral in their overall fitness effect (45% and 55% posterior probability of positive and negative effects; Fig S22).

## Variance buffering strengthens under increased environmental variability

To simulate increased variability, we repeated the decomposition of  $\lambda_S$  for two alternative forecast scenarios, randomly sampling transition matrices that represented either the six most extreme years experienced by each species or the two most extreme years, subsets of the thirteen transition matrices across the 14-year study period. Increased variability elicited stronger mutualistic benefits of endophyte symbiosis (Fig. 3) than ambient variability (overall effect of the symbiosis increased by > 130%). This increase was driven by increased contributions from the variance buffering mechanism (from a 24% contribution in the ambient scenario to a 66% contribution in the most variable scenario) rather than from greater mean effects. In the most variable scenario,

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<sup>2</sup> Could update this to include the VR decomposition

599 the relative importance of mean and variance effects reversed, with variance buffering  
600 contributions that were 1.5 times greater than contributions from mean benefits,  
601 averaged across species (Fig. 4).

602

## 603 Discussion

604

605 Across seven host species, eight vital rates, 14 years, and 16,789 individual plants, our  
606 analysis provided the first empirical evidence of symbiont-mediated variance buffering.  
607 When mean and variance effects of symbionts were considered together, none of the  
608 host-symbiont pairings were antagonistic (i.e., with endophytes that both decreased  
609 mean fitness and increased variance) (Fig. 2C), suggesting that variation across host  
610 species and vital rates in mean and variance effects may reflect alternative strategies  
611 that yield similar net benefits of endophyte symbiosis. These alternative strategies  
612 may to the long-term stability of these mutualism

613 Therefore, host species with long lifespans that produce few, large offspring should  
614 benefit less from symbiont-mediated variance buffering than species with fast life cycles  
615 that produce many smaller offspring with low per-capita chance of success [57, 58].

616 Considering fungal life history traits, the three host species for which the net mutualism  
617 benefit was weakest (*Elymus villosus*, *Elymus virginicus*, and *Poa sylvestris*)  
618 (Fig. 2C) were the only hosts for which we observed fungal stromata, fruiting bodies  
619 capable of horizontal (contagious) transmission (Table S2). This result supports the  
620 theoretical expectation that strict vertical transmission drives the evolution of strong  
621 host-symbiont mutualism [26, 59]. Conclusions about life histories are somewhat con-  
622 strained by the narrow range of trait values among closely related species in the grass  
623 sub-family Pooideae and their co-evolving symbionts. Our understanding of how life his-  
624 tory variation modulates the fitness consequences of microbial symbiosis would profit  
625 from tests across a wider span of taxonomic groups [60].

626 Simulations of increased environmental variability, a key prediction of climate  
627 change forecasts [2], indicated that mutualism with microbial symbionts, and their  
628 variance buffering effects in particular, will take on increased importance for hosts in  
629 a more variable future climate.

630 Reduced sensitivity to drought, as has been reported for some *Epichloë* symbioses  
631 [39], is a candidate mechanism that could generate a signature of variance buffering:  
632 drought conditions may have weaker fitness costs for S+ hosts, reducing fluctuations in  
633 fitness through time. Accordingly, analysis of climate-explicit matrix models indicated  
634 that, for five of seven taxa, S+ populations were less sensitive to annual or growing  
635 season drought (12-month or 3- month drought index; Standardized Precipitation-  
636 Evapotranspiration Index [61]) than S- populations (Supporting Information Text;  
637 Fig. S24-S25; Table S3). However, we did not find a strong relationship between the  
638 magnitude of variance buffering and relative drought sensitivities, suggesting that  
639 other climatic factors or other temporally-varying aspects of the environment may  
640 elicit benefits of endophyte symbiosis, including documented resistance to herbivory  
641 for six of these host taxa [62, 63].

642 To forecast how symbionts may affect hosts in future climates across their ranges,  
643 we need to consider that this is a field experiment in one location.

644

Thus, variance buffering – a cryptic microbial influence that manifests only over long time scales – is poised to become the dominant way in which grasses benefit from symbiosis with fungal endophytes in more variable climates of the future.	645
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To DO: remake size-struct plot for each species	648
Remake size structure for only recruit plantsecoles	649
- The fact that this is a field experiment in one location	650
SPEI analysis? and climate; implicit to explicit treatment of drivers; types of envrionemtnal variability	651
- Evolutionary context: i.e. different alternative strategies of mean and variance; diverse microbiome, bet-hedging	652
S+ and S- independent	653
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<b>Conclusion</b>	658
Ecologists increasingly recognize the importance of symbiotic microbes for host organisms and the populations, communities, and ecosystems in which their hosts reside [64–67]. Despite awareness of these ubiquitous interactions, long-term studies of microbial symbiosis are very rare. Our analysis of taxonomically-replicated, long-term field experiments that manipulated the presence/absence of fungal symbionts in plants demonstrates for the first time that heritable microbes can commonly benefit hosts not only through improved mean fitness – the focus of most previous research – but also through buffering against environmental variance. Our results provide an important advance to improve forecasts of the responses of populations (and symbiota) to increasing environmental stochasticity under global change, suggesting that, for some host species, microbial symbiosis may compensate for the lack of intrinsic tolerance of variability conferred by “slow” life history traits. We found that, relative to mean fitness benefits, symbiont-mediated variance buffering made weak contributions to host-symbiont mutualism under the current regime of environmental variability. However, variance buffering is likely to become the dominant benefit that fungal endophytes confer to grass hosts in more variable future environments. 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.	659
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691 **Acknowledgments.** We thank Mark Sheehan, Ali Campbell, Kyle Dickens, Blaise  
692 Willis, and Sar Lindner for contributions to field data collection. We also thank Volker  
693 Rudolf, Daniel Kowal, Lydia Beaudrot and Judie Bronstein for helpful comments on  
694 and discussion of this project. This research was supported by the National Science  
695 Foundation (grants 1754468 and 2208857).

696 **Supplementary information.** Supplementary information for this paper includes  
697 Supplementary Methods, Figs. A1 to A28, and Tables A1 to A3.  
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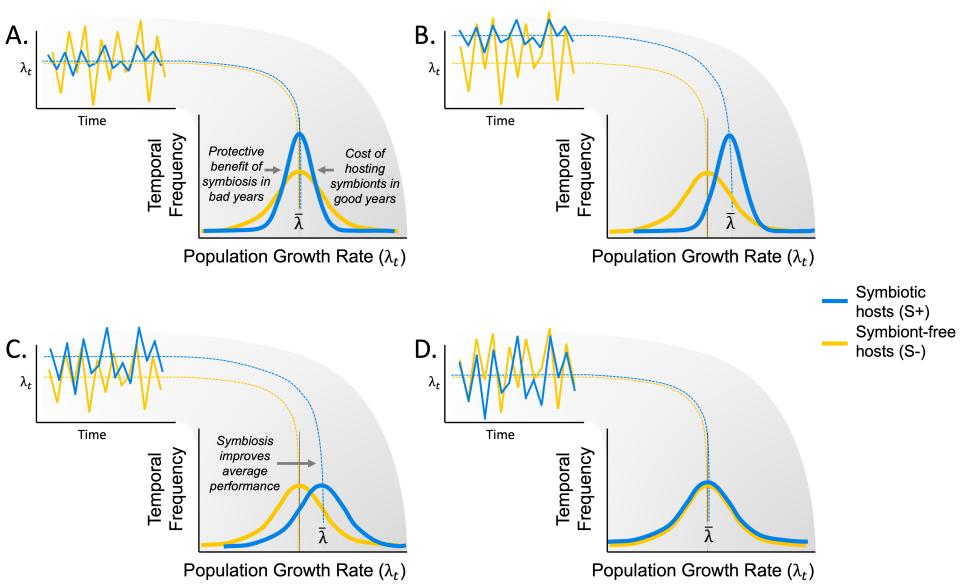
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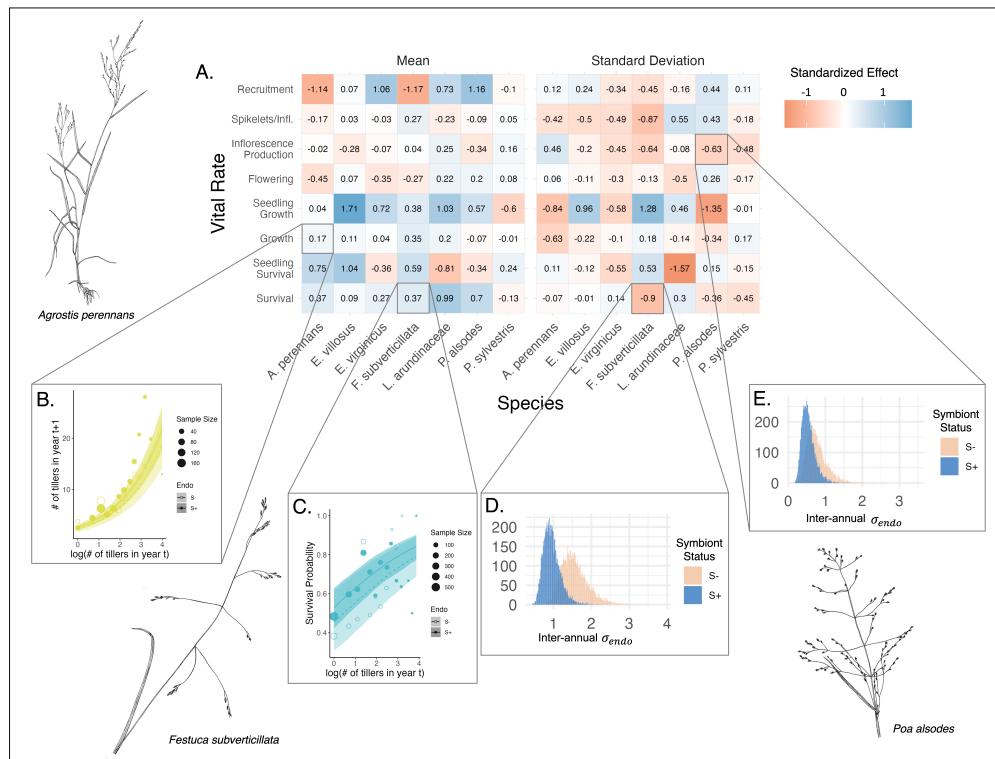
## Figures

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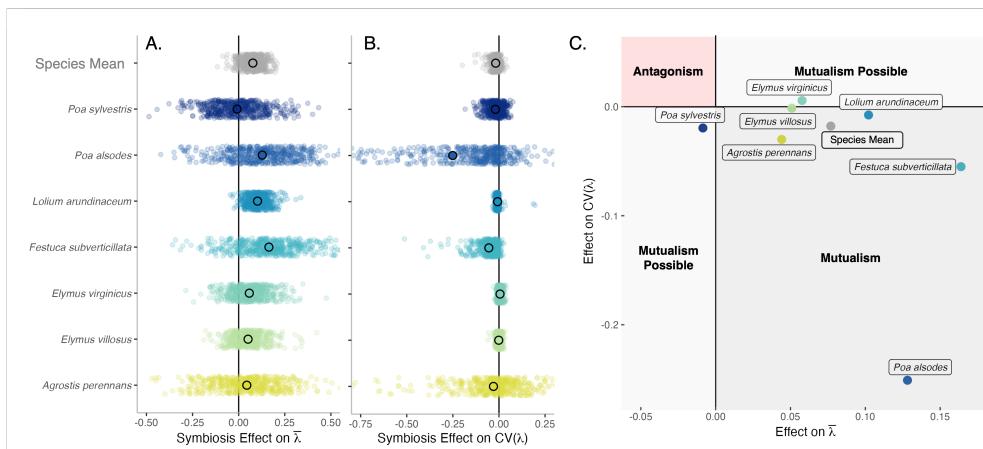
**Fig. 1** Hypothesized effects of symbiosis on the mean and variance of annual population growth rates. (A) Context-dependent symbiosis may provide benefits to hosts during harsh years while being neutral or costly during benign years. Temporal variance in populations growth rates of symbiotic host 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.

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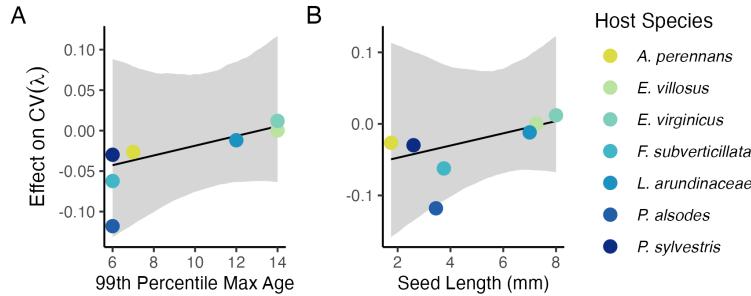


**Fig. 2** Endophyte symbiosis altered host vital rates.(A) Shading represents the posterior mean standardized effect size (Cohen's D) of endophyte symbiosis on mean or standard deviation of host vital rates (blue indicates that symbiosis increased the mean or standard deviation and red indicates a reduction). 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, mean vital rate estimates are shown with 80% credible intervals along with data binned by size for symbiotic (S+) and symbiont-free (S-) plants, while panels D-E show estimated posterior distributions of endophyte-status specific inter-annual standard deviation ( $\sigma_{\tau_{e,h}}^2$ ) for each vital rate for S+ (blue) and S- (beige) populations. Organism silhouettes modified from "Festuca subverticillata" by Cindy Roché and "Agrostis hyemalis" and "Poa alsodes" by Sandy Long ©Utah State University.

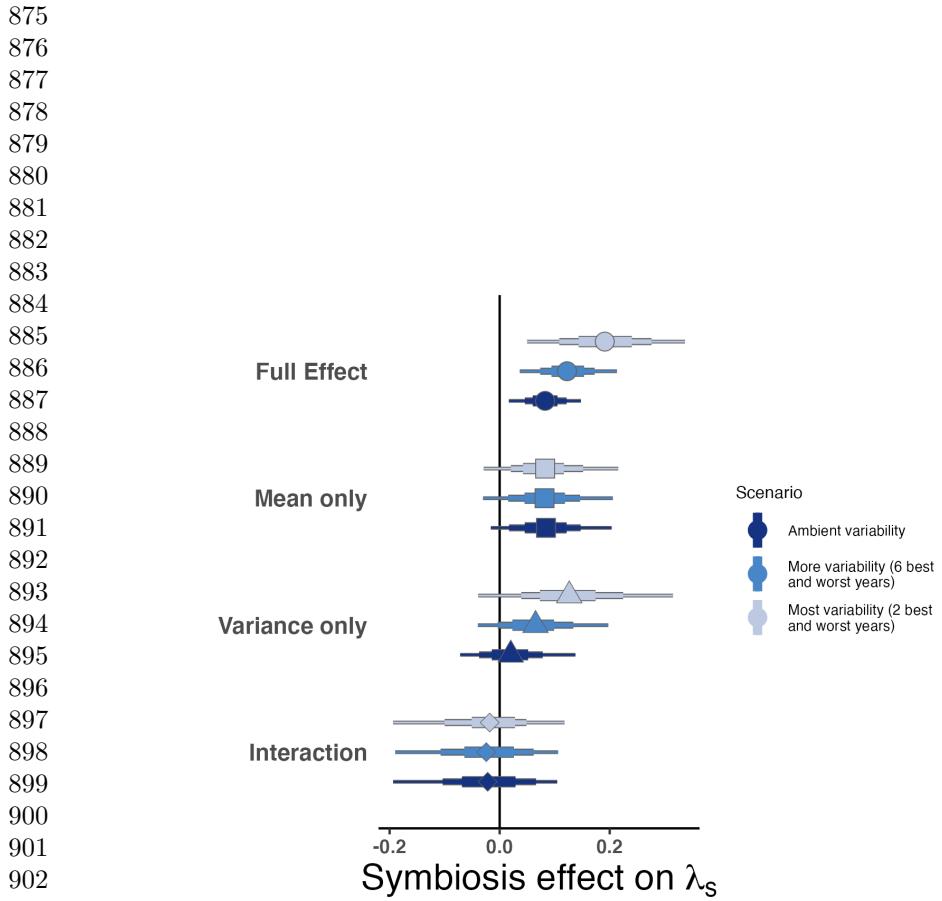
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**Fig. 3** Mean and variance-buffering effects on fitness. Black circles indicate the average effect of endophytes along with 500 posterior draws (smaller colored circles) on the (A) mean and (B) coefficient of variation in  $\lambda$  for each host 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.



**Fig. 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 coefficient of variation in population growth rate ( $\lambda$ ). Each panel shows the fitted mean relationship (line) along with the 95% credible interval.



904 **Fig. 5** Cross-species average endophyte contributions to stochastic growth rates under observed and  
 905 elevated variance. Endophyte symbiosis contributes to the total effect of mutualism on  $\lambda_S$  through  
 906 benefits to mean growth rates and through variance buffering as well as the interaction between  
 907 mean and variance effects. Shapes indicate the posterior mean of each contribution averaged across  
 908 the seven focal symbiota, along with bars for the 50, 75 and 95% credible intervals. The full effect of  
 909 the symbiosis (circles) becomes more mutualistic under scenarios of increased variance (represented  
 910 by color shading). Relative to the ambient scenario sampling transition matrices for all 13 transition  
 911 years during the study period, simulations increased variance by sampling the most extreme six or  
 912 two years, leading to increased contributions from variance buffering effects (triangles) and a  
 913 constant contribution from mean effects (squares).

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<b>Supporting Information</b>	921
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<b>Supplemental Methods</b>	923
<b>Estimating climate drivers of environmental context-dependence</b>	924
	925
To connect the variance buffering effects of endophytes with inter-annual variability in climate, we built climate-explicit stochastic matrix population models from the vital rate data in addition to the climate-implicit model described in the main text.	926
Identifying the potentially complex relationships between vital rates and environmental drivers remains a key challenge for accurate forecasts of the ecological impacts of environmental stochasticity [68]. We first downloaded temperature and precipitation data from a weather station in Bloomington, IN, approx. 27 km from our study site, using the rnoaa package [69]. Compared to other weather stations in the area, the measurements from Bloomington contain the most complete climate record across the study period and are correlated with more local measurements from Nashville, IN for years in which local data are available (total daily precipitation: $R^2 = .76$ ; mean daily temperature: $R^2 = .94$ ). The mean annual temperature across the study period was $11.9 C^\circ$ (SD: $1.05 C^\circ$ ) and the average annual precipitation was 1237.9 mm/year (SD: 204.89 mm/year) (Fig. S24). Given the known role of endophytes in promoting host drought tolerance, we calculated the Standardised Precipitation-Evapotranspiration Index (SPEI) for 3 and 12 months preceding each annual censuses, reflecting drought during the growing season and across the year [61]. To calculate SPEI, we used the Thornthwaite equation to model potential evapotranspiration as implemented in the SPEI R package [70]	927
We repeated the process of fitting statistical models for each vital rate as described in <b>Materials and Methods</b> with the inclusion of a parameter describing the influence of SPEI. We fit separate vital rate models incorporating either the growing season or annual drought index for each vital rate, except for the model describing the mean number of seeds per inflorescence. This model was fit without climate effects because the data came from only a few years. Initial analyses indicated similar fits for models including only a linear term and those with both linear and quadratic terms describing the relationship between the climate driver and the vital rate response, and so we proceeded with models including only the linear term. We expected that including climate predictors into the models would explain some inter-annual variance in vital rates, shrinking the variance associated with the fitted year random effects. We assessed model fit with graphic posterior predictive checks and convergence diagnostics as described for the climate-implicit analysis. Finally, we next built matrix projection models incorporating the climate-dependent vital rate functions to assess the response of symbiotic (S+) vs symbiont-free (S-) populations to drought. The model is as described in <b>Materials and Methods</b> with the inclusion of parameters describing the slope of the relationship with SPEI. We compared the sensitivity of $\lambda$ to either annual or seasonal SPEI of S+ populations ( $\frac{\Delta\lambda^+}{\Delta SPEI}$ ) with those of S- populations ( $\frac{\Delta\lambda^-}{\Delta SPEI}$ ) (Fig. S25; Table S).	928
Most species were slightly more responsive to growing season rather than annual drought conditions, and for most species symbiotic populations were less sensitive to	929
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967 SPEI than symbiont-free populations (Fig. S25; Table S3). However, these drought  
968 indices did not explain the full extent of inter-annual variability in demographic  
969 vital rates. For example, flowering in *A. perennans* had one of the strongest climate  
970 signals (82% probability of a positive relationship with SPEI), yet the estimated inter-  
971 annual variance  $\sigma_{\tau_p}^2$  for symbiont-free plants shrank from 6.7 to 6.1 after including  
972 3-month SPEI as a covariate, suggesting that other factors contribute to inter-annual  
973 variability.

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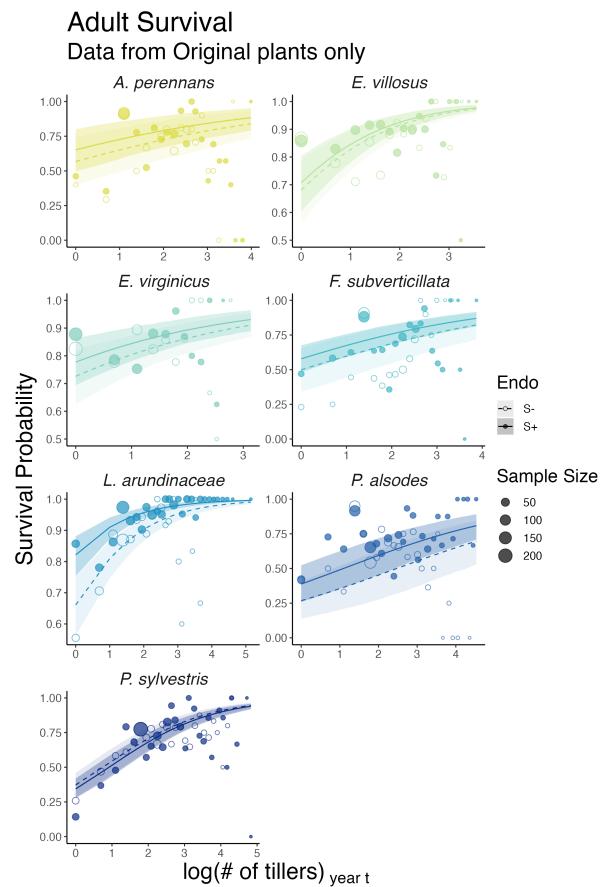
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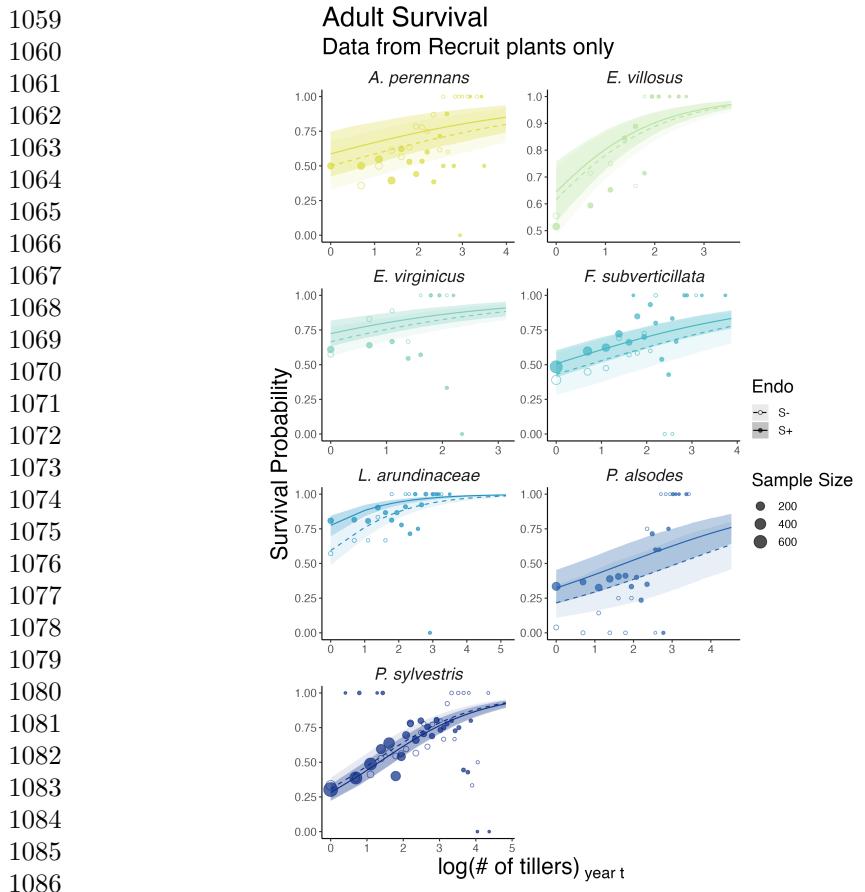
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## Supplemental Figures S1-S28



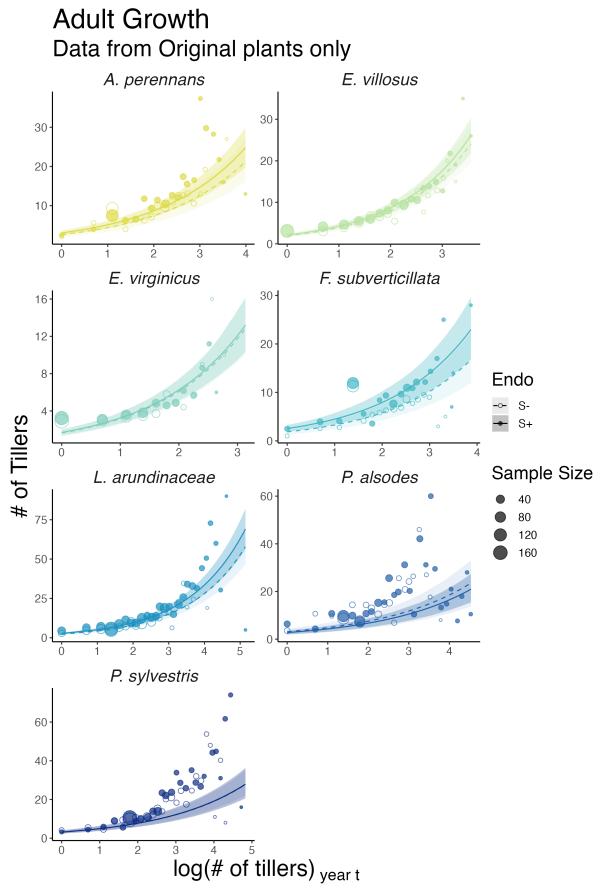
**Fig. S1** Effect of endophyte symbiosis on mean adult survival. Fitted curves represent the size-specific mean survival probability for original plants along with data binned by size shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading for S-.

