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

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

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## Introduction

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

Classic theory predicts that long-term population growth rates (equivalently, population mean fitness) will decline under increased environmental stochasticity because costs of bad years outweigh benefits of good years – a consequence of nonlinear averaging (Lewontin and Cohen, 1969; Tuljapurkar, 1982). For example, in unstructured populations, the long-term stochastic growth rate in a fluctuating environment ( $\lambda_S$ ) will always be lower than the arithmetic mean of annual growth rates ( $\bar{\lambda}_t$ ) by an amount proportional to the environmental variance ( $\sigma^2$ ):

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

Populations structured by size or stage experience similar costs of temporal variability (Cohen, 1979; Tuljapurkar, 2013). There are accordingly two pathways to increase population viability in variable environments: increase the arithmetic mean growth rate and/or dampen temporal fluctuation in growth rates, also called “demographic buffering”.

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

Most multicellular organisms host symbiotic microbes that affect growth and performance (Rodriguez et al, 2009; McFall-Ngai et al, 2013), many of which are vertically transmitted from maternal hosts to offspring (Funkhouser and Bordenstein, 2013).

139 Vertical transmission links the fitness of hosts and symbionts in a feedback loop that  
140 selects for mutual benefits (Fine, 1975). These mutualistic microbes can protect hosts  
141 from stressful environmental conditions including drought, extreme temperatures, or  
142 natural enemies (Russell and Moran, 2006; Kivlin et al, 2013). Some well studied  
143 examples include bacterial symbionts of insects that provide hosts with thermal toler-  
144 ance through the production of heat-shock proteins (Dunbar et al, 2007), and fungal  
145 symbionts of plants that produce anti-herbivore and drought-protective compounds  
146 (Reyna et al, 2012; Saikonen et al, 2013; Neyaz et al, 2022). However, these diverse  
147 protective symbioses are context-dependent: the magnitude of benefits depends on  
148 environmental conditions (Chamberlain et al, 2014; Catford et al, 2022) and thus  
149 will vary temporally in stochastic environments (Jordano, 1994). We hypothesized  
150 that context-dependent benefits from symbionts may buffer host populations against  
151 variability through strong benefits during harsh periods and neutral or even costly  
152 outcomes during benign periods, reducing the impacts of host exposure to extremes  
153 and dampening inter-annual variance relative to non-symbiotic hosts (Fig. 1A). Vari-  
154 ance buffering is a previously unexplored mechanism by which symbionts may benefit  
155 their hosts instead of or in addition to elevating average fitness (Fig. 1C), the focus  
156 of most previous research.

157 To test the hypothesis that context-dependent benefits of symbiosis dampen inter-  
158 annual variance in host fitness, we used a combination of long-term field experiments  
159 and stochastic demographic modeling. We used cool-season grasses and *Epichloë* fun-  
160 gal endophytes, a tractable experimental model in which non-symbiotic plants can be  
161 derived from naturally symbiotic plants through heat treatment, providing a contrast  
162 of symbiont effects that controls for the confounding influence of host genetic back-  
163 ground. *Epichloë* endophytes are specialized symbionts growing intercellularly in the  
164 aboveground tissue of ~ 30% of *C<sub>3</sub>* grass species (Leuchtmann, 1992). These fungi are  
165 primarily transmitted vertically from maternal plants through seeds (Cheplick et al,  
166 2009). They produce a variety of alkaloids that can protect host plants from natural  
167 enemies (Brem and Leuchtmann, 2001) and drought stress (Decunta et al, 2021).

168 Over 14 years (2007–2021), we collected longitudinal demographic data on the  
169 survival, growth, reproduction, and recruitment of all plants within replicated  
170 endophyte-symbiotic and endophyte-free populations at our field site in southern Indi-  
171 ana, USA. Through taxonomic replication (seven host-symbiont species pairs) we  
172 aimed to understand whether host life history traits could explain inter-specific vari-  
173 ation in the magnitude of demographic buffering through symbiosis. We used this  
174 long-term data to parameterize Bayesian stochastic population projection models.  
175 Specifically, we (1) quantified the effect of symbiosis on the mean and variance of host  
176 vital rates (survival, growth and reproduction) and fitness, (2) evaluated the relation-  
177 ship between host life history traits and the magnitude of symbiont-mediated variance  
178 buffering, (3) determined the relative contributions of symbiont-mediated mean and  
179 variance effects to host fitness, and (4) projected how increased environmental stochas-  
180 ticity (expected under future climates) changes the importance of variance buffering  
181 as a pathway of host-symbiont mutualism.

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<b>Materials and Methods</b>	185
<b>Study site and species</b>	186
This study was conducted at Indiana University's Lilly-Dickey Woods Research and Teaching Preserve (39.238533, -86.218150) in Brown County, Indiana, USA. This site is part of the Eastern broadleaf forests of southern Indiana, where the ranges of many understory cool-season grass species overlap. We focused on seven of these grasses ( <i>Agrostis perennans</i> , <i>Elymus villosus</i> , <i>Elymus virginicus</i> , <i>Festuca subverticillata</i> , <i>Lolium arundinaceum</i> , <i>Poa alsodes</i> , and <i>Poa sylvestris</i> ), each of which hosts a unique species of <i>Epichloë</i> endophyte (Table S1). All are native to eastern North America except the Eurasian species <i>L. arundinaceum</i> .	187
Seeds from local, naturally symbiotic populations of the seven focal host species were collected during summer-fall 2006. Seeds were disinfected with a heat treatment or left untreated to generate symbiont-free (S-) and symbiotic (S+) plants from the same genetic lineages. In fall of 2007 and spring of 2008, we established 10 3x3 m plots for <i>A. perennans</i> , <i>E. villosus</i> , <i>E. virginicus</i> , <i>F. subverticillata</i> , and <i>L. arundinaceum</i> and 18 plots for <i>P. alsodes</i> and <i>P. sylvestris</i> . Each plot was randomly assigned to be planted with 20 evenly spaced symbiotic (S+) or symbiont-free (S-) plants. Full details of endophyte removal, plant propagation and field set-up are provided in <i>Supporting Information - Supplemental Methods and Table S1</i> .	188
Long-term demographic data collection	197
Each summer (2008–2021) we censused all individuals in each plot for survival, growth and reproduction. Plots contained 13.3 individuals/m <sup>2</sup> on average during the study. Each census year was a sample of inter-annual variation (n = 14 years, comprising 13 demographic transition years). We censused each species during its peak fruiting stage (May: <i>Poa alsodes</i> , <i>Poa sylvestris</i> ; June: <i>Festuca subverticillata</i> ; July: <i>Elymus villosus</i> , <i>Elymus virginicus</i> , <i>Lolium arundinaceum</i> ; September: <i>Agrostis perennans</i> ), such that censuses were pre-breeding and new recruits came from the previous years' seed production (Fig. S1 shows a generalized life cycle diagram). Leaf litter was cleared out of each plot before the census, to aid in locating plants. For each tagged plant, we determined survival, measured size as a count of tillers, and collected reproductive data as counts of reproductive tillers and seed-bearing spikelets on up to three reproductive tillers. We also tagged all unmarked recruits from the previous years' seed production and collected the same demographic data. New recruits typically had one tiller and were non-reproductive. In 2008 through 2010, we took counts of seeds per inflorescence for all reproducing individuals in the plots to relate inflorescence and spikelet counts to seed production. In 2018, we stopped collecting data for <i>L. arundinaceum</i> , which had very high survival and low recruitment, and consequently low variation in population size across years. In total, the dataset included demographic information for 16,789 individual host-plants and 31,216 transition-year observations.	198
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231 **Vital rate modeling**

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

255 We built stochastic matrix projection model for each host species. We parameter-  
256 ized the models using the fitted statistical vital rate models in a manner similar to  
257 continuous IPM models ([Ellner et al, 2016](#)), while accounting for the discrete data rep-  
258 resenting our focal species' growth ([Ellner et al, 2022](#)) Each matrix projection model  
259 included two state variables:  $r_t$  (the number of newly recruited individuals in year  $t$   
260 which we assume to be non-reproductive), and  $\mathbf{n}_t$  (a vector including all non-seedling  
261 individuals of discrete sizes  $x \in \{1, 2, \dots, U\}$  ranging from one to the maximum number  
262 of tillers  $U$ ). We use these two state variables to avoid assuming demographic equiv-  
263 alence between seedling and non-seedling one-tiller plants. We used the same model  
264 structure, corresponding to a pre-breeding census, for each species and endophyte  
265 status (not shown in model notation for readability; Fig. S1).

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

$$267 \quad r_{t+1} = \sum_{x=1}^U P(x; \boldsymbol{\tau}_P) F(x; \boldsymbol{\tau}_F) K(x; \boldsymbol{\tau}_K) D R(\boldsymbol{\tau}_R) n_t^x \quad (2)$$

268 The total number of seeds produced by a maternal plant of size  $x$  is the product of  
269 the size-specific probability of flowering  $P$ , the number of inflorescences conditional  
270 on flowering  $F$ , the number of spikelets per inflorescence  $K$ , and the number of seeds  
271 per spikelet  $D$ . Multiplying by the probability of transitioning from seed to seedling  
272  $R$  gives a per-capita seedling production rate, which is multiplied by the number of  
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plants of size  $x$  ( $n_t^x$ , the  $x^{\text{th}}$  element of  $n_t$ ) and summed over all sizes. Each function also depends on species- and endophyte-specific year random effects for that vital rate ( $\boldsymbol{\tau}$ , a vector of year-specific values). 277  
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The number of  $y$ -sized plants in year  $t + 1$  is given by: 280  
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$$n_{t+1}^y = Z(y; \boldsymbol{\tau}_Z)B(\boldsymbol{\tau}_B)r_t + \sum_{x=1}^U S(x; \boldsymbol{\tau}_S)G(x, y; \boldsymbol{\tau}_G)n_t^x \quad (3)$$

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. 3 represents growth ( $Z$ ) and survival ( $B$ ) of seedling recruits. The second term includes survival of previously  $x$ -sized plants and the growth of survivors from size  $x$  to  $y$ , summed over all  $x$ . To avoid predictions of unrealistic growth outside of the observed size distribution, we capped the growth function for plants at the 97.5<sup>th</sup> percentile of observed sizes for each host species (Williams et al., 2012). We analyzed projection models constructed from parameters representing the dynamics of naturally recruited plants. 282  
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Each vital rate function in Eqns. 2 and 3 has separate intercepts and year random effects for symbiotic and symbiont-free populations, allowing us to calculate the effect of endophyte symbiosis on the mean, variance, and coefficient of variation (CV) of  $\lambda_t$ , the dominant eigenvalue of the year- and endophyte-specific projection matrix. This model treats climate drivers implicitly through year-specific random effects. We also developed a climate-explicit version with additional parameters defining the relationship between either annual or growing season drought index and each vital rate (Supporting Information - Supplemental Methods).

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 (rather than independently sampling regression coefficients) produces models that realistically capture inter-annual variation by preserving vital rate correlations (Metcalf et al., 2015). We tallied total population size at each time step as  $N_t = r_t + \sum_{x=1}^U n_t^x$  and calculated the stochastic growth rate as  $\log(\lambda_S) = E[\log(\frac{N_t}{N_{t+1}})]$  (Caswell, 2001; Rees and Ellner, 2009). We calculated total effects of endophyte symbiosis as the difference in  $\lambda_S$  between S+ and S- populations. We propagated uncertainty from the vital rates to the calculation of  $\lambda_S$  using 500 draws from model posteriors.

## Life History Analysis

We collected metrics describing each host species' life history to test the relationship between pace of life and variance buffering (Table S2). We recorded seed size as the average lemma length from the Flora of North America (of North America Editorial Committee, 1993). We calculated the 99th percentile of maximum observed age for symbiont-free plants from the census data for each species. Using the Rage package (Jones et al., 2022), we calculated generation time, longevity, net reproductive rate  $R_0$ , Keyfitz entropy (describing survivorship across lifespan), and Demetrius

323 entropy (describing reproduction across lifespan) from the mean transition matrix for  
324 symbiont-free populations. Next, we fit Bayesian phylogenetic mixed-effects models  
325 using the brms package (Bürkner, 2017) to test the relationship between each life his-  
326 tory trait and the effect of symbiosis on the CV of  $\lambda_t$  (a measure of variance buffering)  
327 while controlling for phylogenetic non-independence. We pruned species-level phylo-  
328 genies of plants (Zanne et al, 2014) and *Epichloë* fungi (Leuchtmann et al, 2014) to  
329 include the focal species (or a congener for one host), and defined separate phylo-  
330 genetic covariance matrices from these pruned trees for host and symbiont species. We  
331 propagated uncertainty in the estimated variance buffering effect with a measurement  
332 error model, described in full in the *Supporting Information - Supplemental Methods*.  
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### 334 Mean-variance decomposition

335 We decomposed total endophyte effects on  $\lambda_S$  into contributions from effects on vital  
336 rate means, and variances. Specifically, we repeated the calculation of S+ and S-  $\lambda_S$   
337 described above for two additional “treatments”: (1) endophyte effects on mean vital  
338 rates only, with inter-annual variances shared between S+ and S- at the S- reference  
339 level for all vital rates, and (2) endophyte effects on vital rate variances only, with  
340 vital rate means shared between S+ and S- at the S- reference level. The combination  
341 of all four  $\lambda_S$  treatments (S+ vital rate means and variances, S- means and variances,  
342 S+ means with S- variances, S- means with S+ variances) allowed us to quantify  
343 the extent that overall effects of symbiosis derive from changes in vital rates means,  
344 variances, and their interaction. The interaction occurs because the variance penalty  
345 to stochastic growth is proportional to the arithmetic mean of annual growth rates  
346 (as in Eq. 1, for example) such that variance is more detrimental for populations with  
347 lower average growth rates. To quantify how mean and variance effects of symbionts  
348 arise through effects on different vital rates, we performed an additional decomposition  
349 described in *Supporting Information Supplemental Methods* that isolates symbiont  
350 effects on growth and survival from effects on fertility and recruitment.  
351

352 We simulated scenarios of increased variance relative to that observed during our  
353 study by sampling subsets of the 13 observed annual transition matrices. We created  
354 two scenarios of increased environmental variance by sampling the transition matrices  
355 associated with the set of either six or two most extreme  $\lambda_t$  values for S- populations.  
356 These extreme  $\lambda_t$  values represent the best and worst years experienced by symbiont-  
357 free populations. By sampling away from an average year in both directions, the six-  
358 and two- years scenarios increased standard deviation of annual host growth rates by  
359 1.3 and 2.1 times, respectively, without changing mean growth rates (< 2.1% difference  
360 in  $\bar{\lambda}_t$  between simulation treatments, Fig. S80). We performed the same mean-variance  
361 decomposition for these scenarios as described above.

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<b>Results</b>	369
<b>Symbionts buffer host demographic variance</b>	370
Across 14 census years, endophytes reduced inter-annual variance for 66% (37/56) of host species-vital rate combinations (average Cohen's D for effects on vital rate standard deviation: -0.15) (Fig. 2A; Figs. S22 - S29). Endophytes also increased mean vital rates for the majority (36/56) of host species-vital rate combinations (average Cohen's D for effects on vital rate mean: 0.15), and benefits were particularly strong for host survival, plant growth and recruitment (Fig. 2A; Fig. S2 - S11). The magnitude of mean and variance effects differed among hosts and vital rates. Symbiont effects on vital rate variance were as large and even exceeded mean effects for certain species. For example, endophytes modestly increased mean adult survival (Fig. 2C) and strongly reduced variance in survival (Fig. 2D) for <i>Festuca subverticillata</i> , while for <i>Poa alsodes</i> , variance buffering was more apparent in seedling growth and inflorescence production (Fig. 2E). Additionally, some vital rates showed costs of symbiosis. Symbiotic individuals of <i>A. perennans</i> grew larger than symbiont-free hosts (Fig. 2B), yet endophytes also reduced this species' mean recruitment (Fig. 2A). Similarly, endophytes increased variance for certain species' vital rates, including seedling growth for <i>Elymus villosus</i> and <i>Festuca subverticillata</i> (Fig. 2A).	371
Because not all vital rates contribute equally to fitness, we used stochastic matrix models to integrate diverse vital rate effects described above into comprehensive measures for the arithmetic mean and variance of year-to-year fitness ( $\lambda_t$ ). On average across host species, mean fitness of S+ populations increased by more than 10% (> 92% confidence that endophytes increased $\lambda_t$ ) and inter-annual variability in fitness was 26% lower (> 86% confidence that endophytes decreased the coefficient of variation of $\lambda_t$ ) than S- populations (Fig. 3). For some host species, the CV of $\lambda_t$ declined by more than 62% ( <i>P. alsodes</i> , <i>F. subverticillata</i> ), while for others, endophyte effects on variance were substantially smaller (5% lower for <i>E. villosus</i> , 13% lower for <i>A. perennans</i> ), or even positive (37% increase for <i>E. virginicus</i> ). Considering mean and variance effects together, none of the host-symbiont pairings were antagonistic (i.e., with endophytes that both decreased mean fitness and increased variance) (Fig. 3C)	372
<b>Faster life histories predict stronger symbiont-mediated variance buffering</b>	373
Hosts with slow life history trait values experienced weaker variance buffering from endophytes than those with fast life histories (Fig. 4). Variance buffering was stronger for host species with shorter lifespan (Fig. 4A; 67% probability of positive relationship with empirically observed maximum plant age) and smaller seeds (Fig. 4B; 65% probability of positive relationship with seed length). Other life history traits similarly had weak, positive support for the prediction that faster life history traits correlate with stronger variance buffering (Fig. S83-S85). Models indicate moderate phylogenetic signal in the effect of variance buffering (average Pagel's $\lambda$ of 0.22 (90% CI: 0-0.8) and of 0.56 (90% CI: 0-0.9) from models including host and symbiont phylogeny respectively (Table S2)).	374
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415 **Contributions from variance buffering are weak relative to  
416 mean effects**

417 To evaluate the relative importance of mean fitness benefits and variance buffering as  
418 alternative pathways of mutualism, we decomposed the overall effect of the symbiosis  
419 on stochastic growth rates  $\lambda_S$  using simulations including either the full symbiosis  
420 effect (both mean and variance effects), mean effects alone, variance effects alone, or  
421 neither mean nor variance effects. Overall, the full effect of symbiosis on  $\lambda_S$ , averaged  
422 across host species, provided strong evidence of grass-endophyte mutualism (99% cer-  
423 tainty of a positive total effect on  $\lambda_S$ ) (Fig. 5; see Fig. S81 for individual host species).  
424 Contributions to this full effect derived from both mean and variance buffering effects,  
425 as well as a slightly negative interaction (i.e., the combined influence of mean and  
426 variance effects was smaller than the sum of their individual effects). Endophytes' con-  
427 tributions to  $\lambda_S$  from mean effects were four times greater, averaged across species,  
428 than contributions from variance buffering (Fig. 5), suggesting that, under the regime  
429 of environmental variability represented by our 14-year study, damped fluctuations  
430 in fitness via variance buffering was a less important element of symbiont benefits than  
431 increased mean fitness. Decomposing this result further into contributions through  
432 different vital rates demonstrated that demographic buffering arose primarily from  
433 symbionts' effects on host survival and growth, rather than from effects on repro-  
434 duction (Fig. S82). Results for individual host species were largely consistent with  
435 cross-species trends (Fig. S81). The full effect of symbiosis on  $\lambda_S$  was positive for  
436 five out of seven host species, with statistical confidence ranging from 78% to > 99%  
437 certainty. The exceptions were *P. sylvestris* and *A. perennans*, for which our analy-  
438 sis indicated effectively neutral symbionts in their overall fitness effect (42% and 57%  
439 posterior probability of positive effects respectively; Fig. S81).

441  
442 **Variance buffering strengthens under increased environmental  
443 variability**

444 To simulate increased variability, we repeated the decomposition of  $\lambda_S$  for two alterna-  
445 tive scenarios, randomly sampling transition matrices that represented either the six or  
446 two most extreme years, subsets of the thirteen transition matrices across the 14-year  
447 study period. Increased variability elicited stronger mutualistic benefits of endophyte  
448 symbiosis than ambient variability (Fig. 5; overall effect of the symbiosis increased by  
449 ~2fold). This increase was driven by increased contributions from variance buffering  
450 (from a 16% contribution in the ambient scenario to a 54% contribution in the most  
451 variable scenario) rather than from greater mean effects. In the most variable scenario,  
452 the relative importance of mean and variance effects reversed, with variance buffering  
453 contributions that were 1.2 times greater than mean contributions, averaged across  
454 species (Fig. 5).

456  
457 **Discussion**

458 Across seven host species, eight vital rates, 14 years, and 16,789 individuals, our anal-  
459 ysis provided the first empirical evidence, to our knowledge, of demographic buffering  
460

conferred by microbial symbionts. Our taxonomically-replicated, long-term field experiments that manipulated the presence/absence of fungal symbionts in plants revealed that heritable microbes can commonly benefit hosts not only through improved mean fitness – the focus of most previous research – but also through buffering against environmental variance (Fig. 1). Benefits to mean fitness dominated the overall fitness advantage of endophyte symbiosis under observed environmental variability. However, the strongest symbiotic benefits derived from the combination of both mean effects and variance buffering (Fig. 1B), and simulation experiments point to an increasing role for demographic buffering under increased temporal environmental stochasticity (Fig. 5; Figs. S81-S82). There is growing interest in demographic buffering as a potential source of resilience against increased stochasticity under global change (Hilde et al, 2020). Our results suggest that biotic interactions, and microbial mutualisms in particular, may be an under-appreciated mechanism of demographic buffering. In fact, any interaction that is subject to context-dependence – where magnitudes of cost or benefit depends on harshness of the environment – holds potential to modify demographic variance across years. However, long-term experimental data required to detect such an influence are rarely available.

Taxonomic replication of host-symbiont pairs enabled us to generalize beyond the focal taxa and facilitated inference about the *types* of species in which demographic buffering may be more or less likely. Because host taxa with “slow” life history traits, such as long lifespan, may be intrinsically buffered from environmental variability (Rees, 1996; Moles and Westoby, 2004; Morris et al, 2008), we predicted that buffering effects of endophyte symbiosis would be stronger in hosts with faster pace of life. Supporting this prediction, we found that shorter-lived and smaller-seeded host species experienced stronger reductions in demographic variance through endophyte symbiosis. Thus, microbial symbiosis may compensate for the lack of intrinsic tolerance of variability conferred by slow life history traits. Future studies may consider fungal life history traits, such as diversity in biologically-active alkaloids, or the production of stromata - fruiting bodies capable of horizontal (contagious) transmission. The host species for which the net mutualism benefit was greatest (*F. subverticillata* and *L. arundinaceum*) (Fig. S79) were among those never observed to produce fungal stromata (Table S2), supporting theoretical expectations that strict vertical transmission drives evolution of strong host-symbiont mutualism (Fine, 1975; Afkhami and Rudgers, 2008). We caution that inferences on trait correlates of demographic buffering were subject to large uncertainties (Fig. S85), reflecting relatively narrow taxonomic breadth (closely related grass species in the sub-family Pooideae and their co-evolving symbionts). Understanding of how life history variation modulates fitness consequences of microbial symbiosis would profit from tests across a wider span of plant and animal groups (Jeschke and Kokko, 2009). We also found relatively consistent, positive effects of endophyte symbiosis on stochastic fitness (Fig. S78-S79), suggesting that variation across host species and vital rates in mean and variance effects (Fig. 3C) may reflect alternative strategies that yield similar net benefits.

While our results highlight symbiont-mediated demographic buffering as a potential source of resilience against increased environmental stochasticity, much work remains to connect symbiont effects on mean and variance to quantitative forecasts of

host-symbiont dynamics under global change. Like most temporally stochastic population projection models, our approach quantified demographic variance across years (and simulated increasing variance) without attributing its cause(s). Realistic forecasts for host-symbiont dynamics under environmental change will require explicit connections between driver variables and demographic responses. Reduced sensitivity to drought, as is common in *Epichloë* symbioses (Reyna et al, 2012; Saikkonen et al, 2013; Neyaz et al, 2022; Decunta et al, 2021), is a candidate mechanism that could generate a signature of variance buffering: drought conditions may be less costly for S+ hosts, dampening the effects of drought years and reducing fluctuations in fitness through time (Fig. 1). Preliminary climate-explicit analyses indicated that symbionts reduced sensitivity to drought indices for five of seven host taxa (Supporting Information; Fig. S88-S89; Table S3). However, we did not find a strong relationship between magnitude of variance buffering and relative drought sensitivities, suggesting that other climatic factors or temporally-varying aspects of the environment may elicit benefits of symbiosis, including documented resistance to herbivory for six of these host taxa (Rudgers and Clay, 2008; Crawford et al, 2010). Identifying the type and timescale of relevant drivers would allow more direct connections between demographic models and outputs from global climate models.

Symbiont-mediated demographic buffering is a potential target of selection for improved holobiont fitness (Vandenkoornhuyse et al, 2015) and carries implications for the evolution of bet-hedging strategies in variable environments. Demographic buffering may be considered a bet-hedging strategy if reduced temporal variance comes at the cost of arithmetic mean fitness (Childs et al, 2010). This may be unlikely in this system, where most host species exhibited both reduced variance and elevated mean fitness through symbiosis (Fig. 3C). However, the context-dependent fitness effects that underlie demographic buffering may favor other forms of evolutionary bet-hedging. Theory suggests that imperfect transmission (the production of S- offspring from S+ parent) may be an adaptive host strategy in spatially or temporally varying environments when fitness effects of symbionts are environment-dependent by extending phenotypic variance of offspring and improving the odds of some having the optimal symbiont status for their environment (Brown and Akçay, 2019; Bruijning et al, 2022; Lange et al, 2023). Imperfect vertical transmission is well-documented in grass-endophyte symbioses (Afkhami and Rudgers, 2008), including our focal taxa (Table S2), and could be incorporated into our model by dynamically linking S+ and S- populations (Yule et al, 2013; Chung et al, 2015). A further step could incorporate diverse symbiont partners (e.g. different strains of *Epichloë* fungi or multiple species within the microbiome) to understand how microbial diversity contributes to host genotypic and phenotypic variance (Henry et al, 2021).

Several limiting features of our study point to new directions and valuable next steps. We focused explicitly on temporal variation and intentionally averaged over spatial heterogeneity. Endophytes may dampen spatial heterogeneity in host fitness in ways that parallel their effects on temporal variance, and this hypothesis could be explored by leveraging the plot replication in our experiment. At larger spatial scales, buffering effects of symbionts may vary across the broad geographic distributions

of these eastern North American grass species, especially since historical and projected trends in climate variability are geographically heterogeneous (Bathiany et al, 2018). Finally, our demographic modeling framework could be further “unpacked” to explore other elements of fitness in stochastic environments. We identified damping variance in survival and growth as the key avenue by which symbionts’ variance effects contributed to host fitness (Fig. S82). Elasticity analyses could explore the selection that drives diverse symbiont effects across host vital rates. Small changes in variance of vital rates that are highly important to population growth (i.e. those with high elasticities) may be more strongly selected for than larger changes in less important vital rates (Doak et al, 2005), and symbionts may even provide an adaptive advantage by increasing temporal variance in certain vital rates (i.e. demographic lability) (Koops et al, 2009). Further, our simulations assumed an independently distributed environmental distribution through time, but environmental auto-correlation can be an important component of stochastic population projections (Tuljapurkar and Haridas, 2006) and might modify the fitness consequences of symbiont-mediated variance buffering. Similarly, correlated responses of multiple vital rates could amplify or dampen demographic variance (Tuljapurkar, 2013; Davison et al, 2013; Compagnoni et al, 2016). Our “matrix sampling” approach accounted for vital rate correlations implicitly (Metcalf et al, 2015) but exploring whether and how endophyte symbiosis alters the correlation structure of host vital rates could add nuance to understanding of symbionts’ contributions to variance buffering.

**Conclusion**

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

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604 **Supplementary information** Supplementary information for this paper includes  
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606

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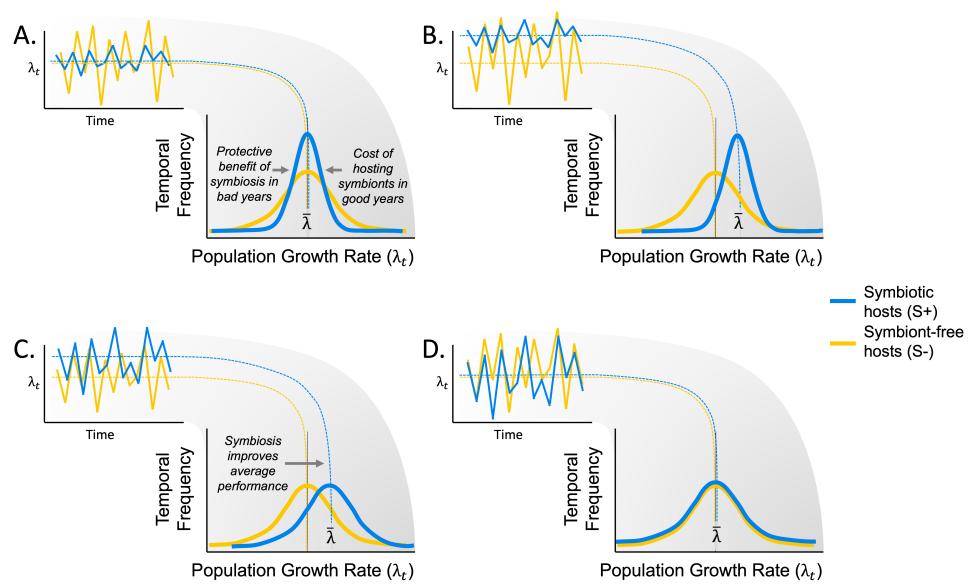
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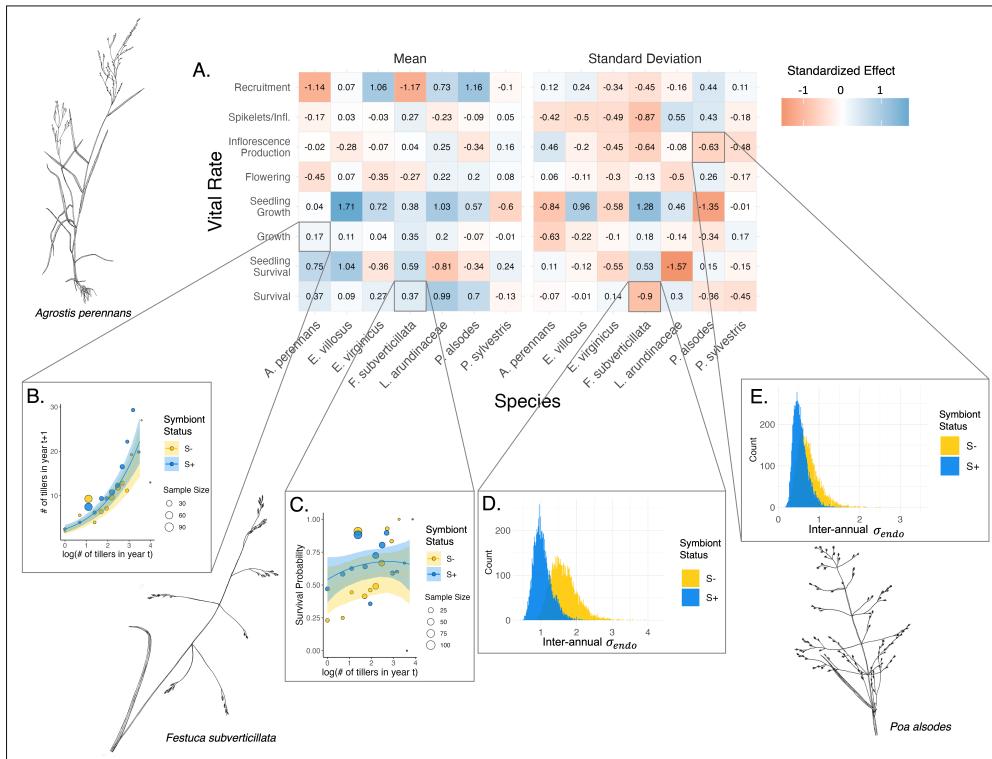
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875 **Figures**

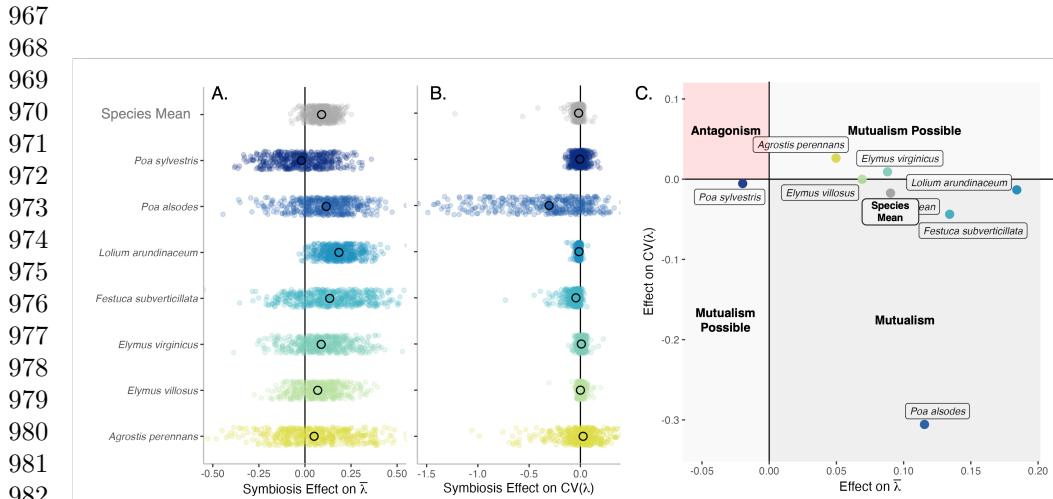


897 **Fig. 1:** Hypothesized effects of symbiosis on the mean and variance of annual popula-  
 898 tion growth rates. (A) Context-dependent symbiosis may provide benefits to hosts  
 899 during harsh years while being neutral or costly during benign years. Temporal vari-  
 900 ance in populations growth rates of symbiotic host populations (S+; blue lines) is  
 901 expected to decrease relative to symbiont-free hosts (S-; yellow lines). (B) Symbiosis  
 902 may improve average performance across years in addition to reducing temporal vari-  
 903 ance. (C) Consistent benefits of symbiosis could improve average performance across  
 904 years with no influence on temporal variance. (D) Symbiosis may have an effectively  
 905 neutral effect on population growth rates.