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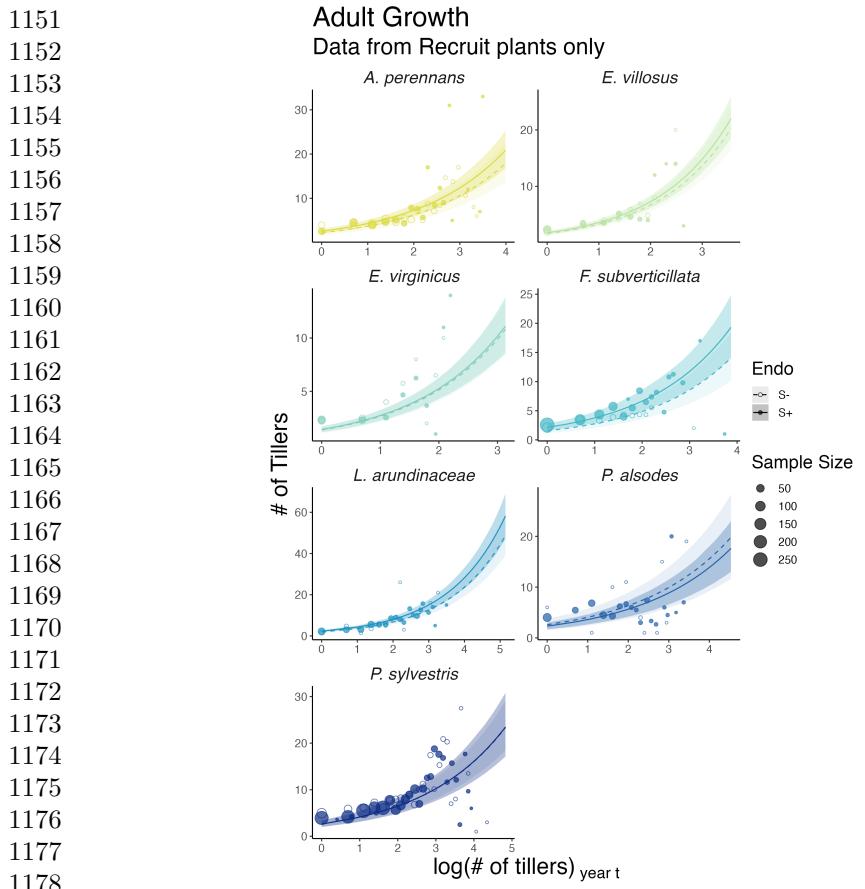
1087 **Fig. S2** Effect of endophyte symbiosis on mean adult survival. Fitted curves represent the size-  
1088 specific mean survival probability for recruited plants along with data binned by size shown as open  
1089 circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent  
1090 symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading  
1091 for S-.

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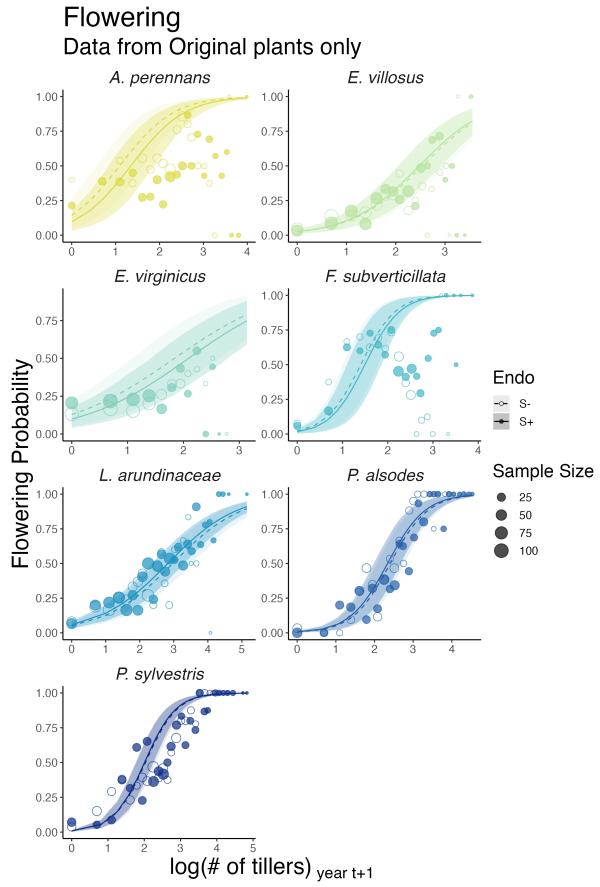
**Fig. S3** Effect of endophyte symbiosis on mean adult growth. Fitted curves represent the size-specific mean expected plant size for original plants along with data binned by size shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading for S-.

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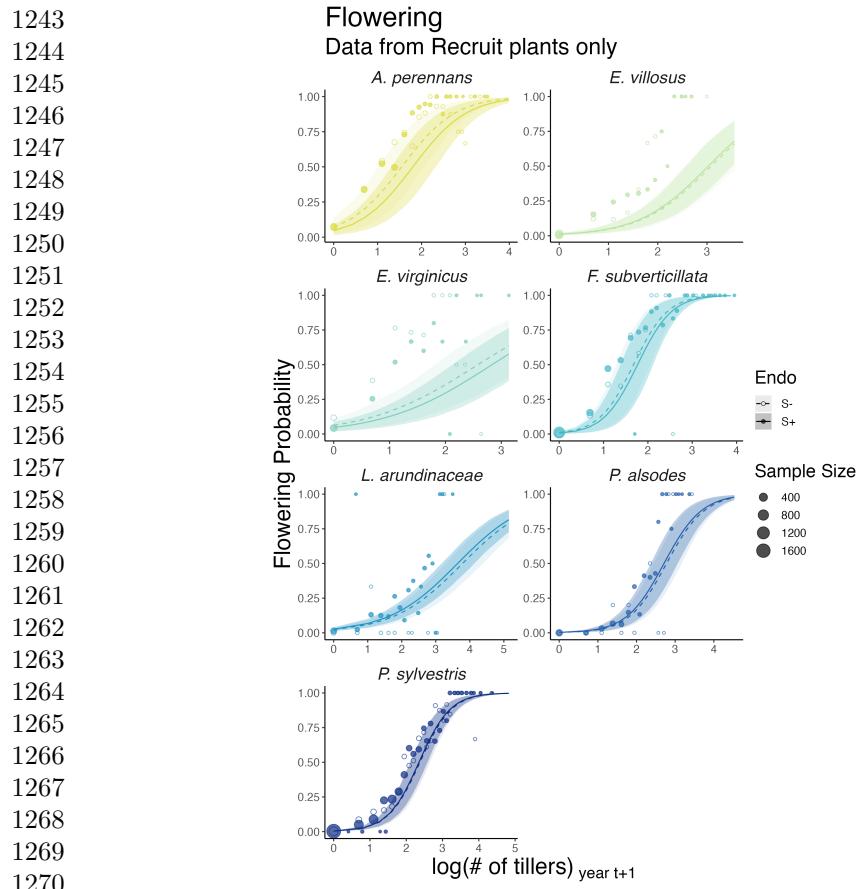


1179 **Fig. S4** Effect of endophyte symbiosis on mean adult growth. Fitted curves represent the size-  
1180 specific mean expected plant size for recruited plants along with data binned by size shown as open  
1181 circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent  
1182 symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading  
1183 for S-.

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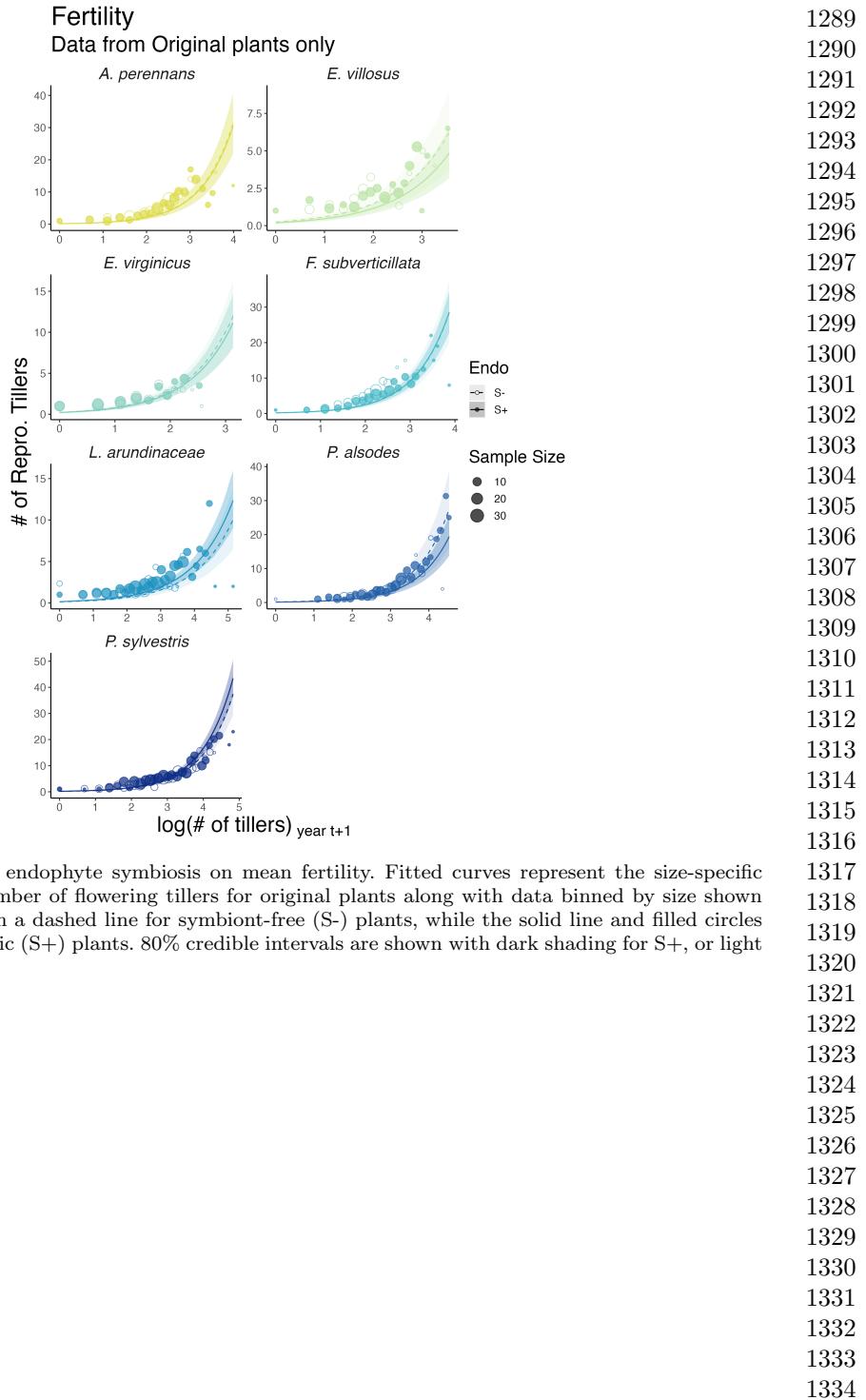


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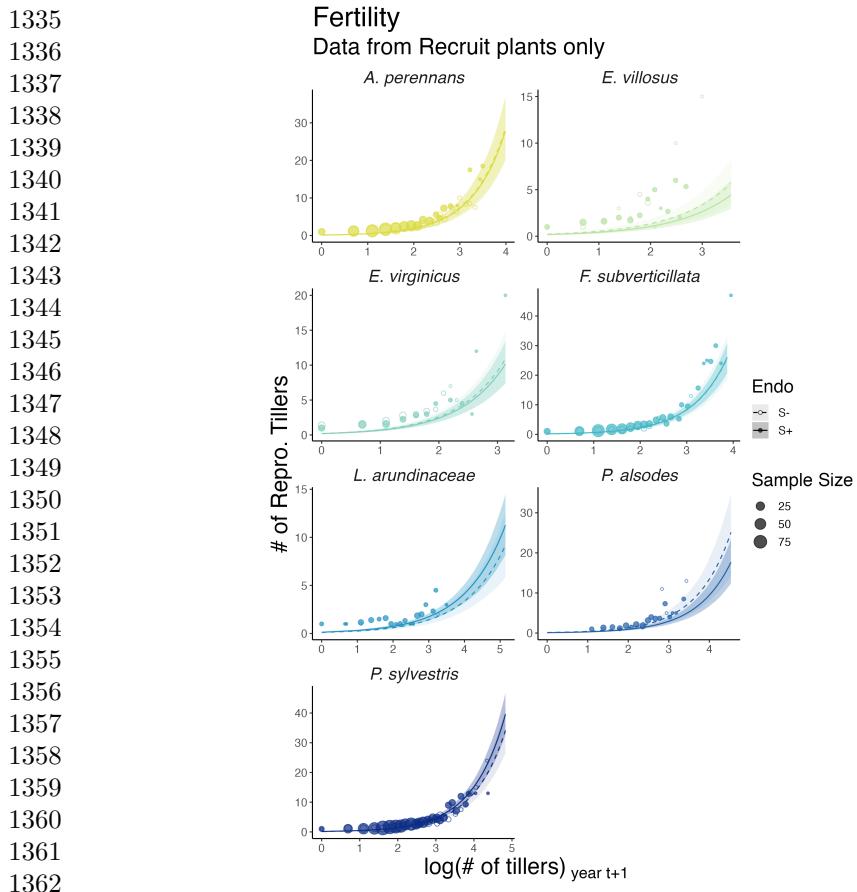


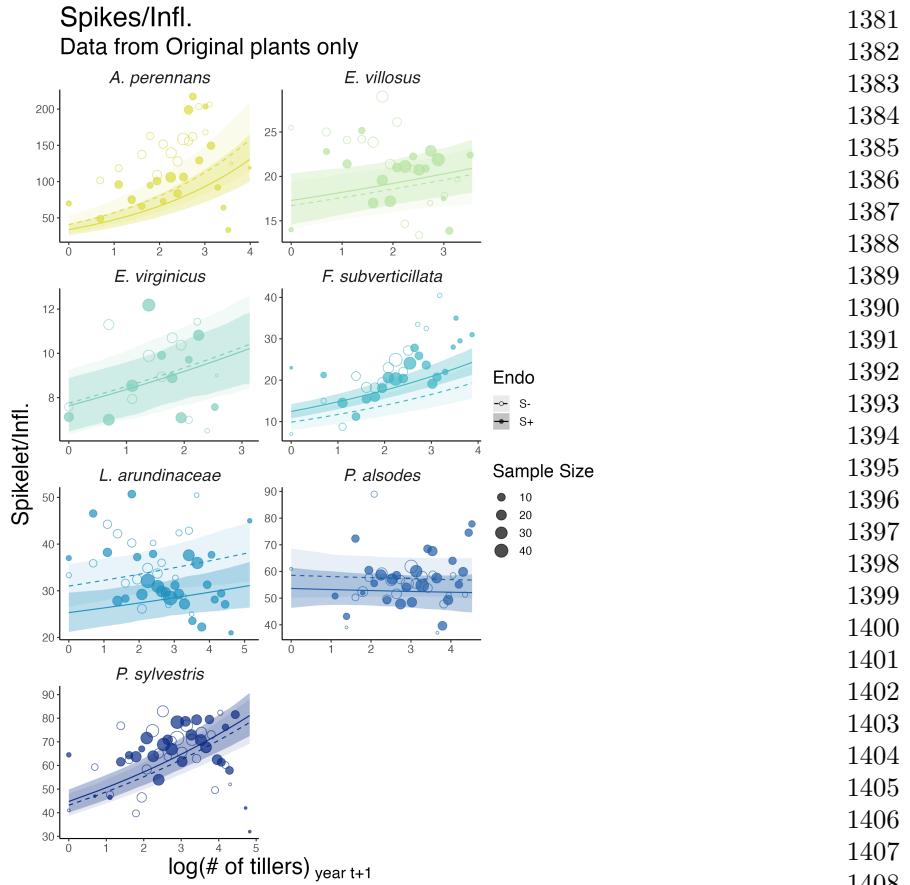
1271 **Fig. S6** Effect of endophyte symbiosis on mean flowering. Fitted curves represent the size-specific  
1272 mean flowering probability for recruited plants along with data binned by size shown as open circles  
1273 with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent  
1274 symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading  
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**Fig. S7** Effect of endophyte symbiosis on mean fertility. Fitted curves represent the size-specific mean expected number of flowering tillers for original plants along with data binned by size shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading for S-.





**Fig. S9** Effect of endophyte symbiosis on mean spikelet production. Fitted curves represent the size-specific mean expected number of spikelets per inflorescence for original plants along with data binned by size shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading for S+, or light shading for S-.

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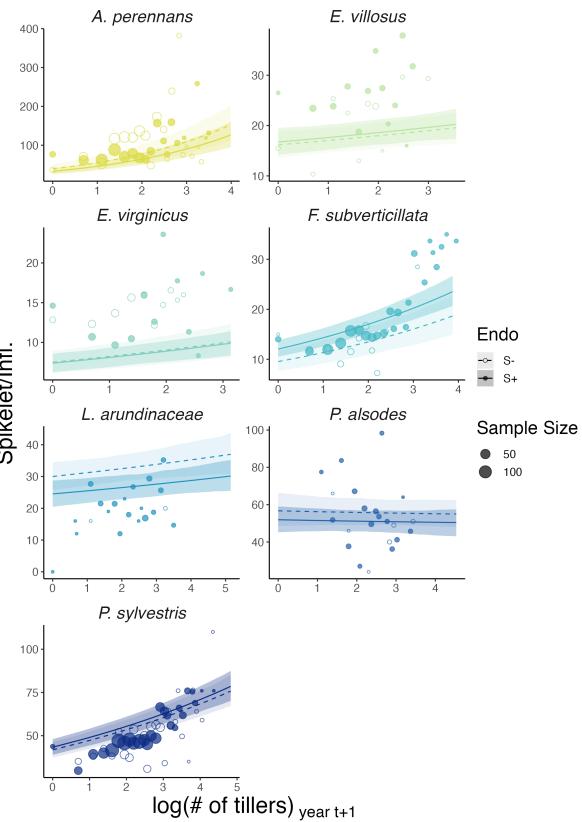
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**Spikes/Infl.  
Data from Recruit plants only**



1455 **Fig. S10** Effect of endophyte symbiosis on mean spikelet production. Fitted curves represent the  
1456 size-specific mean expected number of spikelets per inflorescence for recruited plants along with data  
1457 binned by size shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid  
1458 line and filled circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark  
1459 shading for S+, or light shading for S-.

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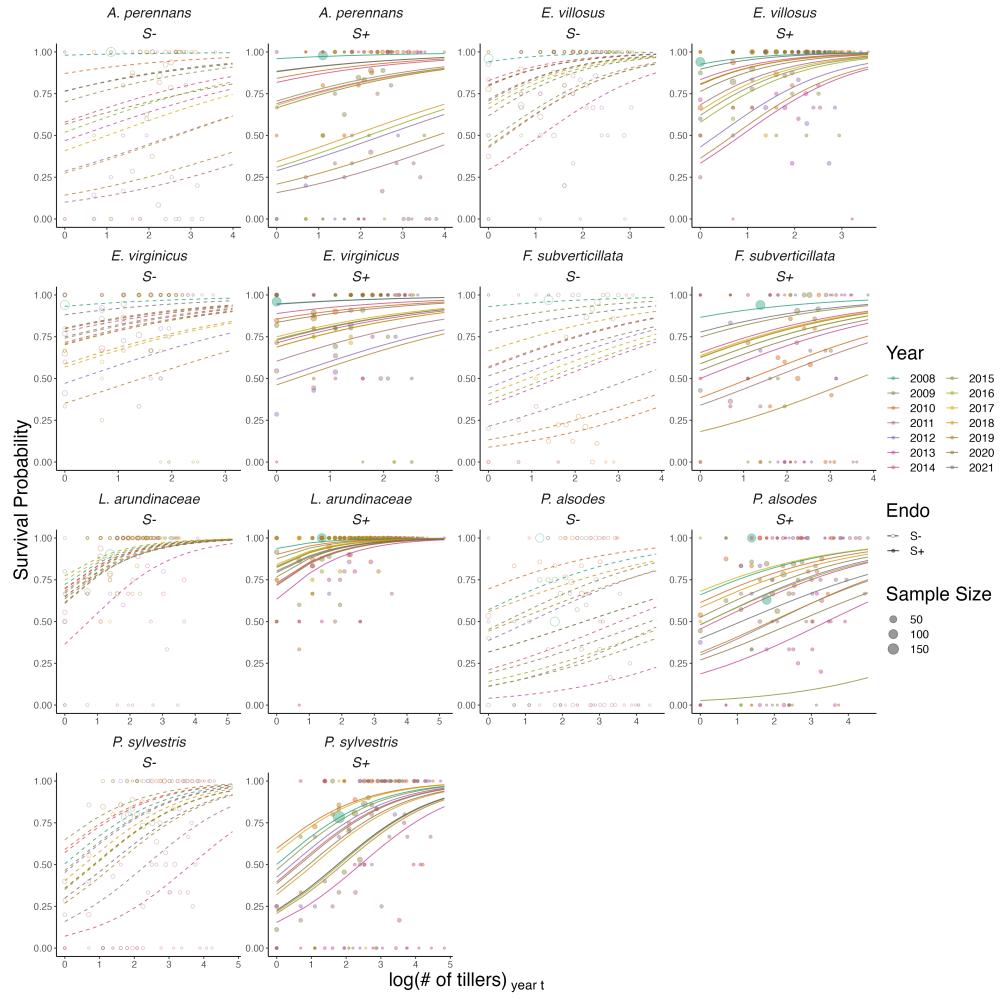
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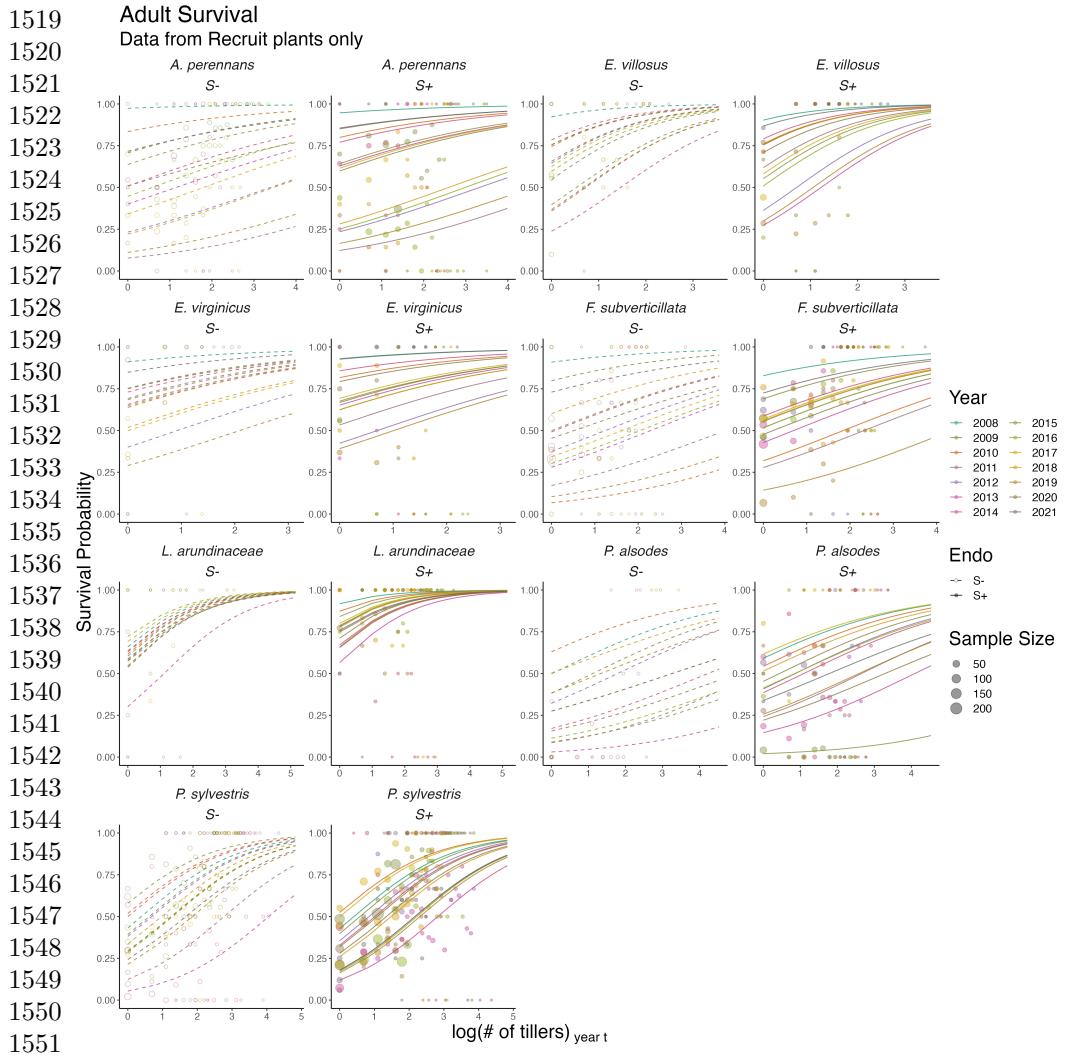
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**Adult Survival**  
Data from Original plants only

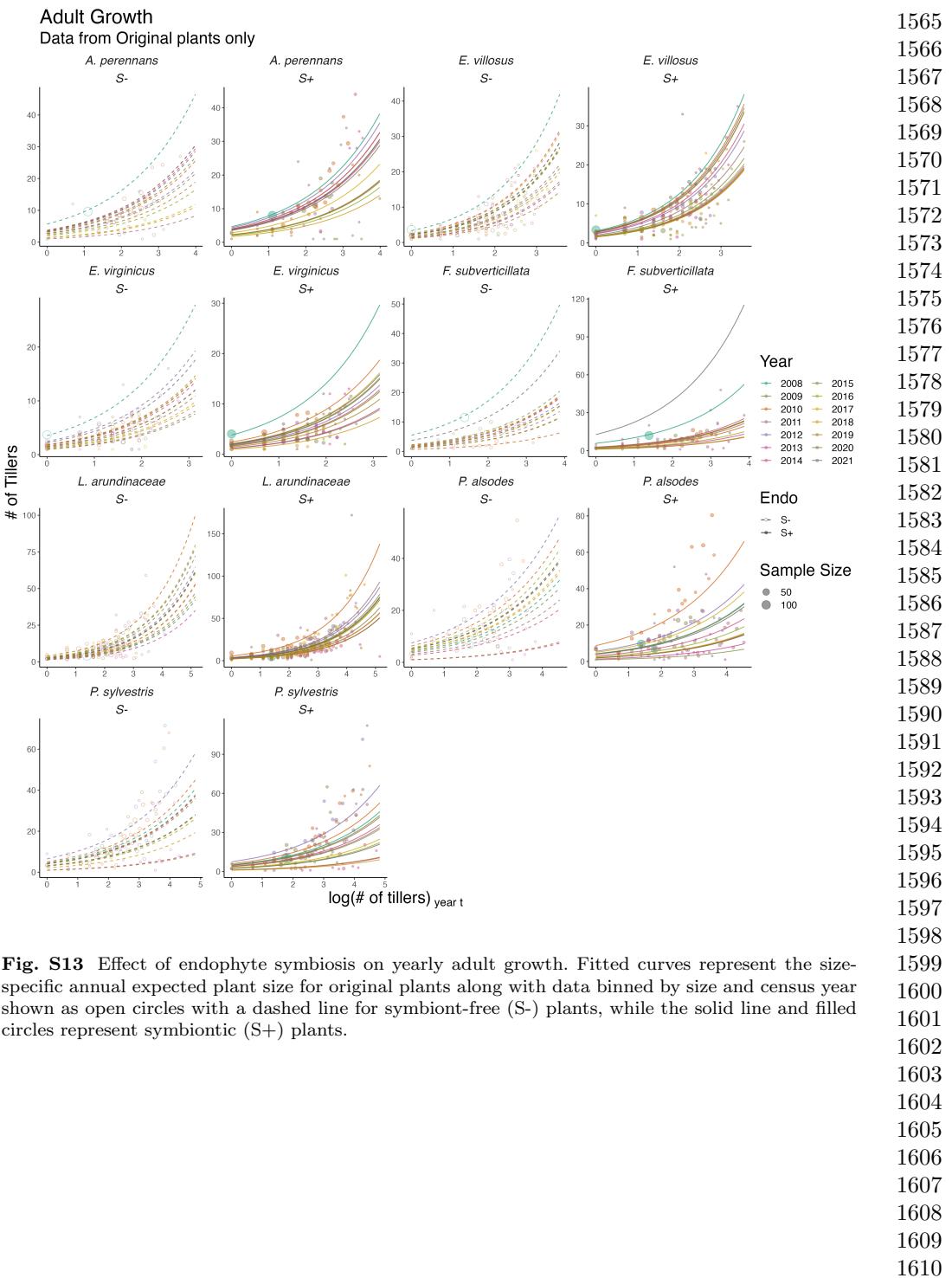


**Fig. S11** Effect of endophyte symbiosis on yearly adult survival. Fitted curves represent the size-specific annual survival probability for original plants along with data binned by size and census year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.

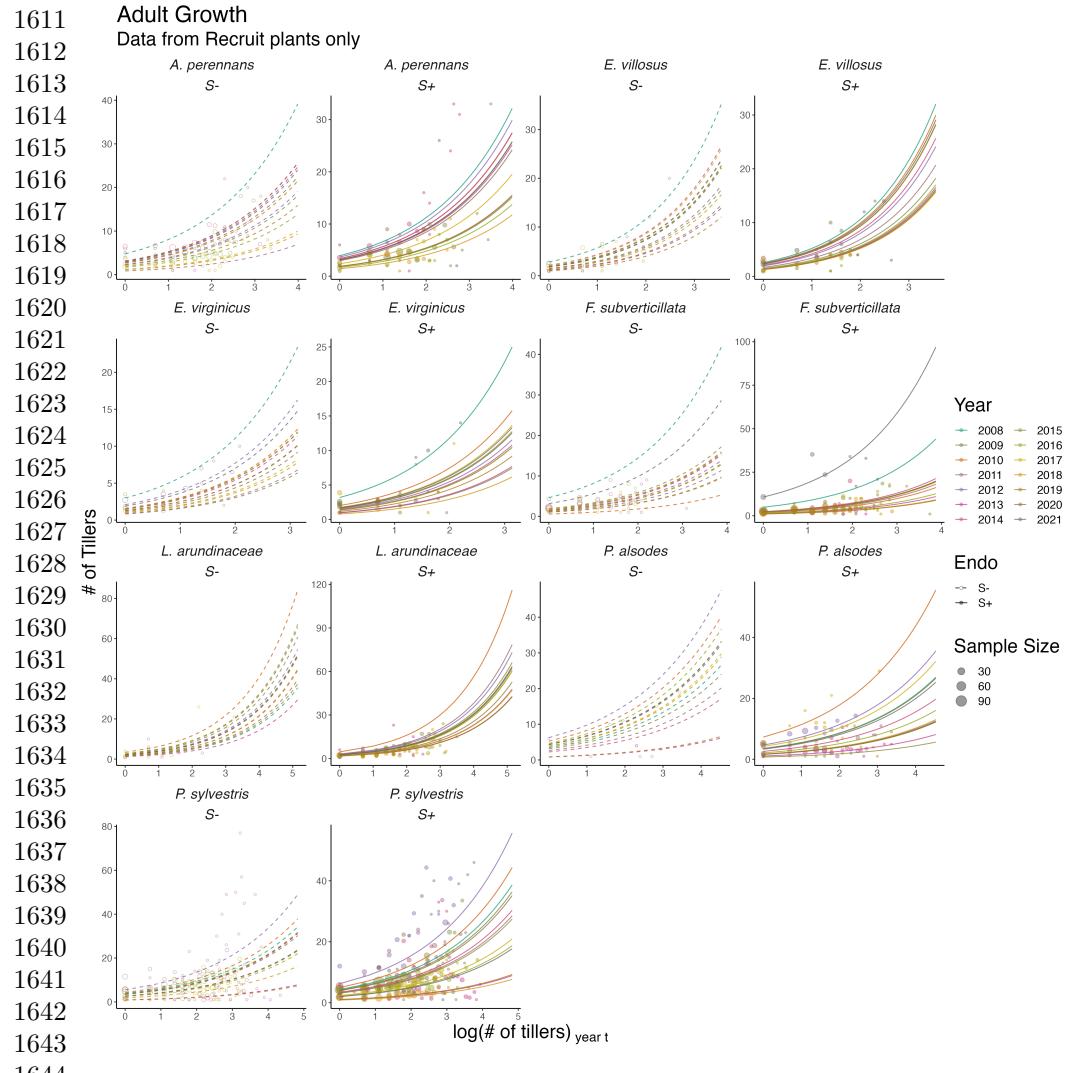
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1553 **Fig. S12** Effect of endophyte symbiosis on yearly adult survival. Fitted curves represent the size-  
1554 specific annual survival probability for recruited plants along with data binned by size and census  
1555 year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and  
1556 filled circles represent symbiotic (S+) plants.



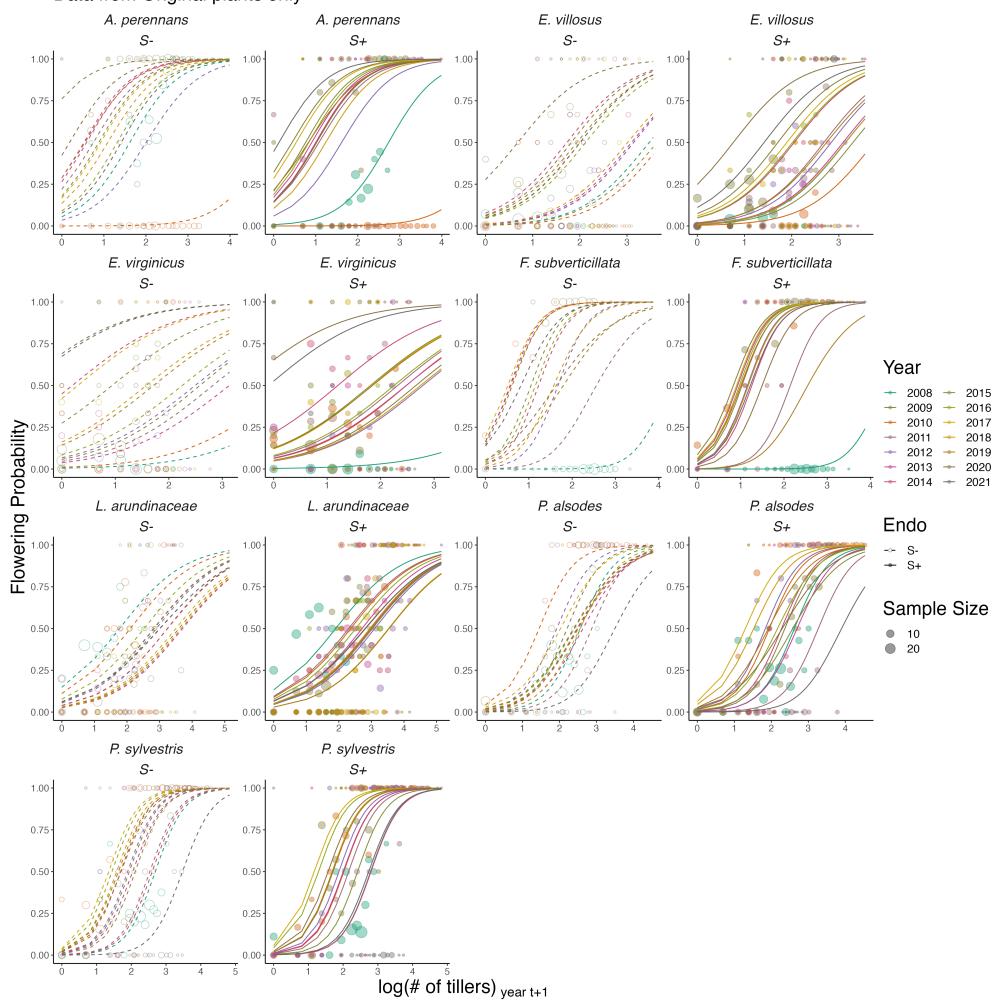
**Fig. S13** Effect of endophyte symbiosis on yearly adult growth. Fitted curves represent the size-specific annual expected plant size for original plants along with data binned by size and census year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



1645 **Fig. S14** Effect of endophyte symbiosis on yearly adult growth. Fitted curves represent the size-  
1646 specific annual expected plant size for recruited plants along with data binned by size and census  
1647 year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and  
1648 filled circles represent symbiotic (S+) plants.

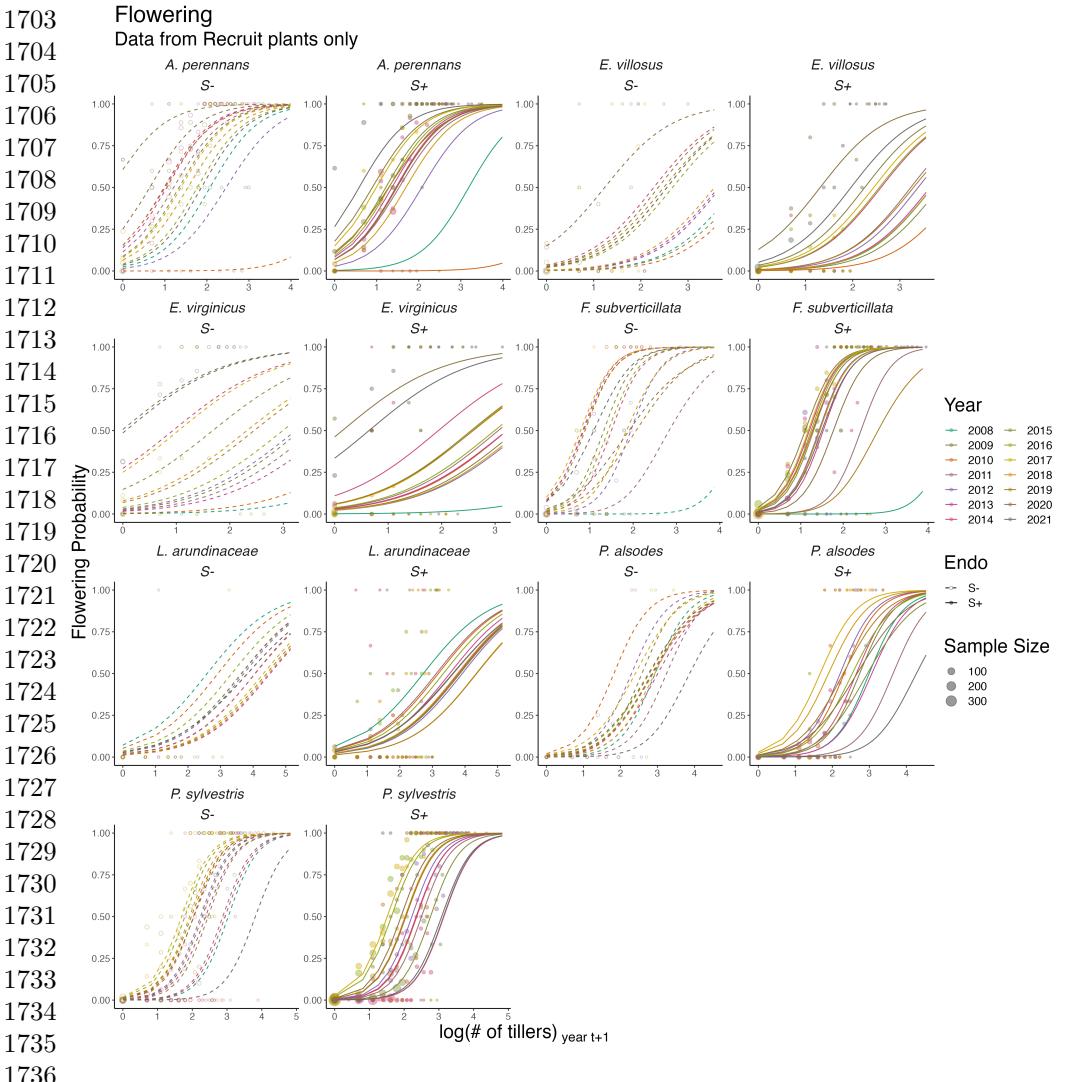
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**Flowering**  
Data from Original plants only



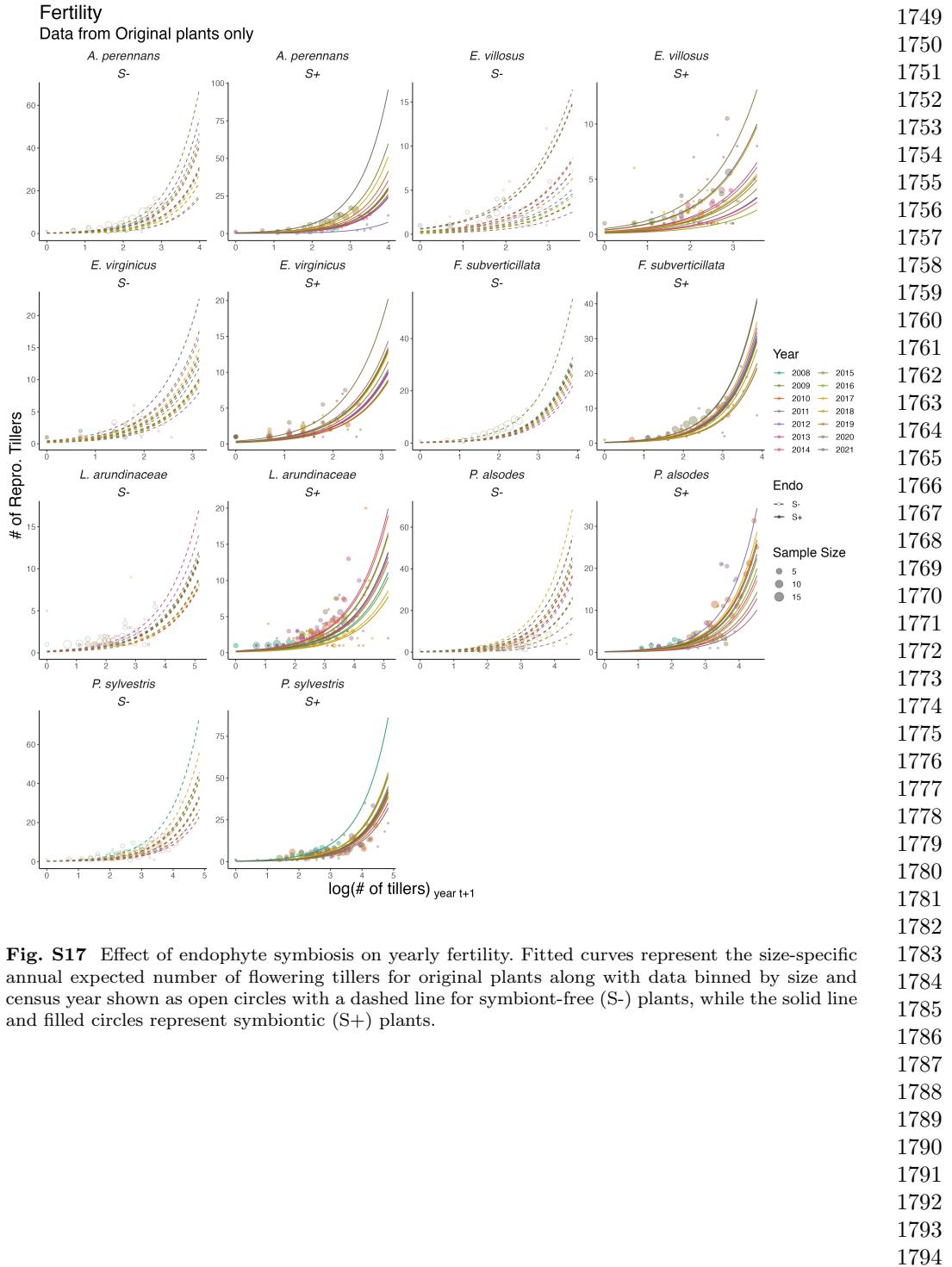
**Fig. S15** Effect of endophyte symbiosis on yearly flowering. Fitted curves represent the size-specific annual flowering probability for original plants along with data binned by size and census year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.

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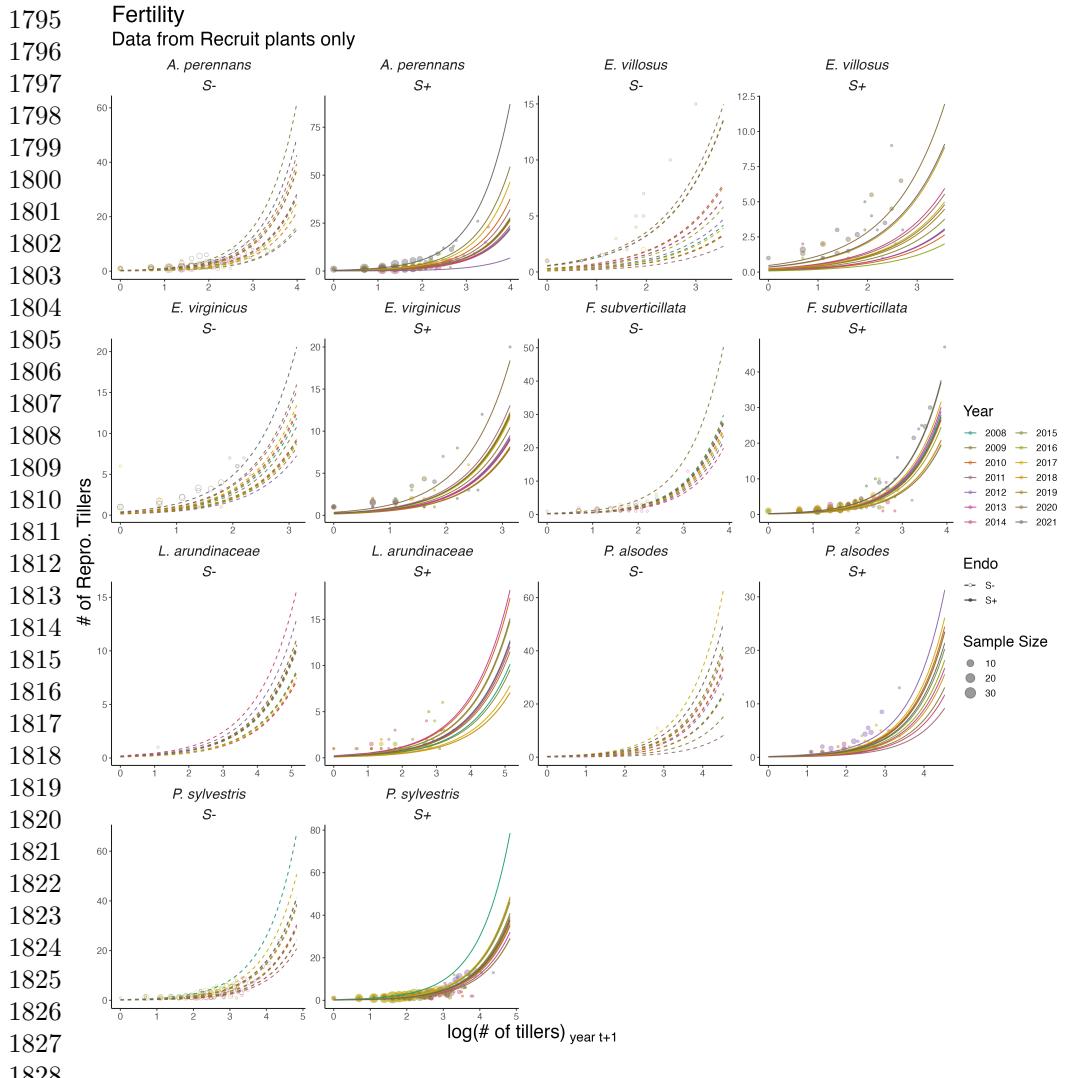


1737 **Fig. S16** Effect of endophyte symbiosis on yearly flowering. Fitted curves represent the size-specific  
1738 annual flowering probability for recruited plants along with data binned by size and census year  
1739 shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled  
1740 circles represent symbiotic (S+) plants.

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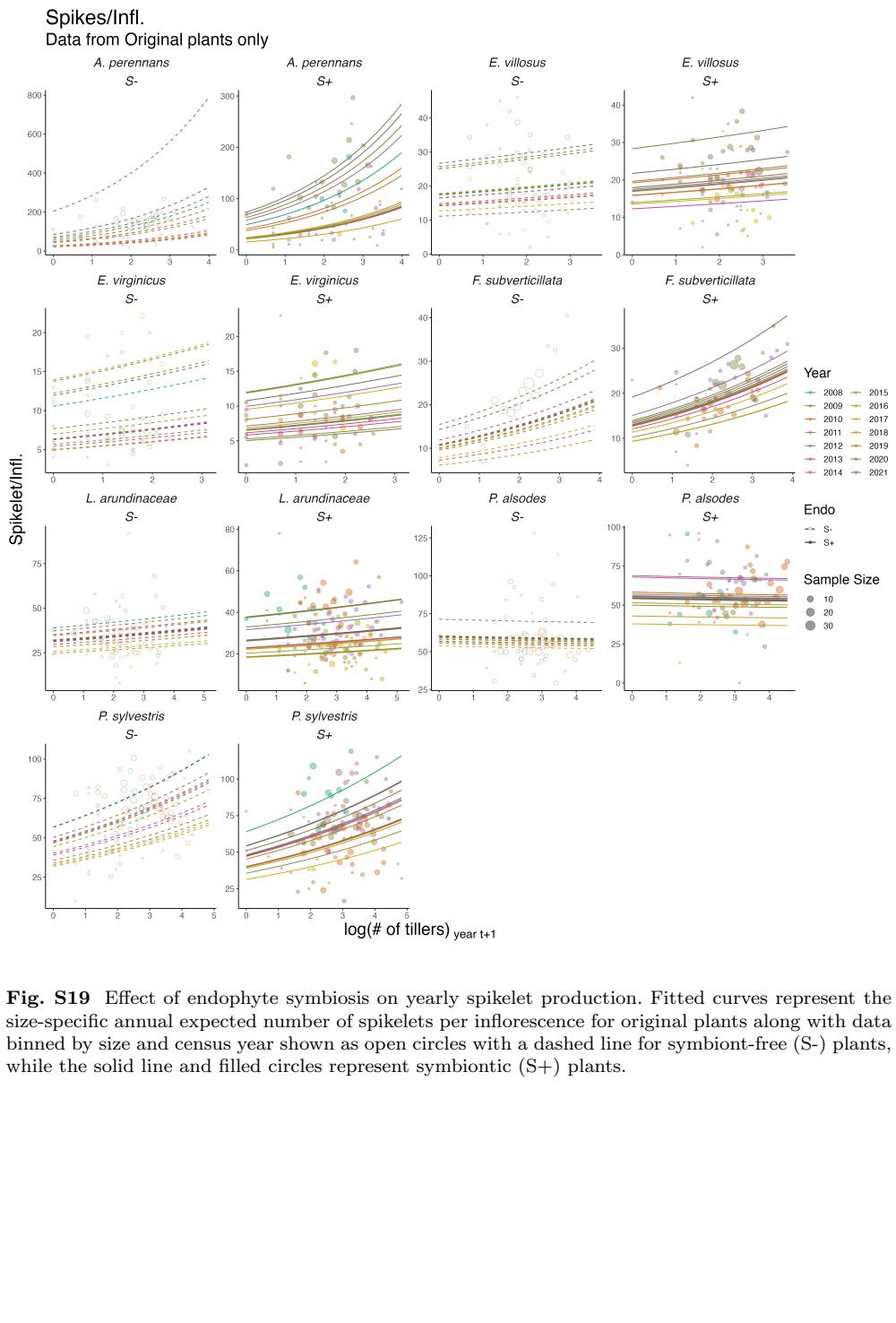


**Fig. S17** Effect of endophyte symbiosis on yearly fertility. Fitted curves represent the size-specific annual expected number of flowering tillers for original plants along with data binned by size and census year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.