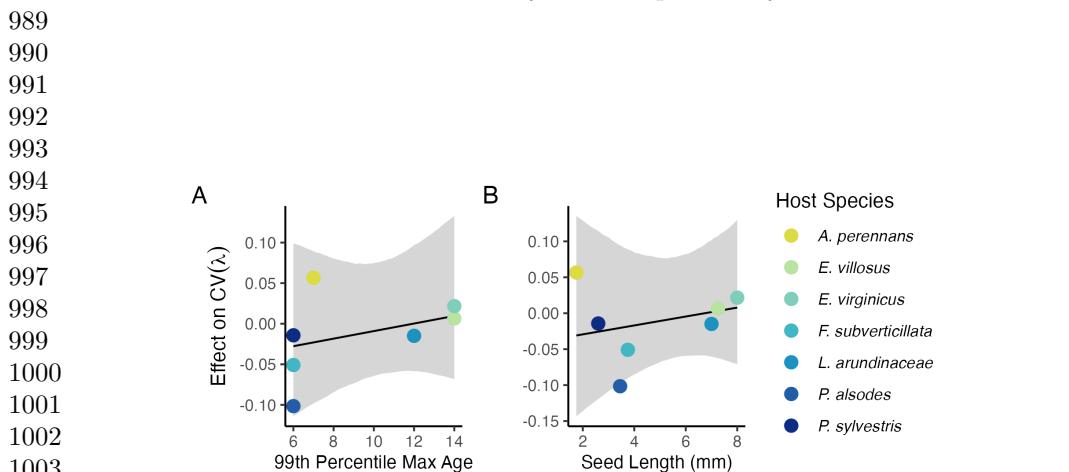
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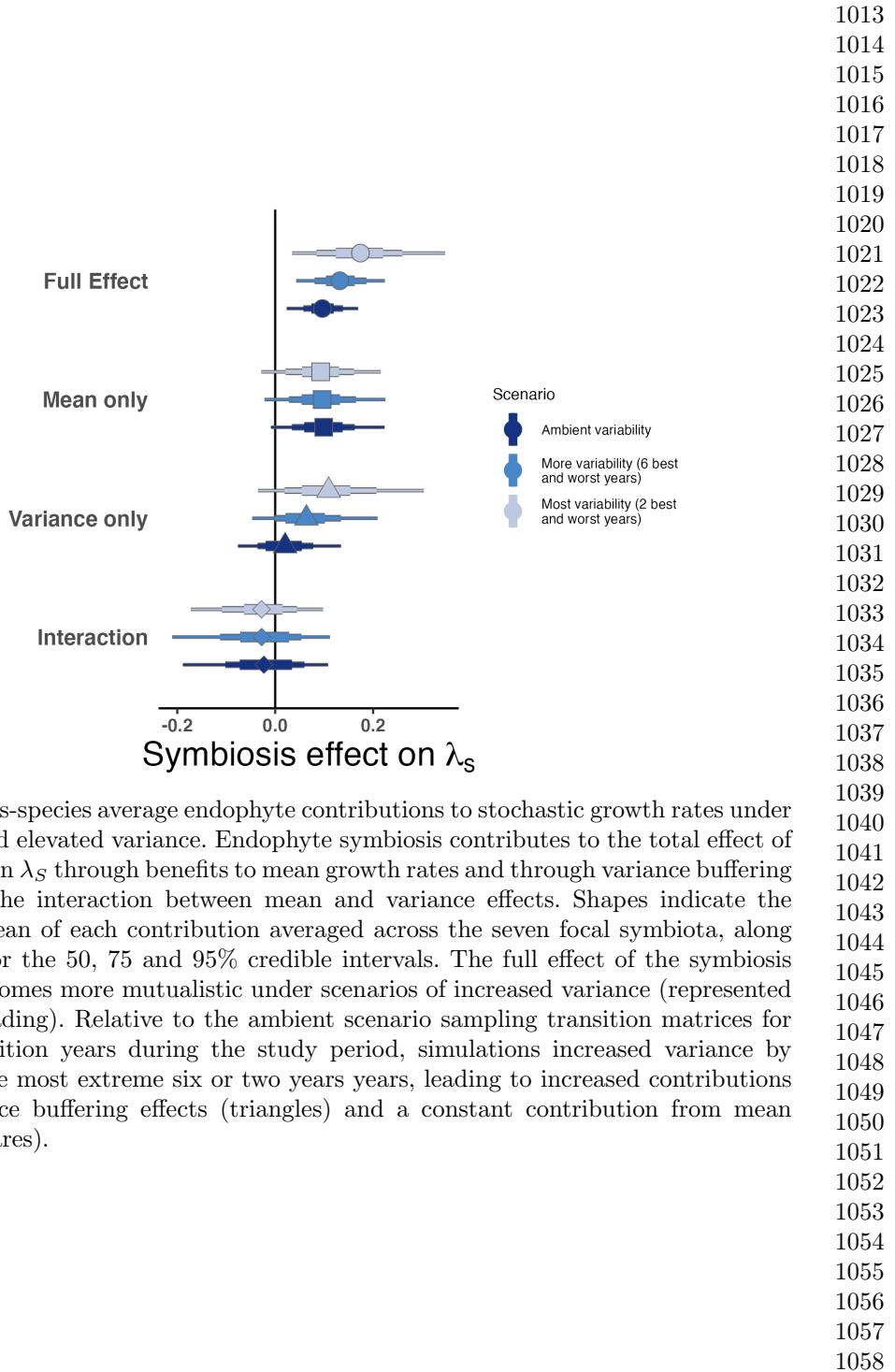
**Fig. 2:** Endophyte symbiosis altered host vital rates.(A) Shading represents the posterior mean standardized effect size (Cohen's D) of endophyte symbiosis on mean or standard deviation of host vital rates (blue indicates that symbiosis increased the mean or standard deviation and red indicates a 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, expected mean vital rates that average across years and plots are shown with 80% credible intervals along with points representing data binned by size for symbiotic (S+) and symbiont-free (S-) plants. Panels D-E show estimated posterior distributions of endophyte-status specific inter-annual standard deviation ( $\sigma_{\tau_{e,h}}^2$ ) 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.



983 **Fig. 3:** Mean and variance-buffering effects on fitness. Black circles indicate the  
984 posterior median effect of endophytes along with 500 posterior draws (smaller colored  
985 circles) on the (A) mean and (B) coefficient of variation in  $\lambda_t$  for each host  
986 species as well as a cross species mean. (C) For all hosts, endophytes either reduce  
987 variance, increase the mean, or both, and consequently when considering stochastic  
988 environments, the interactions are always at least potentially mutualistic.



1004 **Fig. 4:** Host species with faster life history traits experience stronger effects of  
1005 symbiont-mediated variance buffering. Regressions between life history traits describ-  
1006 ing the fast-slow life history continuum ((A) 99th percentile maximum age observed  
1007 during long term censuses in years; (B) Seed size) and the effect of endophyte sym-  
1008 biosis on the coefficient of variation in annual population growth rate ( $\lambda_t$ ). Each panel  
1009 shows the fitted mean relationship (line) along with the 95% credible interval.  
1010  
1011  
1012



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

1059 **Supporting Information**  
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1062 **Table of Contents**  
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1243 **Supplemental Methods**

1244

1245 **Endophyte removal, plant propagation, and field set-up**

1246 Seeds from naturally symbiotic populations of the seven focal host species were col-  
1247 lected during summer-fall 2006 from Lilly-Dickey Woods and the nearby Bayles Road  
1248 Teaching and Research Preserve (39.220167, -86.542683). To generate symbiotic (S+)  
1249 and symbiont-free (S-) plants from the same genetic lineages, seeds from each species  
1250 were disinfected with a heat treatment described in Table S1 or left untreated. The  
1251 heat treatment created symbiont-free plants by warming seeds to temperatures at  
1252 which the fungus becomes inviable but the host seeds can still germinate.

1253 Both heat-treated and untreated seeds were surface sterilized with bleach to remove  
1254 epiphyllous microbes, cold stratified for up to 4 weeks, then germinated in a growth  
1255 chamber before transfer to the greenhouse at Indiana University where they grew for  
1256 ~ 8 weeks. We confirmed endophyte status by staining thin sections of inner leaf  
1257 sheath with aniline blue and examining tissue for fungal hyphae at 200X magnification  
1258 ([Bacon and White, 2018](#)). We established experimental populations with vegetatively  
1259 propagated clones of similar sizes (ranging from one to six tillers).

1260 During the fall of 2007 and spring of 2008, we established 10 3x3 m plots for *A.*  
1261 *perennans*, *E. villosus*, *E. virginicus*, *F. subverticillata*, and *L. arundinaceum* and 18  
1262 plots for *P. alsodes* and *P. sylvestris*. Half of the plots were randomly assigned to be  
1263 planted with either symbiotic (S+) or symbiont-free (S-) plants, and initiated with  
1264 20 evenly spaced individuals labeled with aluminum tags. In spring 2008, we placed  
1265 plastic deer net fencing around each plot to limit deer herbivory and disturbance;  
1266 damaged fences were regularly replaced.

1267 We expected plots to maintain their endophyte status (S+ or S-) because these  
1268 fungal symbionts are almost exclusively vertically transmitted, and plots were spaced  
1269 a minimum of 5 m apart, limiting seed dispersal or horizontal transmission of the  
1270 symbiont between plots. We regularly confirmed endophyte treatment throughout the  
1271 lifetime of the experiment by opportunistically taking subsets of seeds from reproduc-  
1272 tive individuals and scoring them for their endophyte status with microscopy as above.  
1273 Overall, these scores reflected 98% faithfulness of recruits to their expected endophyte  
1274 status across species and plots (Fig. S87; Supplement data). Additionally, we have  
1275 rarely observed fungal stromata, the fruiting bodies by which *Epichloë* are poten-  
1276 tially transmitted horizontally, provided the fly vector is also present ([Bultman et al,](#)  
1277 [1995](#)). For *A. perennans*, *F. subverticillata*, *L. arundinaceum*, and *P. alsodes*, we never  
1278 observed stromata. We observed stromata only infrequently for *E. villosus*, and even  
1279 more rarely for *E. virginicus* and *P. sylvestris* (Table S2). For these species, stromata  
1280 have only been observed irregularly across years on 35, 4, and 6 plants respectively,  
1281 making up < 0.3% of all censused plants.

1282

1283 **Detailed vital rate modeling**

1284

1285 We fit vital rates models in a Bayesian hierarchical framework. Statistical models for  
1286 adult survival, seedling survival, adult growth, seedling growth, flowering (yes or no),  
1287 fertility of flowering plants (number of flowering tillers), production of seed-bearing  
1288

spikelets (number per inflorescence), the average number of seeds per spikelet, and the recruitment of seedlings from the preceding year's seed production, were constructed as follows:

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

$$S_{i,p,e,h,t} \sim Bernoulli(\hat{S}_{i,p,e,h,t}) \quad (S4a)$$

$$\text{logit}(\hat{S}_{i,p,e,h,t}) = \beta_{0_{h,o}} + \beta_{1_h} * \text{endo}_e \quad (S4b)$$

$$+ \beta_{2_{h,o}} * \text{size}_{i,t-1} + \beta_{3_{h,o}} * \text{size}_{i,t-1}^2 + \tau_{e,h,t} + \rho_p \quad (S4c)$$

$$\tau_{e,h,t} \sim \text{Normal}(0, \sigma_{\tau_{e,h}}^2) \quad (S4d)$$

$$\rho_p \sim \text{Normal}(0, \sigma_\rho^2) \quad (S4e)$$

Here,  $\hat{S}$  is the survival probability,  $\beta_{0_{h,o}}$  is an intercept specific to each host species and recruitment origin,  $\beta_{1_h}$  is the endophyte effect,  $\beta_{2_{h,o}}$  is the effect of plant size specific to each species and recruitment origin,  $\beta_{3_{h,o}}$  is a quadratic plant size effect specific to each species and recruitment origin,  $\tau_{e,h,t}$  is a normally distributed year effect for each species and endophyte status with variance  $\sigma_{\tau_{e,h}}^2$ , and  $\rho_p$  is a normally distributed plot effect with variance  $\sigma_\rho^2$  ( $p(e)$  indicates that plot identity is uniquely associated with an endophyte status). We assume that the plot-to-plot variance  $\sigma_\rho^2$  was shared across host species, allowing us to "borrow strength" across the multi-species dataset; other model parameters are unique to host species. We separately modeled the survival of newly recruited seedlings with a similar model but omitting previous size dependence and origin status.

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

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

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

1335     *Spikelets per Inflorescence* - Spikelet production ( $K$ ) was recorded as integer counts  
1336 on up to three inflorescences per reproducing plant. We modeled these data with a neg-  
1337 ative binomial distribution, with the same linear predictor for the mean as described  
1338 above.

1339     *Seed Production per Spikelet* - For individuals with recorded counts of seed pro-  
1340 duction, we calculated the number of seeds per spikelet from our counts of seeds and  
1341 spikelets per inflorescence, and then modeled seeds per spikelet ( $D$ ) as means of a  
1342 Gaussian distribution for each species and endophyte status. Because we had less  
1343 detailed data across years and plants for seed production than for other reproductive  
1344 vital rates, we omitted both plot and year random effects.

1345     *Seedling Recruitment* - We used a binomial distribution to model the recruitment of  
1346 new seedlings ( $R$ ) into the plots from seeds produced in the preceding year, assuming  
1347 no long-lived seed bank. We included an intercept specific to each host and endophyte  
1348 status and the same random effects structure as in other models. We estimated the  
1349 number of seeds per plot in the preceding year by multiplying the total number of  
1350 reproductive tillers per plant by the mean number of spikelets per inflorescence and  
1351 mean number of seeds per spikelet ( $D$ ). For plants with missing fertility or spikelet  
1352 data, we used the expected number of reproductive tillers ( $F$ ) or of spikelets per  
1353 inflorescence from ( $K$ ), drawing from the full posteriors of our models. We rounded  
1354 this value to get the estimated seed production for each individual, and finally summed  
1355 across all reproductive plants in each year and plot to get the total number of seeds  
1356 produced.

### 1357     **Model assessment**

1358 All parameters were given vague priors (Gabry et al, 2019). We ran each vital rate  
1359 model for 2500 warm-up and 2500 MCMC sampling iterations with three chains. We  
1360 assessed model convergence with trace plots of posterior chains and checked for  $\hat{R}$   
1361 values less than 1.01, indicating low within- and between-chain variation (Brooks and  
1362 Gelman, 1998; Gelman and Hill, 2006). For those models that showed poor conver-  
1363 gence, we extended the MCMC sampling to include 5000 warm-up and 5000 sampling  
1364 iterations, which was only necessary for seedling growth. We visualized the interactions  
1365 between plant size, origin status, and endophyte status for both the interannual mean  
1366 expected value for each vital rate (averaging over year and plot variance) (Fig. S2 -  
1367 S11) and for the expected vital rate values specific to each year (averaging over plot  
1368 variance) (Fig. S12 -S21). We graphically checked vital rate model fit with posterior  
1369 predictive checks comparing simulated and observed data (Fig. S30-S68). Initial anal-  
1370 yses including only linear effects of size produced estimates of endophytes' effects on  
1371 vital rate means and inter-annual variances that were similar to those from the more  
1372 flexible quadratic models, but provided worse fit to size-structure in the data in some  
1373 cases. We therefore proceeded with the more flexible quadratic models. Results from  
1374 subsequent matrix model analyses were qualitatively similar regardless of this choice.  
1375

### 1376     **Estimating climate drivers of environmental**

#### 1377     **context-dependence**

1378

1379 To connect the variance buffering effects of endophytes with inter-annual variability  
1380 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. 1381  
Identifying the potentially complex relationships between vital rates and environmental 1382  
drivers remains a key challenge for accurate forecasts of the ecological impacts of 1383  
environmental stochasticity (Ehrlén and Morris, 2015). We first downloaded temperature 1384  
and precipitation data from a weather station in Bloomington, IN, approx. 27 1385  
km from our study site, using the rnoaa package (Chamberlain et al, 2022). Compared 1386  
to other weather stations in the area, the measurements from Bloomington contain 1387  
the most complete climate record across the study period and are correlated with 1388  
more local measurements from Nashville, IN for years in which local data are available 1389  
(total daily precipitation:  $R^2 = .76$ ; mean daily temperature:  $R^2 = .94$ ). The 1390  
mean annual temperature across the study period was  $11.9\text{ }C^\circ$  (SD:  $1.05\text{ }C^\circ$ ) and the 1391  
average annual precipitation was 1237.9 mm/year (SD: 204.89 mm/year) (Fig. S88). 1392  
Given the known role of endophytes in promoting host drought tolerance, we calculated 1393  
the Standardised Precipitation-Evapotranspiration Index (SPEI) for 3 and 12 1394  
months preceding each annual censuses, reflecting drought during the growing season 1395  
and across the year (Vicente-Serrano et al, 2010). To calculate SPEI, we used the 1396  
Thornthwaite equation to model potential evapotranspiration as implemented in the 1397  
SPEI R package (Beguería and Vicente-Serrano, 2013) 1398

We repeated the process of fitting statistical models for each vital rate as described 1399  
above with the inclusion of a parameter describing the influence of SPEI. We fit 1400  
separate vital rate models incorporating either the growing season or annual drought 1401  
index for each vital rate, except for the model describing the mean number of seeds 1402  
per inflorescence. This model was fit without climate effects because the data came 1403  
from only a few years. Initial analyses indicated similar fits for models including only a 1404  
linear term and those with both linear and quadratic terms describing the relationship 1405  
between the climate driver and the vital rate response, and so we proceeded with 1406  
models including only the linear term. We expected that including climate predictors 1407  
into the models would explain some inter-annual variance in vital rates, shrinking the 1408  
variance associated with the fitted year random effects. We assessed model fit with 1409  
graphic posterior predictive checks and convergence diagnostics as described for the 1410  
climate-implicit analysis. Finally, we next built matrix projection models incorporating 1411  
the climate-dependent vital rate functions to assess the response of symbiotic (S+) vs 1412  
symbiont-free (S-) populations to drought. The model is as described in **Materials** 1413  
and **Methods** with the inclusion of parameters describing the slope of the relationship 1414  
with SPEI. We compared the sensitivity of  $\lambda$  to either annual or seasonal SPEI of S+ 1415  
populations ( $\frac{\Delta\lambda^+}{\Delta\text{SPEI}}$ ) with those of S- populations ( $\frac{\Delta\lambda^-}{\Delta\text{SPEI}}$ ) (Fig. S89; Table S). 1416

Most species were slightly more responsive to growing season rather than annual 1417  
drought conditions, and for most species symbiotic populations were less sensitive to 1418  
SPEI than symbiont-free populations (Fig. S89; Table S3). However, these drought 1419  
indices did not explain the full extent of inter-annual variability in demographic vital 1420  
rates. For example, flowering in *A. perennans* had one of the strongest climate signals 1421  
(82% probability of a positive relationship with SPEI), yet the estimated inter-annual 1422  
variance  $\sigma_{\tau_{e,h}}^2$  for symbiont-free plants shrank from 6.7 to 6.1 after including 3-month 1423  
SPEI as a covariate, suggesting that other factors contribute to inter-annual variability. 1424

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1427 **Detailed statistical analysis of life history traits**

1428 We fit Bayesian phylogenetic mixed-effects models using the brms package (Bürkner,  
 1429 2017) to test the relationship between each life history trait and the effect of symbiosis  
 1430 on the CV of  $\lambda_t$  (a measure of variance buffering) while controlling for phylogenetic  
 1431 non-independence. We pruned species-level phylogenies of plants (Zanne et al, 2014)  
 1432 and *Epichloë* fungi (Leuchtmann et al, 2014) to include the focal species. *Agrostis*  
 1433 *perennans* was not included in the published tree, and so we used the congener *A.*  
 1434 *hyemalis*. We defined separate phylogenetic covariance matrices for the pruned tree  
 1435 for host and symbiont species.

1436 We propagated uncertainty in the estimated variance buffering effect  $V$  with a  
 1437 measurement error model:

1439

$$1440 \quad V_{MEAN,h} \sim Normal(V_{EST,h}, V_{SD,h}) \quad (S5a)$$

$$1442 \quad V_{EST,h} \sim Normal(\mu_h, \sigma) \quad (S5b)$$

$$1443 \quad \mu = \alpha + \beta * trait + \pi_j \quad (S5c)$$

$$1444 \quad \alpha \sim Normal(0, .1) \quad (S5d)$$

$$1445 \quad \beta \sim Normal(0, .1) \quad (S5e)$$

$$1447 \quad \sigma \sim Half-Normal(.05, .01) \quad (S5f)$$

$$1448 \quad \pi_h \sim MVN(0, \sigma_\pi \mathbf{A}) \quad (S5g)$$

$$1449 \quad \sigma_\pi \sim Half-Normal(0, .1) \quad (S5h)$$

1450

1451 Here,  $V_{EST}$  is the variance buffering effect for host species  $h$ , estimated from the  
 1452 posterior mean ( $V_{MEAN}$ ) and standard deviation ( $V_{SD}$ ), propagating uncertainty asso-  
 1453 ciated with the effect of symbiosis. The model includes an intercept ( $\alpha$ ) and slope ( $\beta$ )  
 1454 defining the relationship between variance buffering effect and the life history trait.  
 1455 The residual standard deviation is given by ( $\sigma$ ). We used weakly informative priors  
 1456 to aid model convergence. Each prior was centered at zero, except for the residual  
 1457 standard deviation, which we centered at the standard deviation of the estimated  
 1458 variance buffering effect, .05. The phylogenetic random effect ( $\pi$ ), modeled as a multi-  
 1459 variate normal distribution, has a between-species standard deviation ( $\sigma_\pi$ ) structured  
 1460 by the phylogenetic covariance matrix  $\mathbf{A}$ . We ran each MCMC sampling chain for  
 1461 8000 warmup iterations and 2000 sampling iterations. We assessed model convergence  
 1462 as described above for the vital rate models.

1463

1464 **Vital rate mean-variance decomposition**

1465

1466 We performed a mean-variance decomposition to quantify the extent that mean and  
 1467 variance effects on stochastic population growth rates arise through different vital  
 1468 rates. Specifically, we repeated the calculation of  $\lambda_S$  as described in the main text  
 1469 for symbiotic populations as well as symbiont-free populations, as well as for four  
 1470 additional “treatments”. These treatments differentiate between mortality and growth  
 1471 related vital rates (adult survival, adult growth, seedling survival, and seedling growth)  
 1472 and reproductive vital rates (probability of flowering, inflorescence production, spikelet

production, seed production, and recruitment). Each treatment set vital rate mean  
 and interannual variances according to the symbiont-free parameter values across vital  
 rates while introducing (1) endophyte effects on the vital rate means for survival and  
 growth vital rates only, (2) endophyte effects on the vital rate variances for survival and  
 growth vital rates only, (3) endophyte effects on the vital rate means for reproductive  
 vital rates only, and (4) endophyte effects on the vital rate variances for reproductive  
 vital rates only. 1473  
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1519 **Supplemental Figures S1-S89**

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1523 *Census t*

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1525  $n_t^x$

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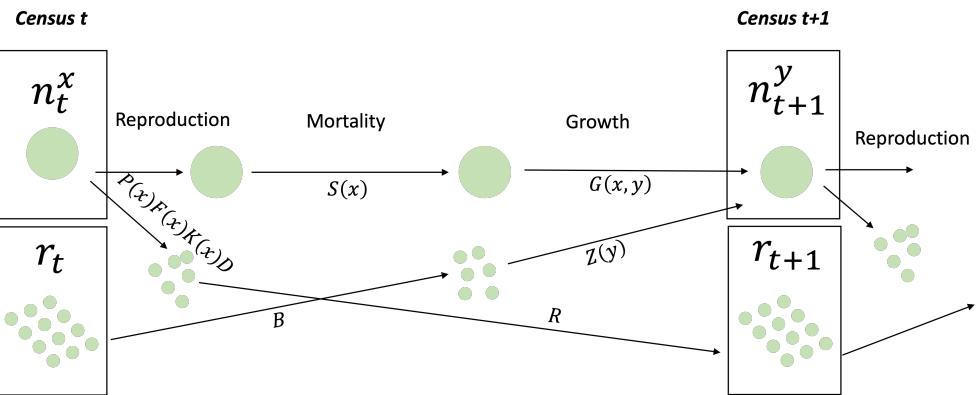
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1535 Figure S1: Life cycle diagram depicting the generalized structure of matrix population  
 1536 model. The population consists of different life stages at each census  $t$  or census  $t+1$ .  
 1537 Individuals transition from size  $x$  to size  $y$ .  $n$  is a vector of discrete sizes representing  
 1538 number of tillers, according to their likelihood of survival ( $S$ ) and growth ( $G$ ). Repro-  
 1539 duction generates new recruits (small circles) through four steps, the probability of  
 1540 flowering ( $P$ ), the number of flowering tillers produced ( $F$ ), the number of spikelets  
 1541 per inflorescence produced ( $K$ ), and the number of seeds per spikelet ( $D$ ). The proba-  
 1542 bility of successful recruitment ( $R$ ) determines the success of these offspring, and any  
 1543 new recruits ( $r$ ) are incorporated into the census. These non-reproductive, typically  
 1544 one-tiller recruits transition into the population of mature individuals with survival  
 1545 ( $B$ ) and growth ( $Z$ ) probability. Symbiotic and symbiont-free populations have the  
 1546 same model structure with species-specific and symbiont status-specific transition  
 1547 probabilities used to construct matrices.

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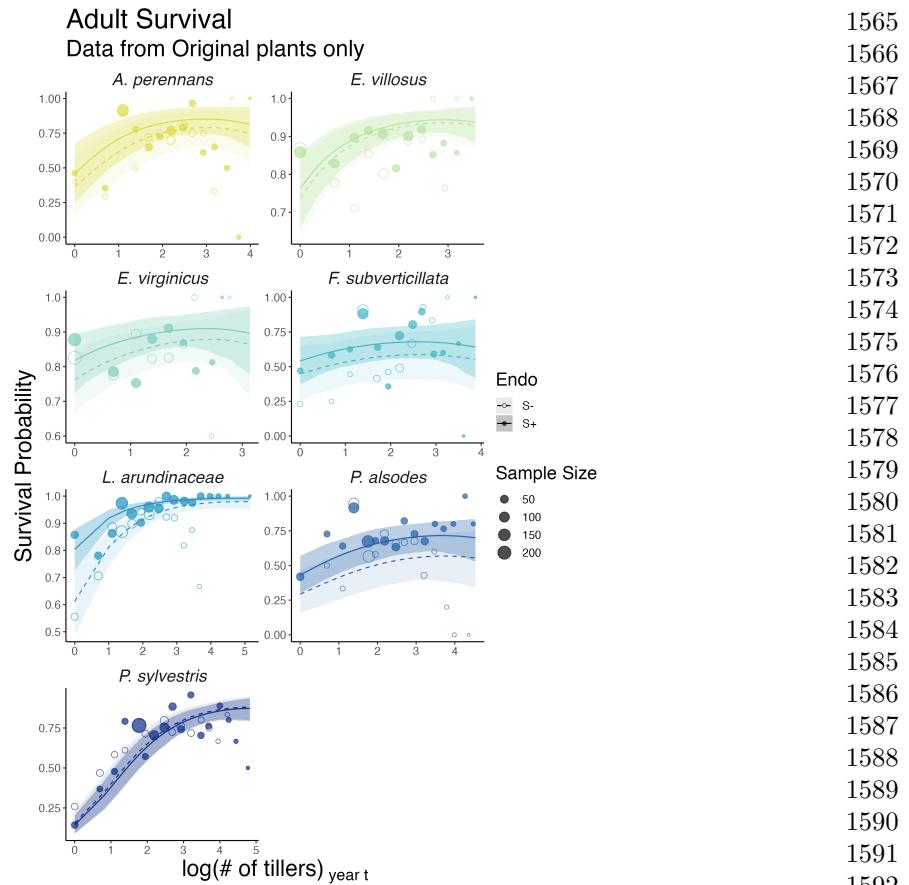
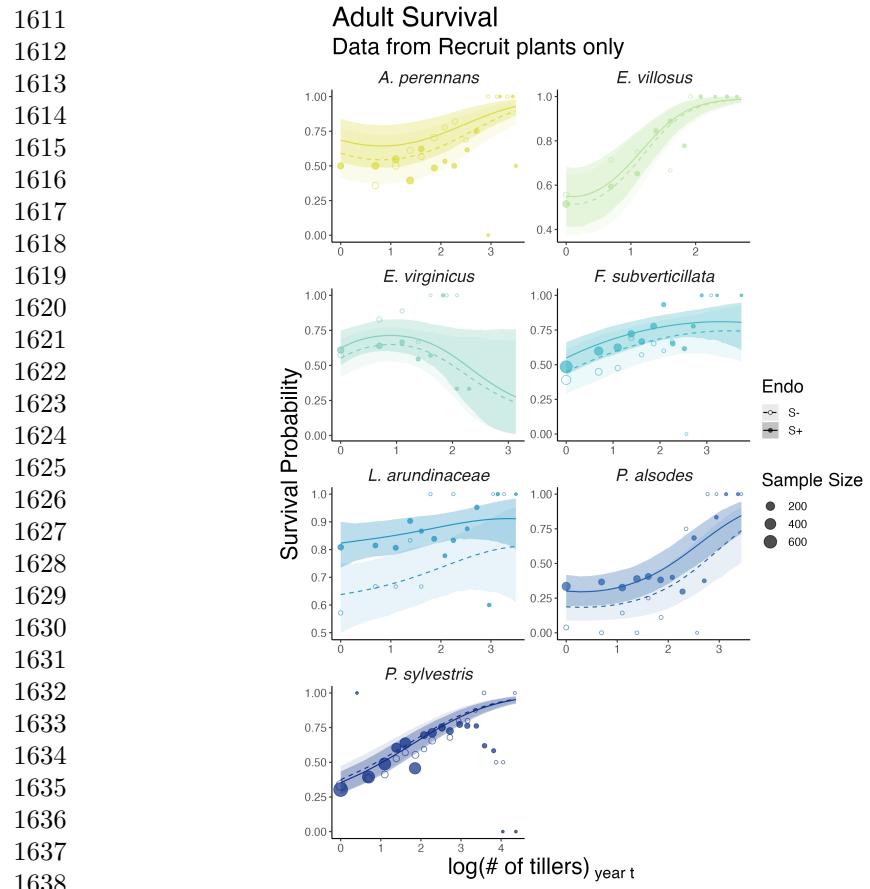


Figure S2: Effect of endophyte symbiosis on mean adult survival. Fitted curves represent the size-specific mean survival probability for originally transplanted plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles with a dashed line for symbiont-free (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-.



1639 Figure S3: Effect of endophyte symbiosis on mean adult survival. Fitted curves rep-  
1640 resent the size-specific mean survival probability for recruited plants along with data  
1641 binned by size and averaged over many individuals, years, and plots shown as open  
1642 circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled  
1643 circles represent symbiotic (S+) plants. 80% credible intervals are shown with dark  
1644 shading for S+, or light shading for S-.