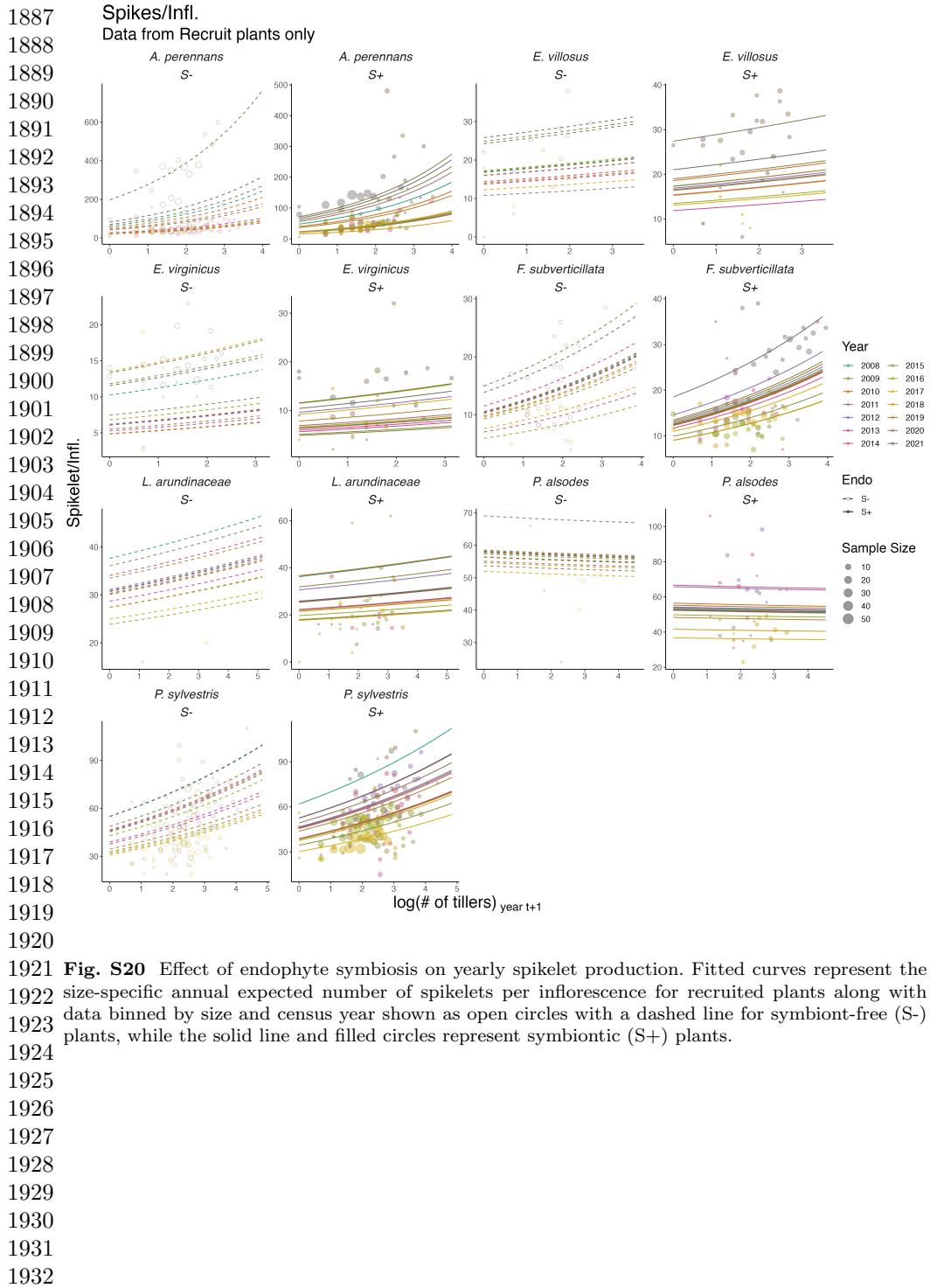


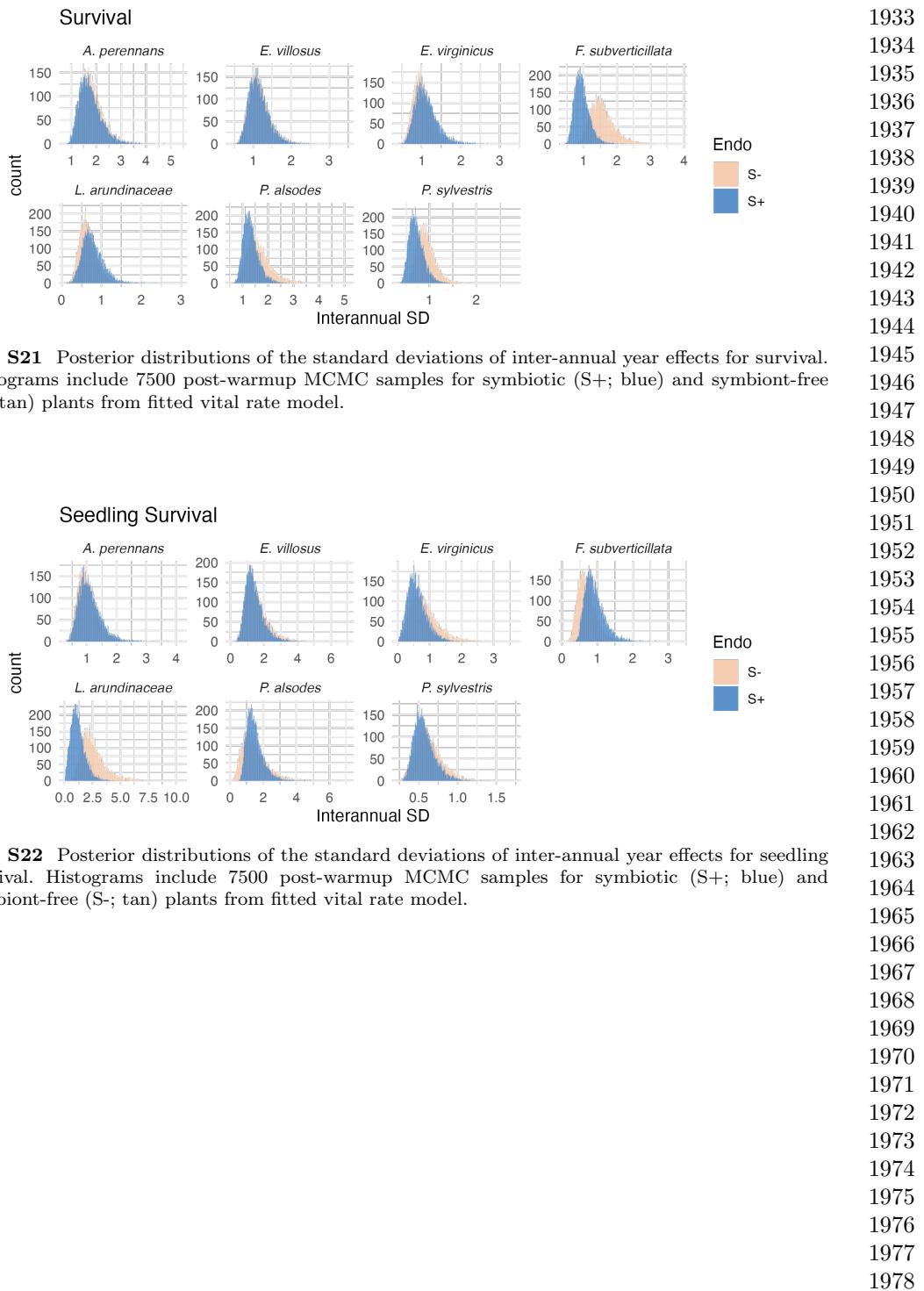
1829 **Fig. S18** Effect of endophyte symbiosis on yearly fertility. Fitted curves represent the size-specific  
 1830 annual expected number of flowering tillers for recruited along with data binned by size and census  
 1831 year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and  
 1832 filled circles represent symbiotic (S+) plants.

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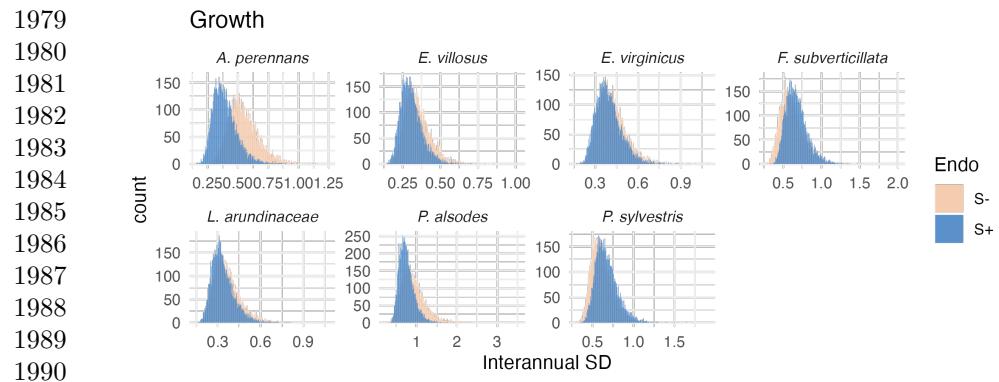
**Fig. S19** Effect of endophyte symbiosis on yearly spikelet production. Fitted curves represent the size-specific annual expected number of spikelets per inflorescence for original plants along with data binned by size and census year shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



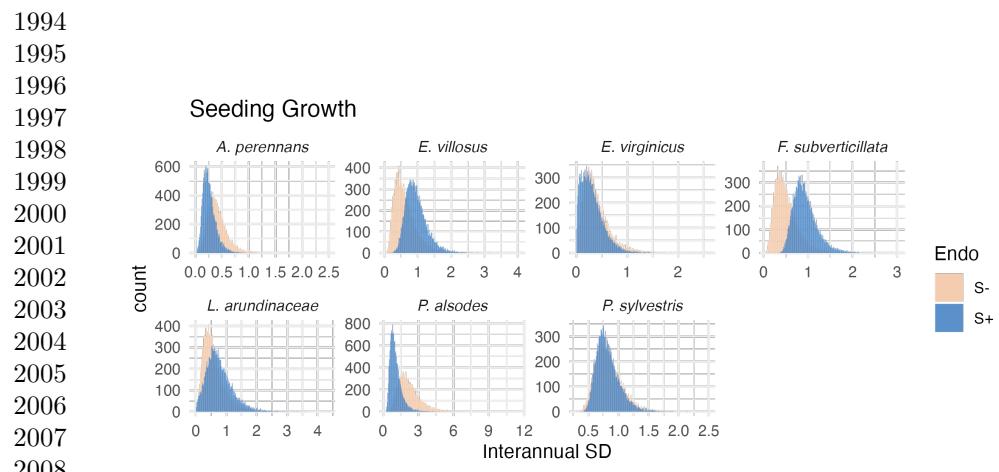


**Fig. S21** Posterior distributions of the standard deviations of inter-annual year effects for survival. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

**Fig. S22** Posterior distributions of the standard deviations of inter-annual year effects for seedling survival. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

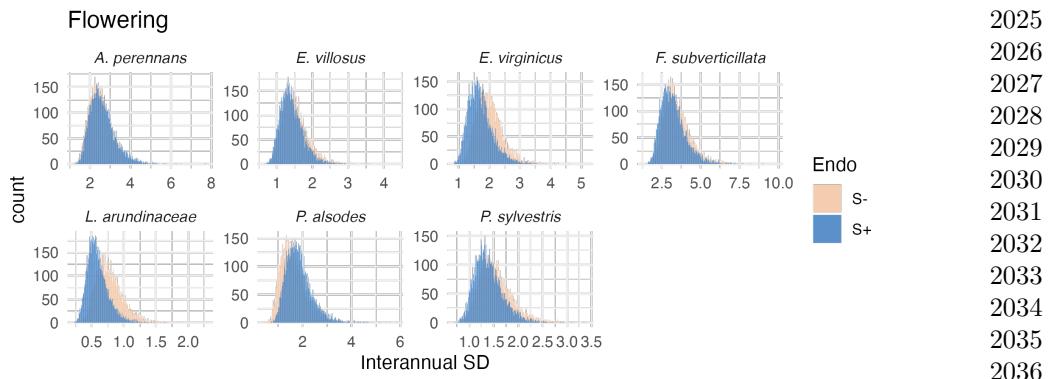


1991 **Fig. S23** Posterior distributions of the standard deviations of inter-annual year effects for growth.  
 1992 Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free  
 1993 (S-; tan) plants from fitted vital rate model.

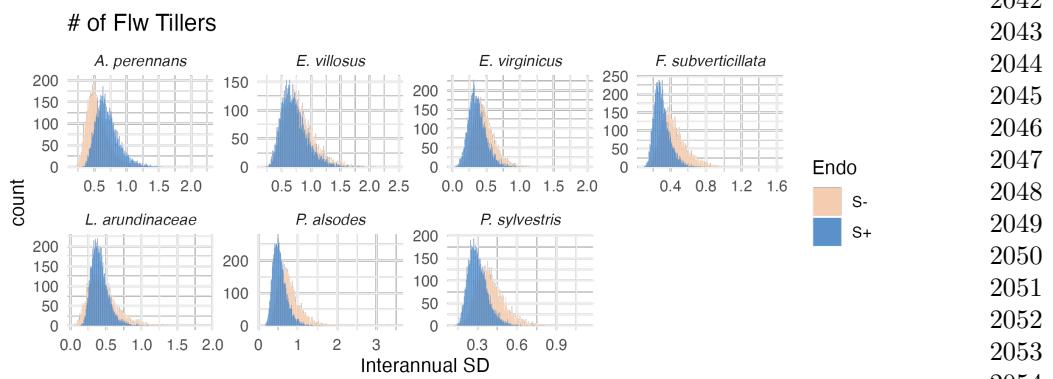


2009 **Fig. S24** Posterior distributions of the standard deviations of inter-annual year effects for seedling growth. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

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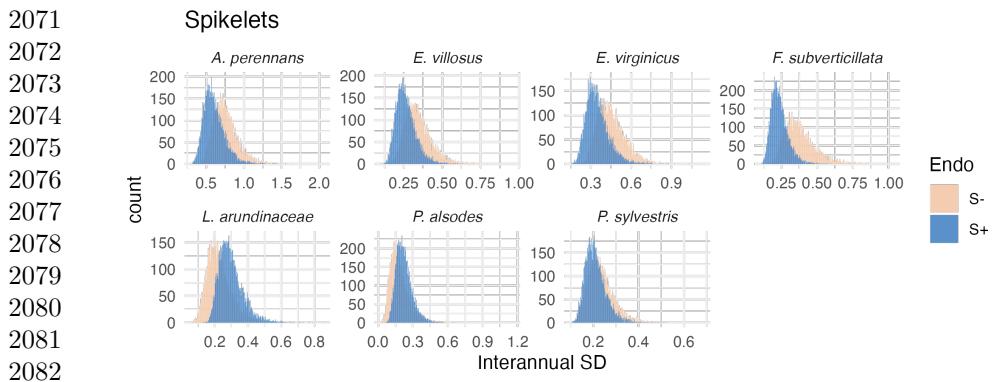


**Fig. S25** Posterior distributions of the standard deviations of inter-annual year effects for flowering probability. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

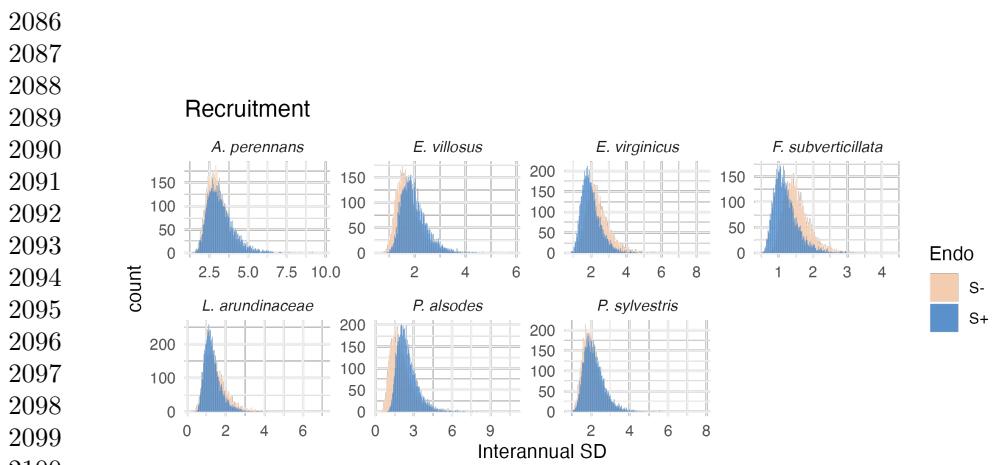


**Fig. S26** Posterior distributions of the standard deviations of inter-annual year effects for fertility (no. of flowering tillers). Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

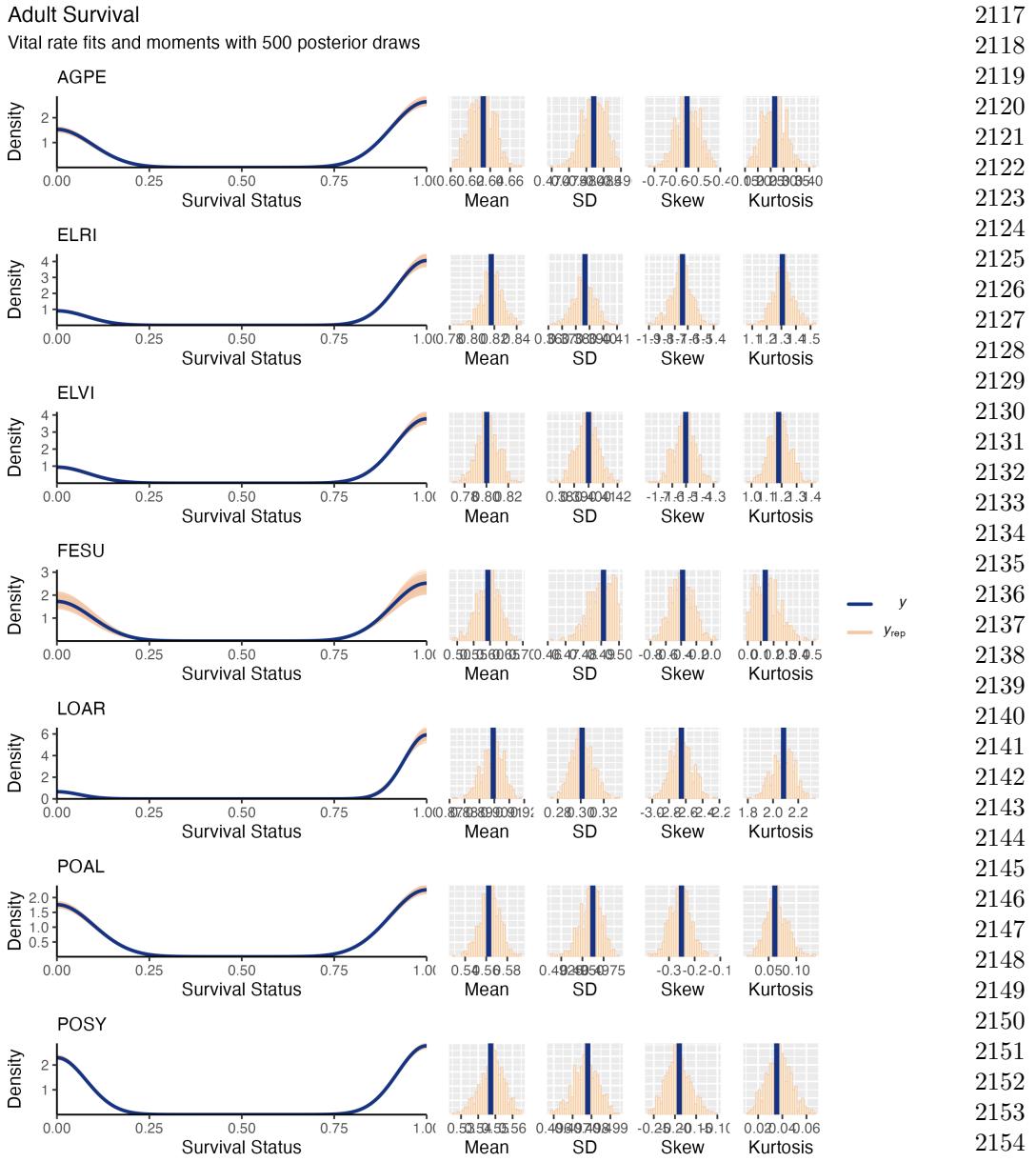
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2083 **Fig. S27** Posterior distributions of the standard deviations of inter-annual year effects for spikelets  
2084 per inflorescence. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue)  
2085 and symbiont-free (S-; tan) plants from fitted vital rate model.

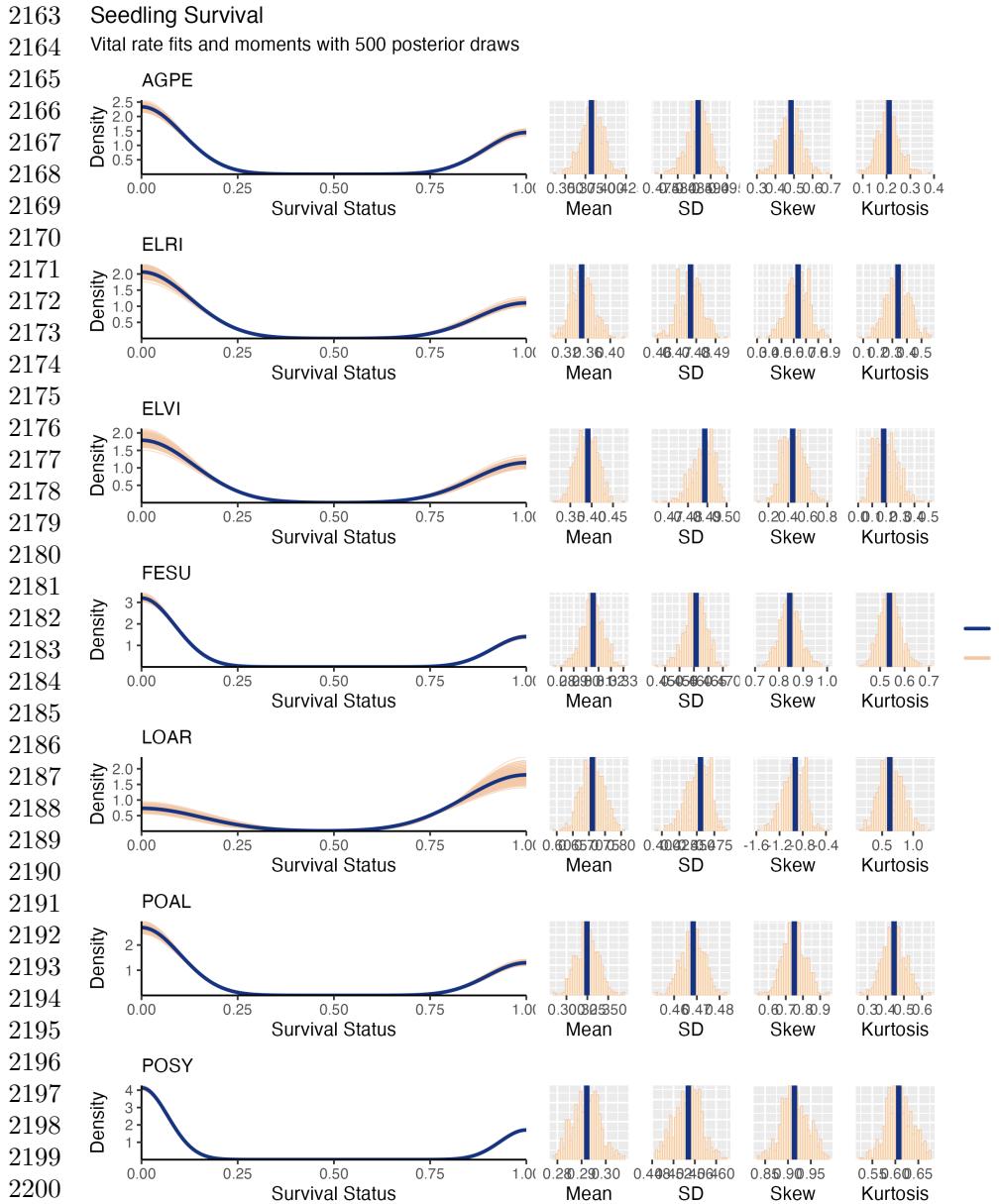


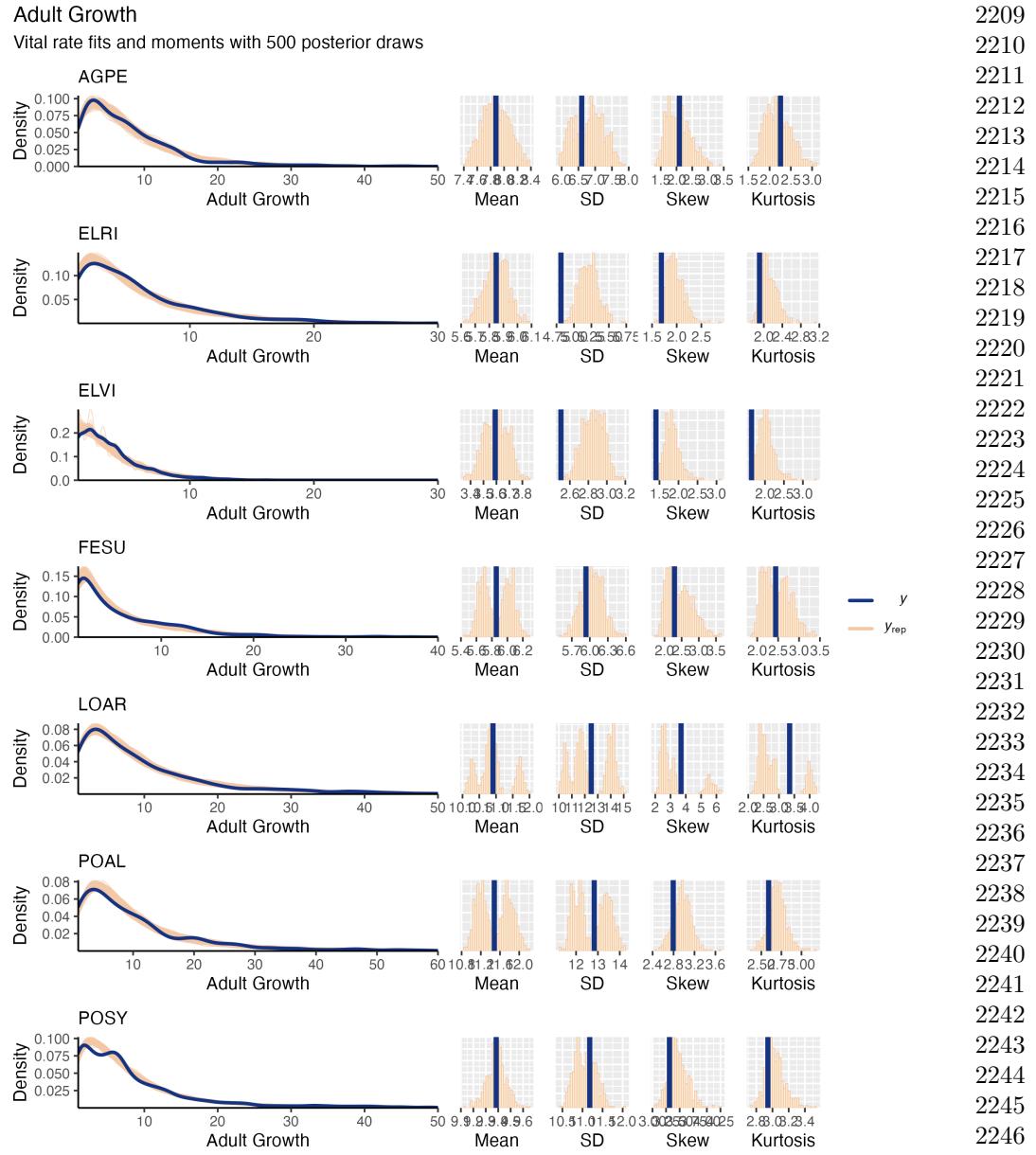
2101 **Fig. S28** Posterior distributions of the standard deviations of inter-annual year effects for  
2102 recruitment. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and  
2103 symbiont-free (S-; tan) plants from fitted vital rate model.  
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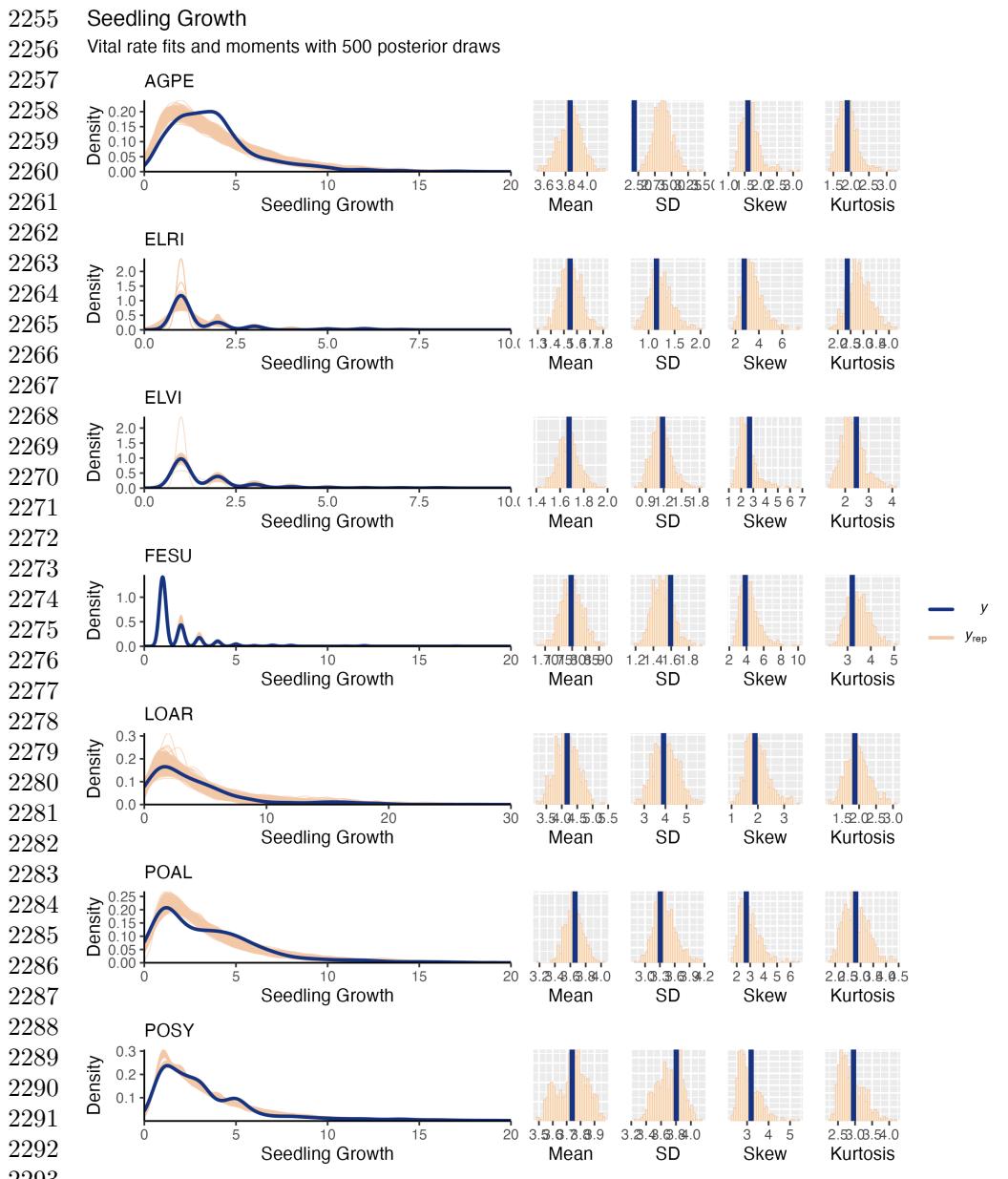
**Fig. S29** Posterior predictive check for statistical model of Adult Survival. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.

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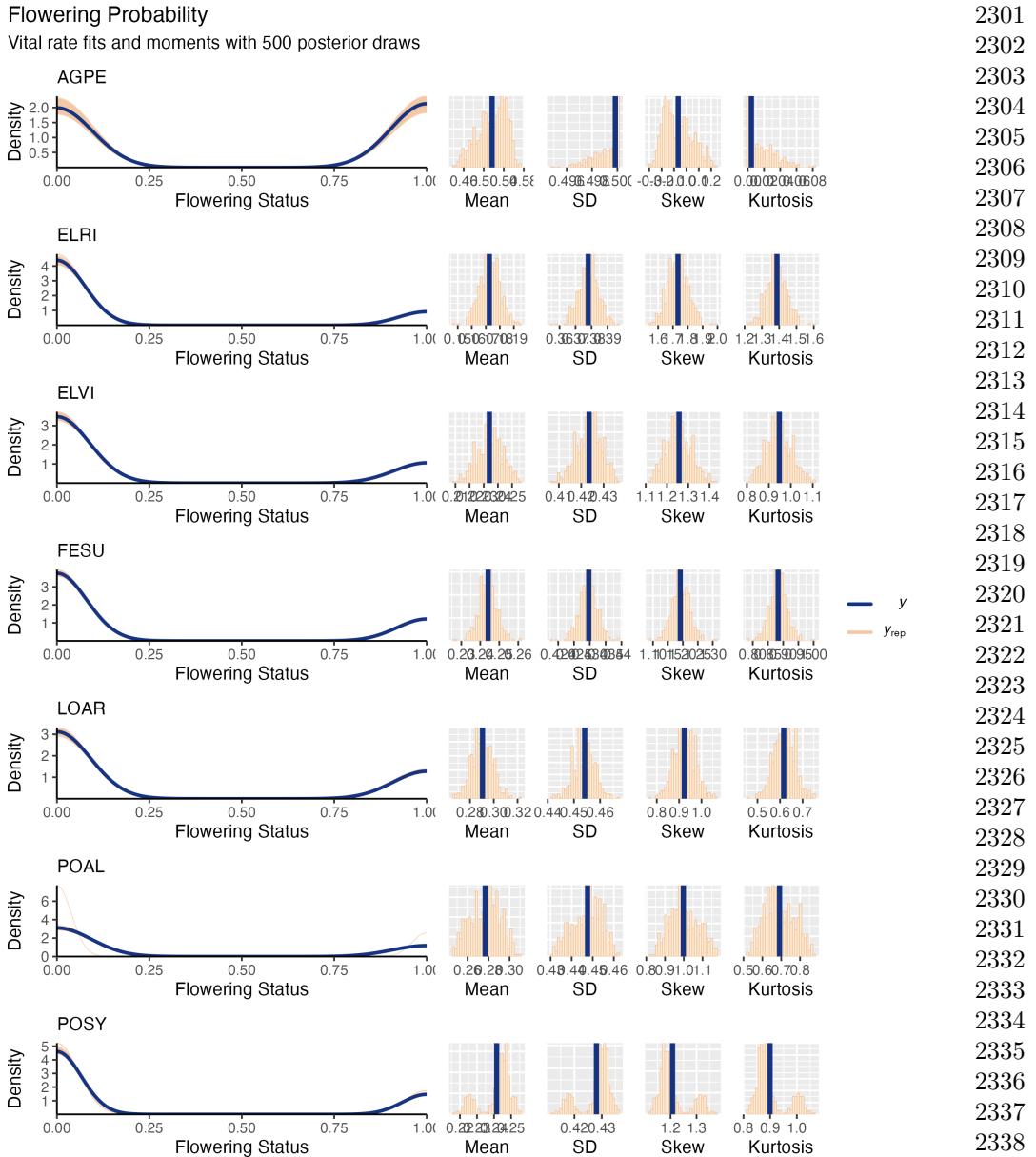


**Fig. S31** Posterior predictive check for statistical model of Adult Growth. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.

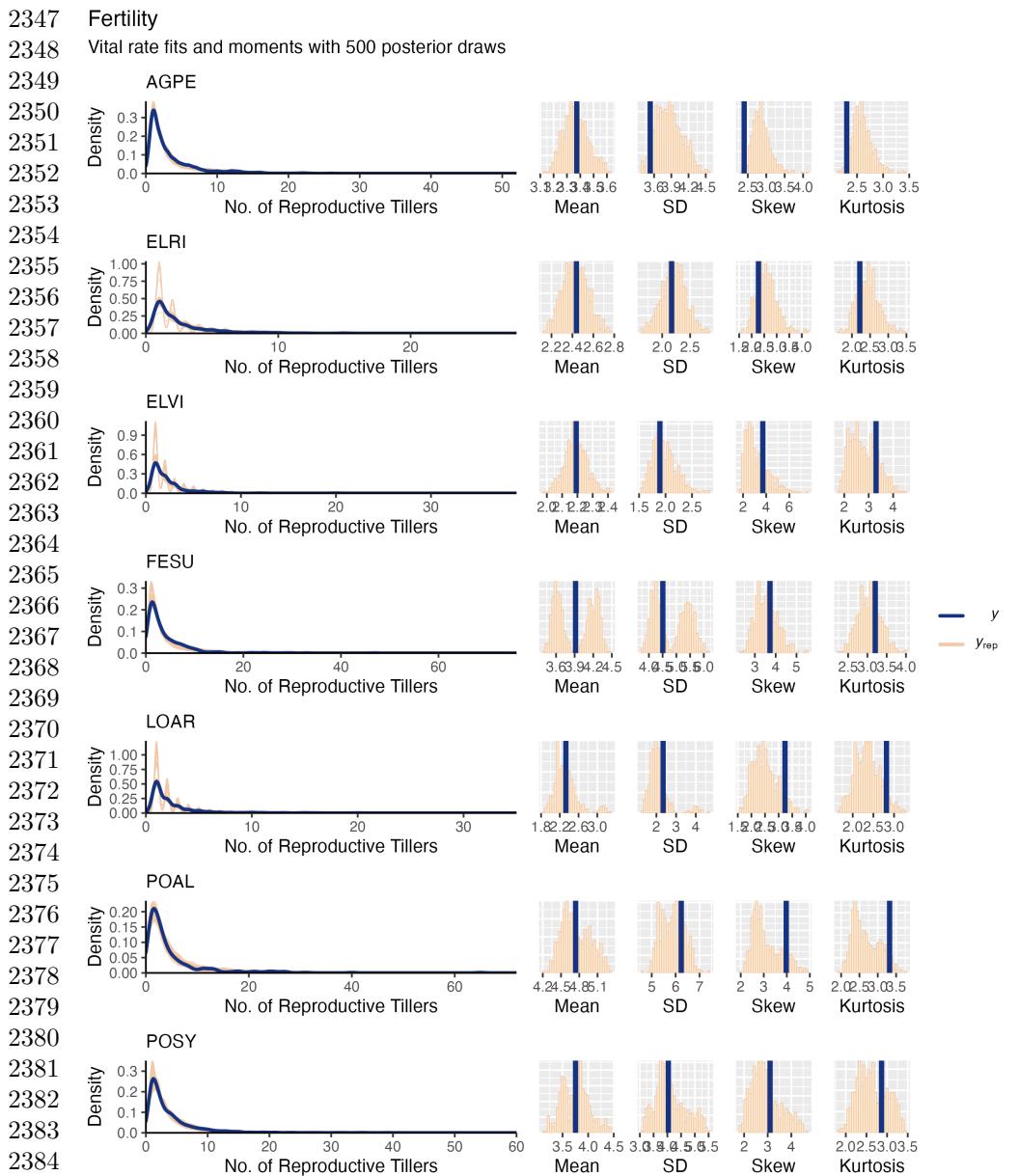


2295 **Fig. S32** Posterior predictive check for statistical model of Seedling Growth. Consistency between  
 2296 real data and simulated values indicates that fitted models describe the data well. Lines show den-  
 2297 sity distributions of observed data (blue line) compared to data simulated from fitted models (tan  
 2298 lines) generated from 500 draws from posterior distributions of model parameters along with the  
 2299 distribution's moments.

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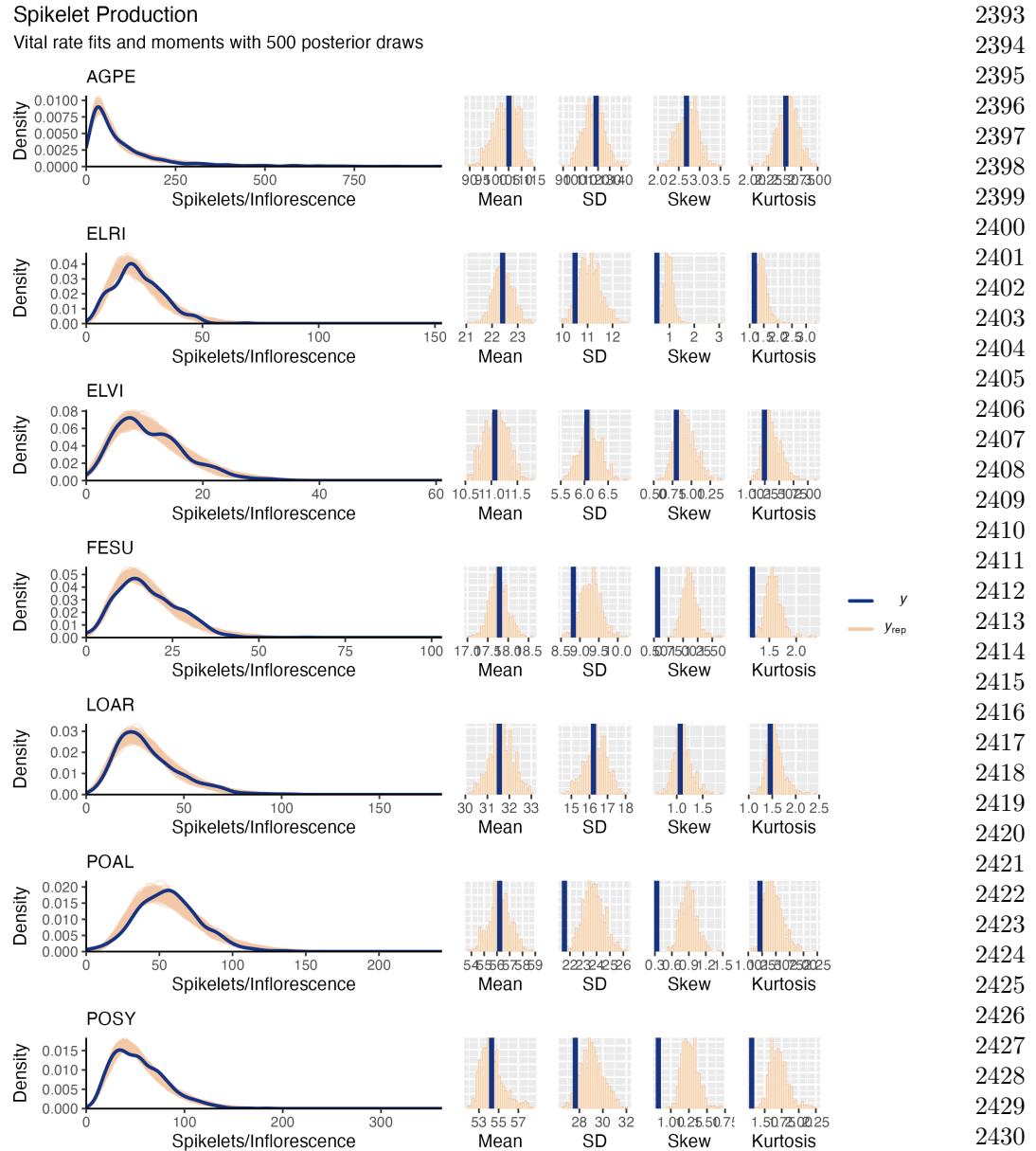


**Fig. S33** Posterior predictive check for statistical model of Flowering Probability. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.

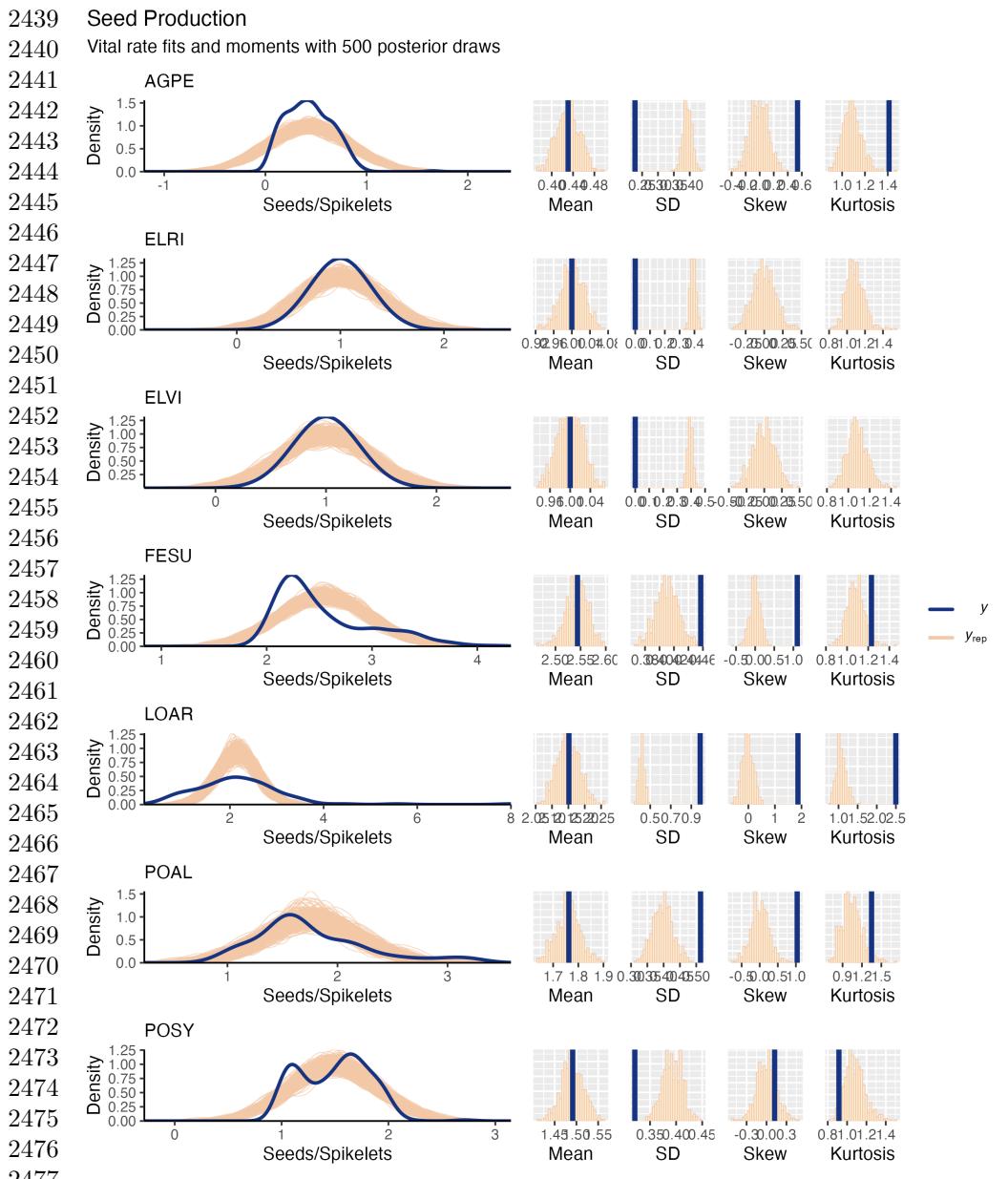


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 2386 Fig. S34 Posterior predictive check for statistical model of Flowering Tiller production. Consistency  
 2387 between real data and simulated values indicates that fitted models describe the data well. Lines  
 2388 show density distributions of observed data (blue line) compared to data simulated from fitted models  
 2389 (tan lines) generated from 500 draws from posterior distributions of model parameters along with the  
 2390 distribution's moments.

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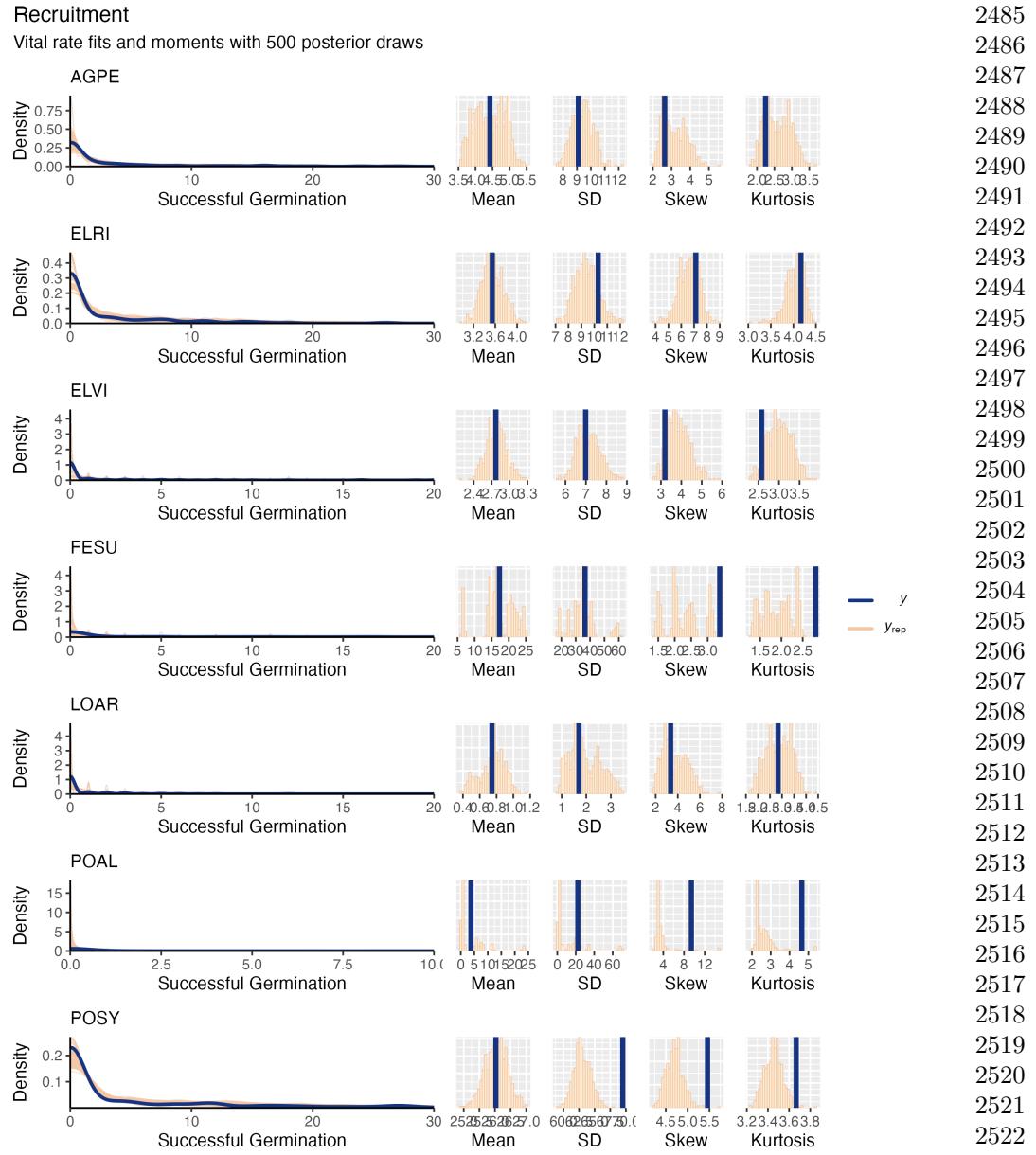


**Fig. S35** Posterior predictive check for statistical model of Spikelets/Inflorescence. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.



2449 Fig. S36 Posterior predictive check for statistical model of Mean Seeds/Spikelet. Consistency  
 2450 between real data and simulated values indicates that fitted models describe the data well. Lines  
 2451 show density distributions of observed data (blue line) compared to data simulated from fitted mod-  
 2452 els (tan lines) generated from 500 draws from posterior distributions of model parameters along with  
 2453 the distribution's moments.

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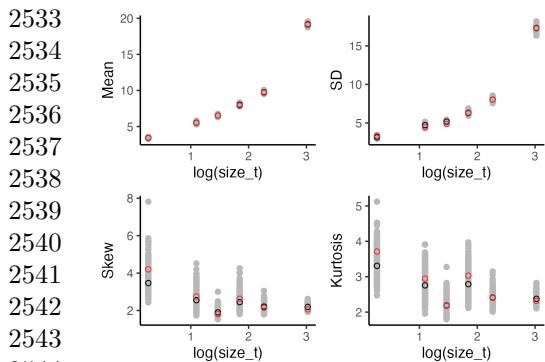


**Fig. S37** Posterior predictive check for statistical model of Recruitment. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.