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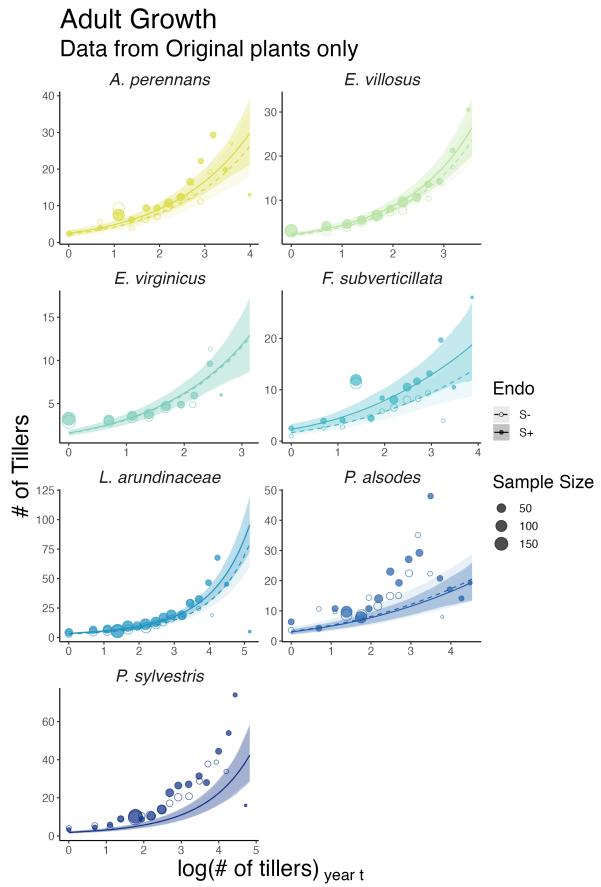
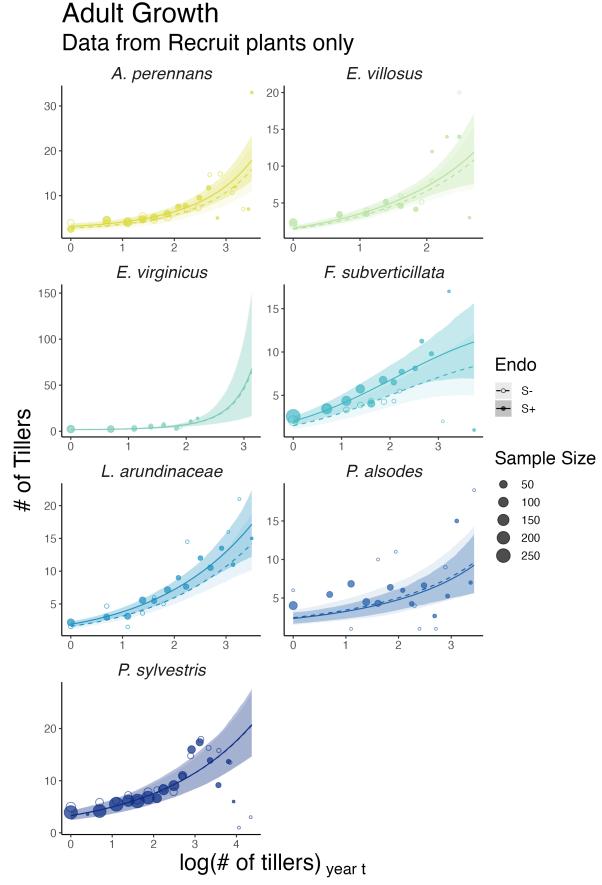


Figure S4: Effect of endophyte symbiosis on mean adult growth. Fitted curves represent the size-specific mean expected plant size for originally transplanted plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles with a dashed line for symbiont-free (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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1731 Figure S5: Effect of endophyte symbiosis on mean adult growth. Fitted curves represent  
1732 the size-specific mean expected plant size for recruited plants along with data binned  
1733 by size and averaged over many individuals, years, and plots shown as open circles  
1734 with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles  
1735 represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading  
1736 for S+, or light shading for S-.

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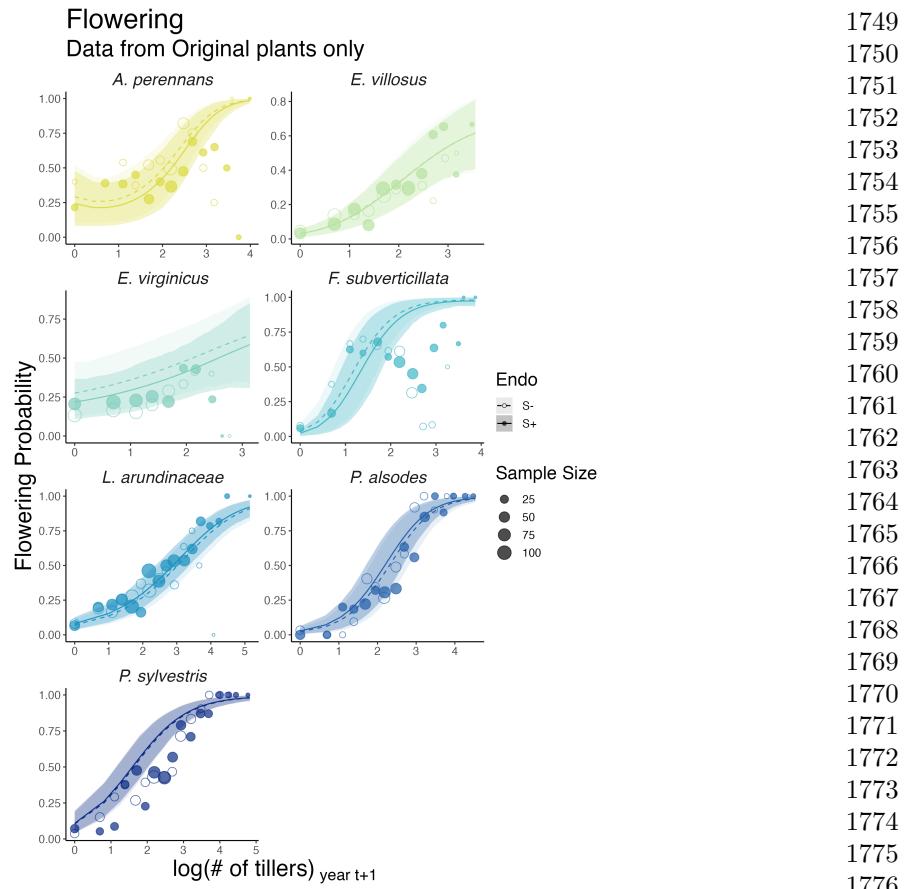
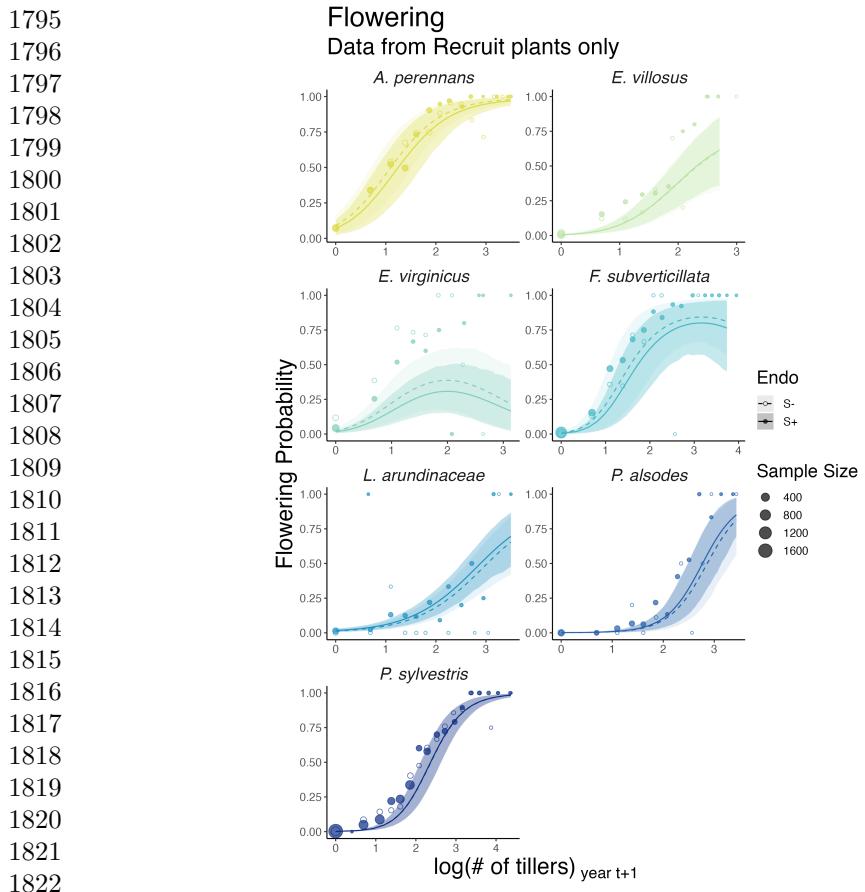


Figure S6: Effect of endophyte symbiosis on mean flowering. Fitted curves represent the size-specific mean flowering probability for originally transplanted plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles with a dashed line for symbiont-free (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-.



1823 Figure S7: Effect of endophyte symbiosis on mean flowering. Fitted curves represent  
 1824 the size-specific mean flowering probability for recruited plants along with data binned  
 1825 by size and averaged over many individuals, years, and plots shown as open circles  
 1826 with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles  
 1827 represent symbiotic (S+) plants. 80% credible intervals are shown with dark shading  
 1828 for S+, or light shading for S-.

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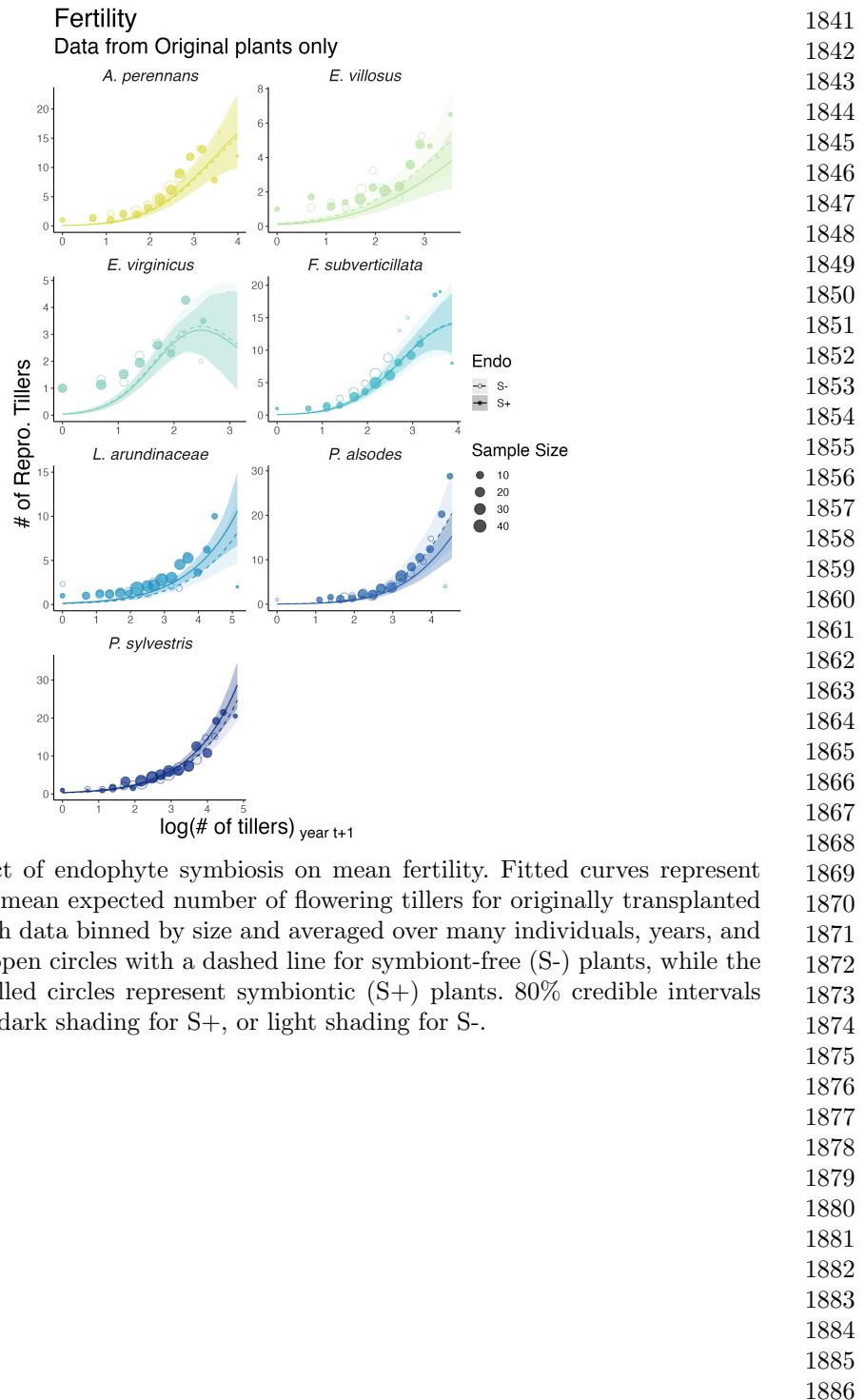


Figure S8: Effect of endophyte symbiosis on mean fertility. Fitted curves represent the size-specific mean expected number of flowering tillers for originally transplanted plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles with a dashed line 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-.

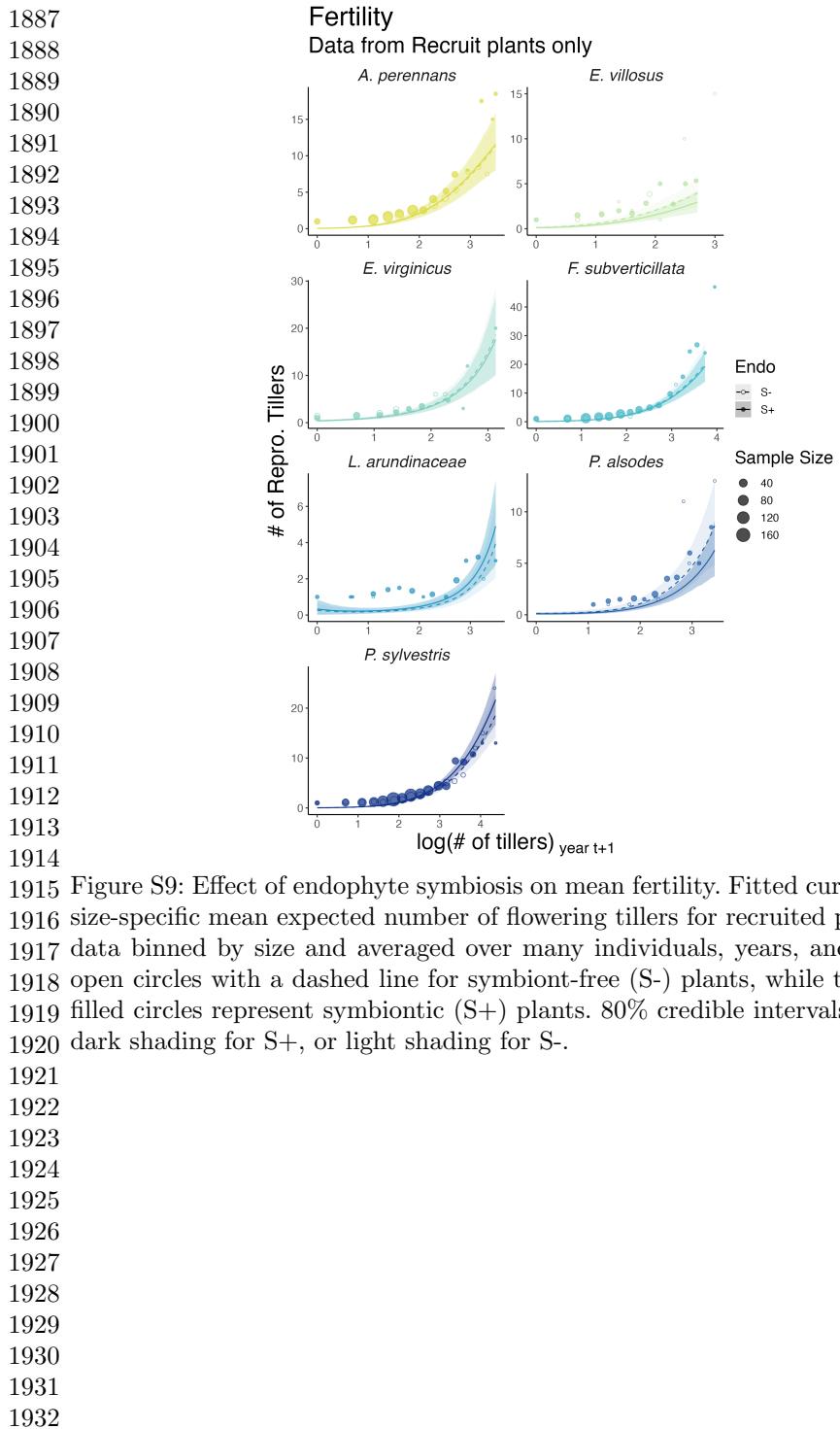


Figure S9: Effect of endophyte symbiosis on mean fertility. Fitted curves represent the size-specific mean expected number of flowering tillers for recruited plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles with a dashed line for symbiont-free (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-.

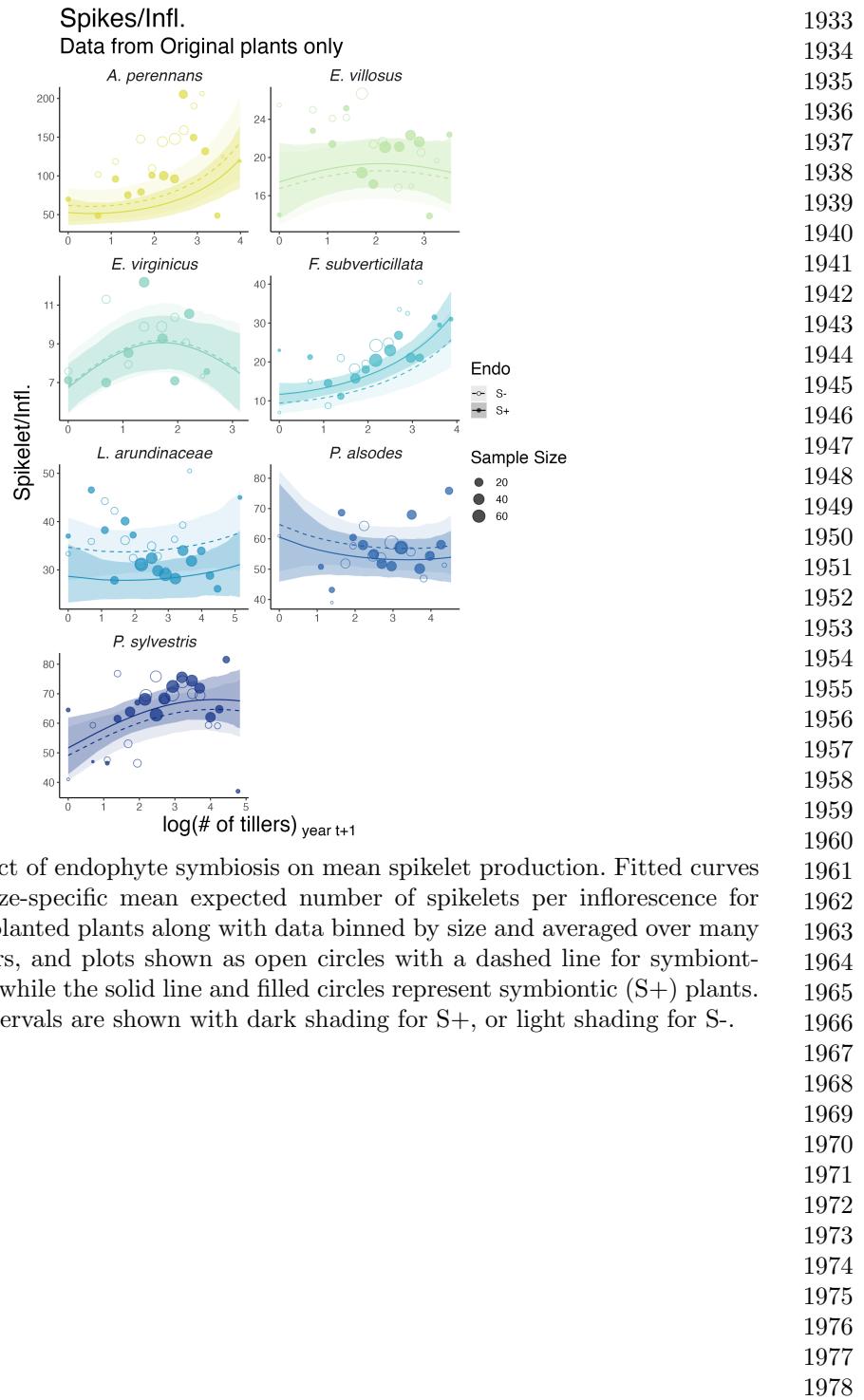
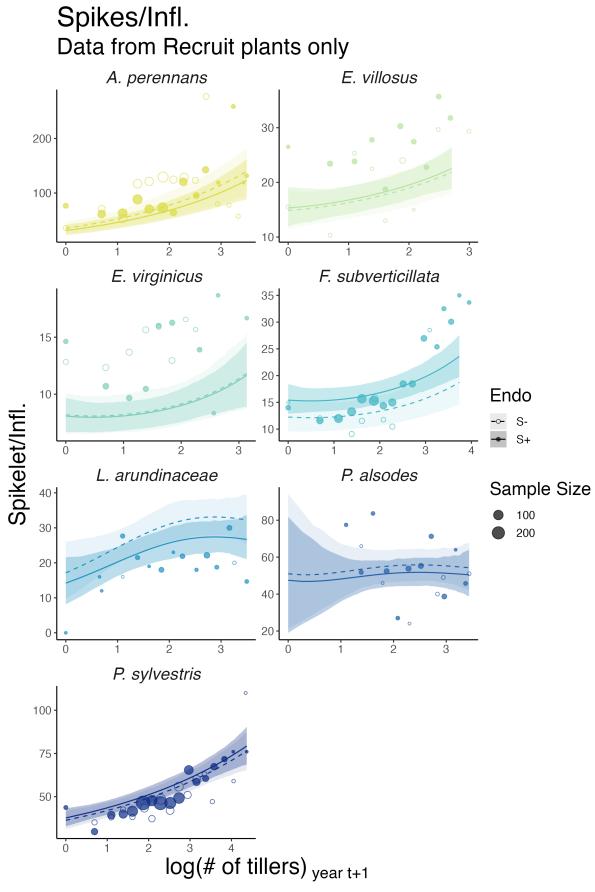


Figure S10: Effect of endophyte symbiosis on mean spikelet production. Fitted curves represent the size-specific mean expected number of spikelets per inflorescence for originally transplanted plants along with data binned by size and averaged over many individuals, years, and plots shown as open circles 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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2007 Figure S11: Effect of endophyte symbiosis on mean spikelet production. Fitted curves  
 2008 represent the size-specific mean expected number of spikelets per inflorescence for  
 2009 recruited plants along with data binned by size and averaged over many individuals,  
 2010 years, and plots shown as open circles with a dashed line for symbiont-free (S-) plants,  
 2011 while the solid line and filled circles represent symbiotic (S+) plants. 80% credible  
 2012 intervals are shown with dark shading for S+, or light shading for S-.

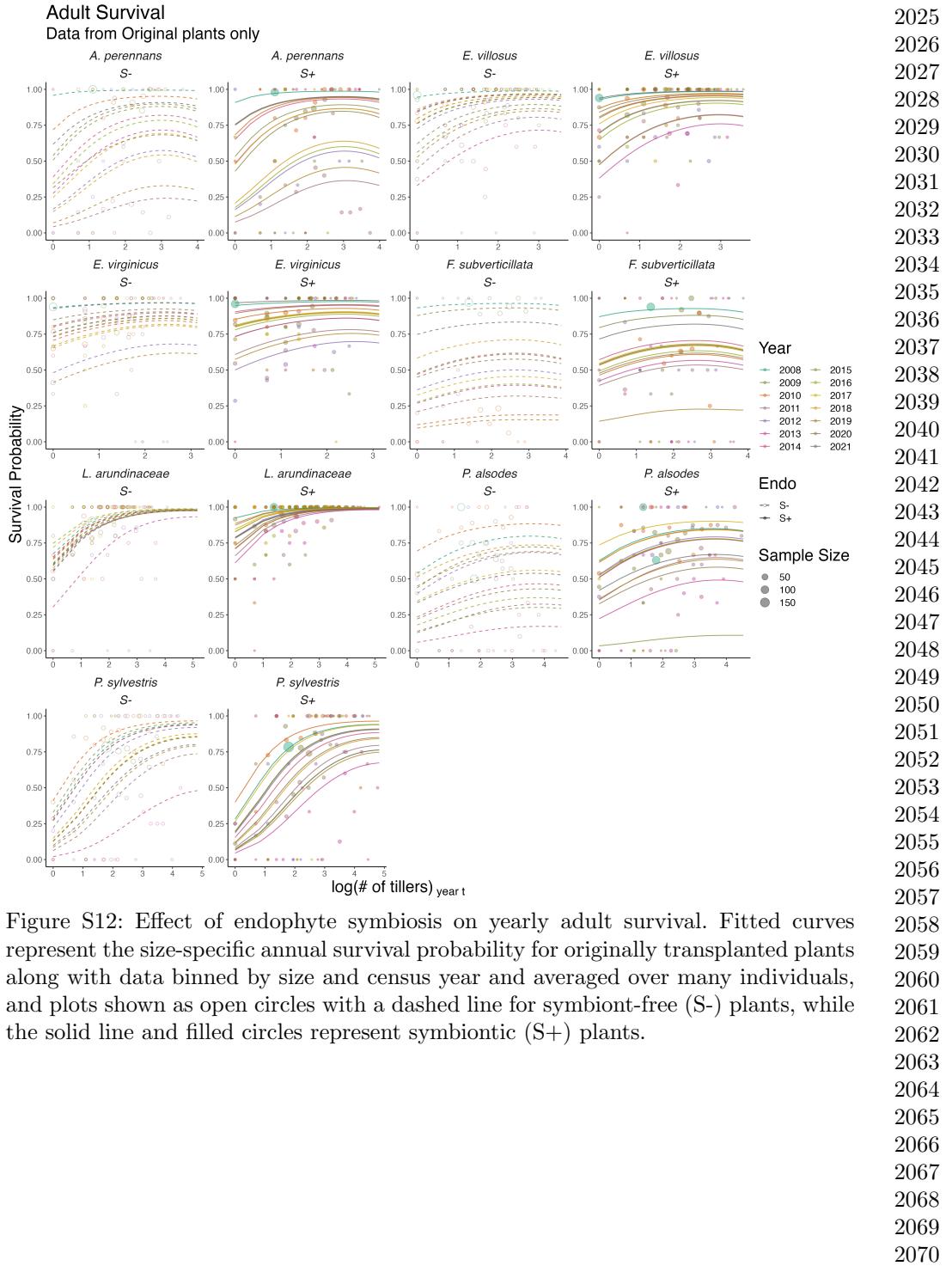
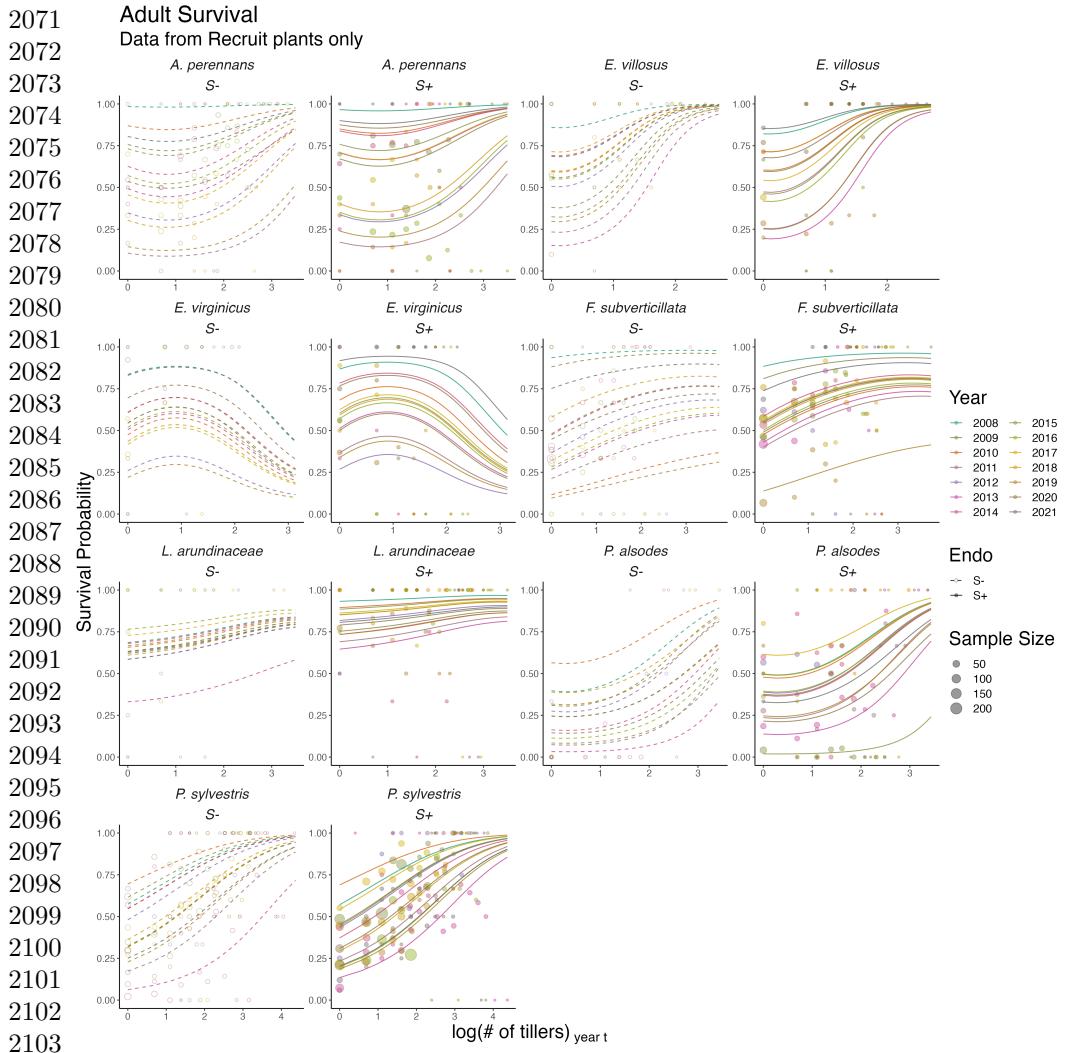


Figure S12: Effect of endophyte symbiosis on yearly adult survival. Fitted curves represent the size-specific annual survival probability for originally transplanted plants along with data binned by size and census year and averaged over many individuals, and plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



2104 Figure S13: Effect of endophyte symbiosis on yearly adult survival. Fitted curves  
2105 represent the size-specific annual survival probability for recruited plants along with  
2106 data binned by size and census year and averaged over many individuals, and plots  
2107 shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid  
2108 line and filled circles represent symbiotic (S+) plants.

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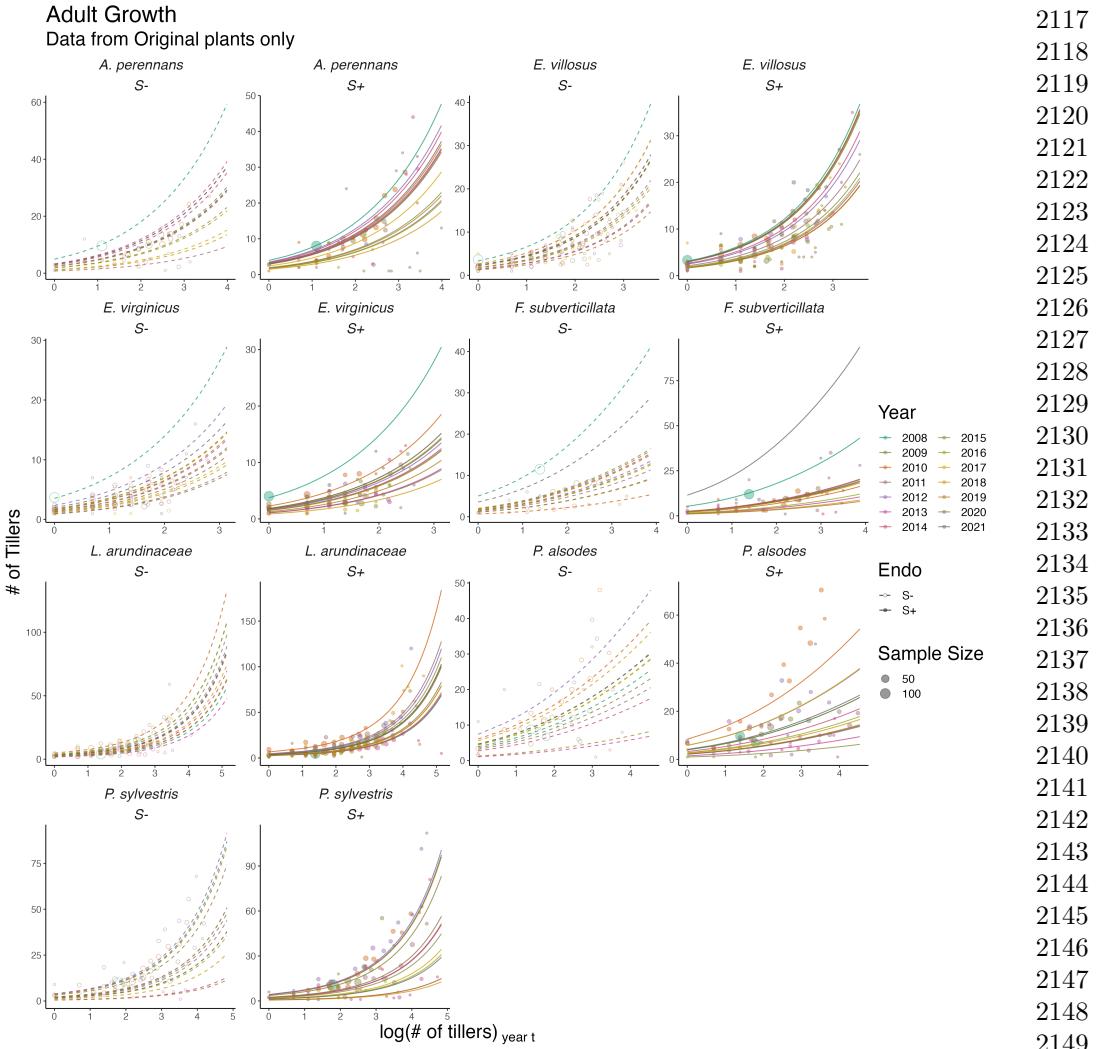
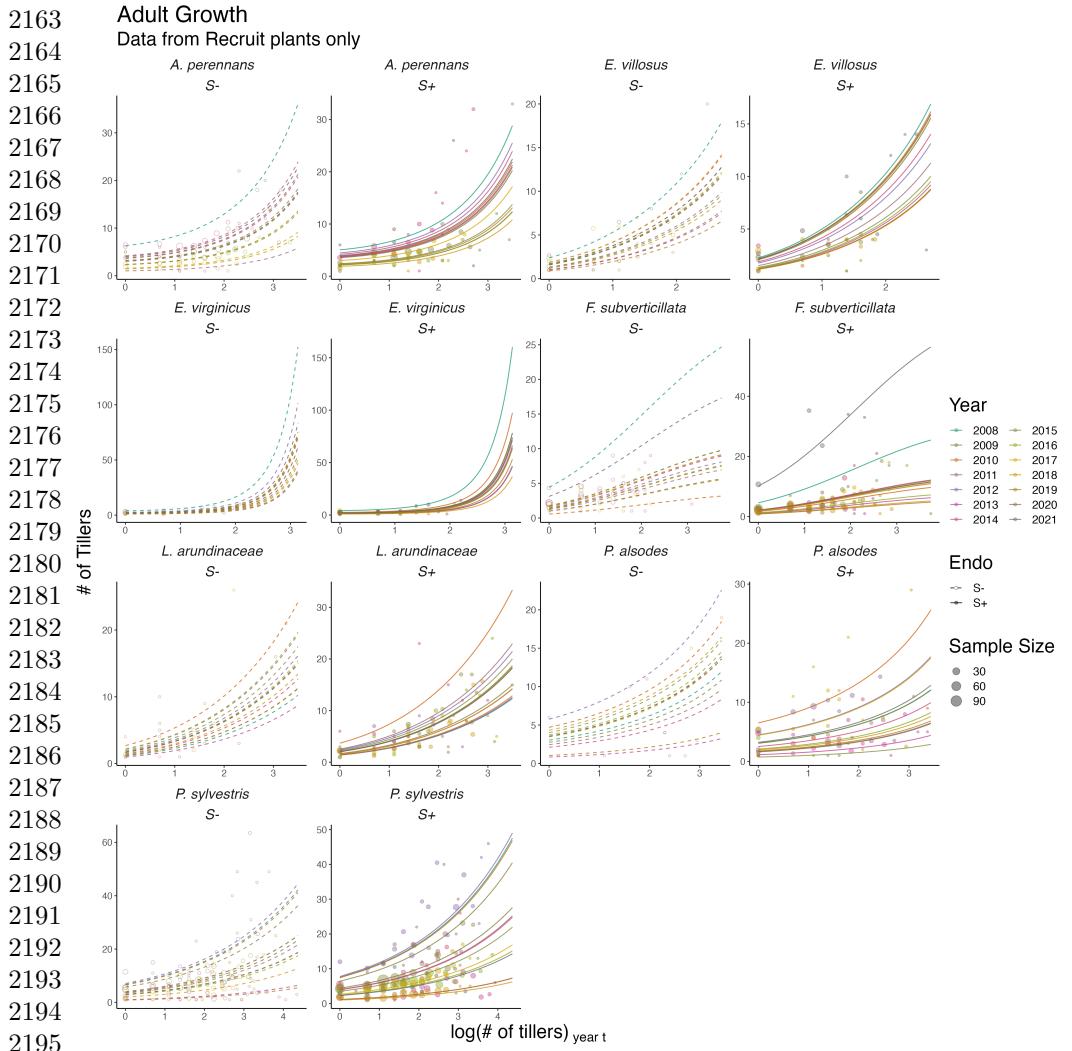


Figure S14: Effect of endophyte symbiosis on yearly adult growth. Fitted curves represent the size-specific annual expected plant size for originally transplanted plants along with data binned by size and census year and averaged over many individuals, and plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



2195      Figure S15: Effect of endophyte symbiosis on yearly adult growth. Fitted curves rep-  
2196 resent the size-specific annual expected plant size for recruited plants along with data  
2197 binned by size and census year and averaged over many individuals, and plots shown  
2198 as open circles with a dashed line for symbiont-free (S-) plants, while the solid line  
2199 and filled circles represent symbiotic (S+) plants.

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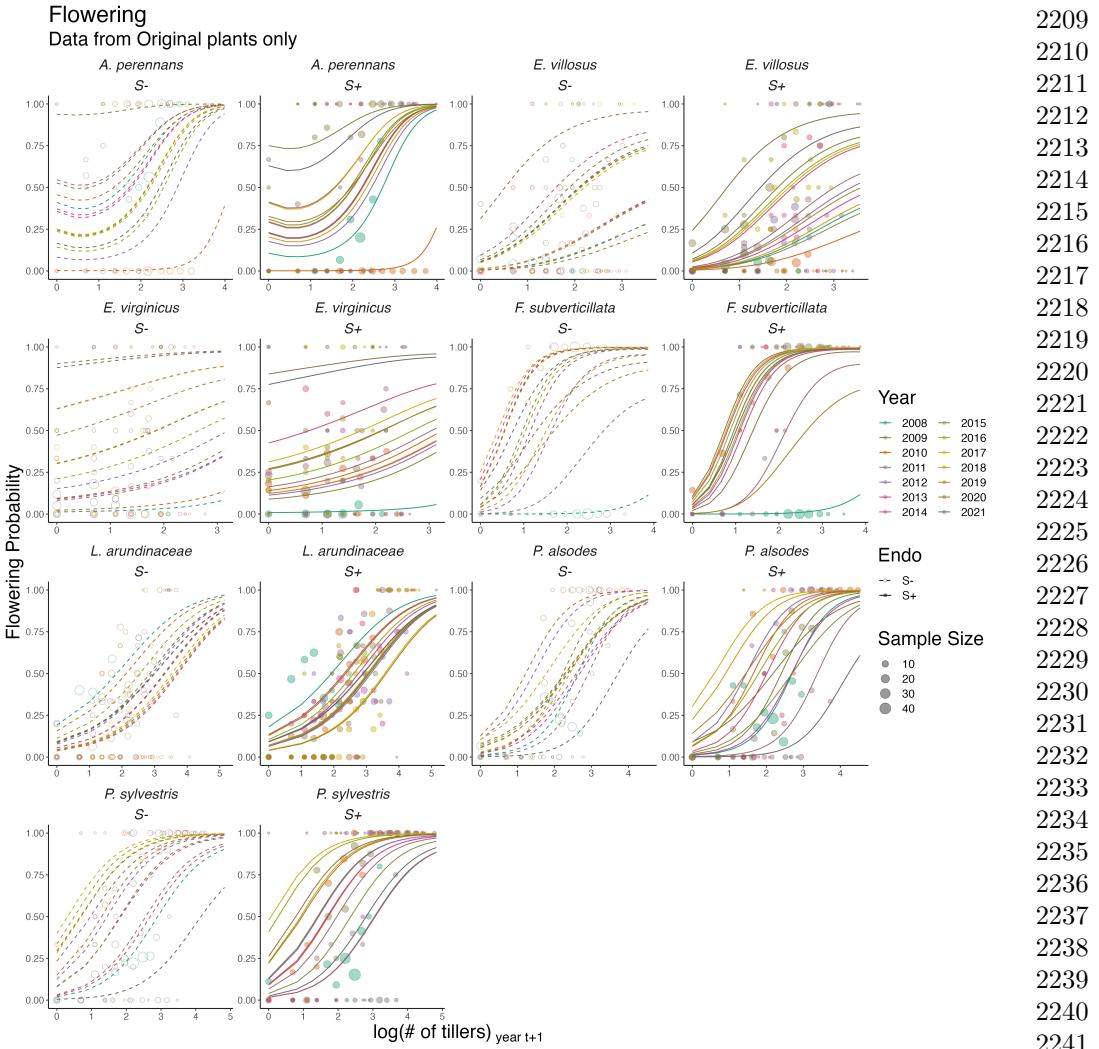
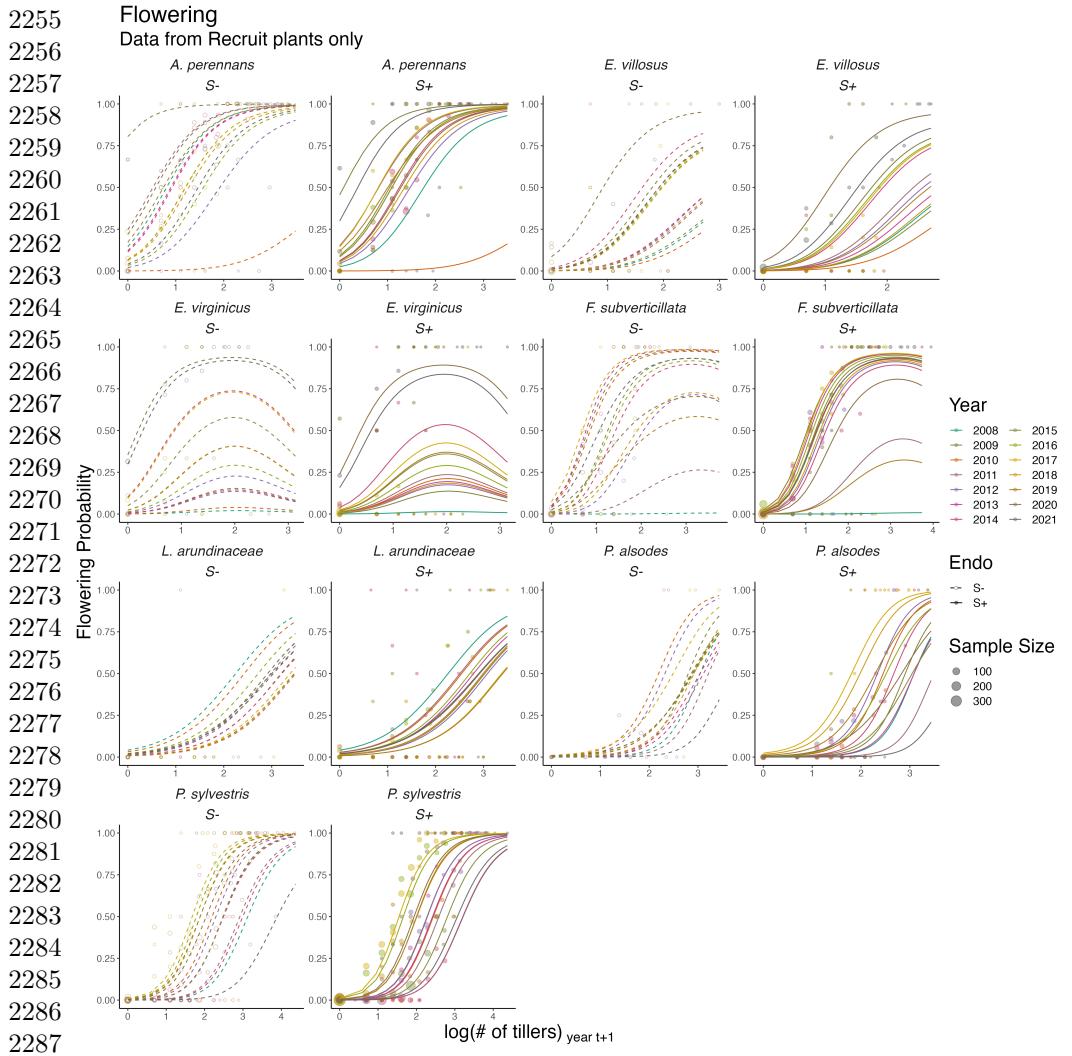


Figure S16: Effect of endophyte symbiosis on yearly flowering. Fitted curves represent the size-specific annual flowering probability for originally transplanted plants along with data binned by size and census year and averaged over many individuals, and plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.

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2288 Figure S17: Effect of endophyte symbiosis on yearly flowering. Fitted curves represent the size-specific annual flowering probability for recruited plants along with data binned by size and census year and averaged over many individuals, and plots 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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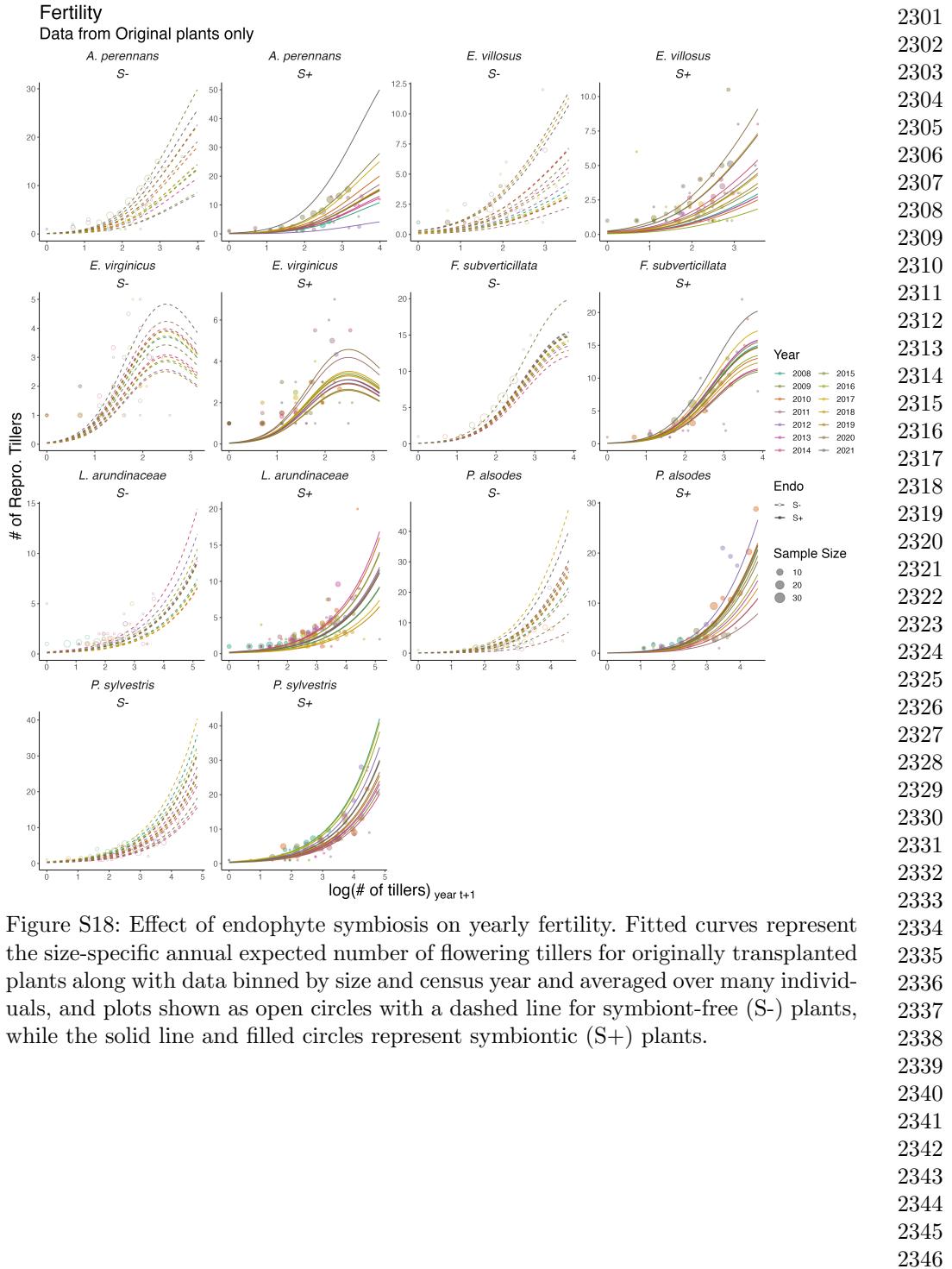
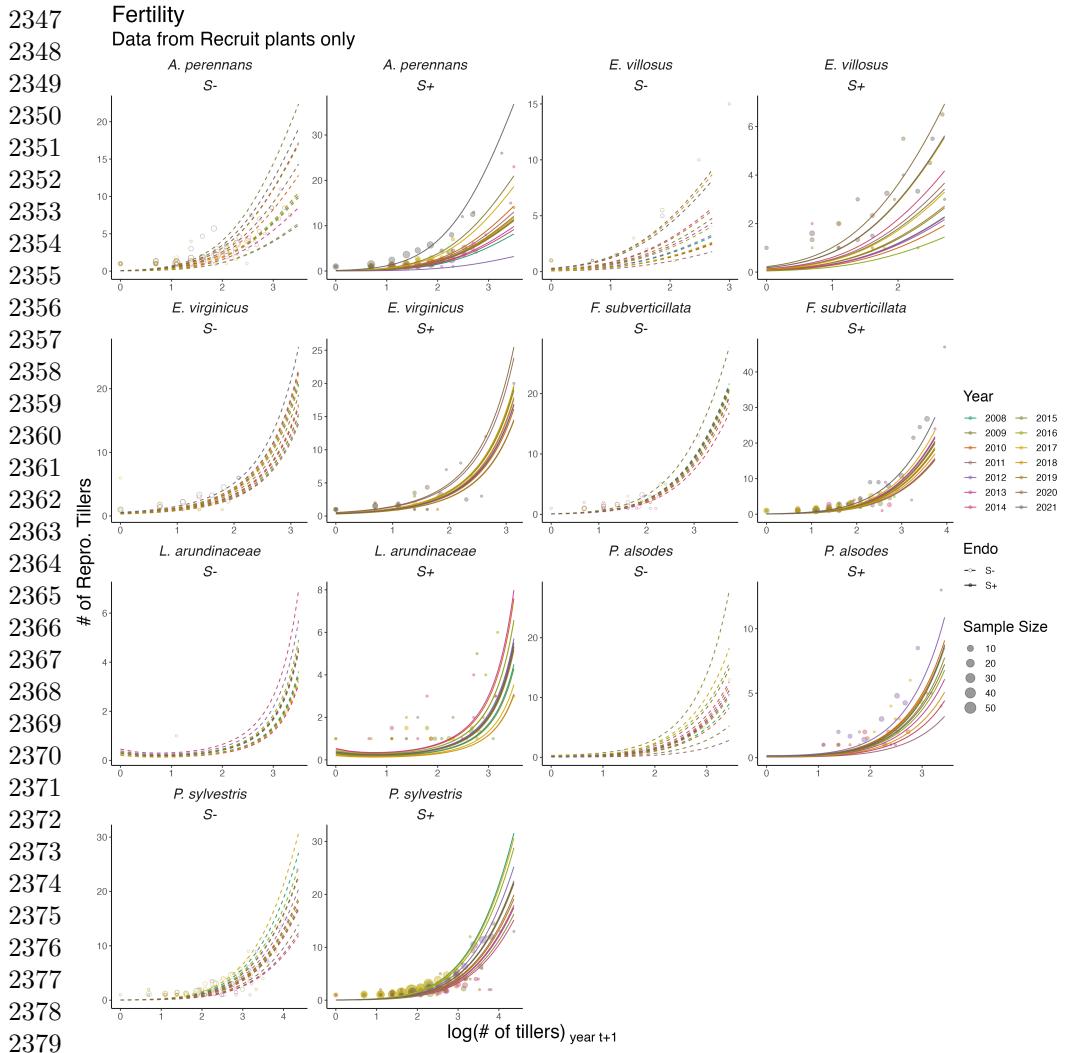


Figure S18: Effect of endophyte symbiosis on yearly fertility. Fitted curves represent the size-specific annual expected number of flowering tillers for originally transplanted plants along with data binned by size and census year and averaged over many individuals, and plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



2380 Figure S19: Effect of endophyte symbiosis on yearly fertility. Fitted curves represent  
 2381 the size-specific annual expected number of flowering tillers for recruited plants along  
 2382 with data binned by size and census year and averaged over many individuals, and  
 2383 plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the  
 2384 solid line and filled circles represent symbiotic (S+) plants.

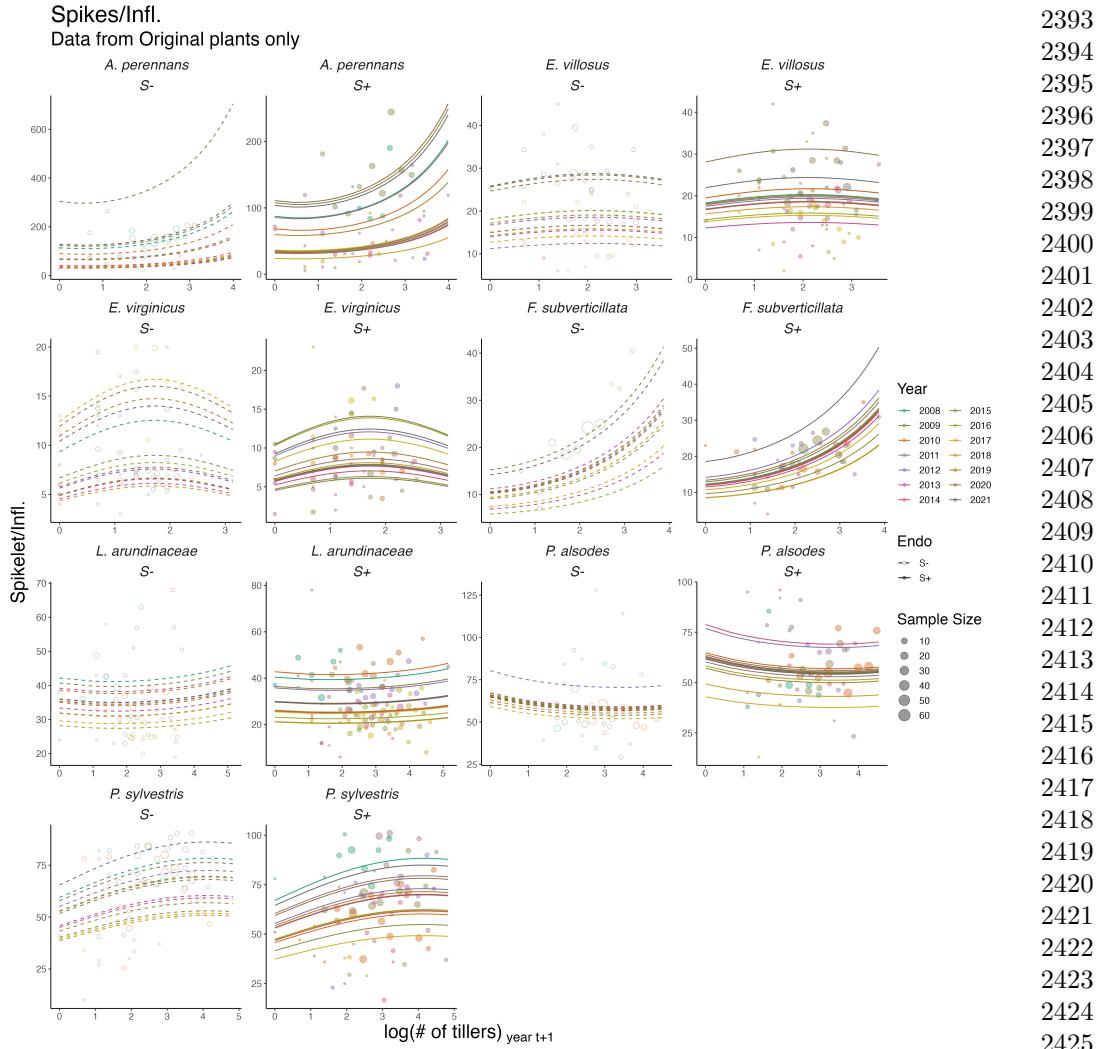
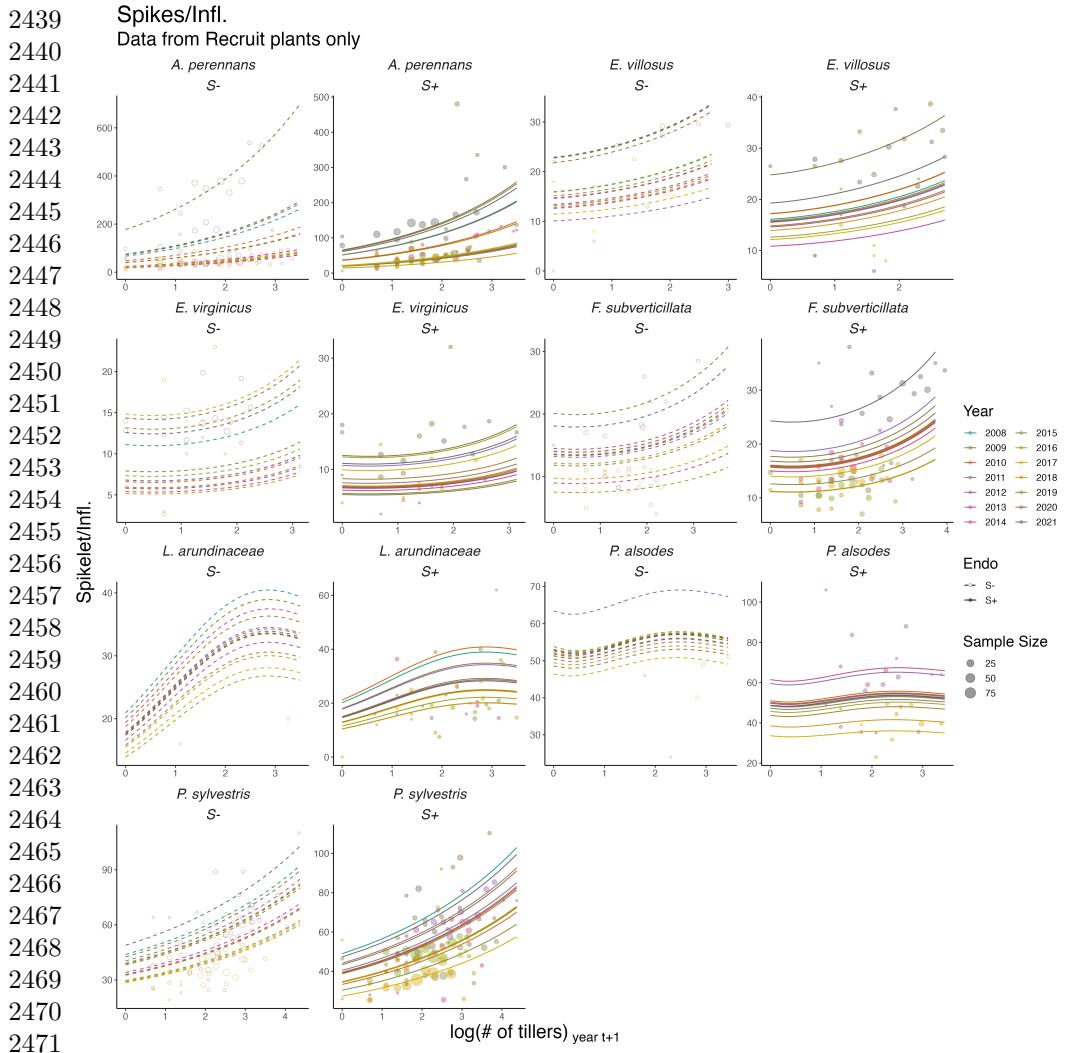


Figure S20: Effect of endophyte symbiosis on yearly spikelet production. Fitted curves represent the size-specific annual expected number of spikelets per inflorescence for originally transplanted plants along with data binned by size and census year and averaged over many individuals, and plots shown as open circles with a dashed line for symbiont-free (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.



2472 Figure S21: Effect of endophyte symbiosis on yearly spikelet production. Fitted curves  
2473 represent the size-specific annual expected number of spikelets per inflorescence for  
2474 recruited plants along with data binned by size and census year and averaged over  
2475 many individuals, and plots shown as open circles with a dashed line for symbiont-free  
2476 (S-) plants, while the solid line and filled circles represent symbiotic (S+) plants.

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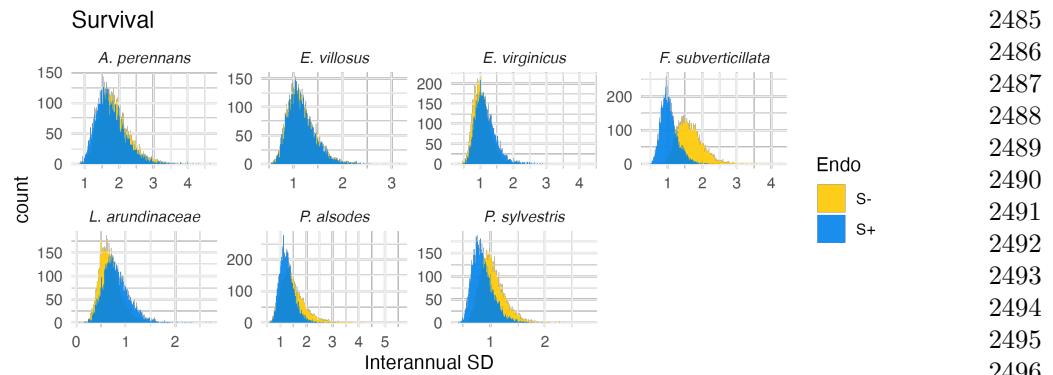


Figure S22: Posterior distributions of the standard deviations of inter-annual year effects for survival. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

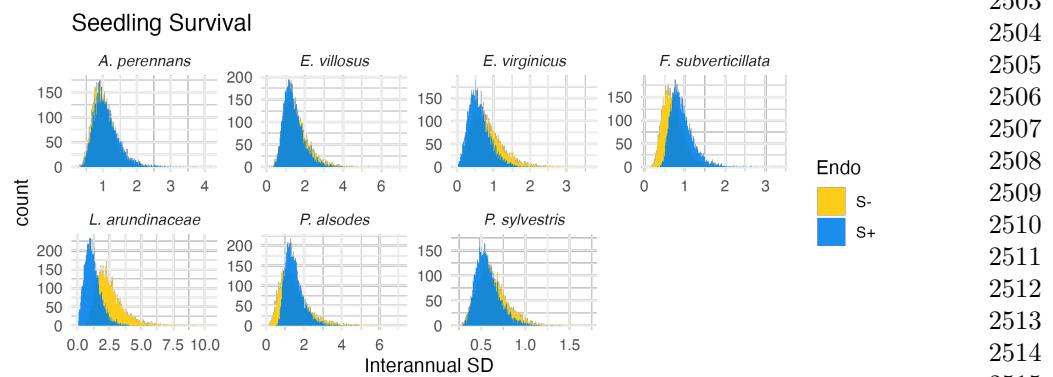
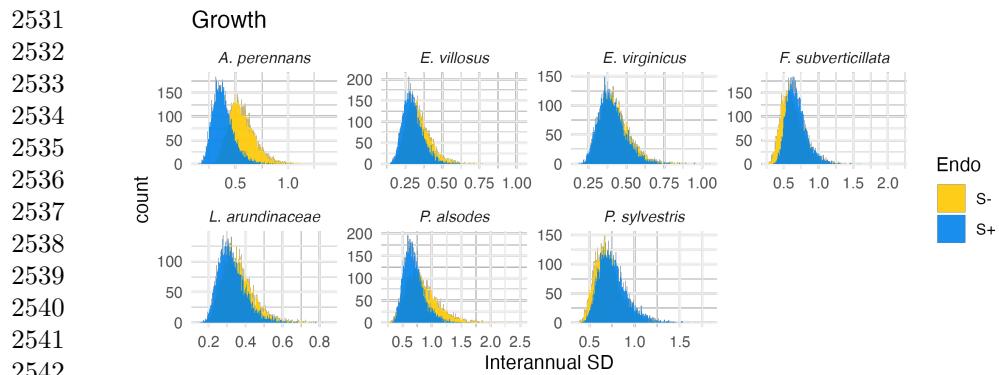
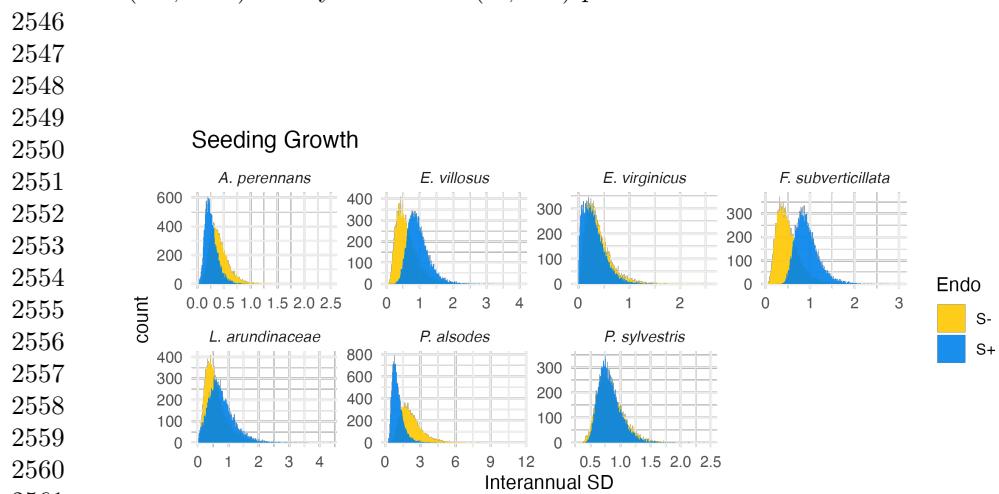


Figure S23: Posterior distributions of the standard deviations of inter-annual year effects for seedling survival. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.