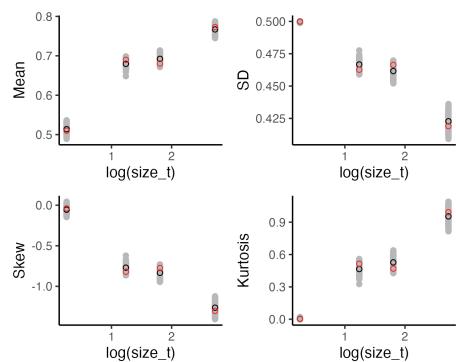
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2531 Size specific vital rate moments

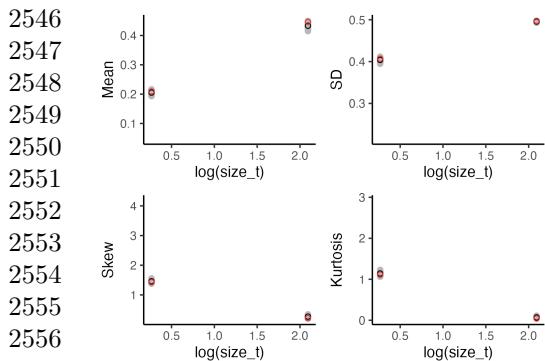
2532 Adult Growth



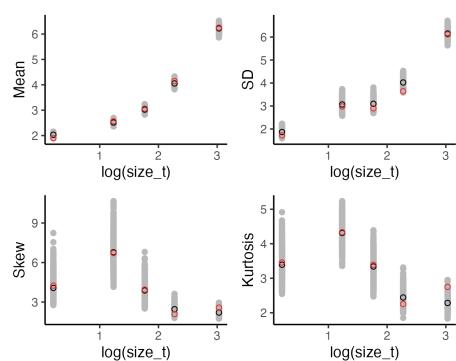
Adult Survival



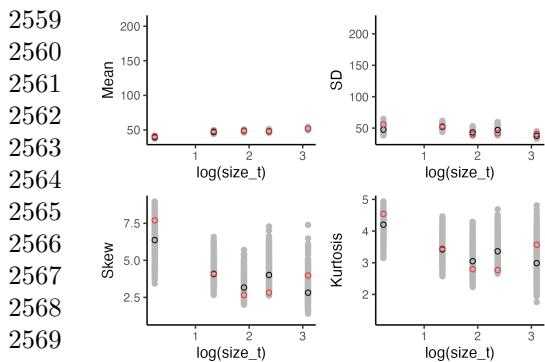
2545 Flowering Probability



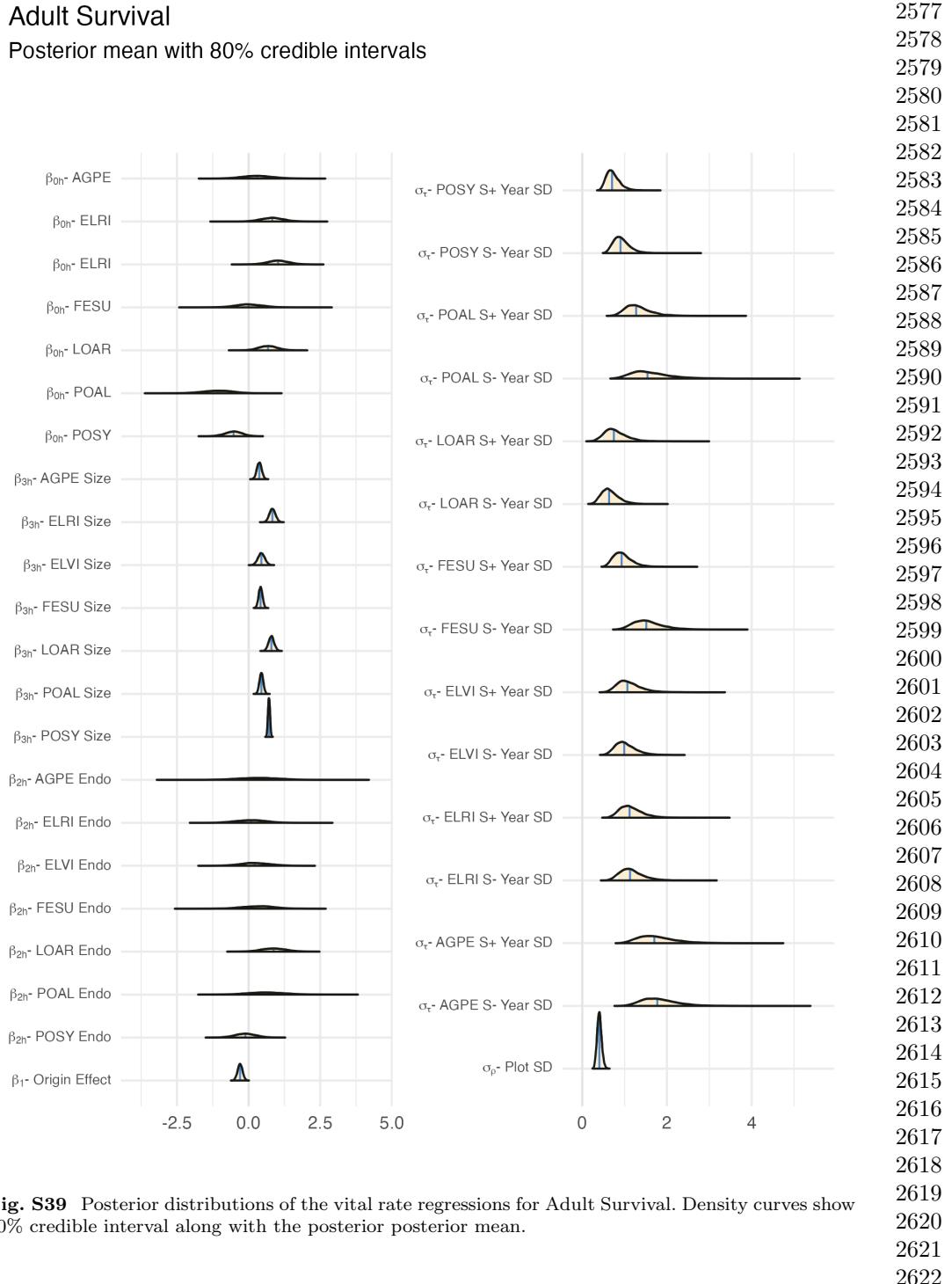
Inflorescence Production



2558 Spikelets/Infl.



2572 **Fig. S38** Consistency between real data and fitted values across sizes indicates that the vital rate  
2573 models are accurately capturing size dependence. Graphs of posterior predictive check for mean and  
2574 higher moments of the vital rate models across size. Points show the value of statistical moments  
2575 binned across size for the observed data (red circles) compared to the simulated datasets (grey circles)  
2576 and the median of the simulated values (black circles) generated from 500 posterior draws from the  
2577 fitted model.



**Fig. S39** Posterior distributions of the vital rate regressions for Adult Survival. Density curves show 80% credible interval along with the posterior mean.

2623 Seedling Survival  
2624 Posterior mean with 80% credible intervals

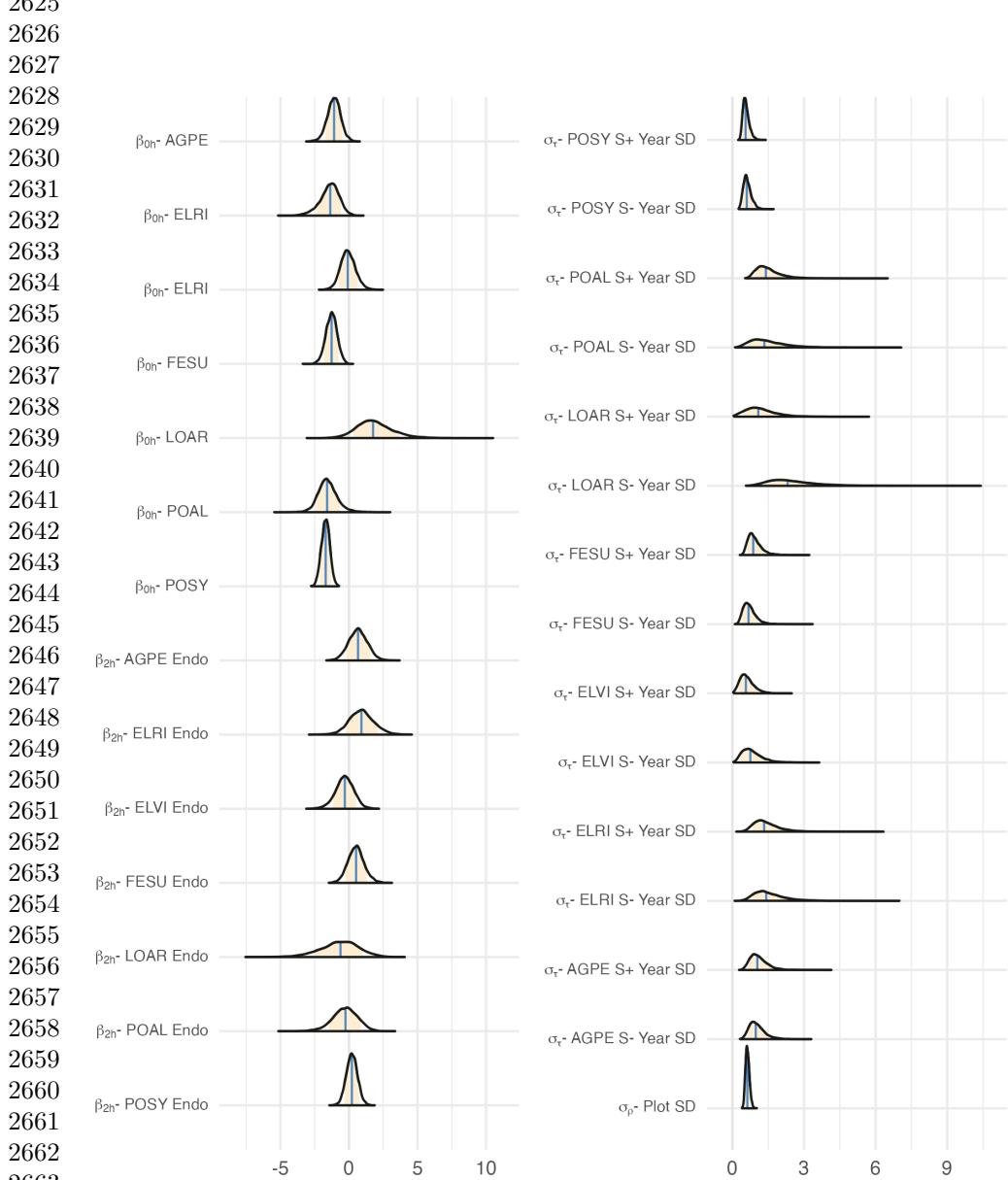
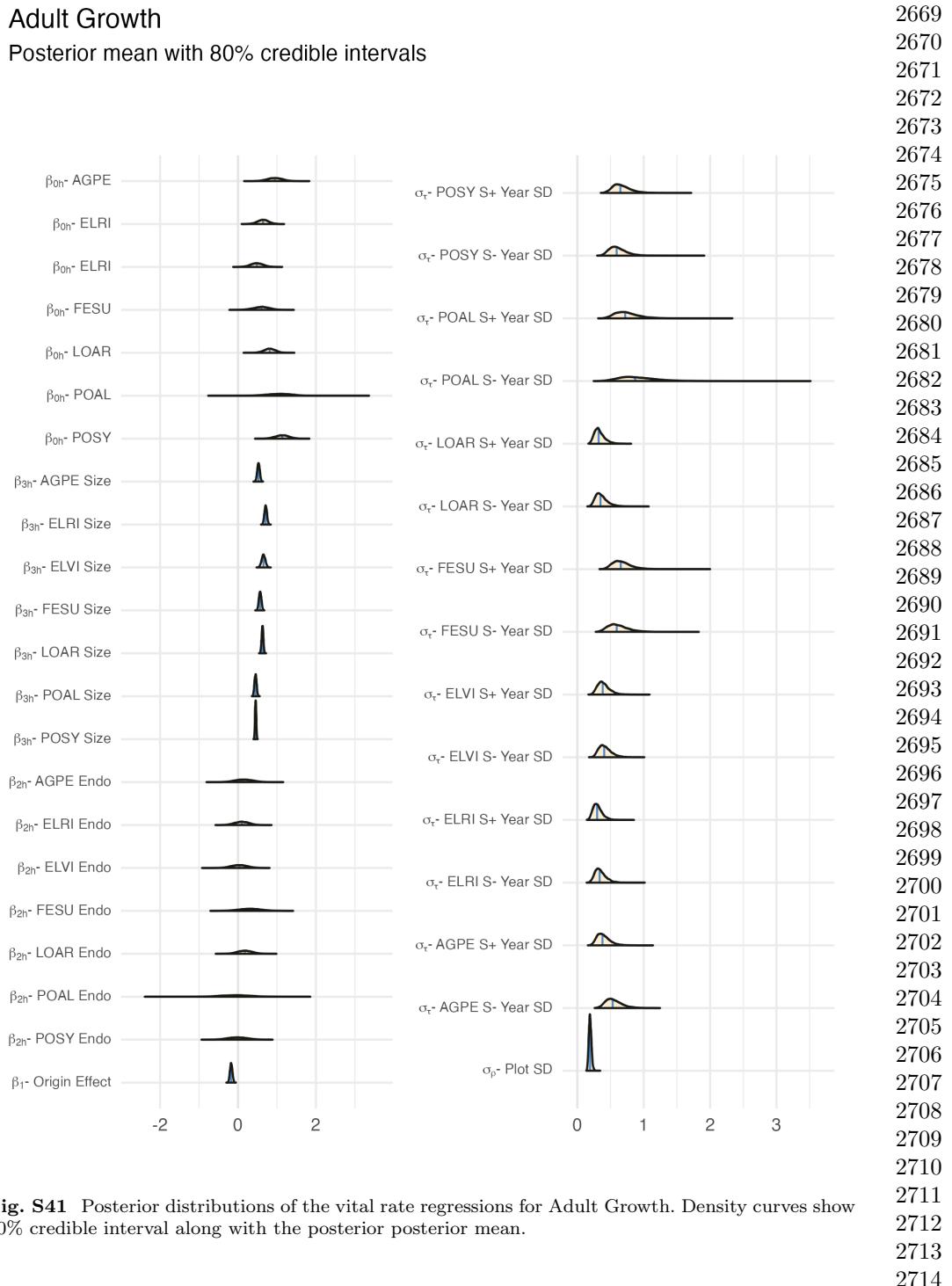


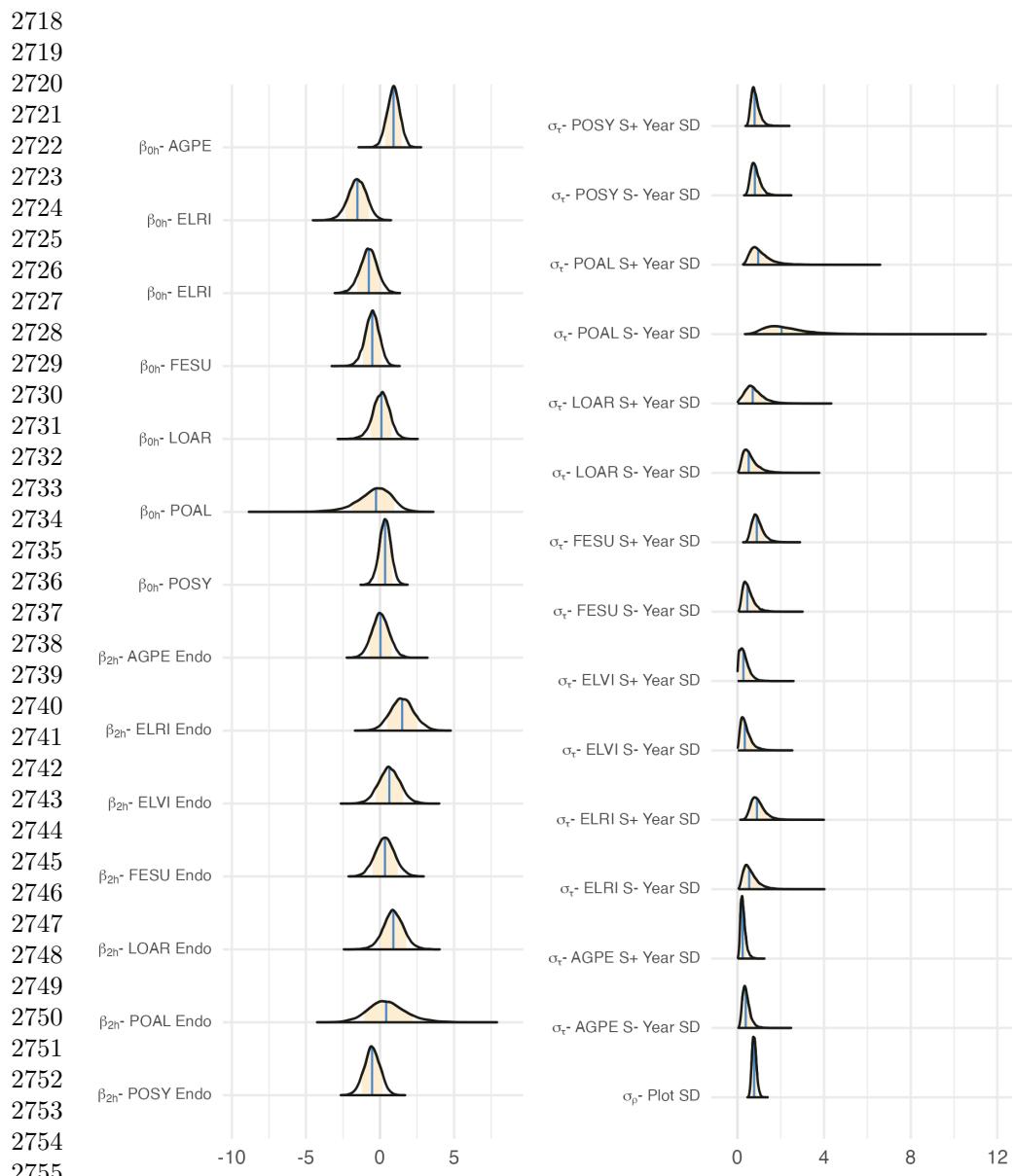
Fig. S40 Posterior distributions of the vital rate regressions for Seedling Survival. Density curves show 80% credible interval along with the posterior posterior mean.

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**Fig. S41** Posterior distributions of the vital rate regressions for Adult Growth. Density curves show 80% credible interval along with the posterior posterior mean.

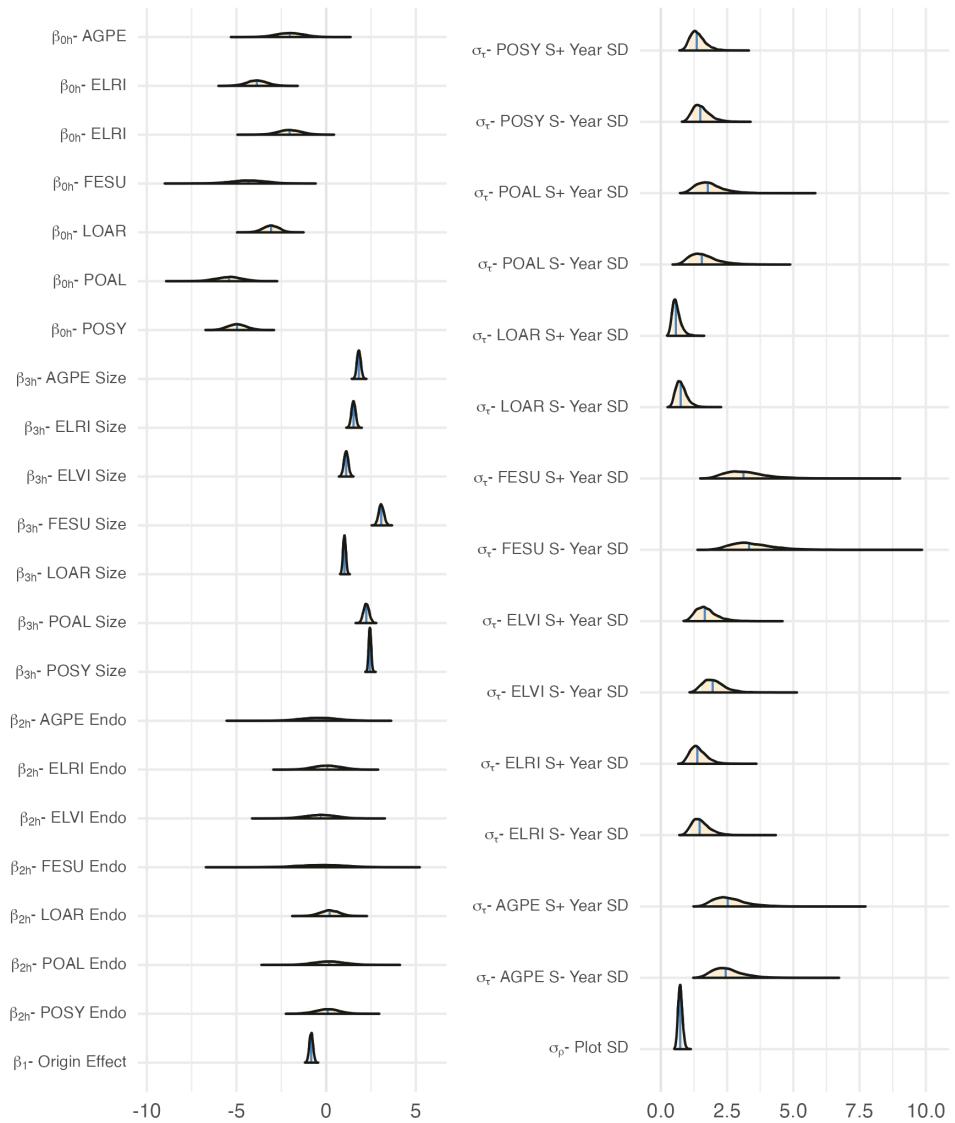
2715 Seedling Growth  
 2716 Posterior mean with 80% credible intervals  
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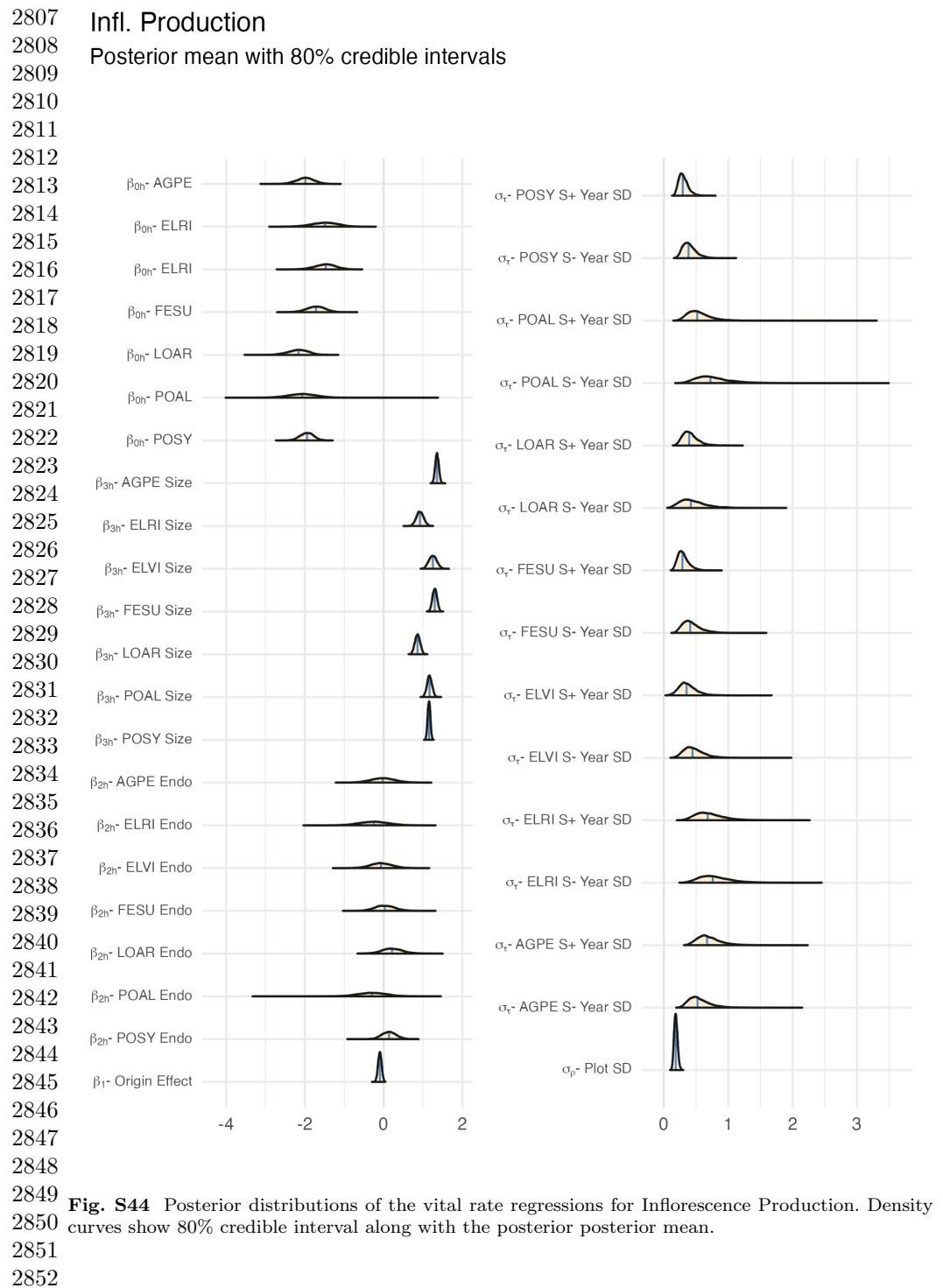
2757 **Fig. S42** Posterior distributions of the vital rate regressions for Seedling Growth. Density curves  
 2758 show 80% credible interval along with the posterior posterior mean.