2543 Figure S24: Posterior distributions of the standard deviations of inter-annual year  
 2544 effects for growth. Histograms include 7500 post-warmup MCMC samples for symbi-  
 2545 otic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.



2561 Figure S25: Posterior distributions of the standard deviations of inter-annual year  
 2562 effects for seedling growth. Histograms include 7500 post-warmup MCMC samples for  
 2563 symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

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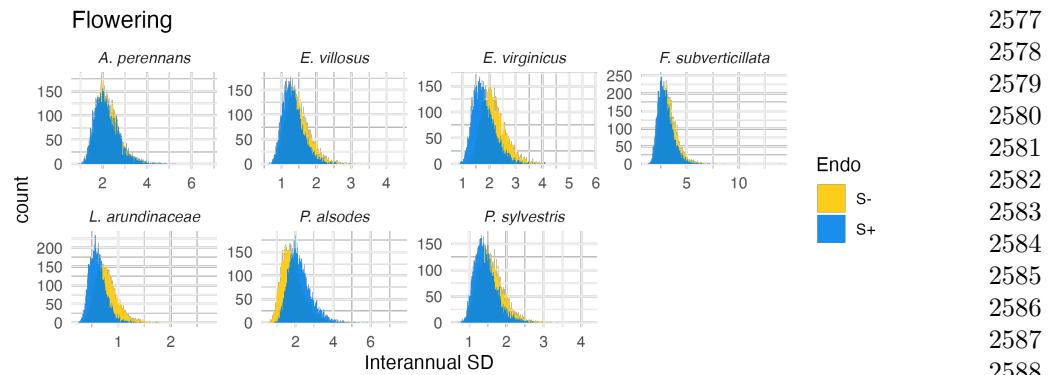


Figure S26: Posterior distributions of the standard deviations of inter-annual year effects for flowering probability. Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.

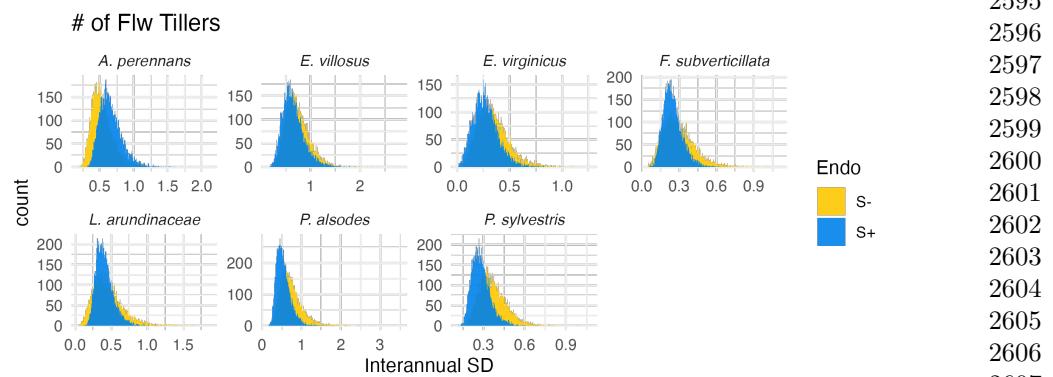
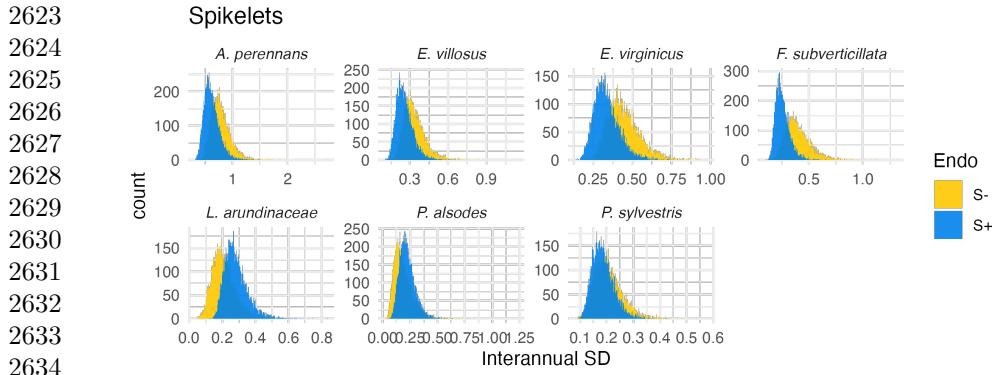
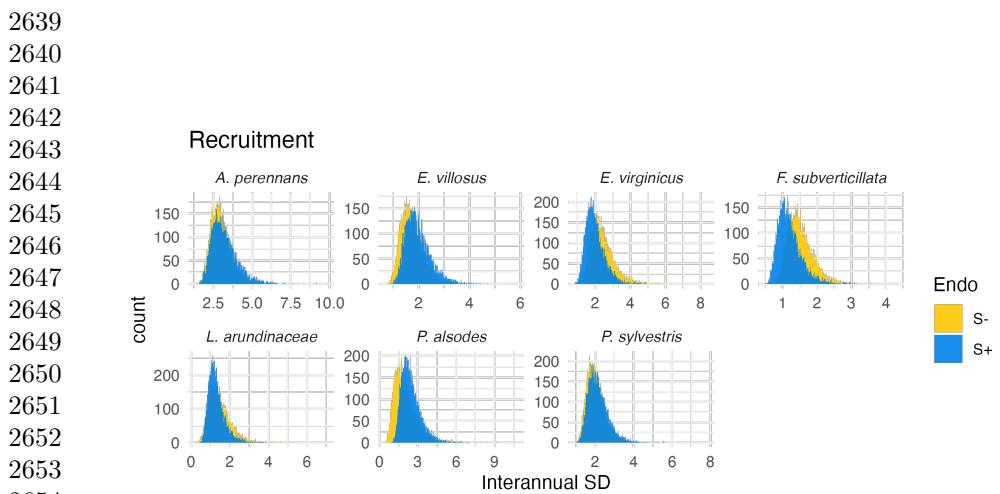


Figure S27: Posterior distributions of the standard deviations of inter-annual year effects for fertility (no. of flowering tillers). Histograms include 7500 post-warmup MCMC samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.



2635 Figure S28: Posterior distributions of the standard deviations of inter-annual year  
 2636 effects for spikelets per inflorescence. Histograms include 7500 post-warmup MCMC  
 2637 samples for symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital  
 2638 rate model.



2654 Figure S29: Posterior distributions of the standard deviations of inter-annual year  
 2655 effects for recruitment. Histograms include 7500 post-warmup MCMC samples for  
 2656 symbiotic (S+; blue) and symbiont-free (S-; tan) plants from fitted vital rate model.  
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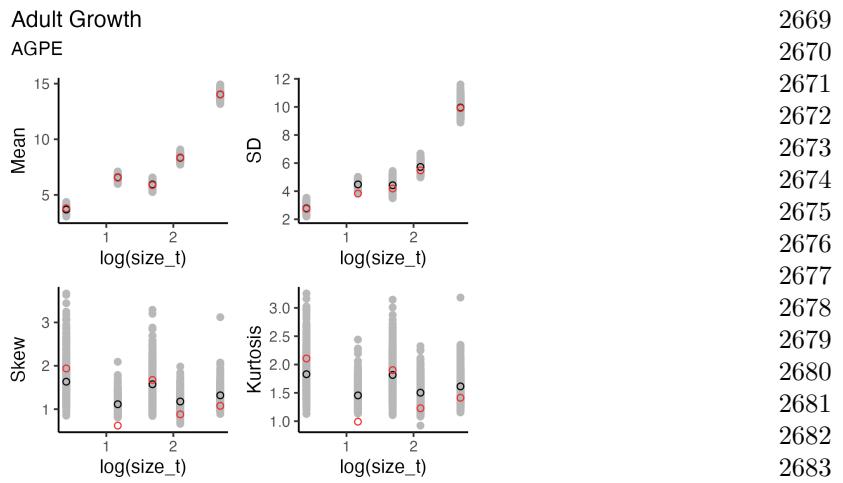


Figure S30: Graphical posterior predictive check for mean and higher moments of *A. perennans* growth model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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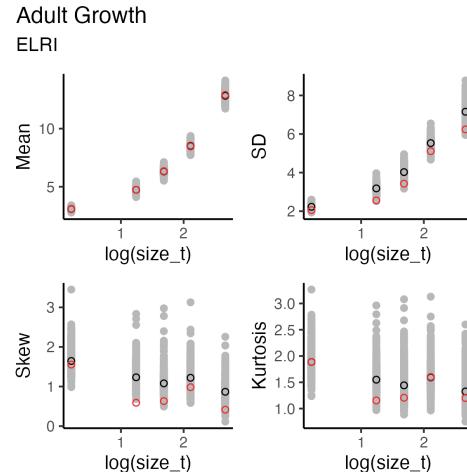
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2730 Figure S31: Graphical posterior predictive check for mean and higher moments of *E.*  
 2731 *villosus* growth model across size. Consistency between real data and fitted values  
 2732 across sizes indicates that the vital rate models are accurately capturing size depen-  
 2733 dence. Points show the value of statistical moments binned across size for the observed  
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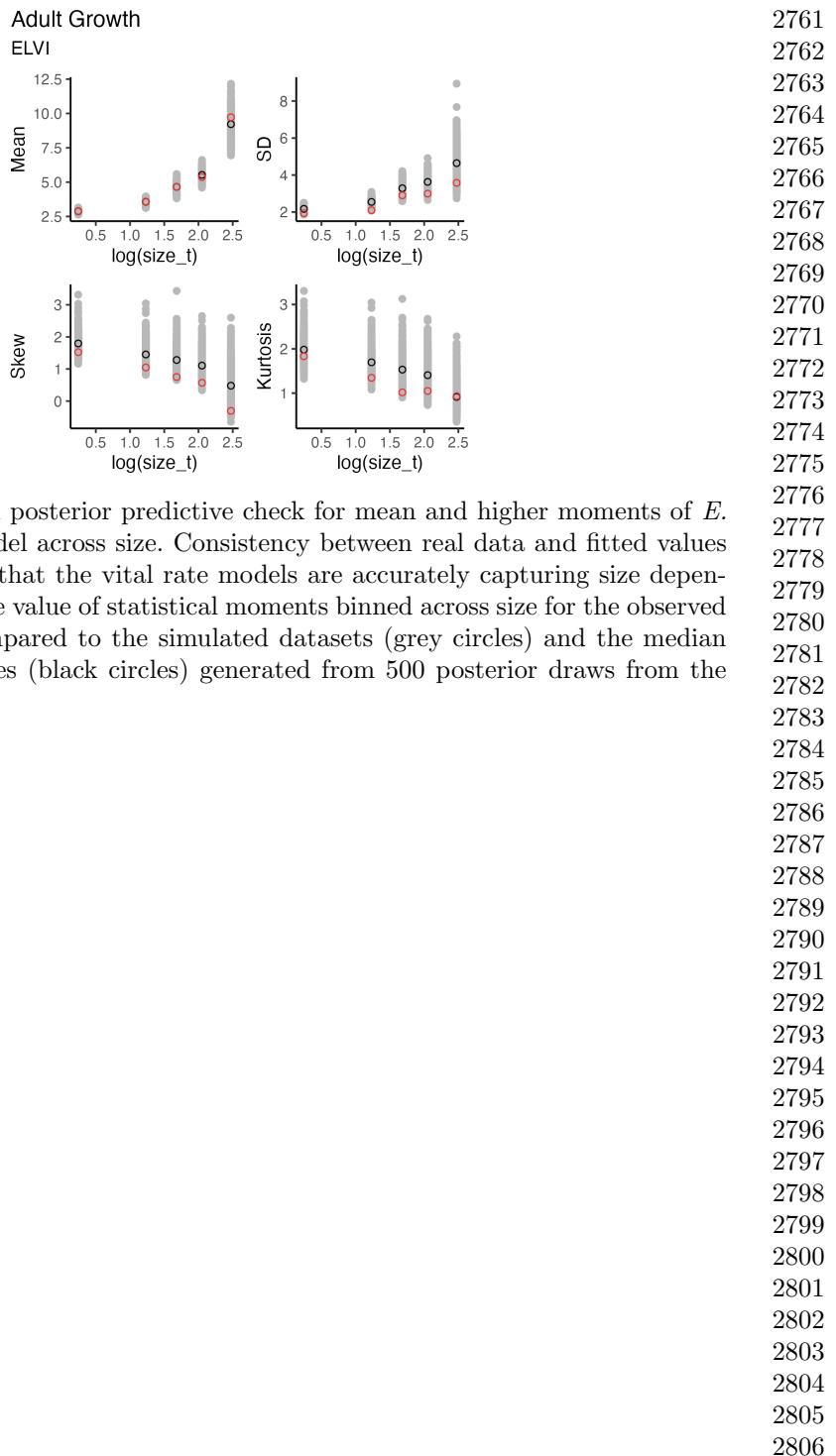


Figure S32: Graphical posterior predictive check for mean and higher moments of *E. virginicus* growth model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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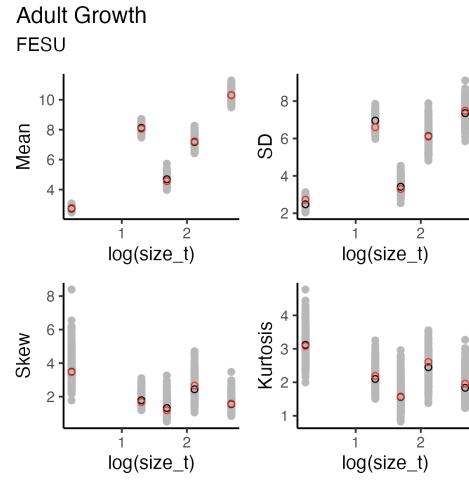
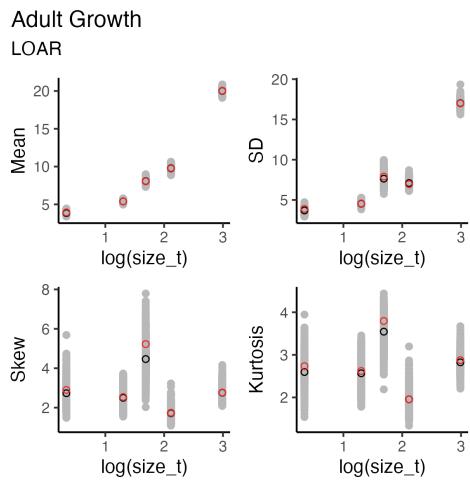


Figure S33: Graphical posterior predictive check for mean and higher moments of *F. subverticillata* growth model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.



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Figure S35: Graphical posterior predictive check for mean and higher moments of *P. alsodes* growth model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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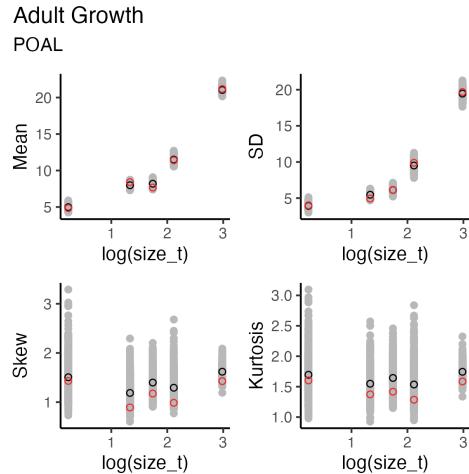
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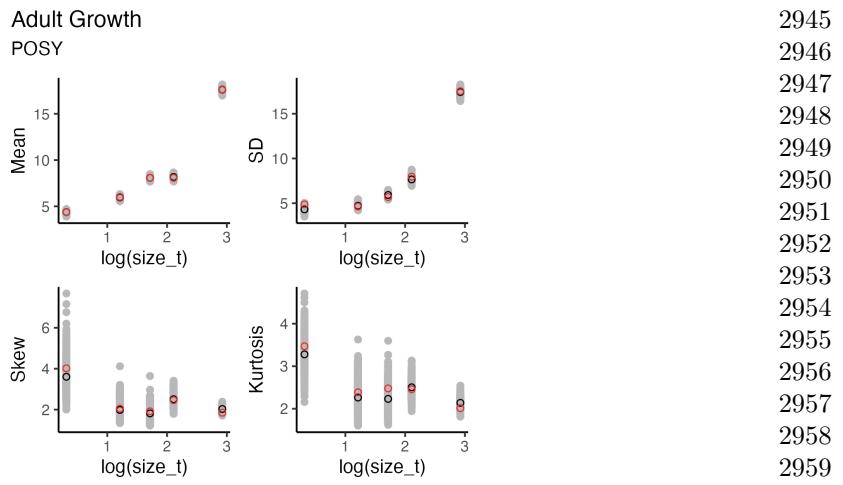


Figure S36: Graphical posterior predictive check for mean and higher moments of *P. sylvestris* growth model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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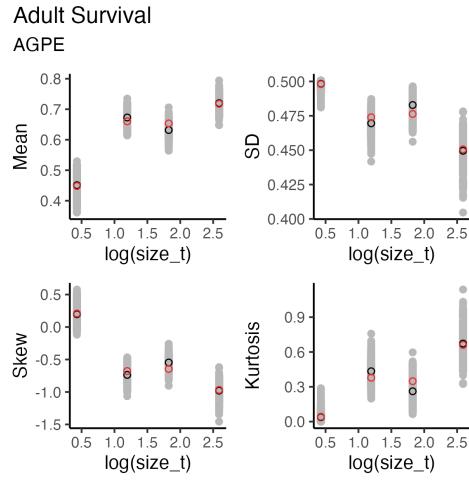


Figure S37: Graphical posterior predictive check for mean and higher moments of *A. perennans* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

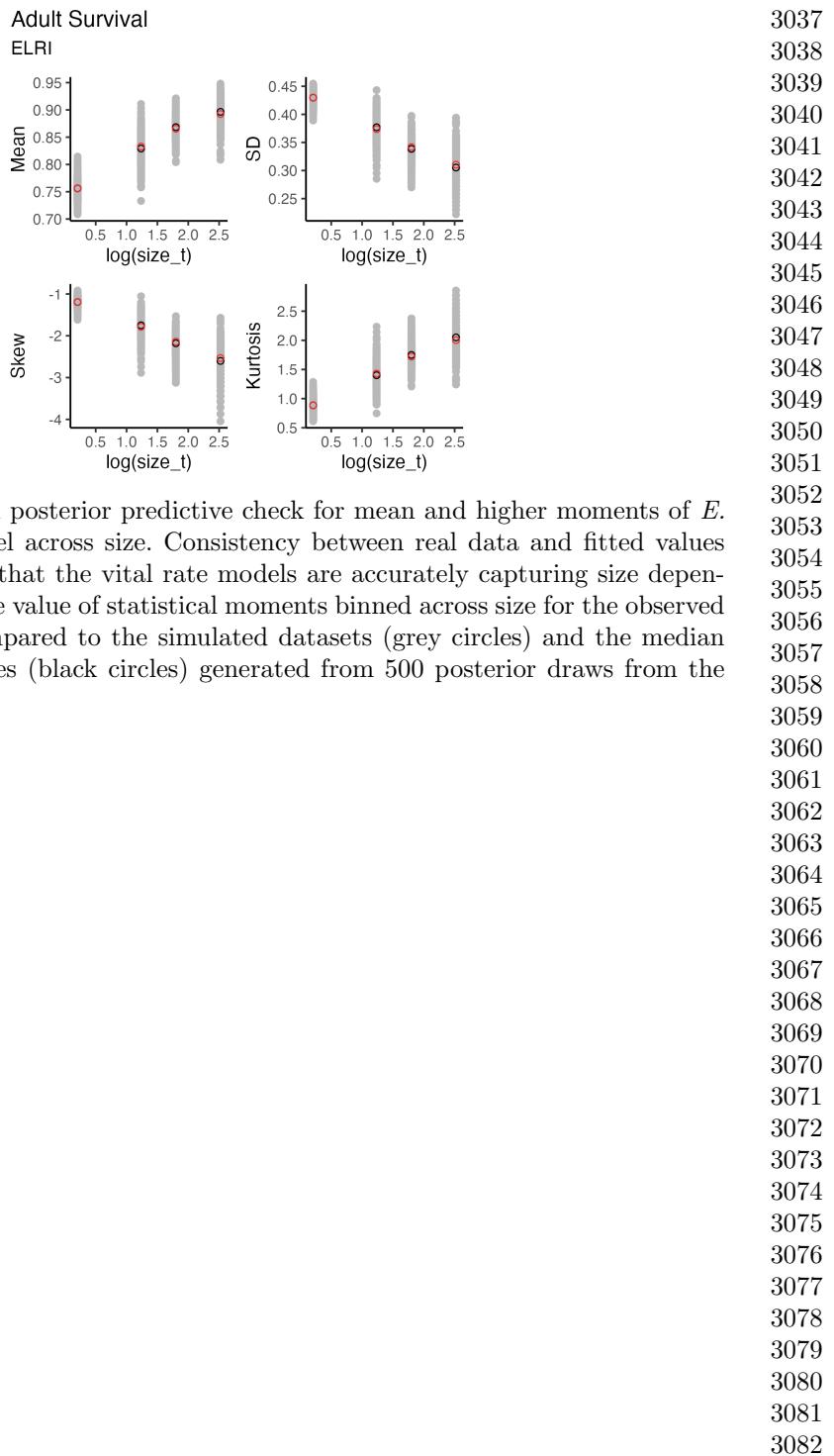


Figure S38: Graphical posterior predictive check for mean and higher moments of *E. villosus* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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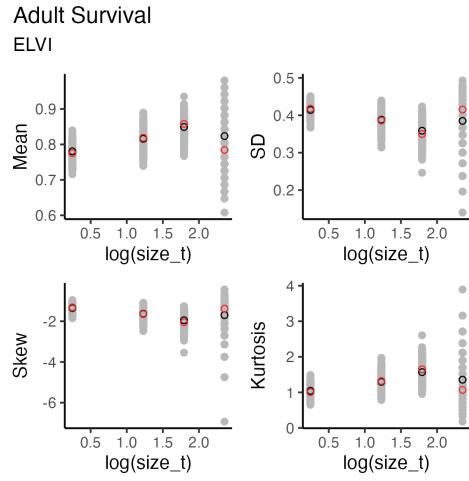


Figure S39: Graphical posterior predictive check for mean and higher moments of *E. virginicus* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

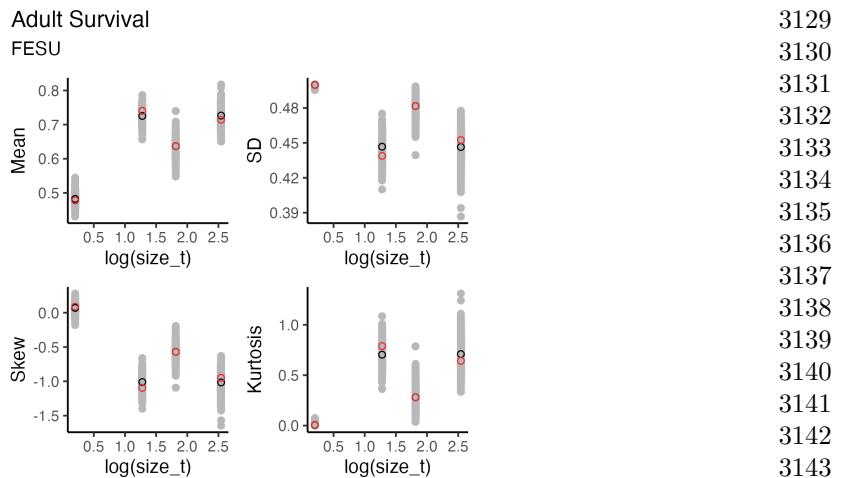


Figure S40: Graphical posterior predictive check for mean and higher moments of *F. subverticillata* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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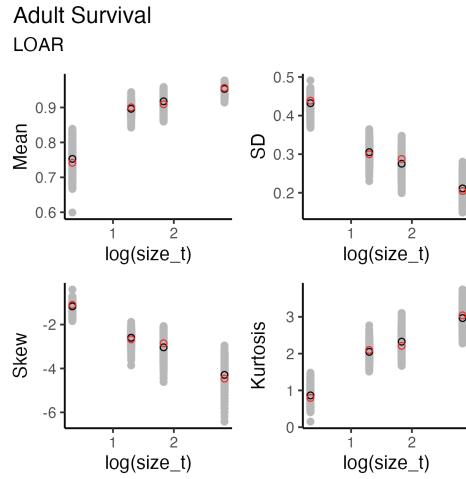


Figure S41: Graphical posterior predictive check for mean and higher moments of *L. arundinacea* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

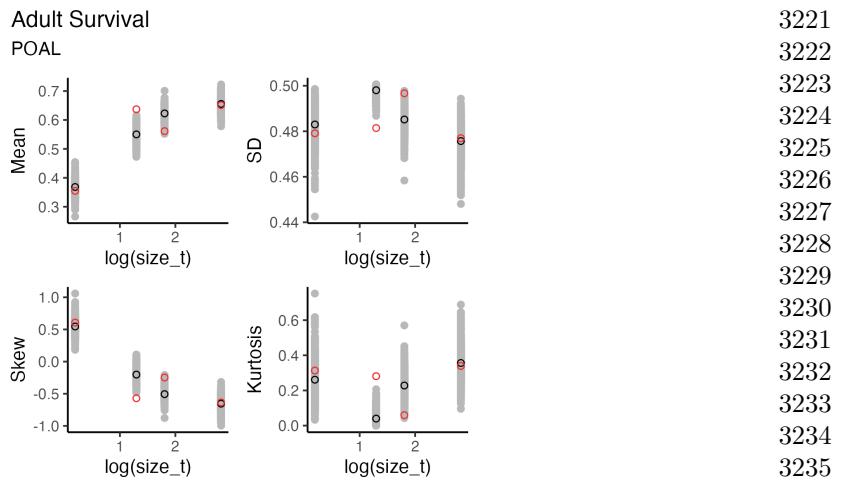


Figure S42: Graphical posterior predictive check for mean and higher moments of *P. alsodes* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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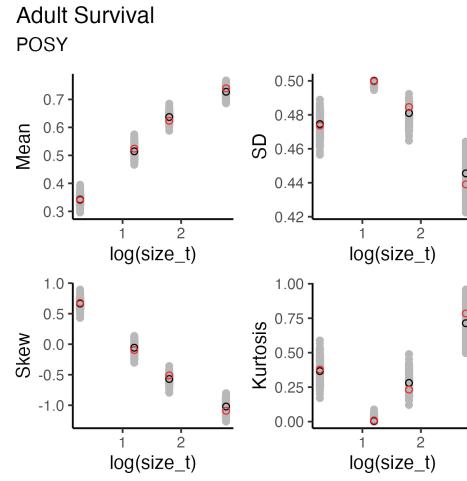
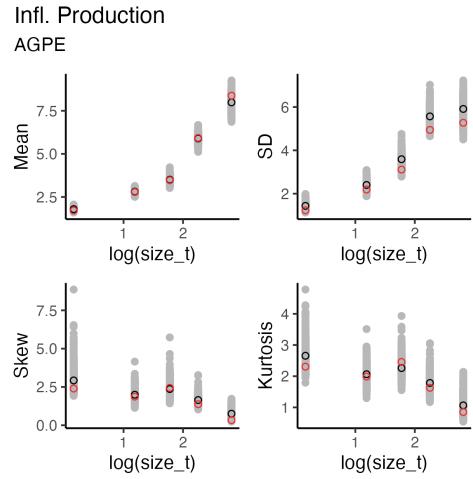


Figure S43: Graphical posterior predictive check for mean and higher moments of *P. sylvestris* survival model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.



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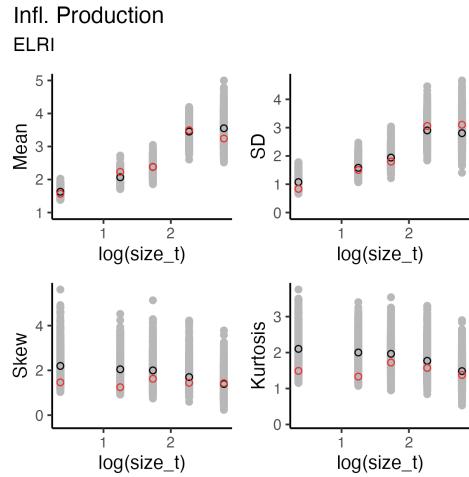
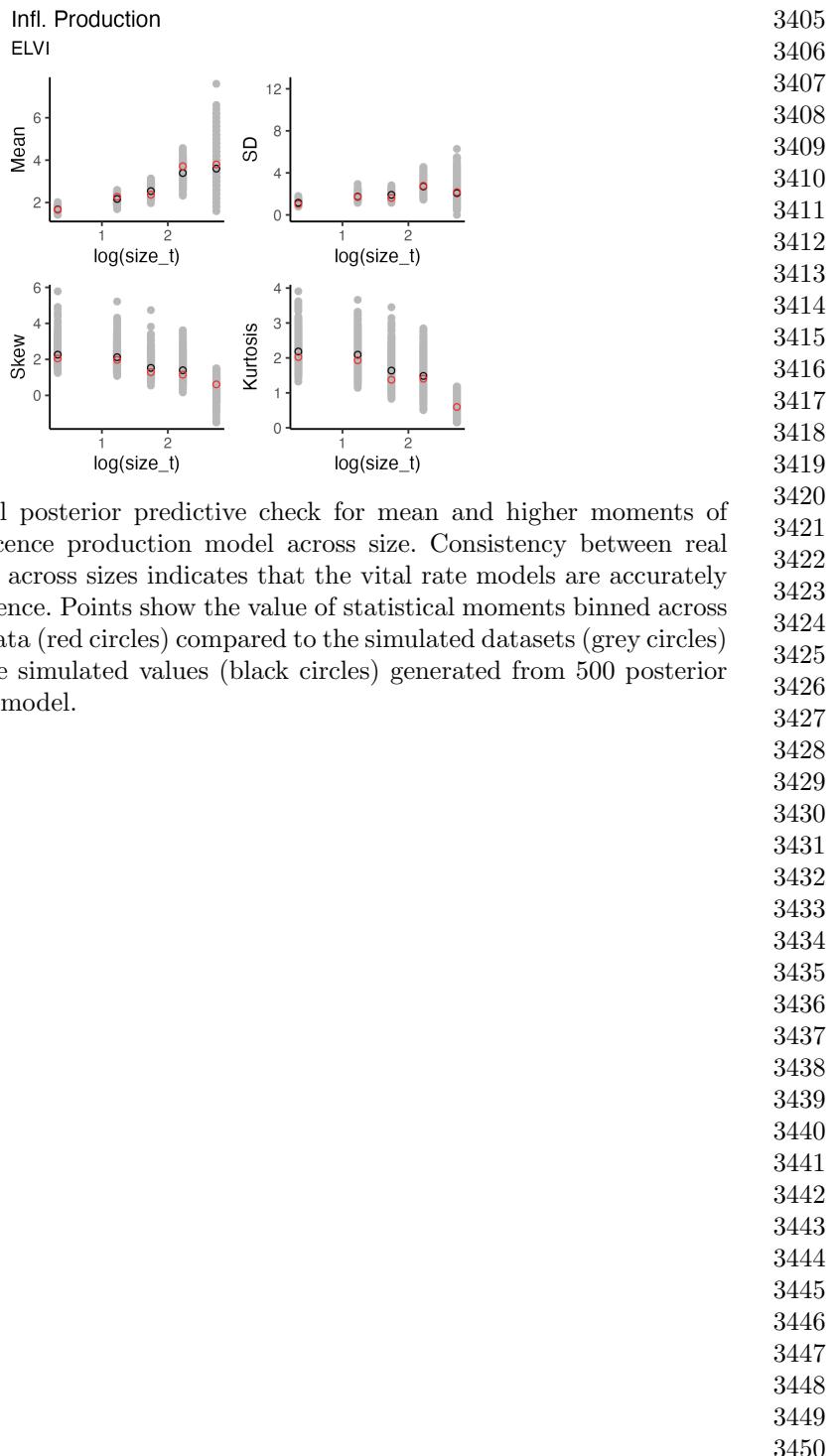


Figure S45: Graphical posterior predictive check for mean and higher moments of *E. villosus* inflorescence production model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.



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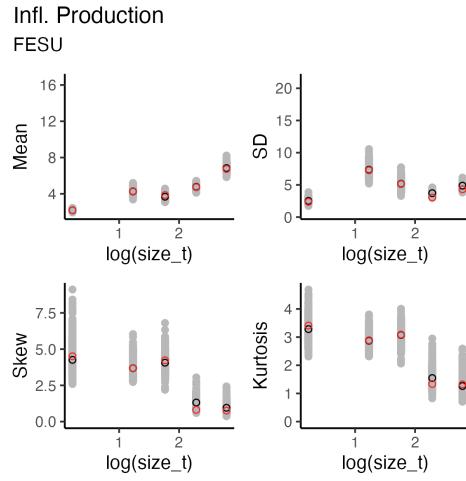


Figure S47: Graphical posterior predictive check for mean and higher moments of *F. subverticillata* inflorescence production model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

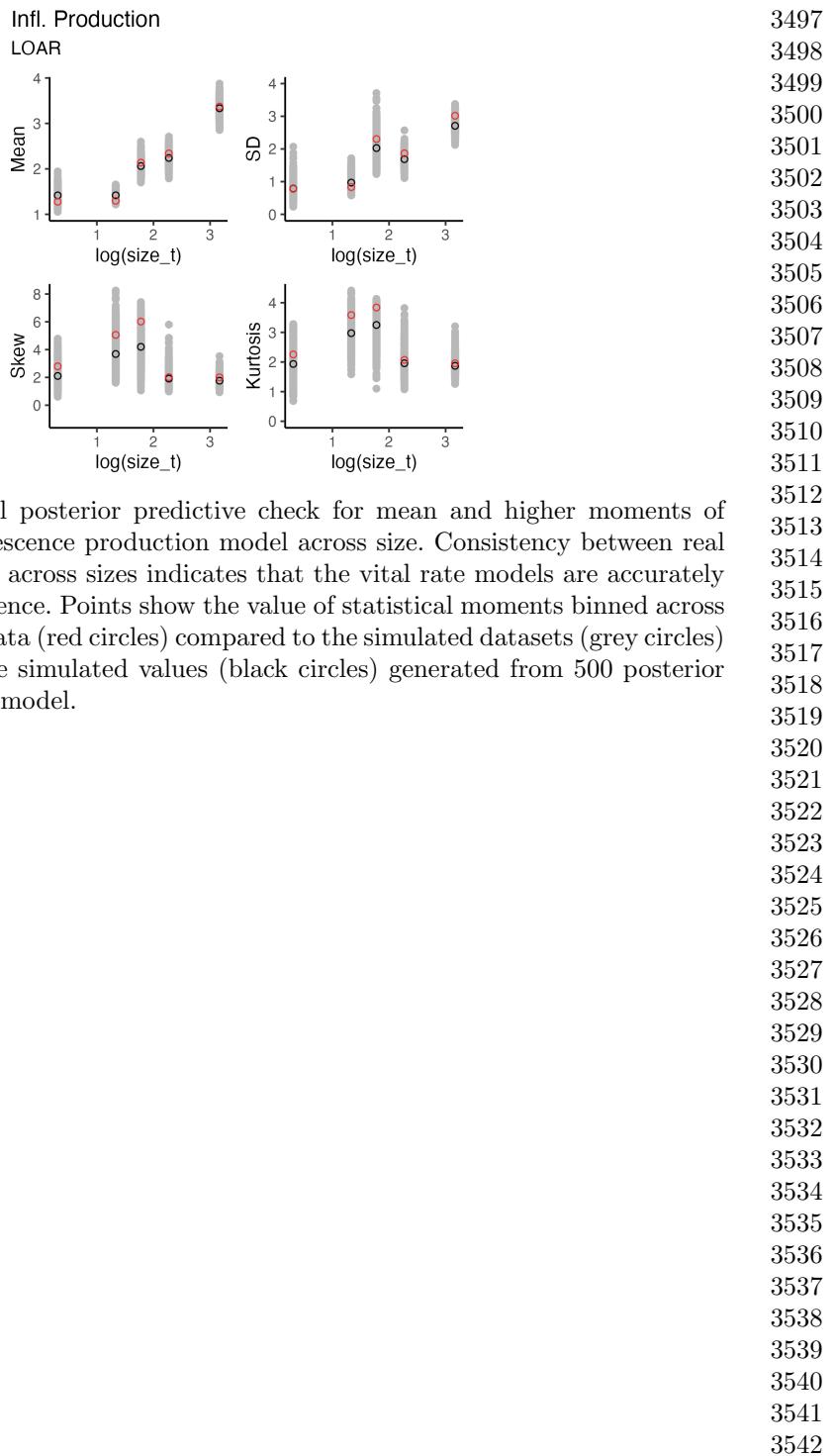


Figure S48: Graphical posterior predictive check for mean and higher moments of *L. arundinacea* inflorescence production model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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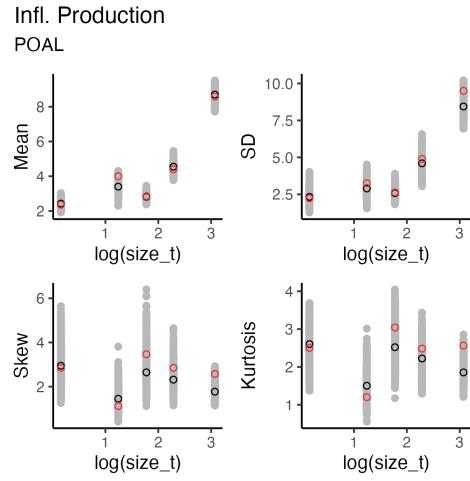


Figure S49: Graphical posterior predictive check for mean and higher moments of  $P$ . *alsodes* inflorescence production model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

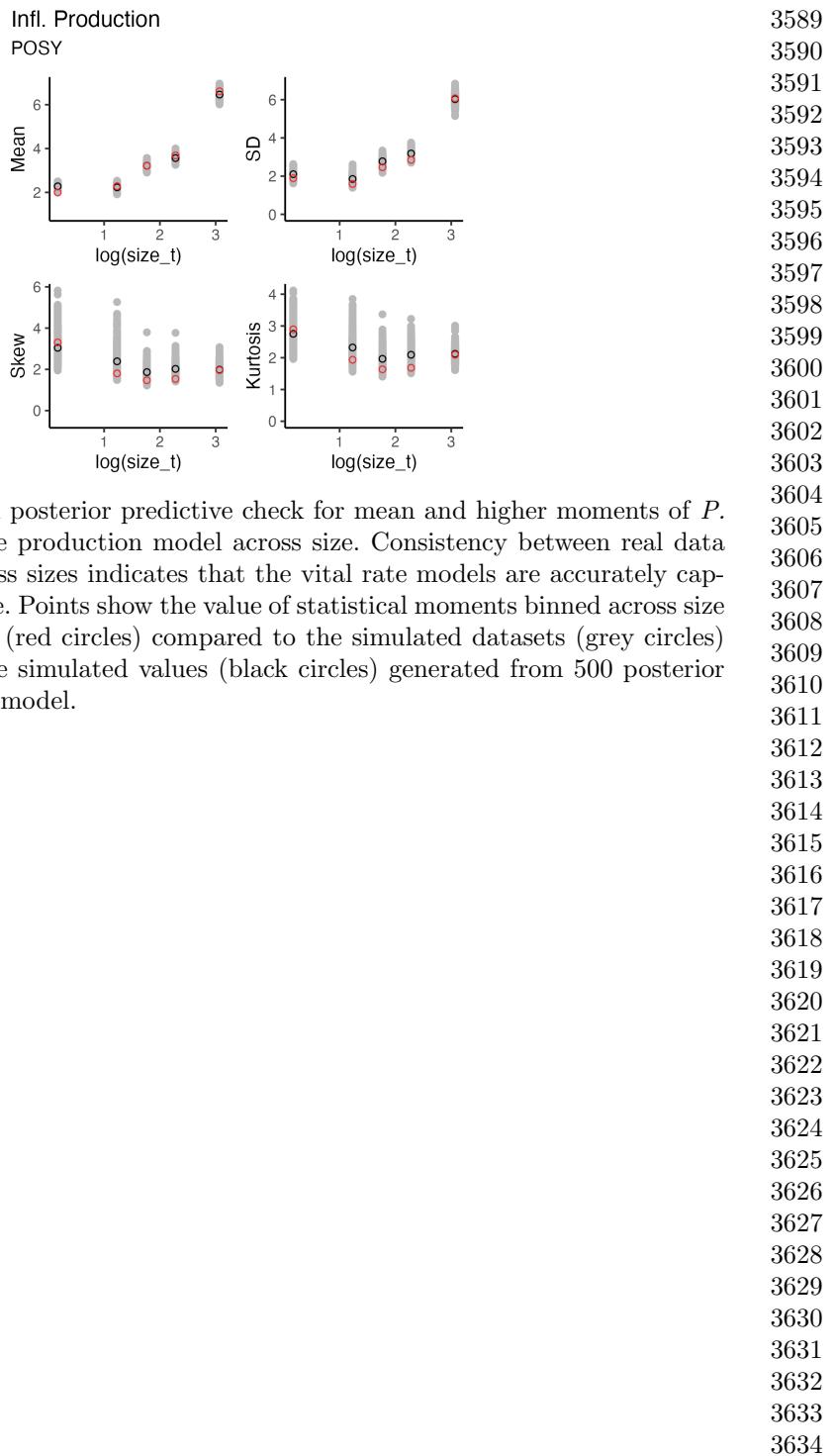


Figure S50: Graphical posterior predictive check for mean and higher moments of *P. sylvestris* inflorescence production model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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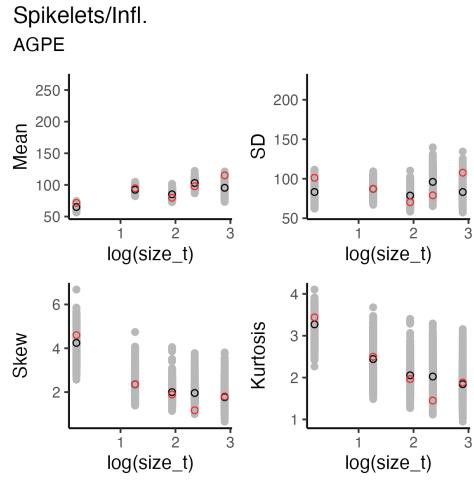


Figure S51: Graphical posterior predictive check for mean and higher moments of *A. perennans* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

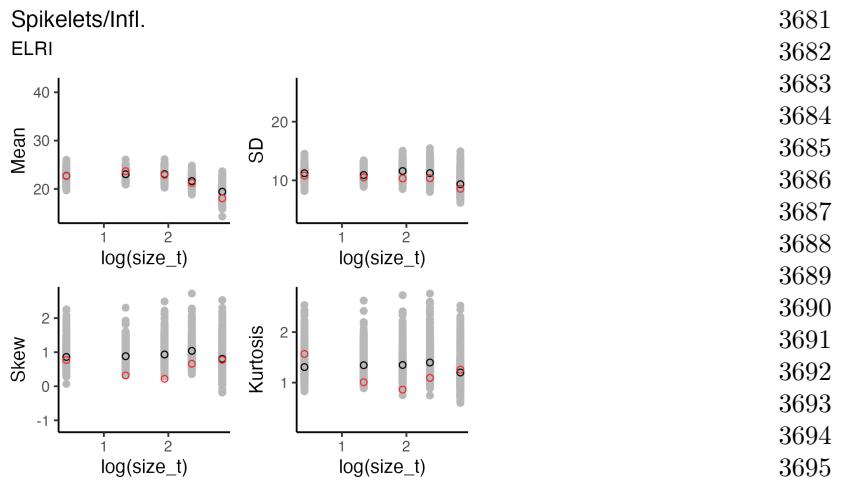


Figure S52: Graphical posterior predictive check for mean and higher moments of *E. villosus* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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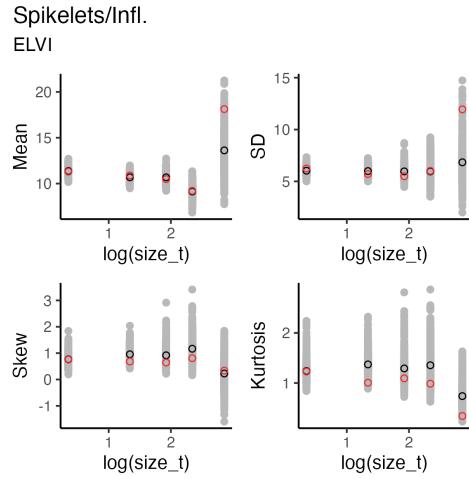


Figure S53: Graphical posterior predictive check for mean and higher moments of *E. virginicus* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

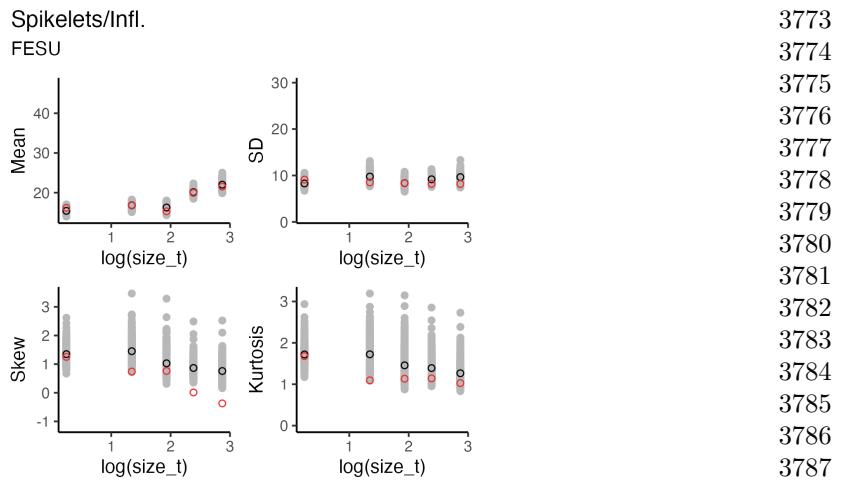


Figure S54: Graphical posterior predictive check for mean and higher moments of *F. subverticillata* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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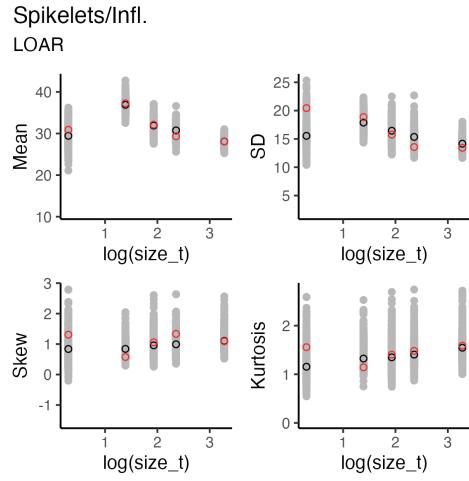


Figure S55: Graphical posterior predictive check for mean and higher moments of *L. arundinacea* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

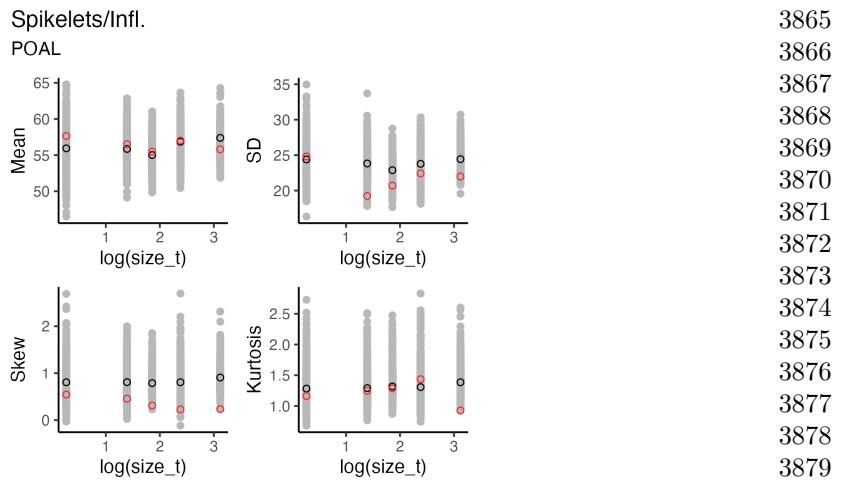


Figure S56: Graphical posterior predictive check for mean and higher moments of *P. alsodes* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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Figure S57: Graphical posterior predictive check for mean and higher moments of *P. sylvestris* spikelet model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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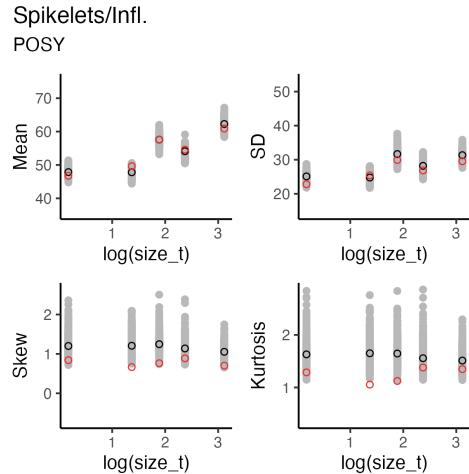
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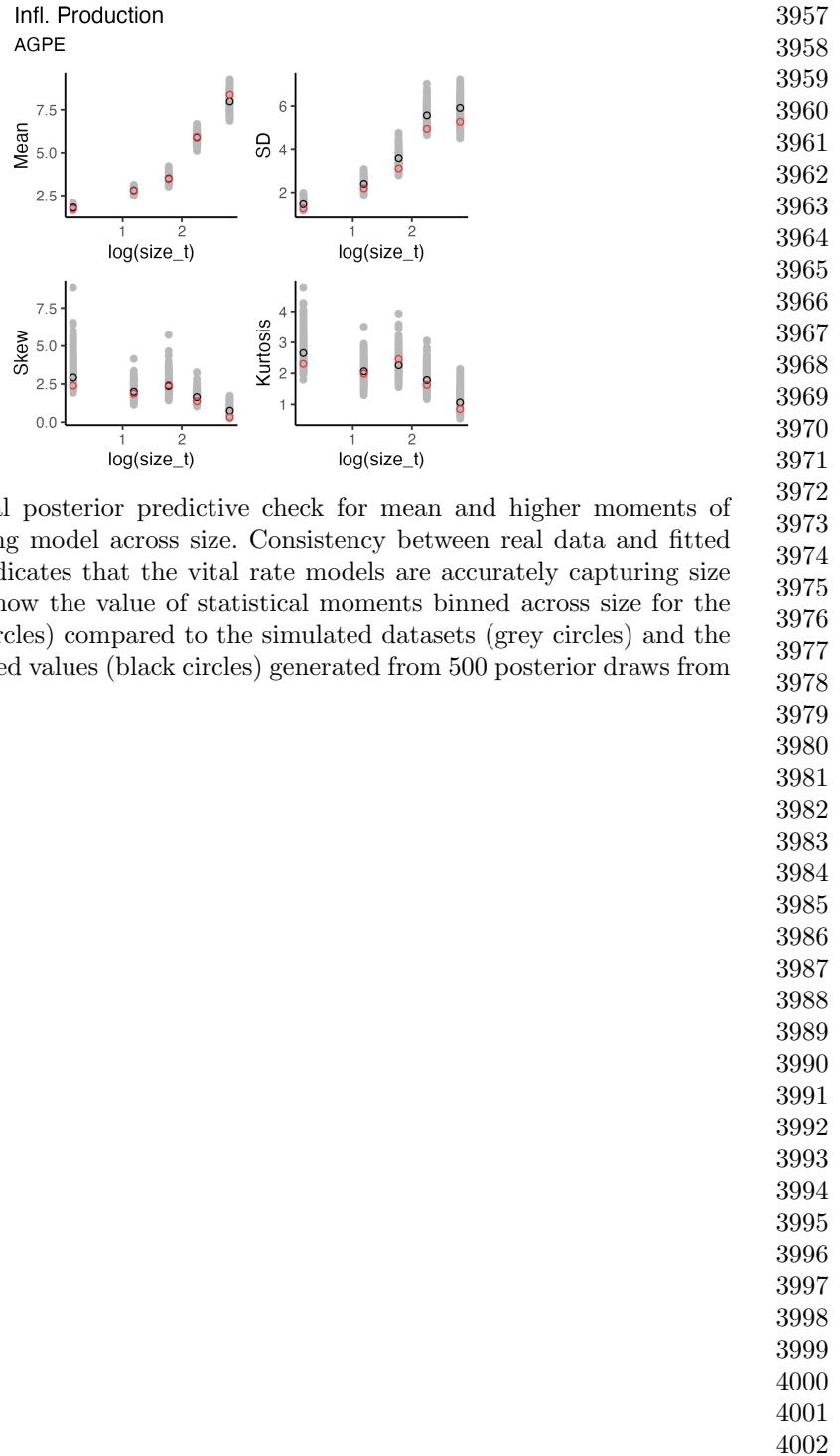


Figure S58: Graphical posterior predictive check for mean and higher moments of *A. perennans* flowering model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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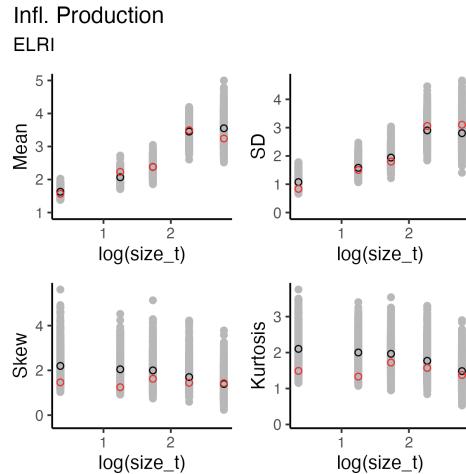
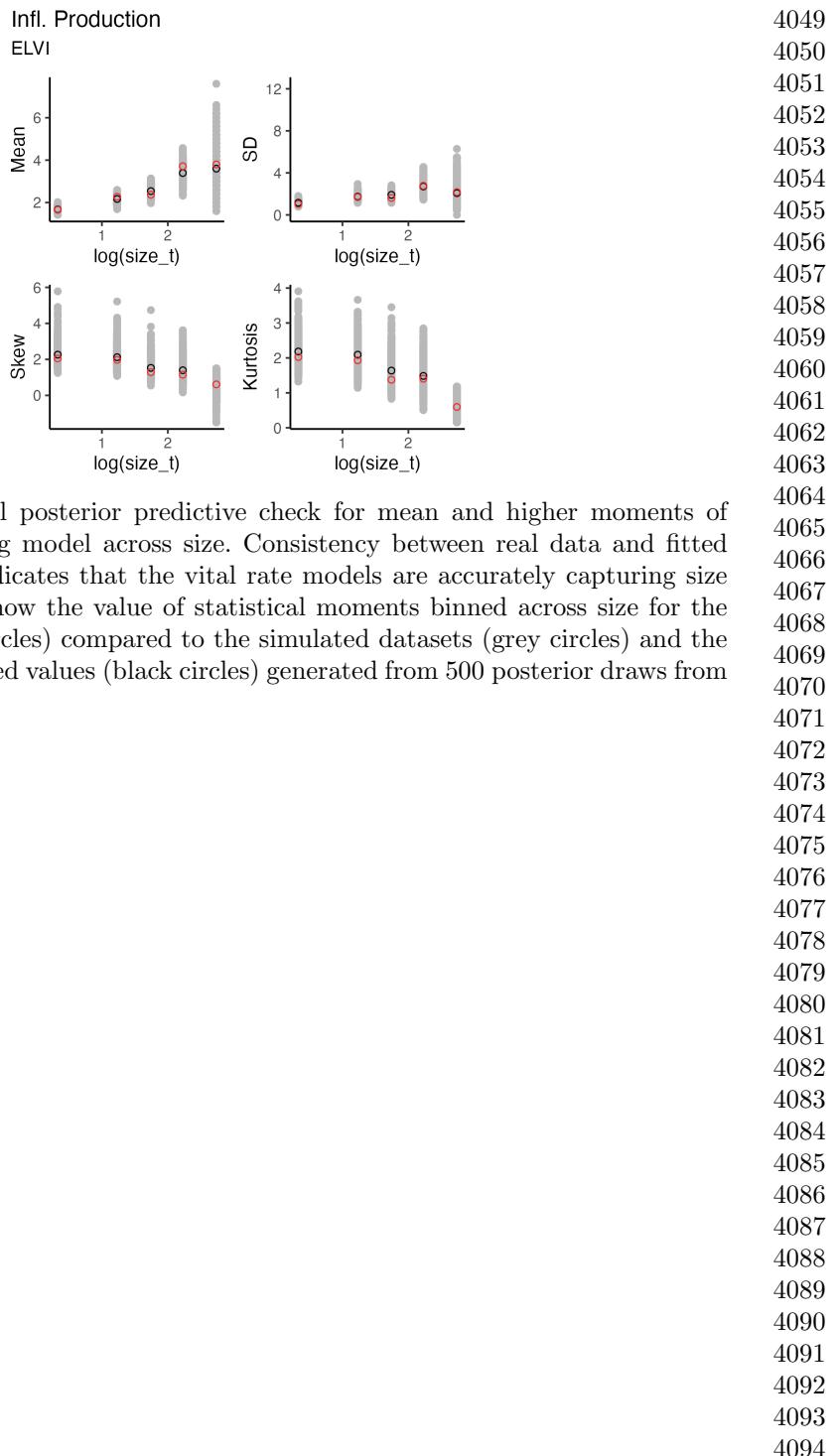


Figure S59: Graphical posterior predictive check for mean and higher moments of *E. villosus* flowering model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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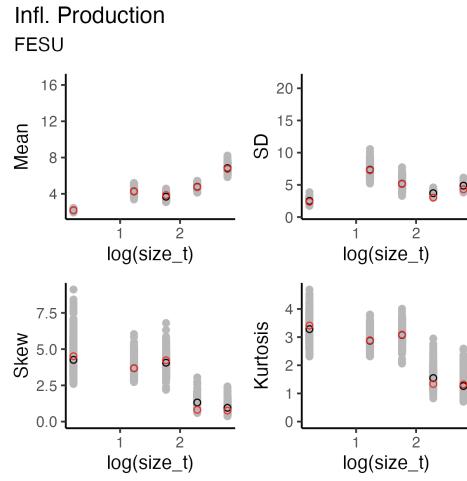


Figure S61: Graphical posterior predictive check for mean and higher moments of *F. subverticillata* flowering model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

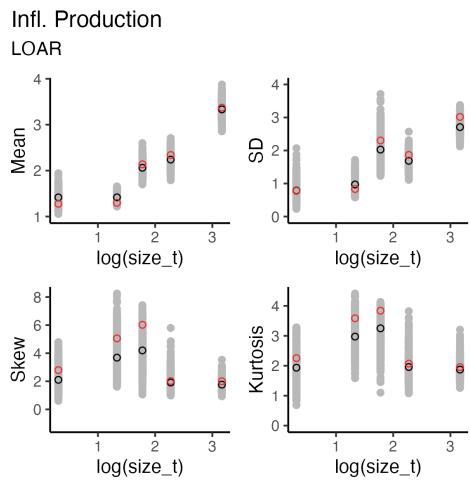
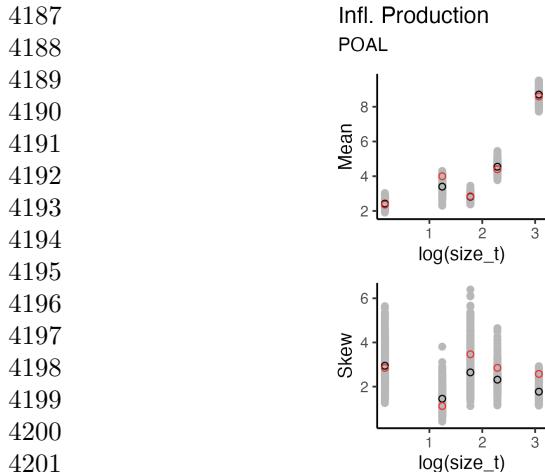


Figure S62: Graphical posterior predictive check for mean and higher moments of *L. arundinacea* flowering model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.

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4203 Figure S63: Graphical posterior predictive check for mean and higher moments of *P.*  
 4204 *alsodes* flowering model across size. Consistency between real data and fitted values  
 4205 across sizes indicates that the vital rate models are accurately capturing size depen-  
 4206 dence. Points show the value of statistical moments binned across size for the observed  
 4207 data (red circles) compared to the simulated datasets (grey circles) and the median  
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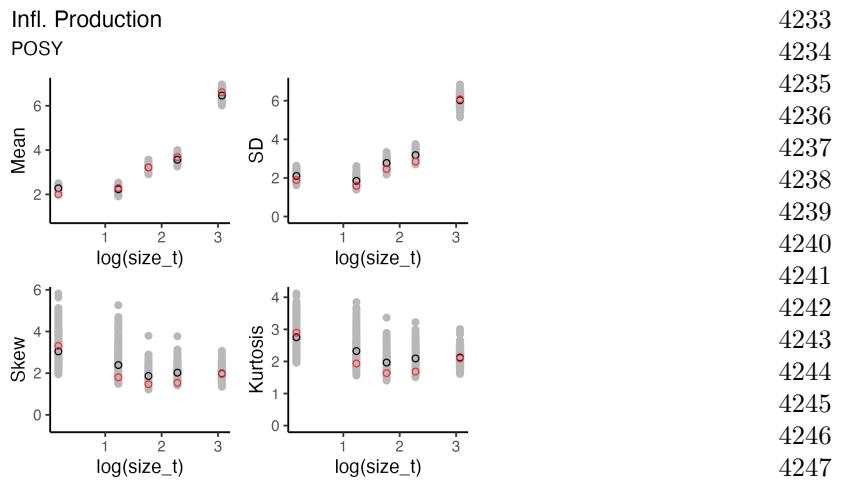
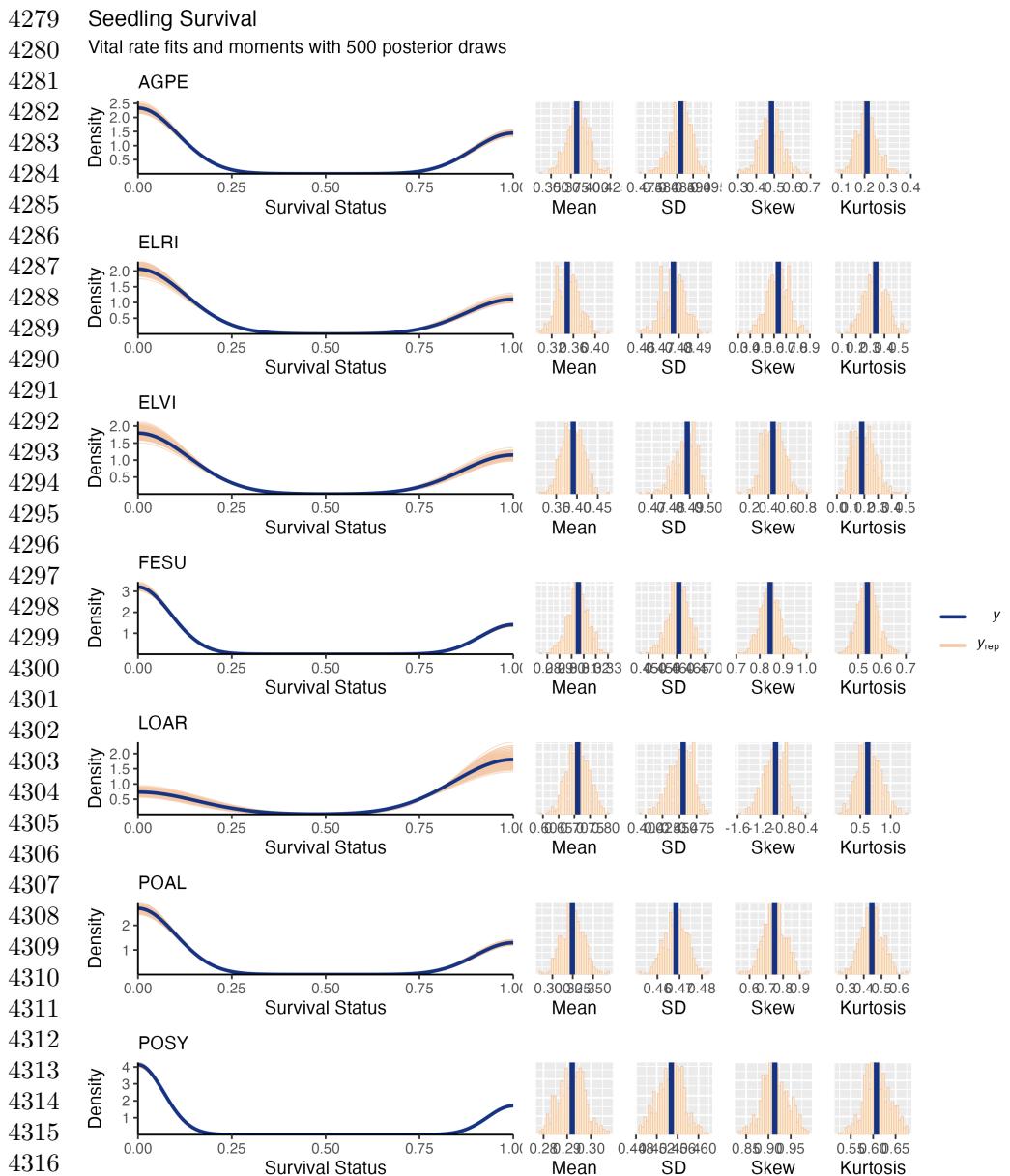


Figure S64: Graphical posterior predictive check for mean and higher moments of *P. sylvestris* flowering model across size. Consistency between real data and fitted values across sizes indicates that the vital rate models are accurately capturing size dependence. Points show the value of statistical moments binned across size for the observed data (red circles) compared to the simulated datasets (grey circles) and the median of the simulated values (black circles) generated from 500 posterior draws from the fitted model.