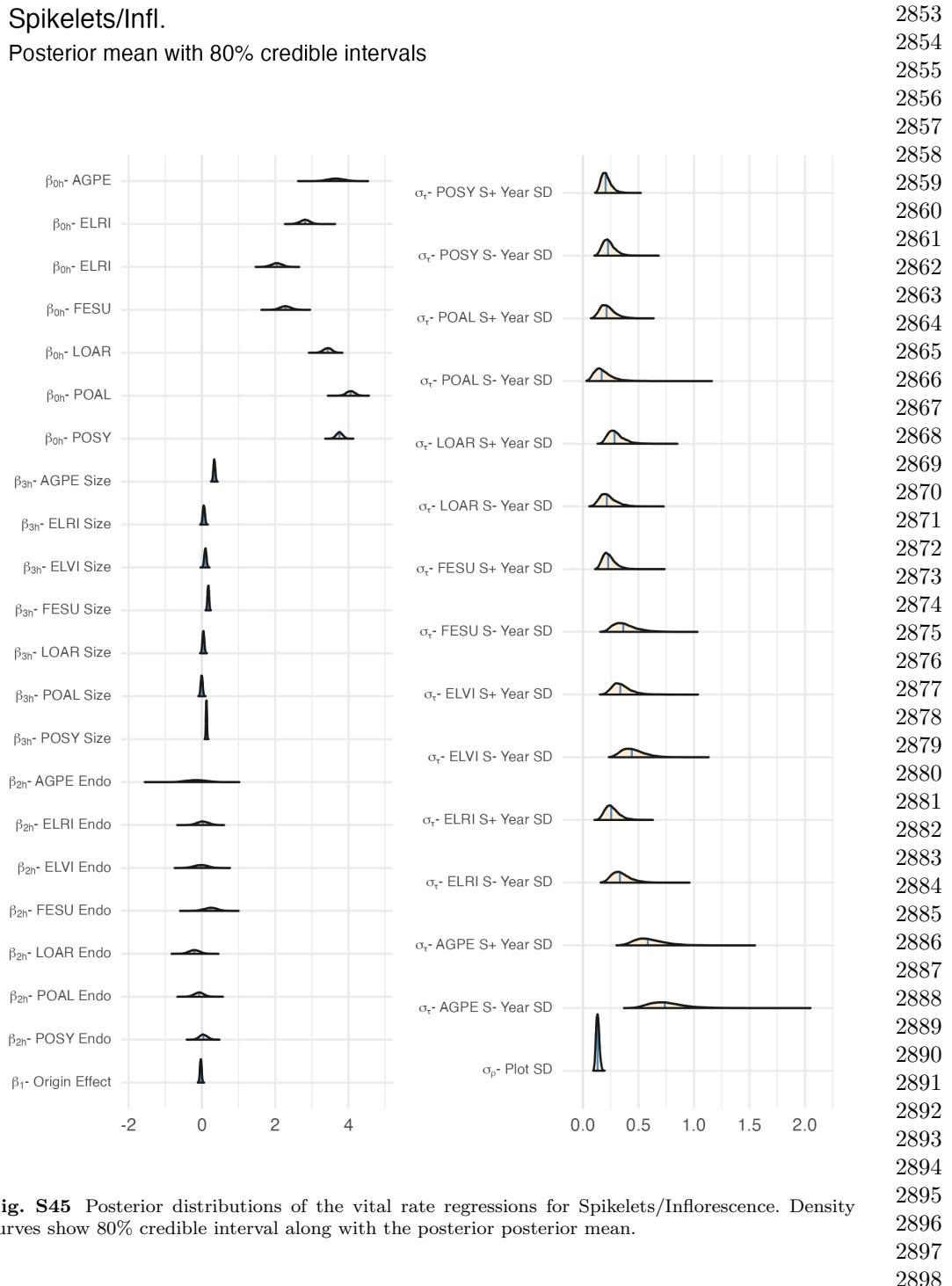
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**Flowering Probability**  
Posterior mean with 80% credible intervals

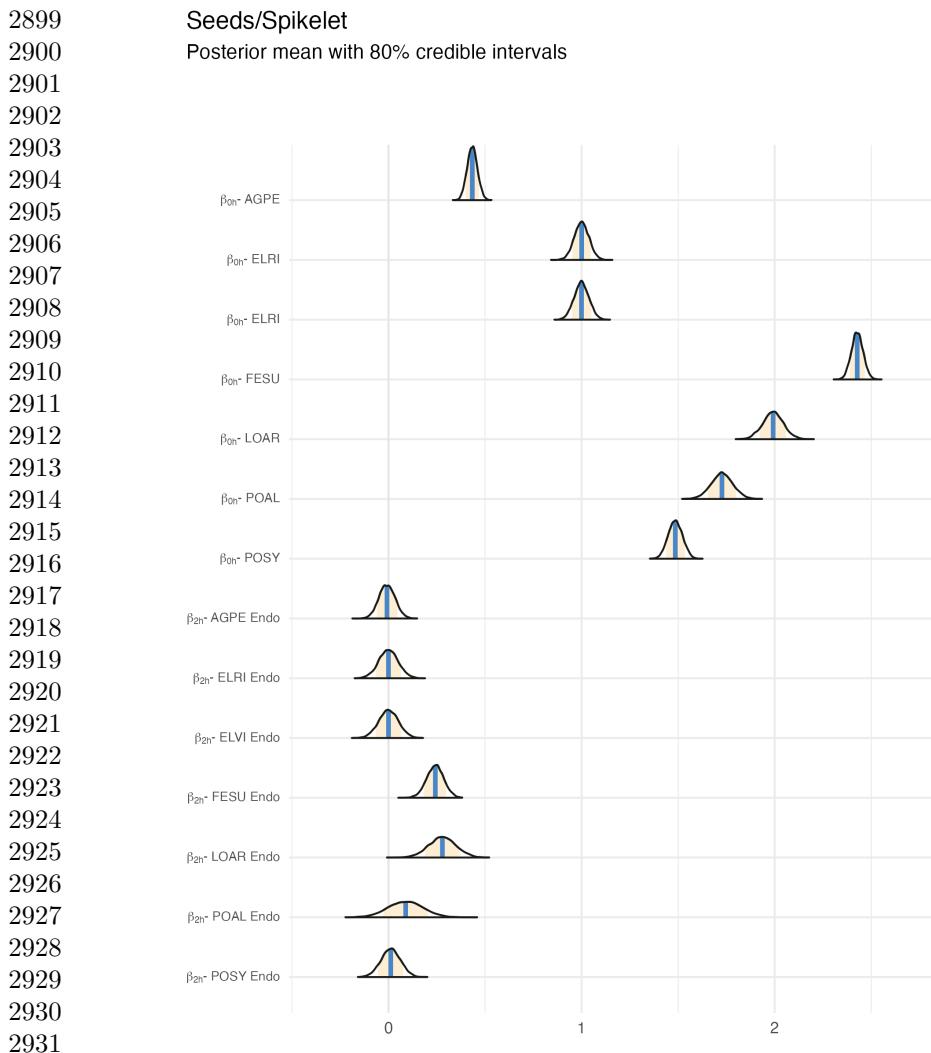


**Fig. S43** Posterior distributions of the vital rate regressions for Flowering Probability. Density curves show 80% credible interval along with the posterior posterior mean.

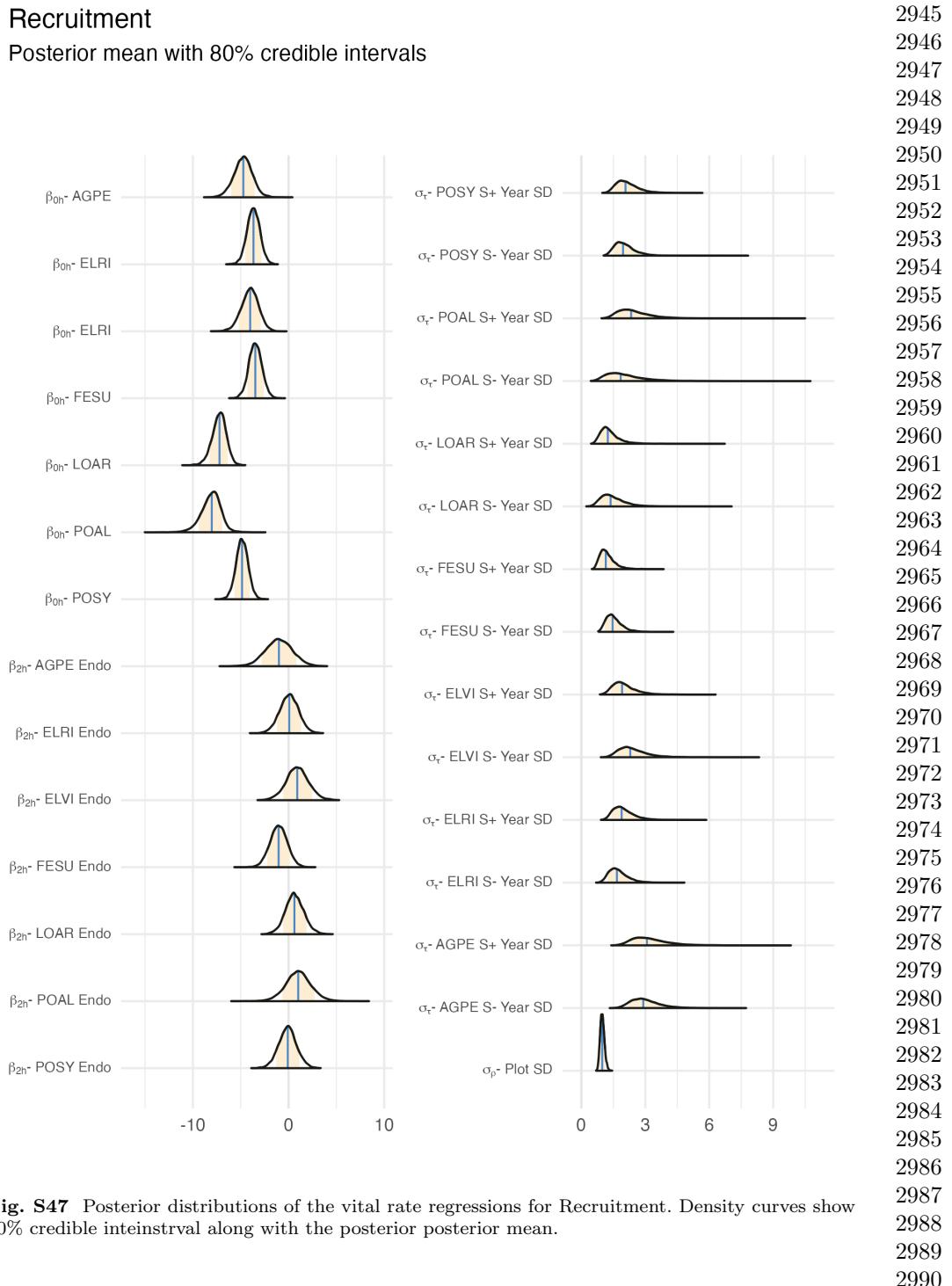




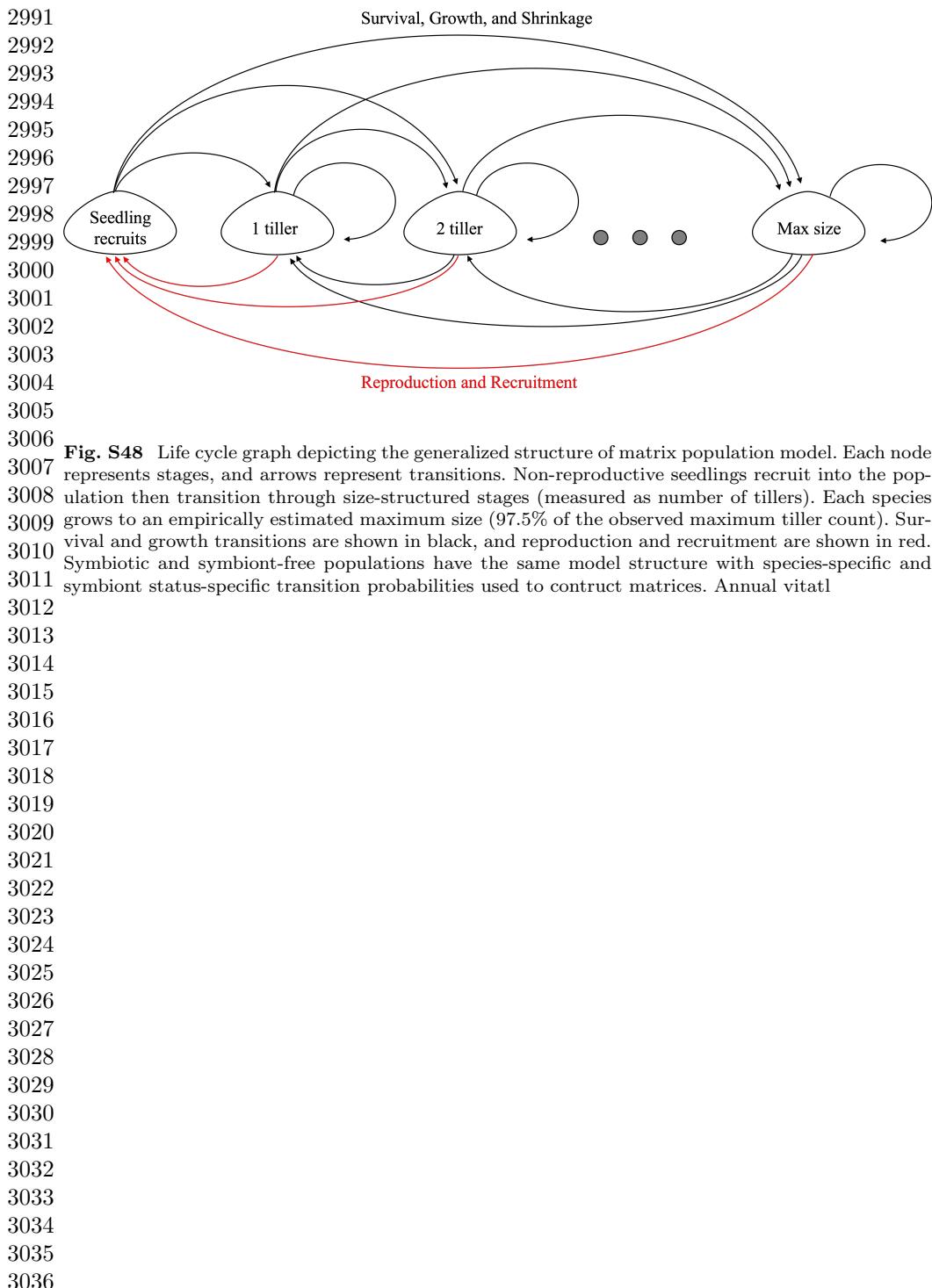
**Fig. S45** Posterior distributions of the vital rate regressions for Spikelets/Inflorescence. Density curves show 80% credible interval along with the posterior posterior mean.

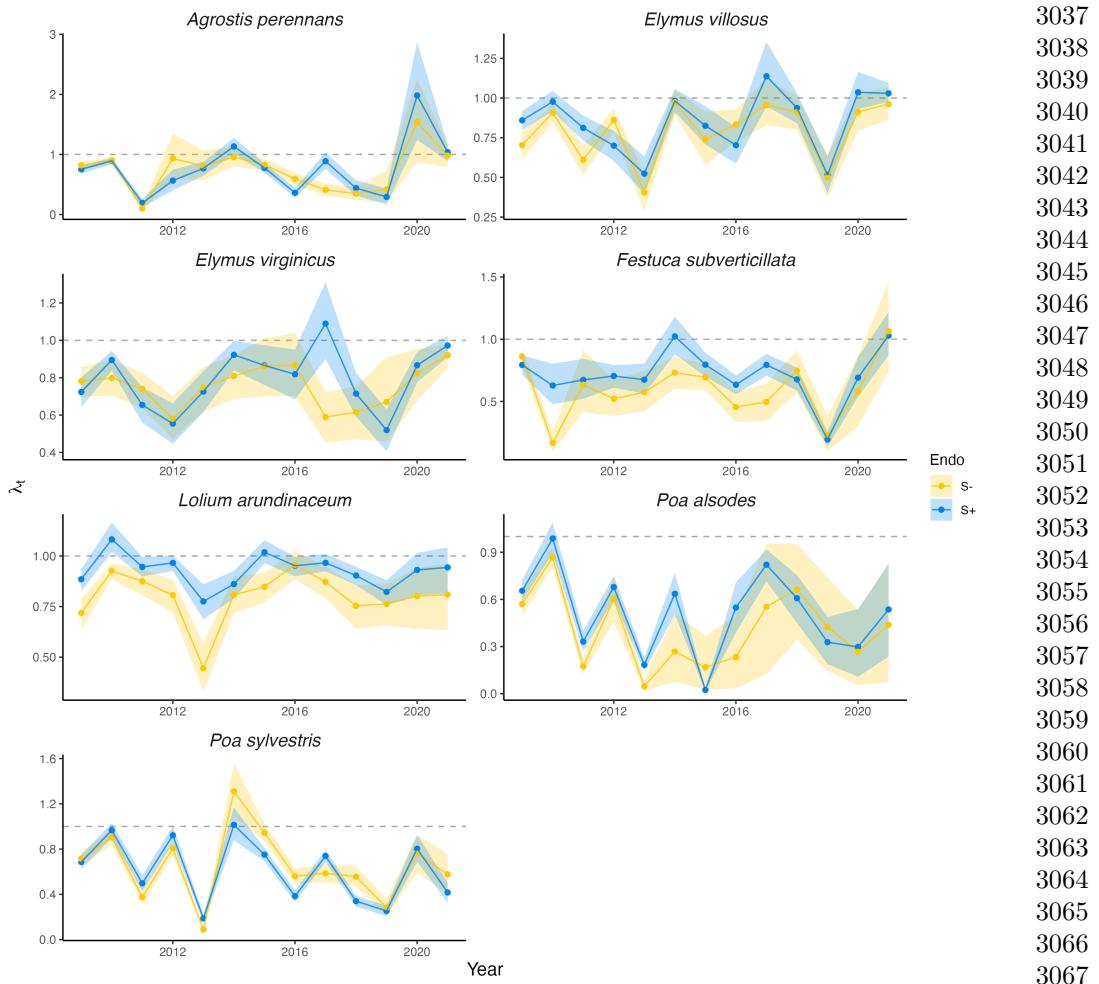


2932 **Fig. S46** Posterior distributions of the vital rate regressions for Seeds/Spikelet. Density curves show  
 2933 80% credible interval along with the posterior posterior mean.  
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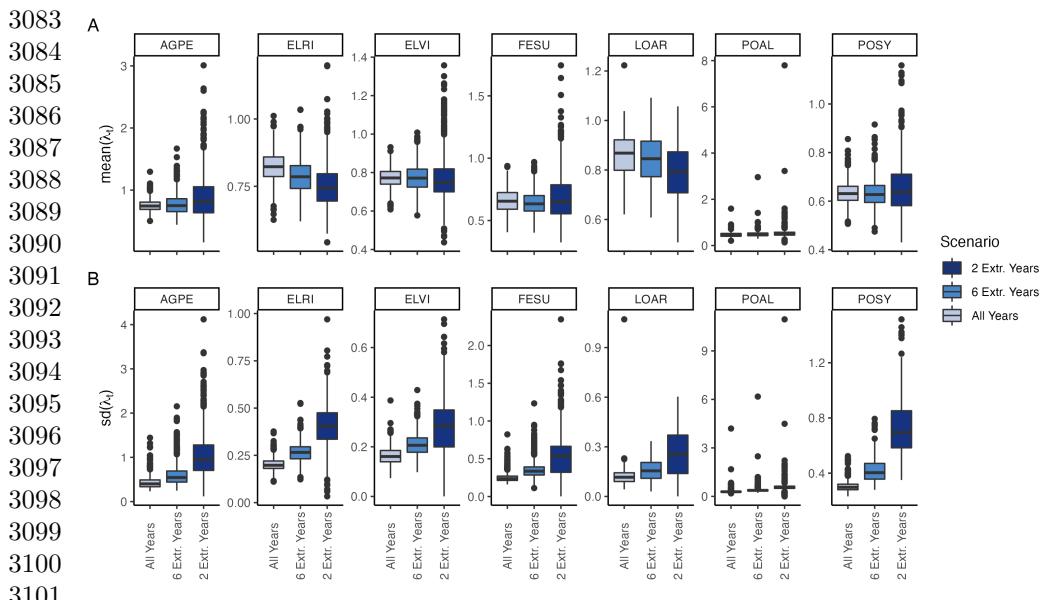
**Fig. S47** Posterior distributions of the vital rate regressions for Recruitment. Density curves show 80% credible intervals along with the posterior mean.





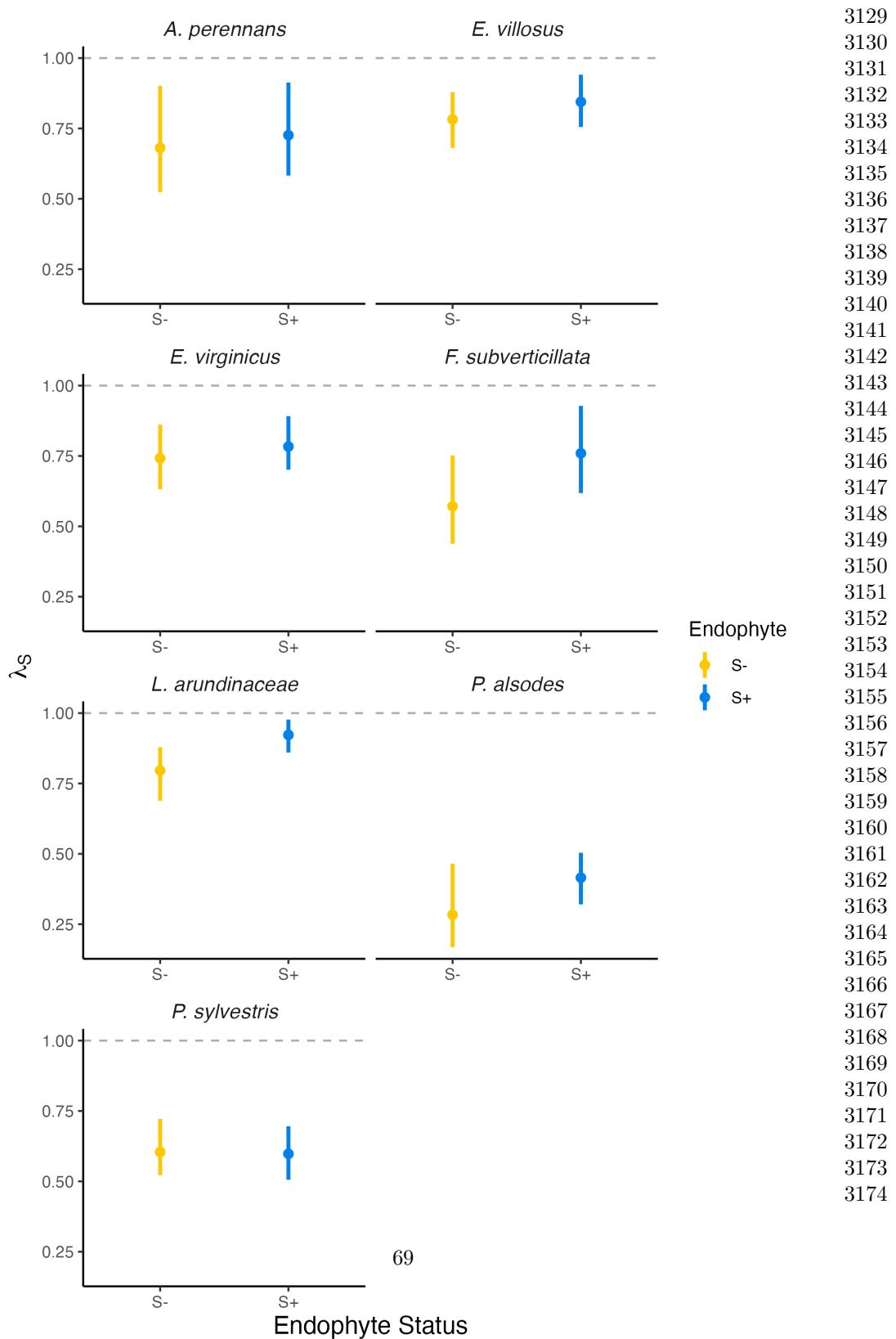
**Fig. S49** Annual growth rate values ( $\lambda_t$ ) over thirteen years. Mean values for symbiotic (blue) and symbiont-free (yellow) population growth rates are show along with 80% credible intervals. Dashed line at ( $\lambda_t = 1$ ) indicates stable population growth rate. All values are calculated from matrix models representing recruit plants.

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3103 **Fig. S50** (A) Mean and (B) standard deviation of annual growth rate values during simulation  
 3104 scenarios. Each scenario selects from observed transition matrixes, increasing the variance by selecting  
 3105 either all observed years, or a set (6 or 2 years) that have the highest and lowest growth rates for  
 3106 symbiont-free populations.

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**Fig. S51** Stochastic population growth rates ( $\lambda_s$ ) for symbiotic (blue) and symbiont-free (yellow) populations. Points show posterior medians along with the 95% credible interval 50% and posterior medians. All values are calculated from matrix models representing recruit plants.