4318 Figure S65: Graphical posterior predictive check for statistical model of Seedling  
4319 Survival. Consistency between real data and simulated values indicates that fitted  
4320 models describe the data well. Lines show density distributions of observed data (blue  
4321 line) compared to data simulated from fitted models (tan lines) generated from 500  
4322 draws from posterior distributions of model parameters along with the distribution's  
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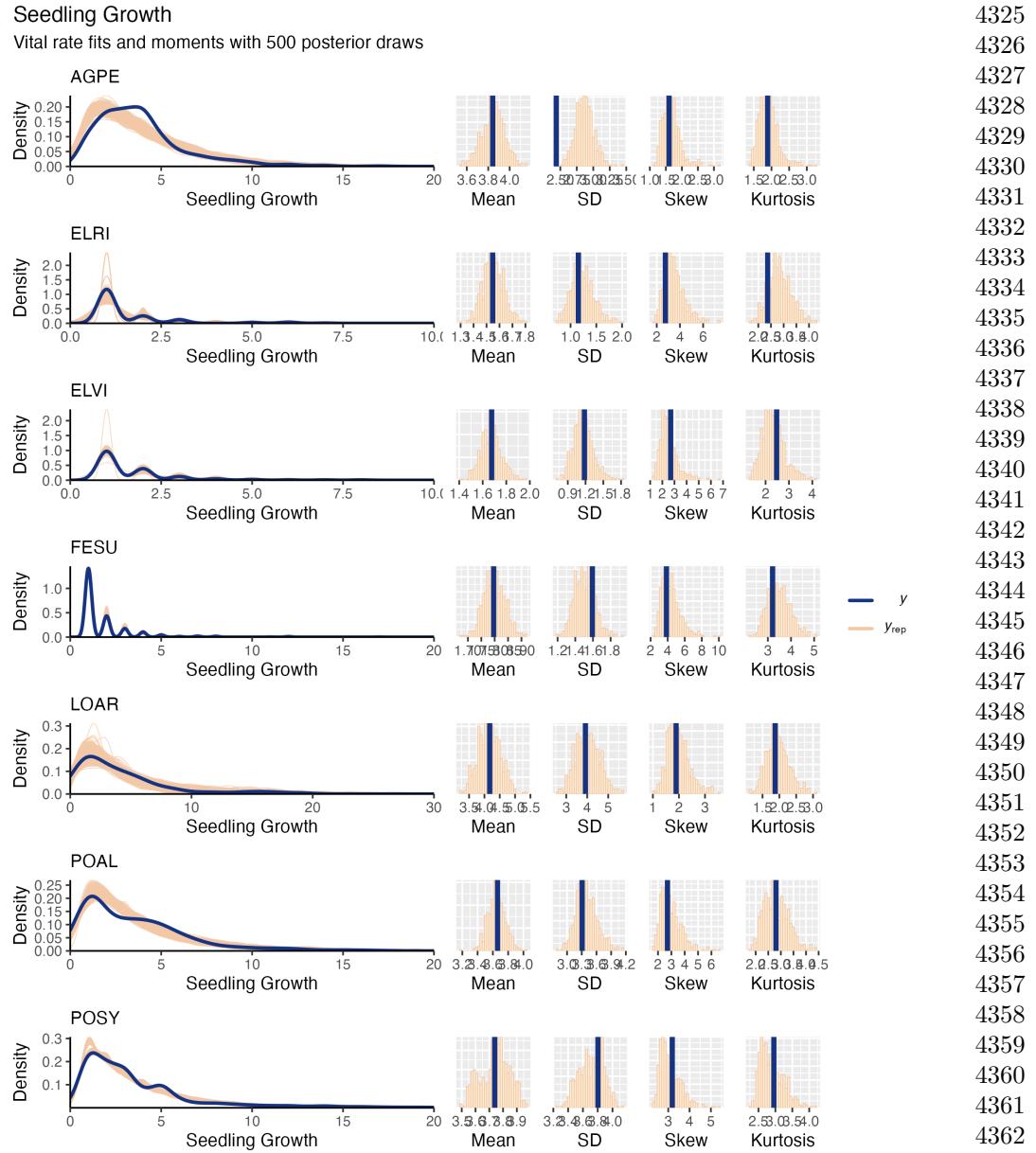
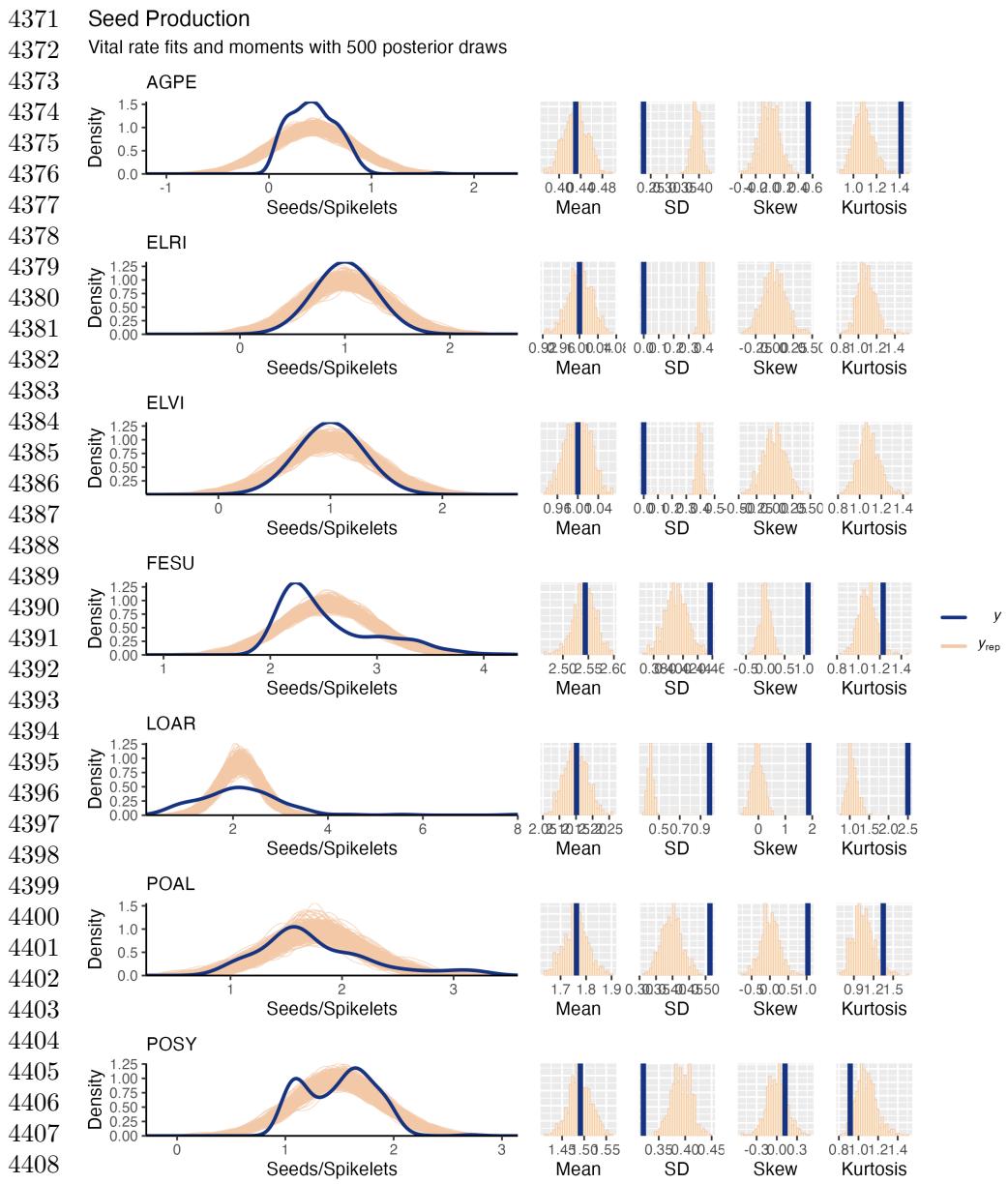


Figure S66: Graphical posterior predictive check for statistical model of Seedling Growth. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.



4409 Figure S67: Graphical posterior predictive check for statistical model of Mean Seed-  
4410 s/Spikelet. Consistency between real data and simulated values indicates that fitted  
4411 models describe the data well. Lines show density distributions of observed data (blue  
4412 line) compared to data simulated from fitted models (tan lines) generated from 500  
4413 draws from posterior distributions of model parameters along with the distribution's  
4414 moments.  
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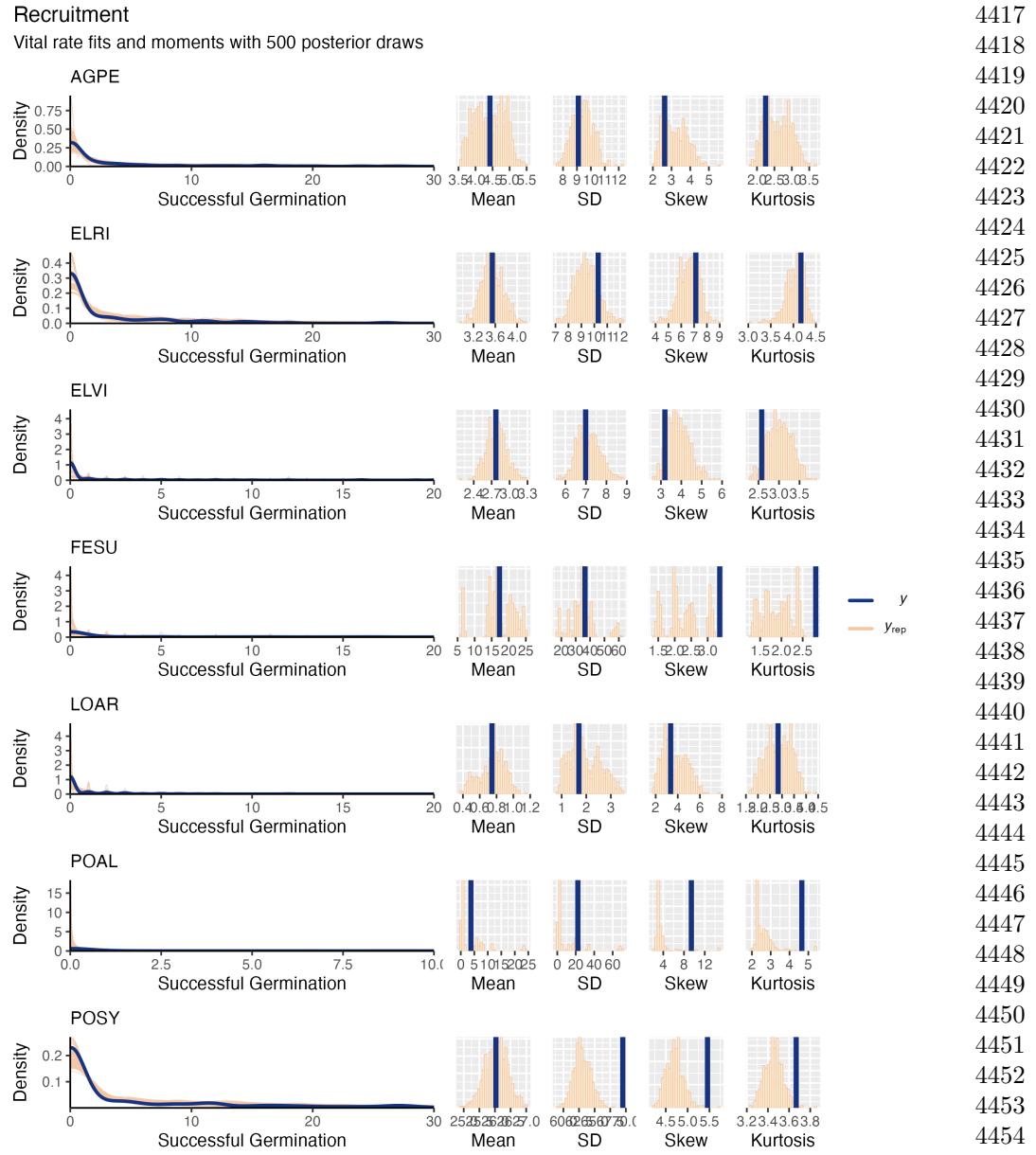


Figure S68: Graphical posterior predictive check for statistical model of Recruitment. Consistency between real data and simulated values indicates that fitted models describe the data well. Lines show density distributions of observed data (blue line) compared to data simulated from fitted models (tan lines) generated from 500 draws from posterior distributions of model parameters along with the distribution's moments.

4463 Adult Survival

4464 Posterior mean with 80% credible intervals

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$\beta_{0ho}$ - AGPE; Orig.

4469  $\beta_{0ho}$ - ELRI; Rec.

4470  $\beta_{0ho}$ - ELRI; Orig.

4471  $\beta_{0ho}$ - FESU; Orig.

4472  $\beta_{0ho}$ - LOAR; Orig.

4473  $\beta_{0ho}$ - POAL; Orig.

4474  $\beta_{0ho}$ - POSY; Orig.

4475  $\beta_{0ho}$ - AGPE; Rec.

4476  $\beta_{0ho}$ - ELRI; Rec.

4477  $\beta_{0ho}$ - FESU; Rec.

4478  $\beta_{0ho}$ - LOAR; Rec.

4479  $\beta_{0ho}$ - POAL; Rec.

4480  $\beta_{0ho}$ - POSY; Rec.

4481  $\beta_{2ho}$ - AGPE Size; Orig.

4482  $\beta_{2ho}$ - ELRI Size; Orig.

4483  $\beta_{2ho}$ - ELVI Size; Orig.

4484  $\beta_{2ho}$ - FESU Size; Orig.

4485  $\beta_{2ho}$ - LOAR Size; Orig.

4486  $\beta_{2ho}$ - POAL Size; Orig.

4487  $\beta_{2ho}$ - POSY Size; Orig.

4488  $\beta_{2ho}$ - AGPE Quadratic; Orig.

4489  $\beta_{2ho}$ - ELRI Quadratic; Orig.

4490  $\beta_{2ho}$ - ELVI Quadratic; Orig.

4491  $\beta_{2ho}$ - FESU Quadratic; Orig.

4492  $\beta_{2ho}$ - LOAR Quadratic; Orig.

4493  $\beta_{2ho}$ - POAL Quadratic; Orig.

4494  $\beta_{2ho}$ - POSY Quadratic; Orig.

4495  $\beta_{2ho}$ - AGPE Quadratic; Rec.

4496  $\beta_{2ho}$ - ELRI Quadratic; Rec.

4497  $\beta_{2ho}$ - ELVI Quadratic; Rec.

4498  $\beta_{2ho}$ - FESU Quadratic; Rec.

4499  $\beta_{2ho}$ - LOAR Quadratic; Rec.

4500  $\beta_{2ho}$ - POAL Quadratic; Rec.

4501  $\beta_{2ho}$ - POSY Quadratic; Rec.

4502  $\beta_{1h}$ - AGPE Endo

4503  $\beta_{1h}$ - ELRI Endo

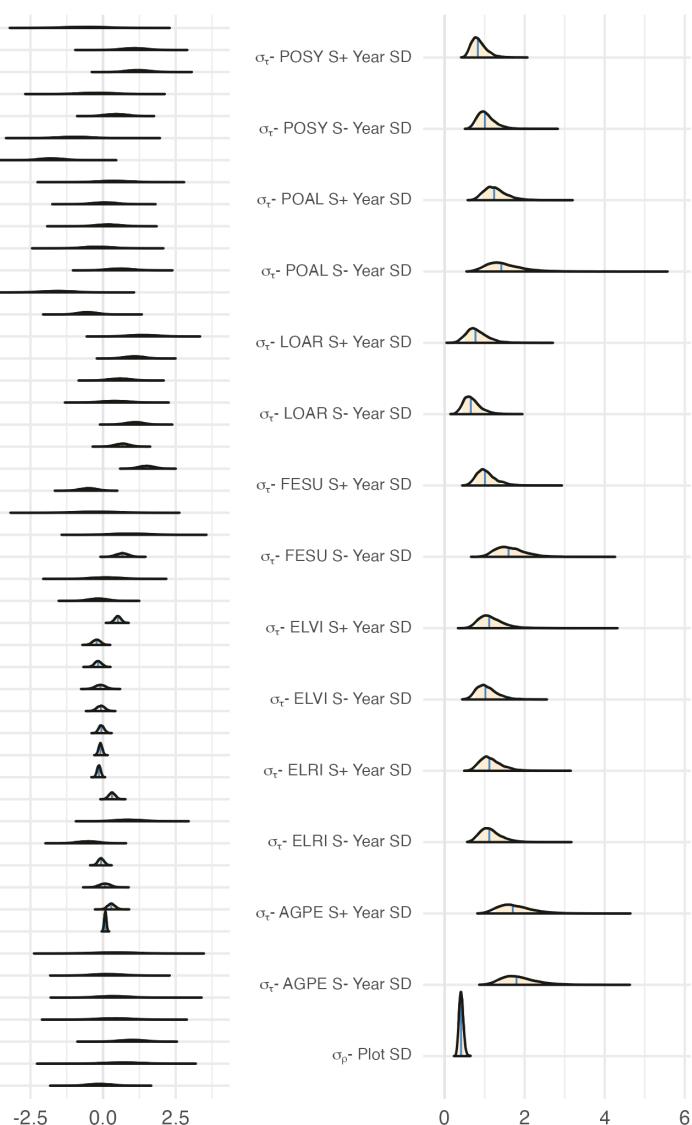
4504  $\beta_{1h}$ - ELVI Endo

4505  $\beta_{1h}$ - FESU Endo

4506  $\beta_{1h}$ - LOAR Endo

4507  $\beta_{1h}$ - POAL Endo

4508  $\beta_{1h}$ - POSY Endo



4504 Figure S69: Posterior distributions of the vital rate regressions for Adult Survival.

4505 Density curves show 80% credible interval along with the posterior posterior mean.

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**Seedling Survival**  
 Posterior mean with 80% credible intervals

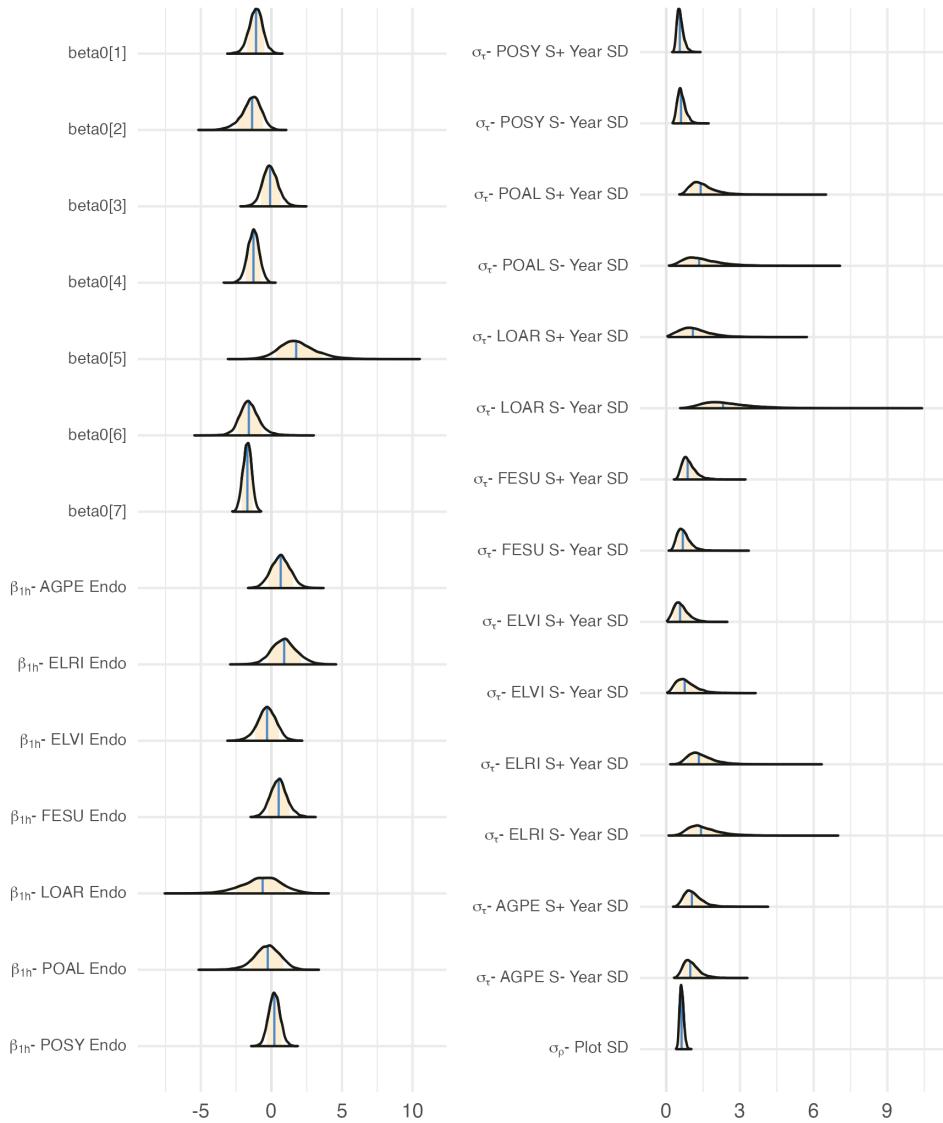
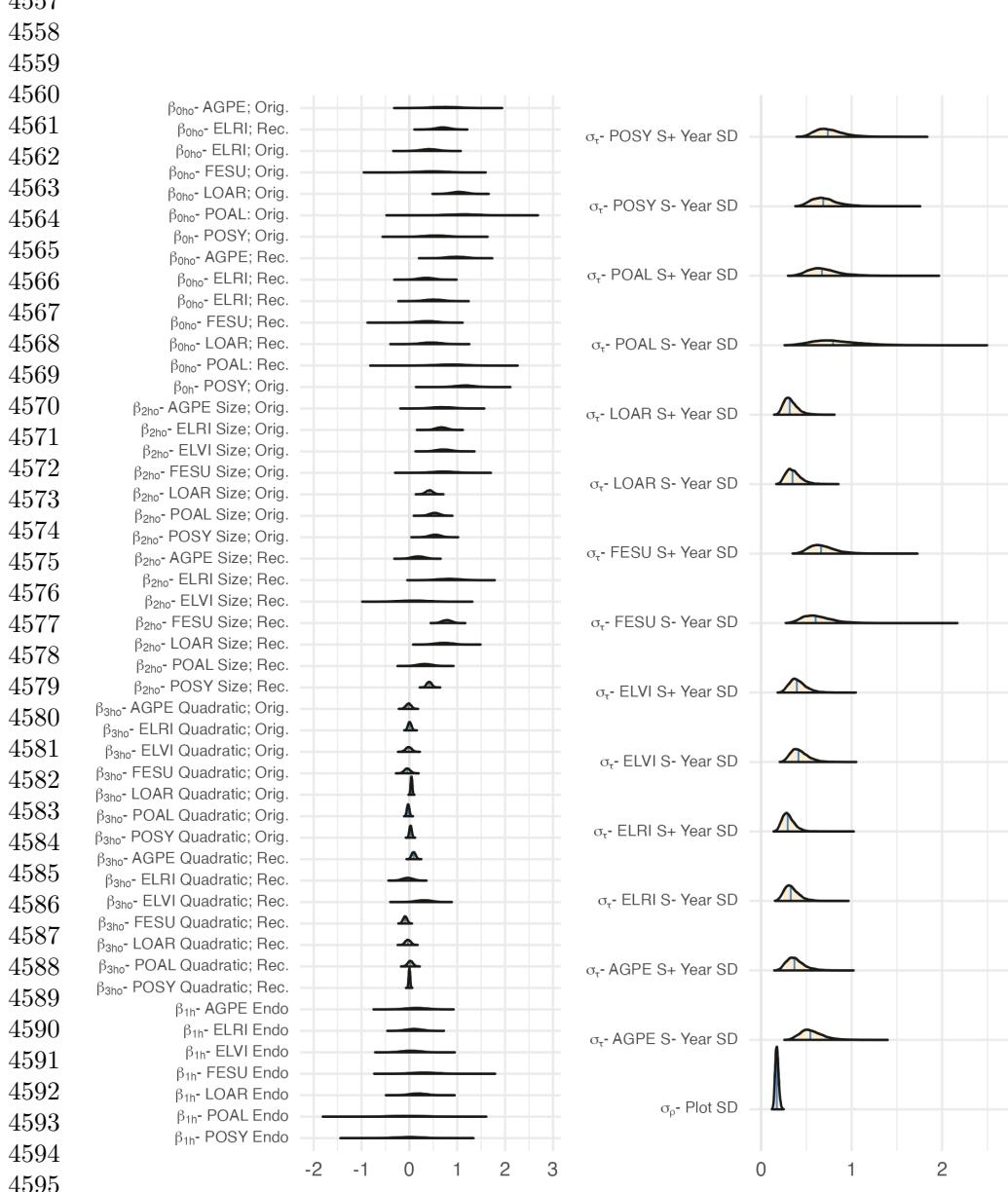


Figure S70: Posterior distributions of the vital rate regressions for Seedling Survival. Density curves show 80% credible interval along with the posterior posterior mean.

4555 Adult Growth  
 4556 Posterior mean with 80% credible intervals



4596 Figure S71: Posterior distributions of the vital rate regressions for Adult Growth.  
 4597 Density curves show 80% credible interval along with the posterior posterior mean.  
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**Seedling Growth**  
 Posterior mean with 80% credible intervals

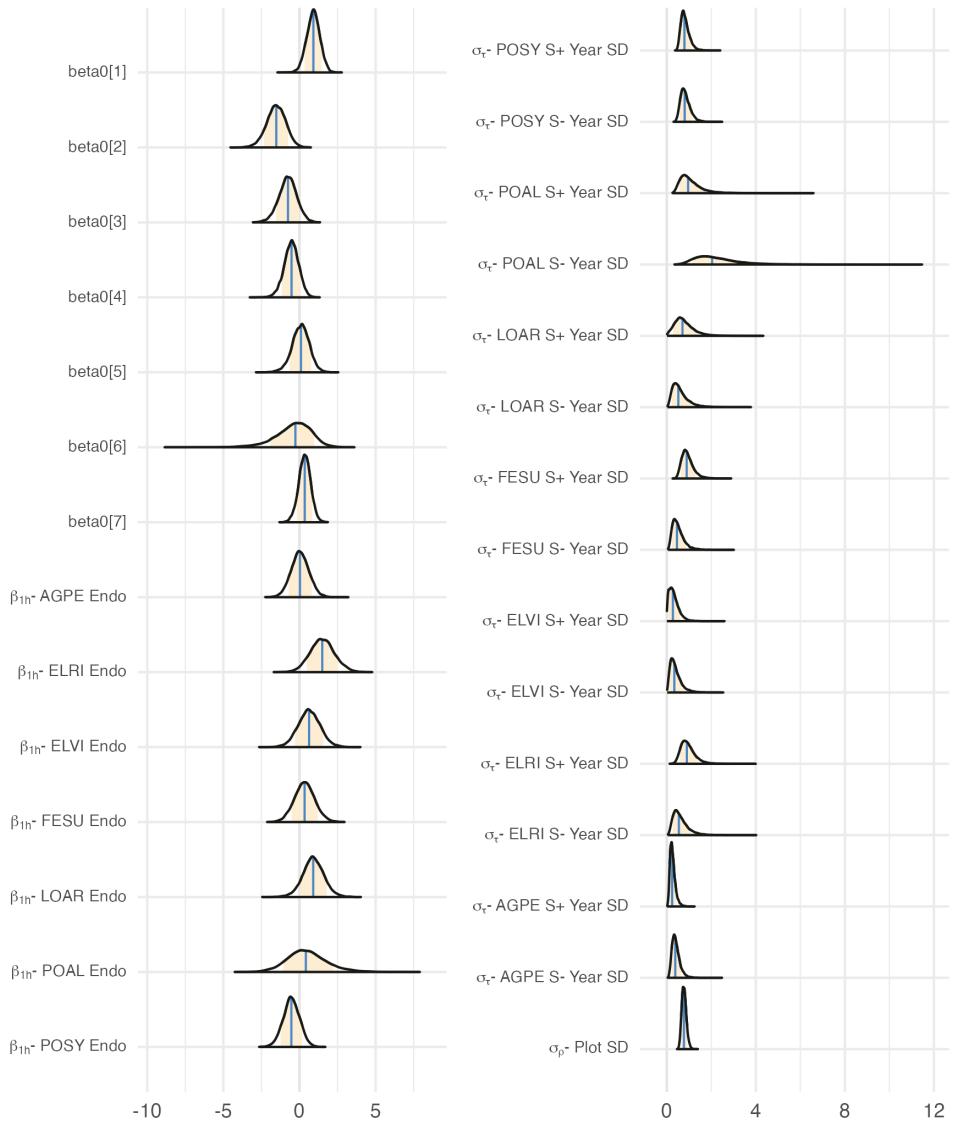
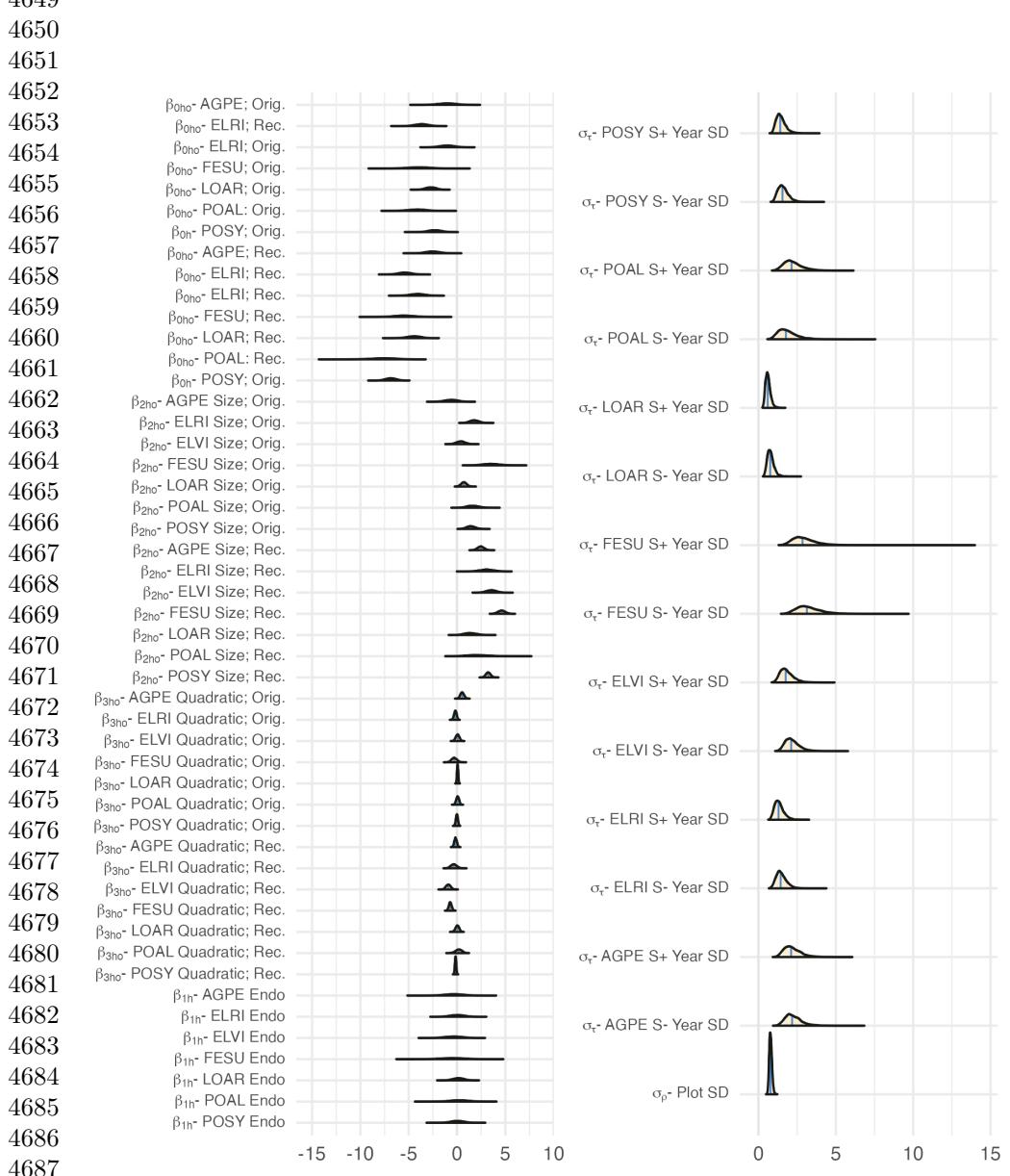


Figure S72: Posterior distributions of the vital rate regressions for Seedling Growth. Density curves show 80% credible interval along with the posterior posterior mean.

4647 Flowering Probability  
 4648 Posterior mean with 80% credible intervals



4688 Figure S73: Posterior distributions of the vital rate regressions for Flowering Probability. Density curves show 80% credible interval along with the posterior posterior mean.