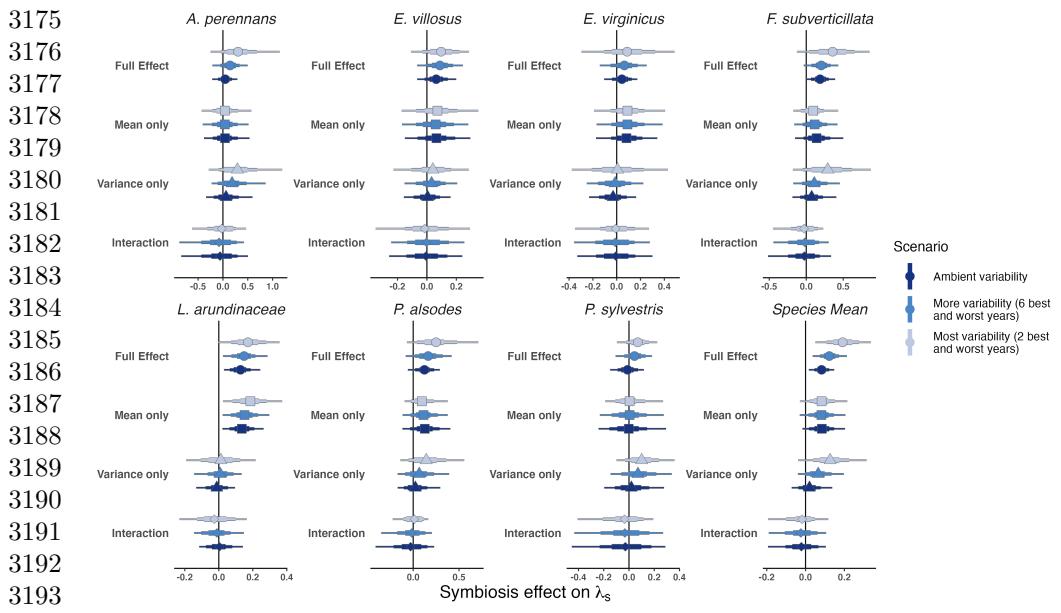
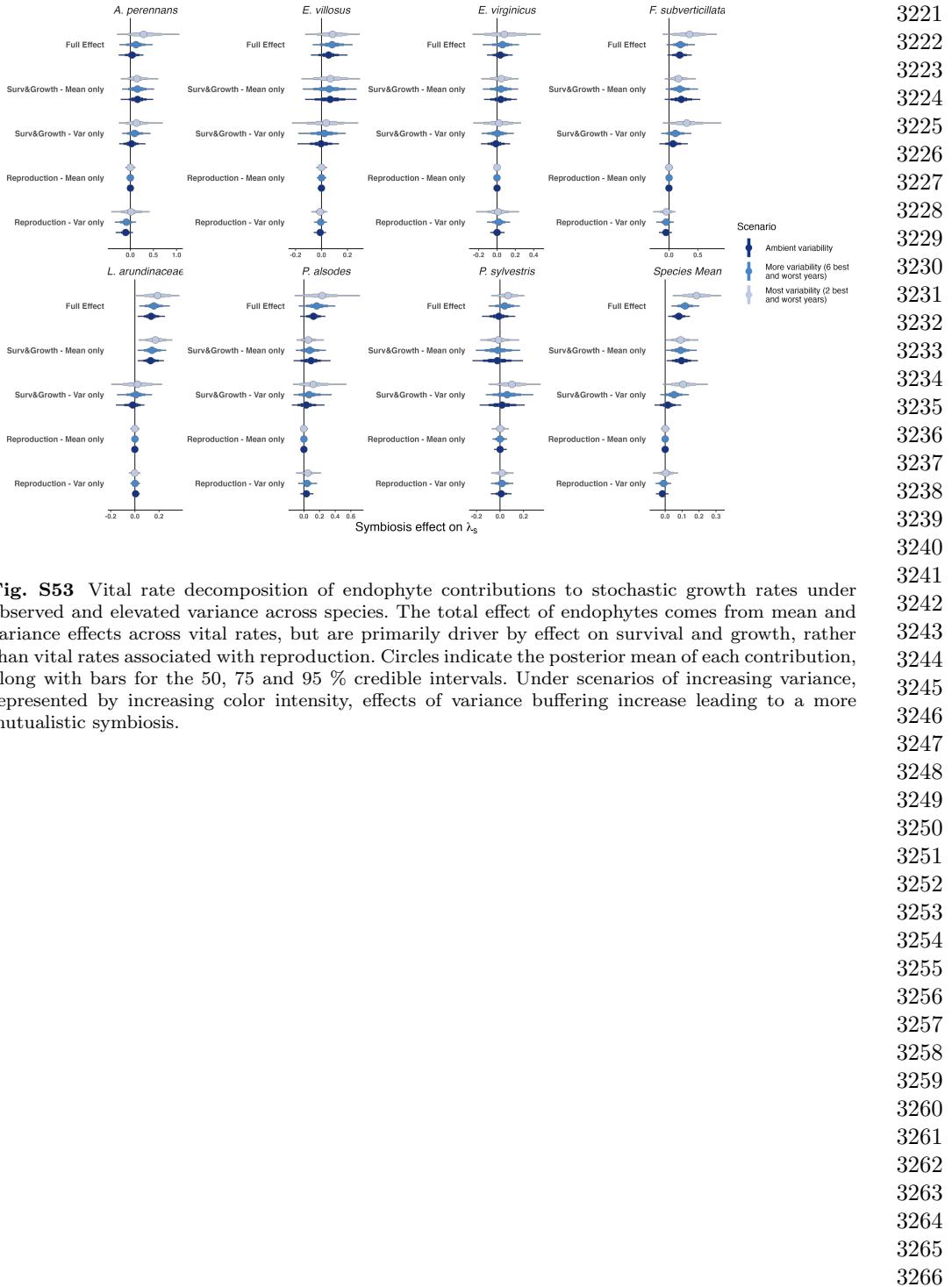


Fig. S52 Endophyte contributions to stochastic growth rates under observed and elevated variance across species. The total effect of endophytes (circle) comes from mean benefits (square) and variance buffering (triangle) as well as the interaction between mean and variance effects (diamond). Shapes indicate the posterior mean of each contribution, along with bars for the 50, 75 and 95 % credible intervals. Under scenarios of increasing variance, represented by increasing color intensity, effects of variance buffering increase leading to a more mutualistic symbiosis.

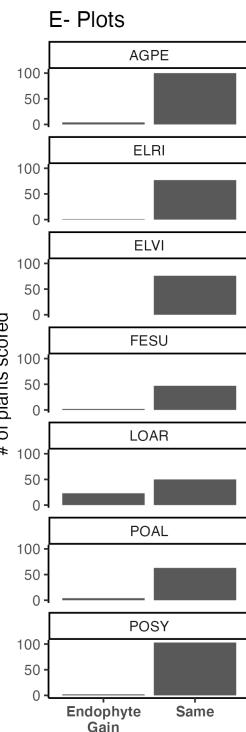
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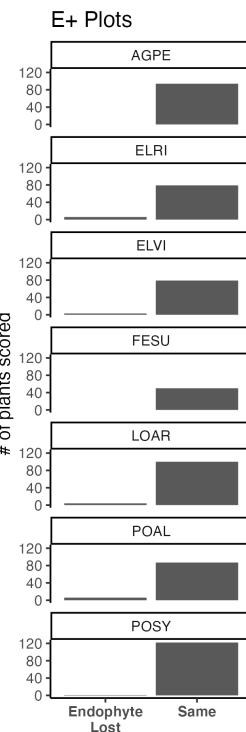
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#### Endophyte Status Checks

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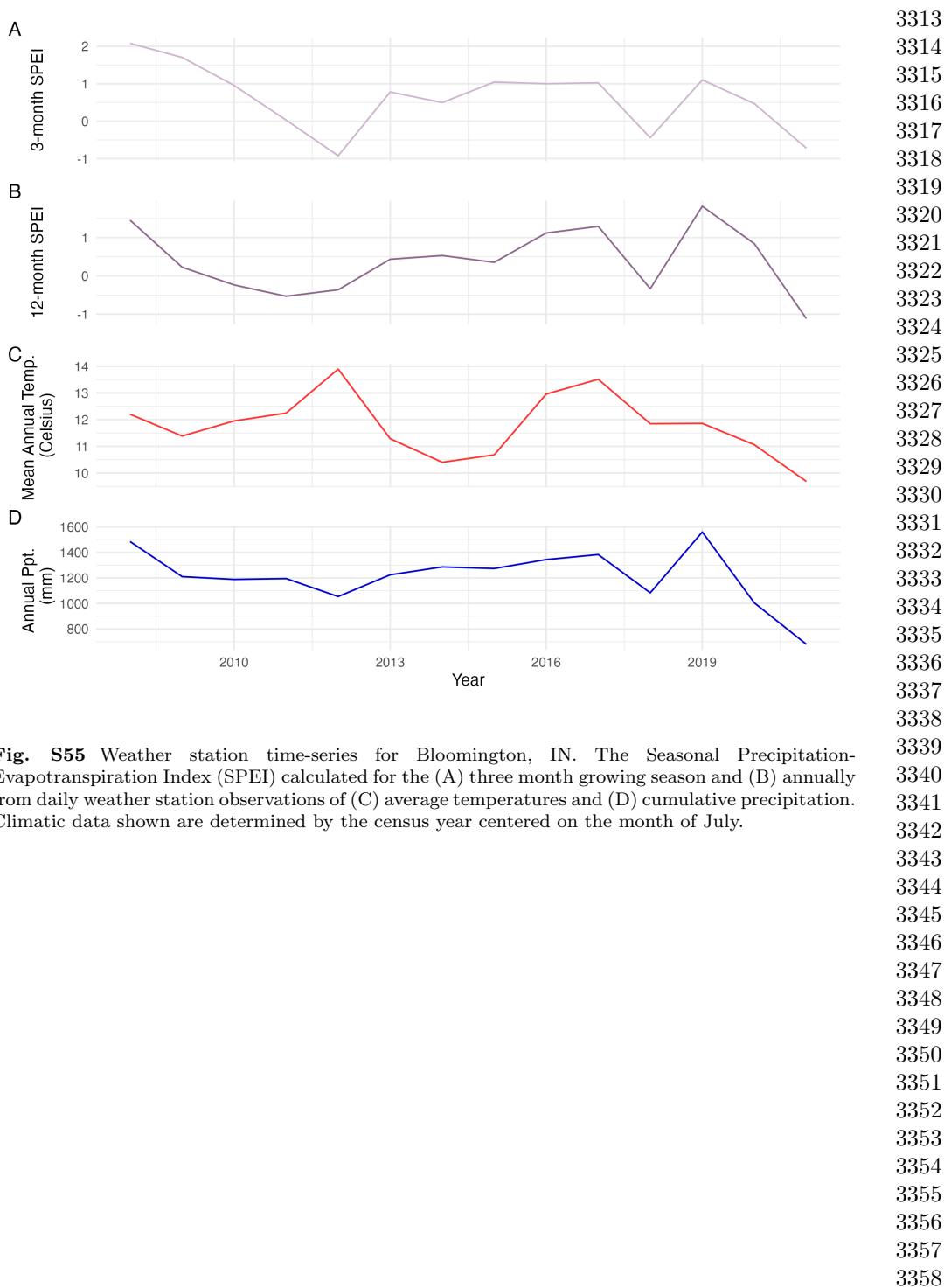


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3293 **Fig. S54** Faithfulness of experimental plots to assigned endophyte status. Counts of plants scored  
3294 with leaf peels or seed squashes to check the faithfulness of recruits to the assigned plot-level endophyte  
3295 status. (A) Endophytic plants may be gained in initially S- plots, or (B) lost in initially S+ plots.

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**Fig. S55** Weather station time-series for Bloomington, IN. The Seasonal Precipitation-Evapotranspiration Index (SPEI) calculated for the (A) three month growing season and (B) annually from daily weather station observations of (C) average temperatures and (D) cumulative precipitation. Climatic data shown are determined by the census year centered on the month of July.

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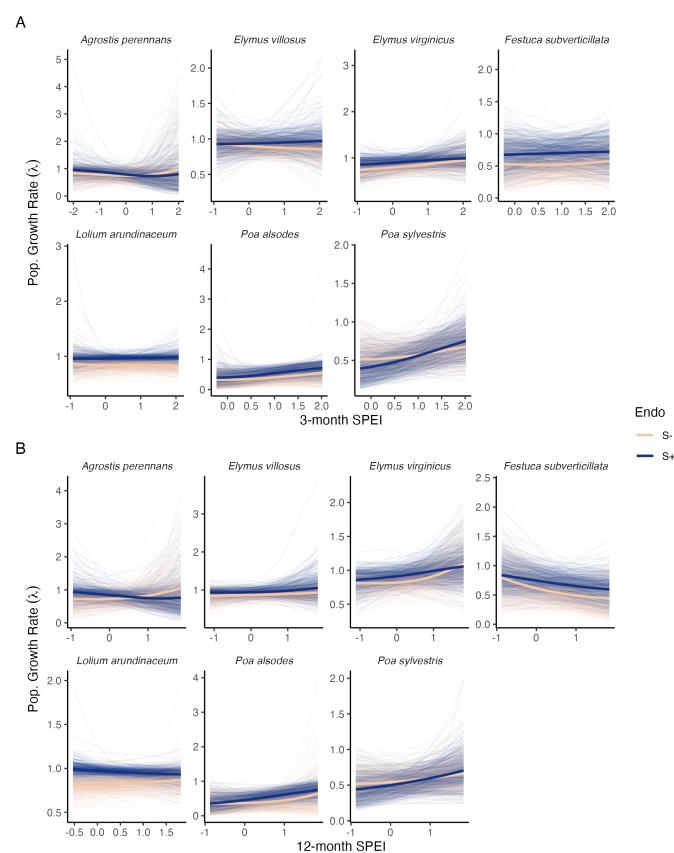
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3386 **Fig. S56** Predicted population growth rates across drought indices. Symbiotic (S+; blue) and  
 3387 symbiont-free (S-; tan) populations respond differently to climate as measured by the (A) 3-month  
 3388 SPEI and (B) 12-month SPEI. Thick lines represent the predicted mean growth rate and thin lines  
 3389 show 500 posterior draws.

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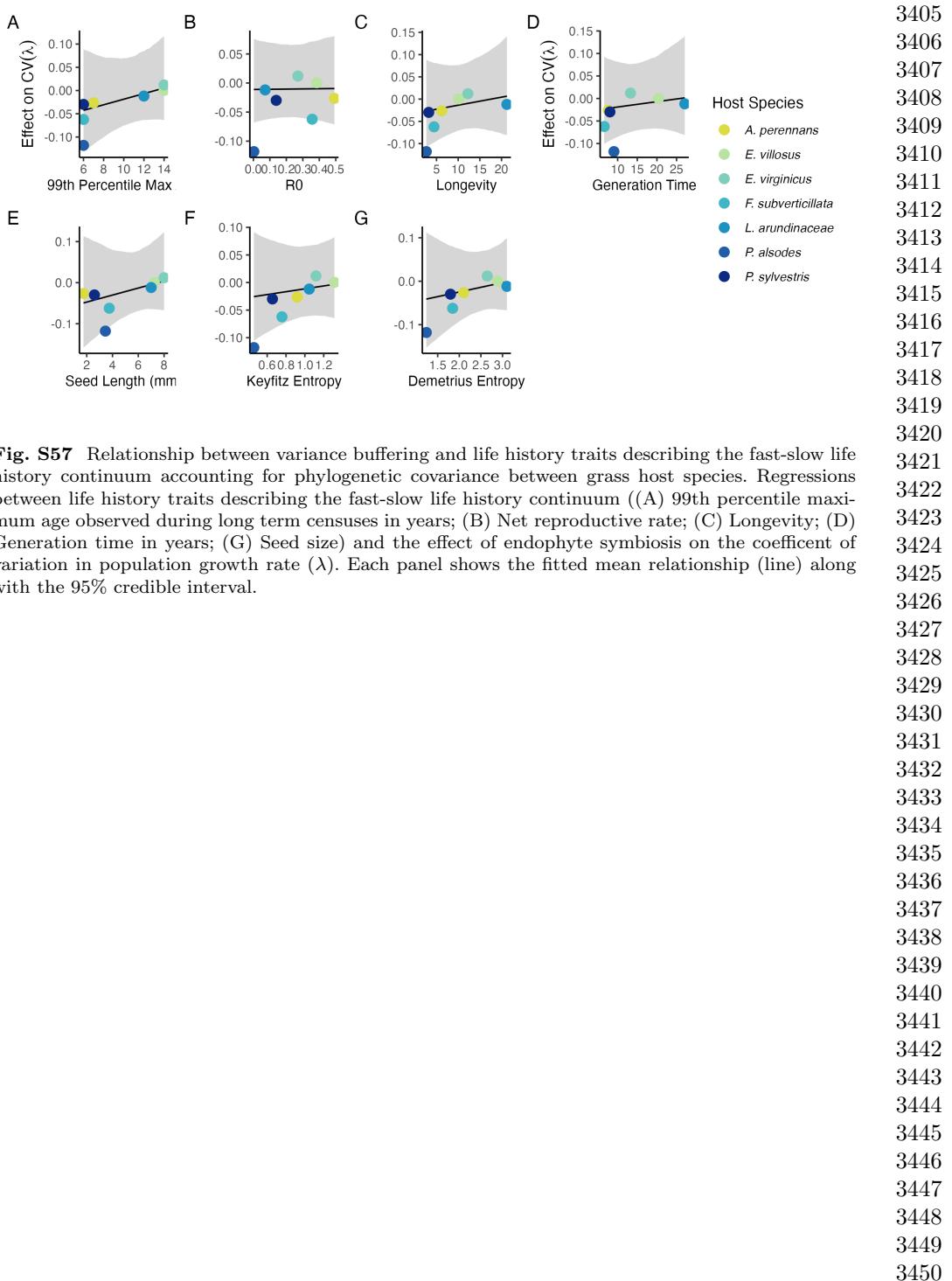
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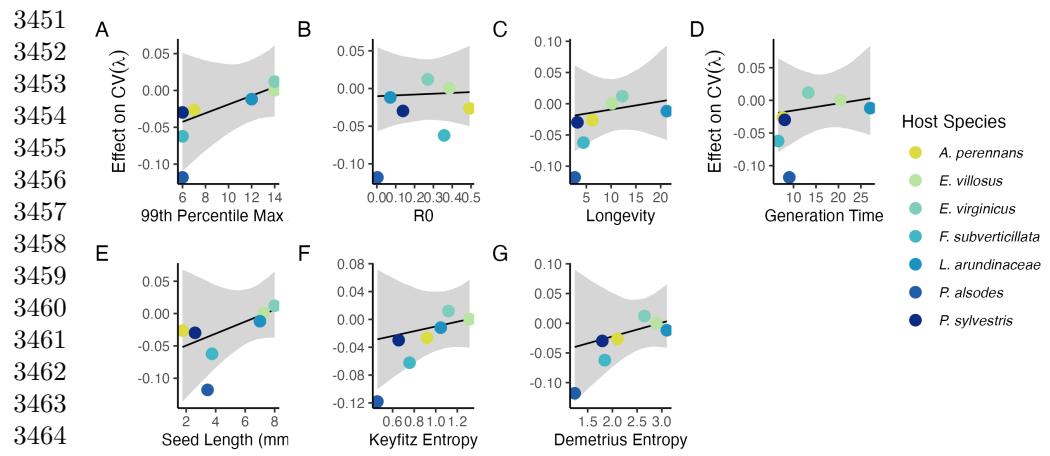
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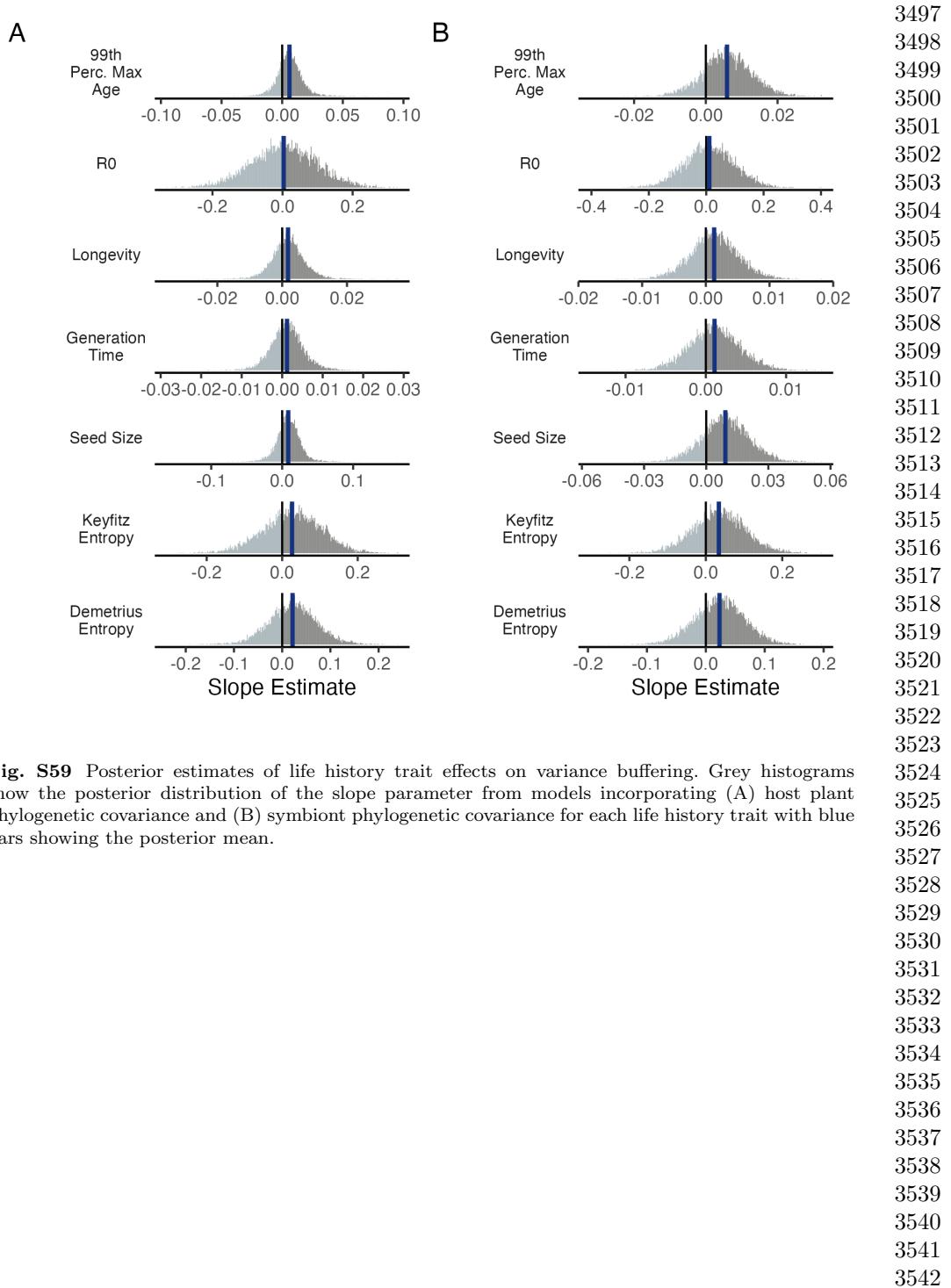
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**Fig. S59** Posterior estimates of life history trait effects on variance buffering. Grey histograms show the posterior distribution of the slope parameter from models incorporating (A) host plant phylogenetic covariance and (B) symbiont phylogenetic covariance for each life history trait with blue bars showing the posterior mean.



<b>Supplemental Tables S1-S3</b>	3589
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**Table S1** Summary of host-endophyte propagation and transplant methods

Host Species	Symbiont Species	Heat treatment duration (Temp.)	Transplant date
<i>Agrostis perennans</i>	<i>E. amarillans</i>	12 min. hot water bath (60 °C)	April 2008 (10 plots)
<i>Elymus villosus</i>	<i>E. elymi</i>	6 days drying oven (60 °C)	April 2008 (10 plots)
<i>Elymus virginicus</i>	<i>E. elymi</i> or <i>EviTG-1</i>	6 days drying oven (60 °C)	April 2008 (10 plots)
<i>Festuca subverticillata</i>	<i>E. starrii</i>	6 days drying oven (60 °C)	April 2008 (10 plots)
<i>Lolium arundinaceum</i>	<i>E. coenophiala</i>	6 days drying oven (60 °C)	Sept. 2007 (10 plots)
<i>Poa alsodes</i>	<i>E. alsodes</i>	7 days drying oven (60 °C)	Sept. 2007 (8 plots)/April 2008 (10 plots)
<i>Poa sylvestris</i>	<i>E. PsyTG-1</i>	7 days drying oven (60 °C)	Sept. 2007 (8 plots)/April 2008 (10 plots)

**Table S2** Summary of focal life history traits

Host Species	Observed max age (years)	99th percentile max age (years)	Generation time (years)	$R_0$	Longevity (years)	Seed length (mm.)	Keyfitz Entropy	Demetrius Entropy	Imperfect transmission rate (%)	Stromata Observed (% of indiv. per species)
<i>Agrostis perennans</i>	11	7	7.6	0.58	6.4	1.75	0.9	2.1	69.8	0.0
<i>Elymus villosus</i>	14	14	20.7	0.35	9.8	7.25	1.3	2.9	100	4.6
<i>Elymus virginicus</i>	14	14	13.4	0.25	12.5	8	1.1	2.6	100	0.6
<i>Festuca subverticillata</i>	9	6	6.6	0.28	4.3	3.75	0.8	1.8	42.7	0.0
<i>Lolium arundinaceum</i>	12*	12*	27.4	0.08	21.3	7	1.1	3.1	100	0.0
<i>Poa alsodes</i>	8	6	9.2	0.0033	2.6	3.45	0.5	1.2	99.9	0.0
<i>Poa sylvestris</i>	12	6	8.0	0.14	3.2	2.6	0.7	1.8	16.6	0.1
Page's $\lambda$ (host)	—	0.27	0.28	0.23	0.28	0.27	0.25	0.25	—	—
Page's $\lambda$ (symbiont)	—	0.63	0.63	0.63	0.63	0.62	0.62	0.62	—	—

\*Censuses for *L. arundinaceum* plots stopped after year 12 of the experiment.

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**Table S3** Summary of host-endophyte drought sensitivities

Host Species	Effect on CV( $\lambda$ )	Effect on Mean( $\lambda$ )	$\frac{\Delta\lambda^-}{\Delta SPEI_3}$	$\frac{\Delta\lambda^+}{\Delta SPEI_3}$	3 month S- to S+ ratio	$\frac{\Delta\lambda^-}{\Delta SPEI_{12}}$	$\frac{\Delta\lambda^+}{\Delta SPEI_{12}}$	12 month S- to S+ ratio
<i>Agrostis perennans</i>	-0.0264	0.0441	0.03	-0.04	0.85	0.11	-0.06	1.82
<i>Elymus villosus</i>	0.0003	0.0509	-0.03	0.01	1.95	0.03	0.04	0.70
<i>Elymus virginicus</i>	0.0120	0.0578	0.07	0.05	1.50	0.10	0.07	1.42
<i>Festuca subverticillata</i>	-0.0622	0.1639	0.02	0.02	1.01	-0.13	-0.09	1.43
<i>Lolium arundinaceum</i>	-0.0118	0.1022	-0.01	0.01	1.32	0.03	-0.03	1.02
<i>Poa alsodes</i>	-0.1179	0.1282	0.10	0.14	0.71	0.11	0.14	0.73
<i>Poa sylvestris</i>	-0.0298	-0.0085	0.07	0.16	0.44	0.05	0.10	0.55

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