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## Infl. Production

Posterior mean with 80% credible intervals

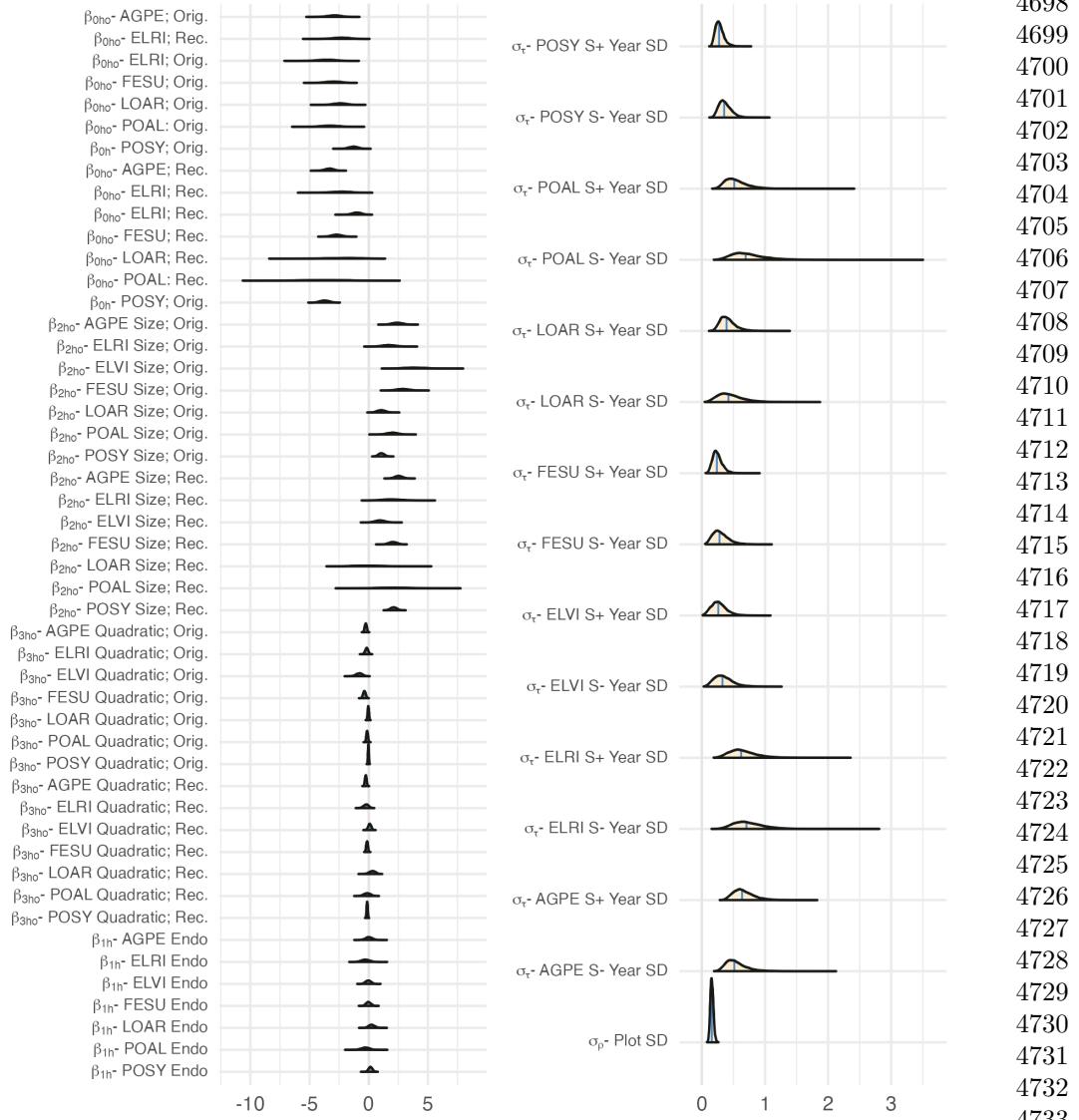
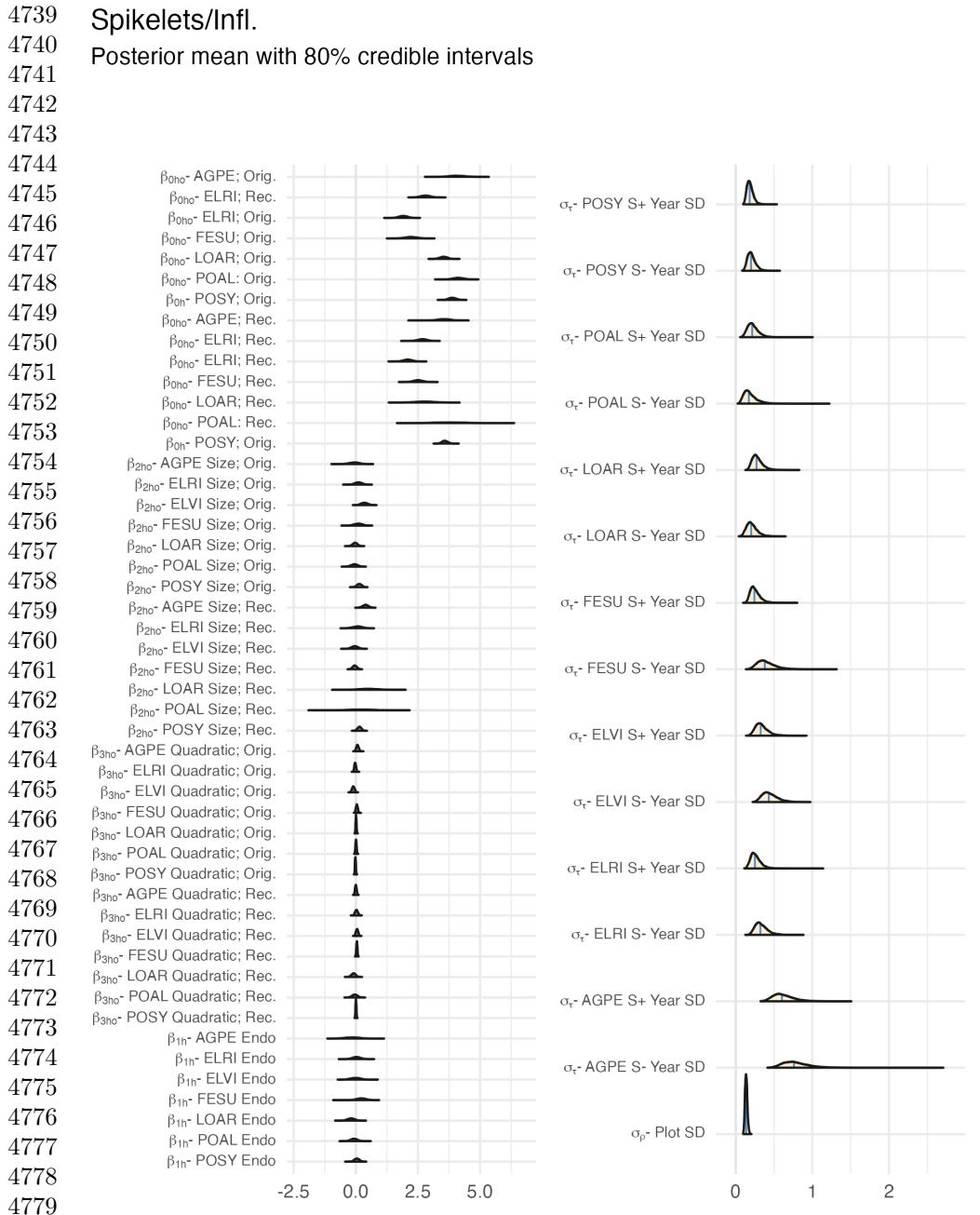


Figure S74: Posterior distributions of the vital rate regressions for Inflorescence Production. Density curves show 80% credible interval along with the posterior posterior mean.



4780 Figure S75: Posterior distributions of the vital rate regressions for Spikelets/Inflorescence. Density curves show 80% credible interval along with the posterior posterior  
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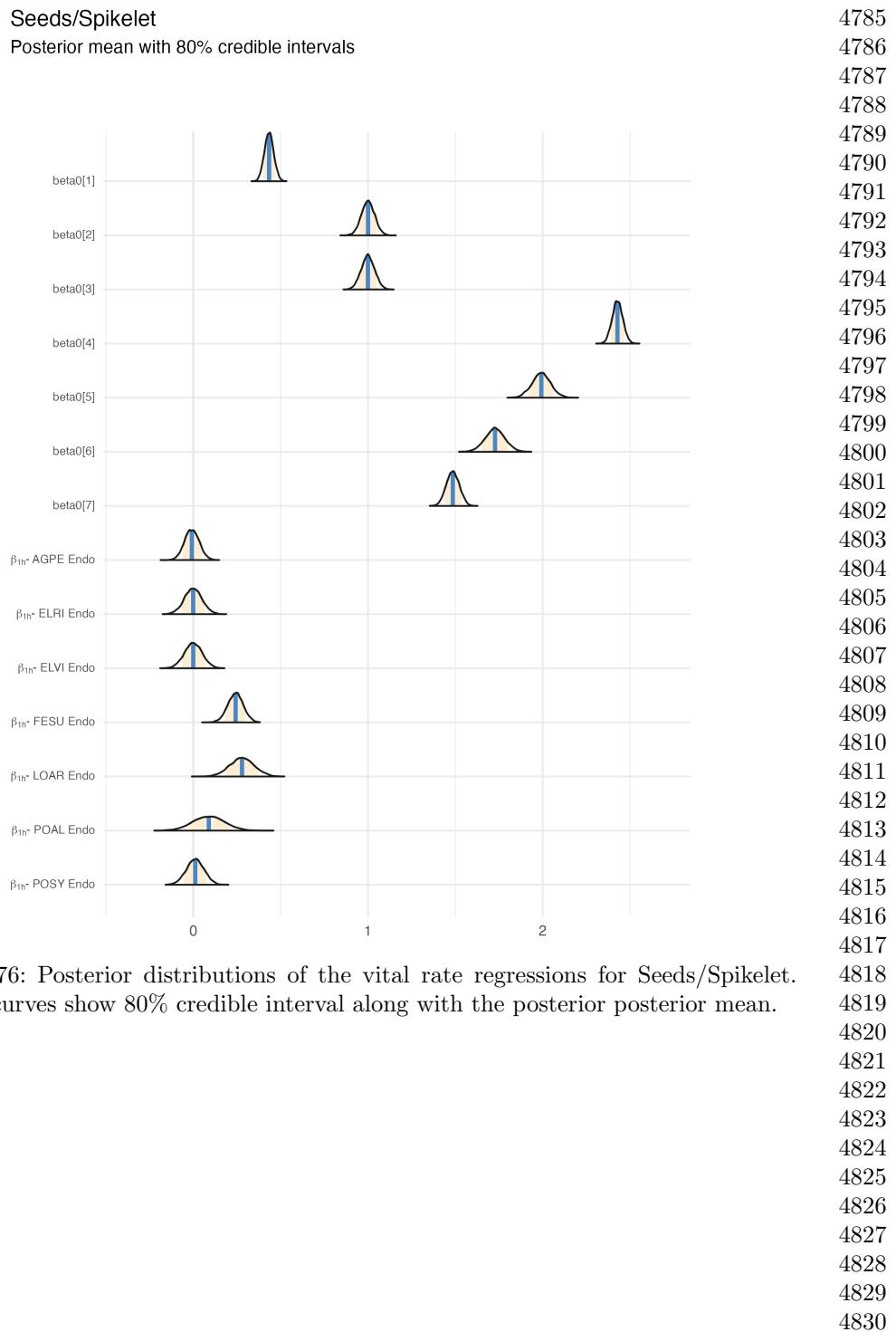
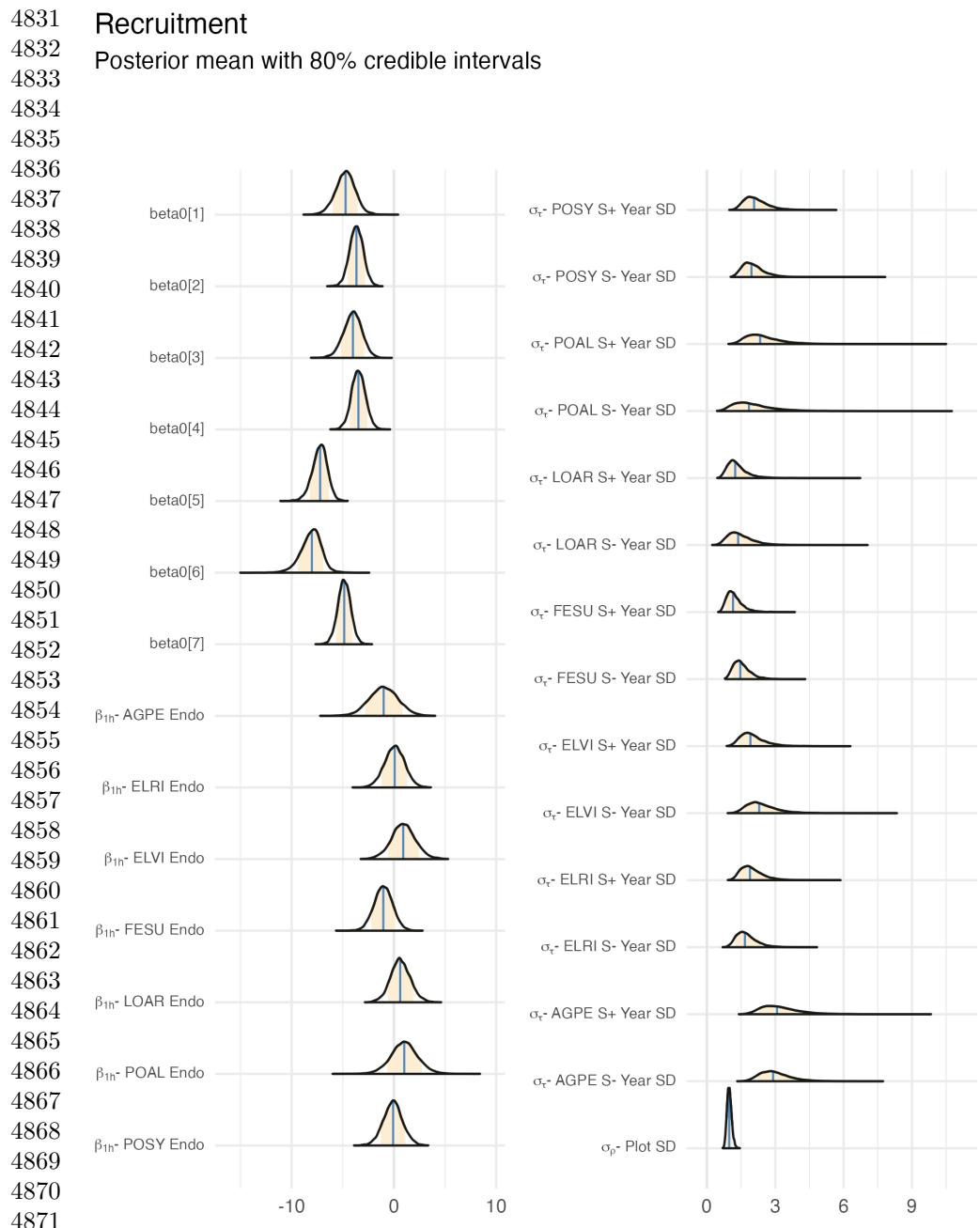


Figure S76: Posterior distributions of the vital rate regressions for Seeds/Spikelet. Density curves show 80% credible interval along with the posterior posterior mean.



4872 Figure S77: Posterior distributions of the vital rate regressions for Recruitment.

4873 Density curves show 80% credible interval along with the posterior posterior mean.

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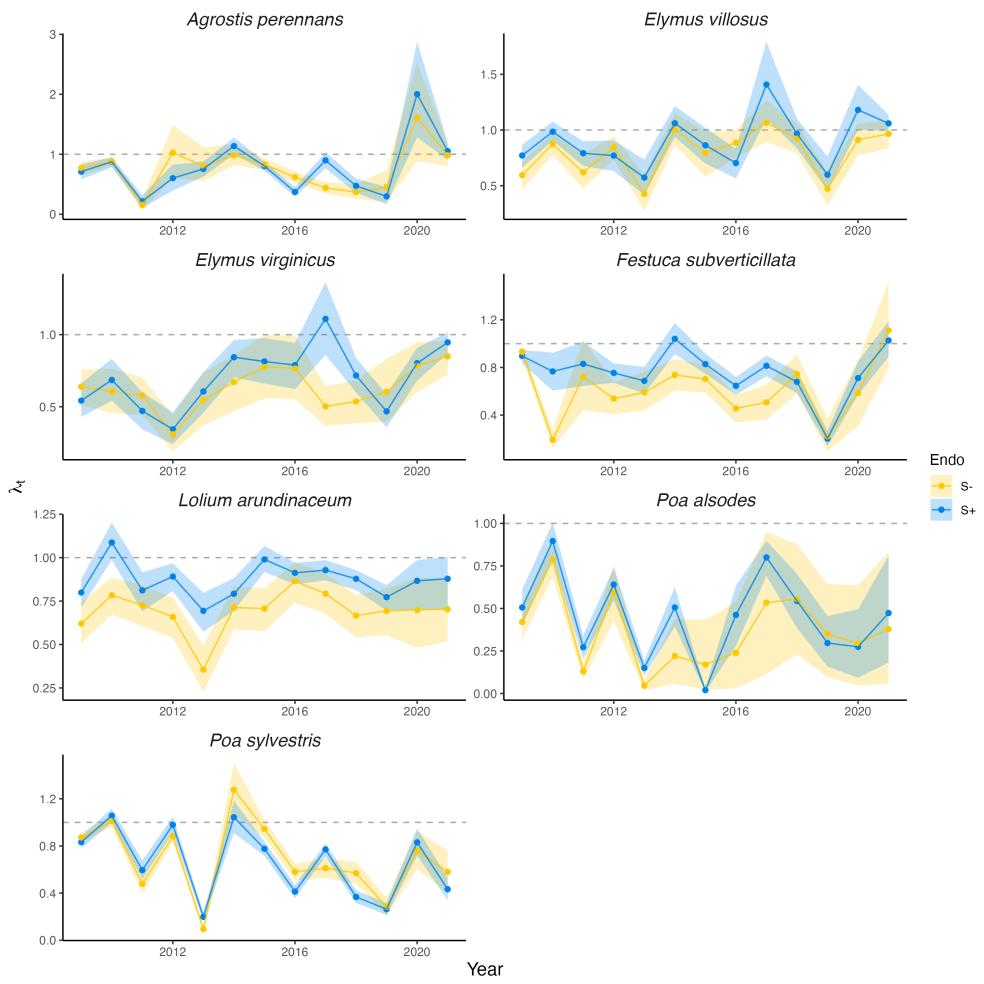


Figure S78: Annual growth rate values ( $\lambda_t$ ) over thirteen years. Mean values for symbiotic (blue) and symbiont-free (yellow) population growth rates are shown along with 80% credible intervals. Dashed line at  $\lambda_t = 1$  indicates stable population growth rate. All values are calculated from matrix models representing recruit plants.

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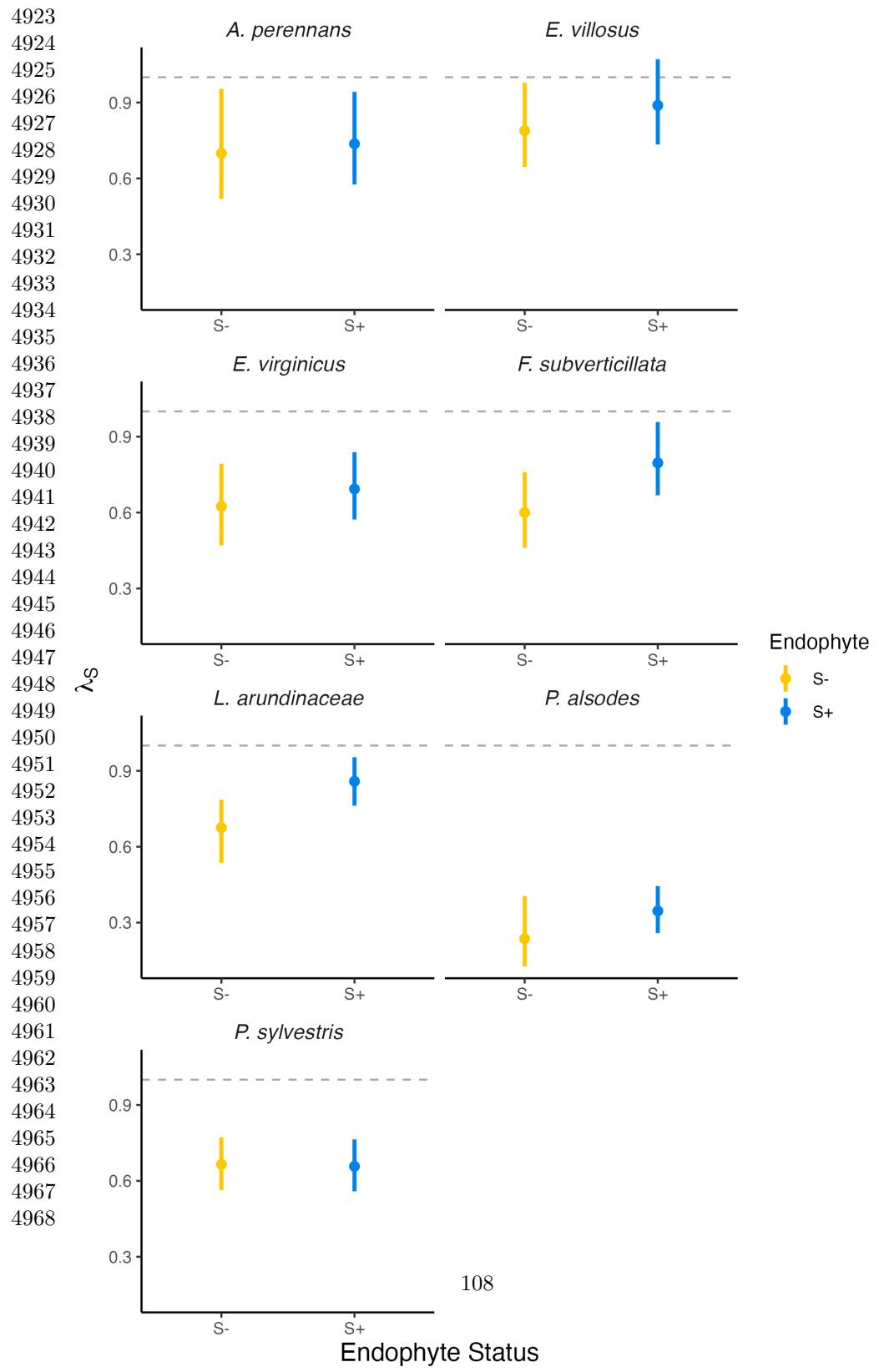
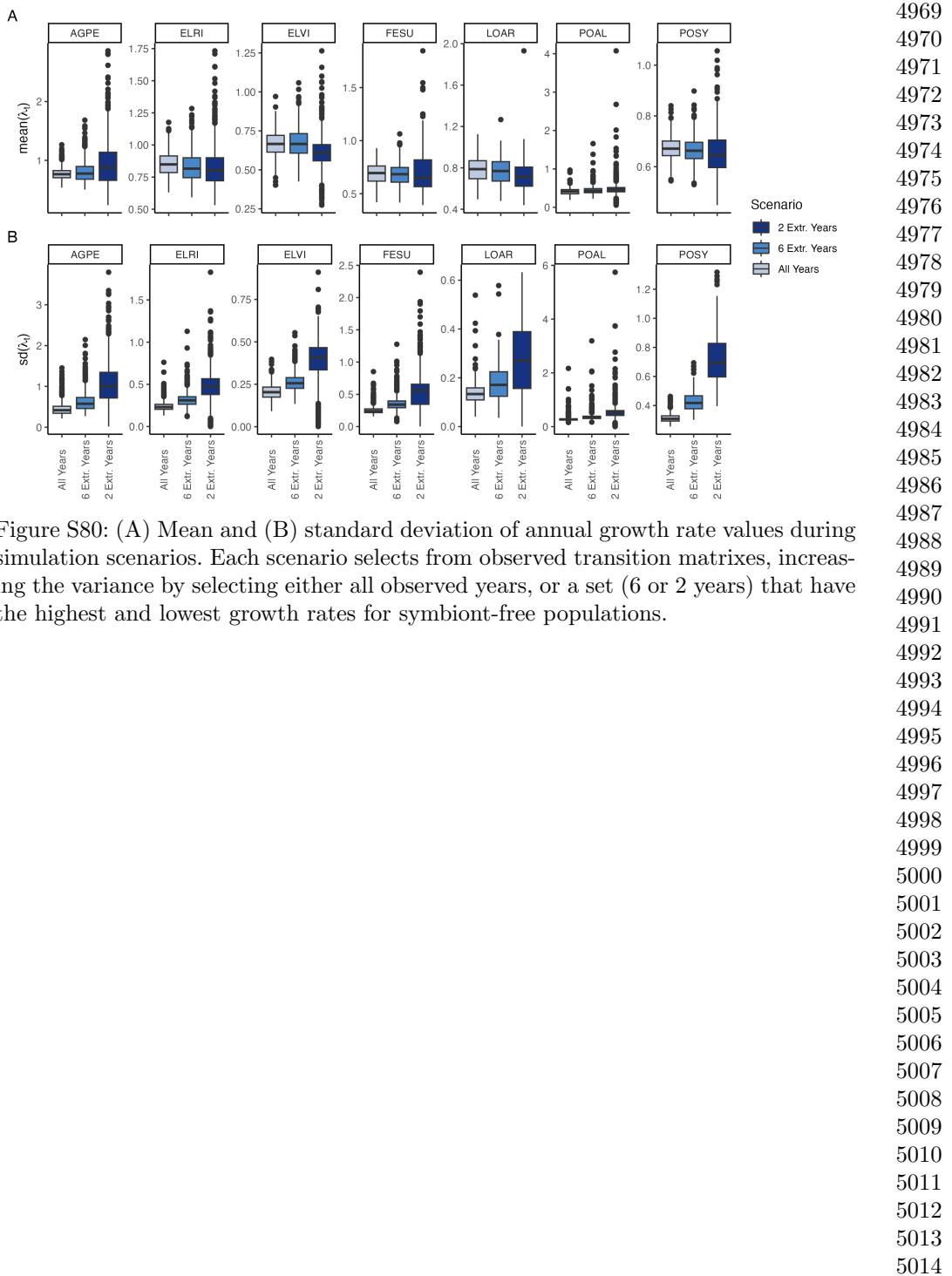
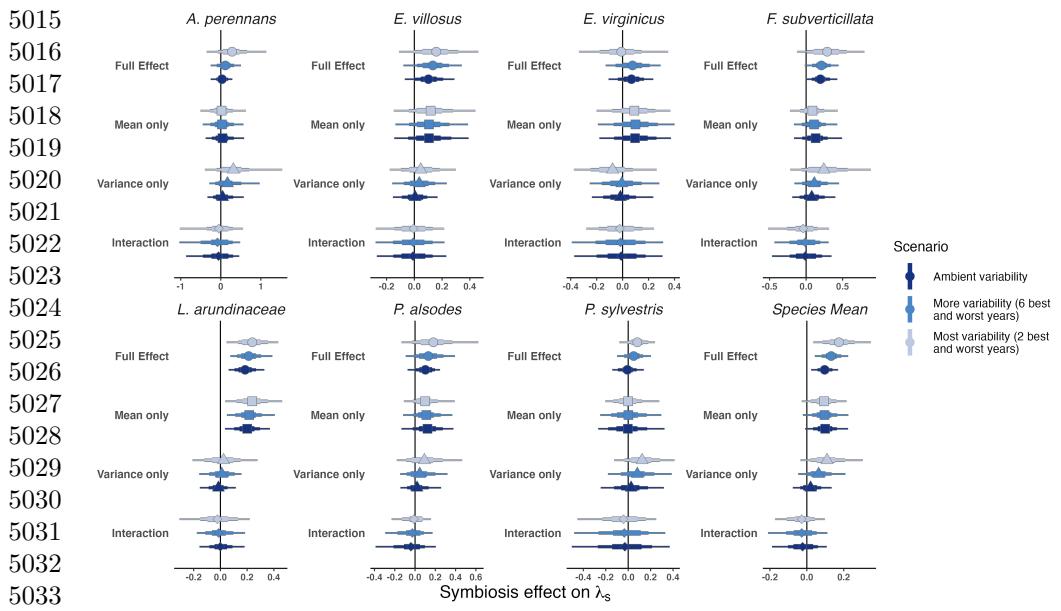


Figure S79: Stochastic population growth rates ( $\lambda_S$ ) for symbiotic (blue) and symbiont-free (yellow) populations. Points show posterior medians along with the 95% credible interval and posterior medians. All values are calculated from matrix models representing recruit plants.





5034 Figure S81: Endophyte contributions to stochastic growth rates under observed and  
 5035 elevated variance across species. The total effect of endophytes (circle) comes from  
 5036 mean benefits (square) and variance buffering (triangle) as well as the interaction  
 5037 between mean and variance effects (diamond). Shapes indicate the posterior mean of  
 5038 each contribution, along with bars for the 50, 75 and 95 % credible intervals. Under  
 5039 scenarios of increasing variance, represented by increasing color intensity, effects of  
 5040 variance buffering increase leading to a more mutualistic symbiosis.

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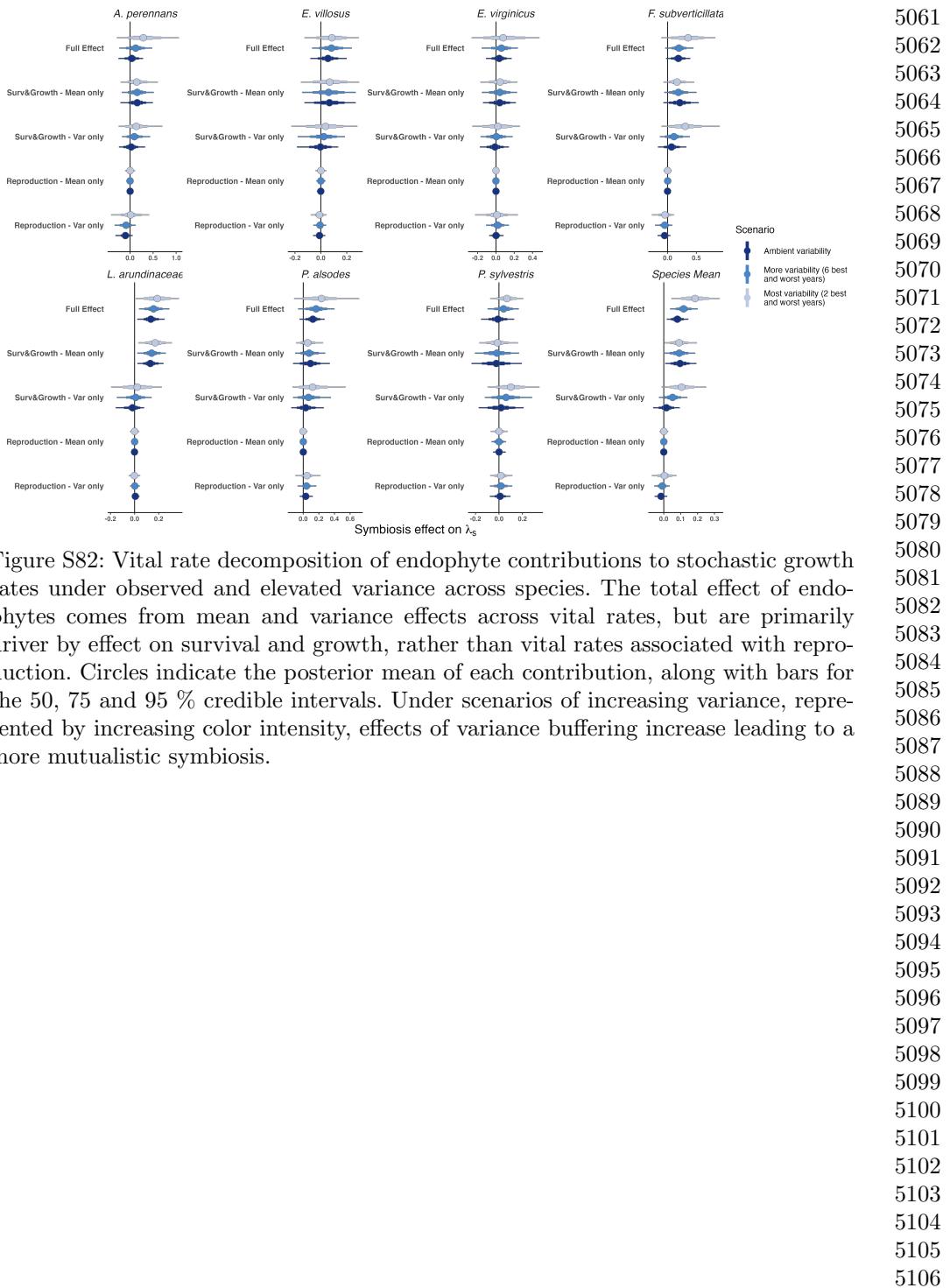
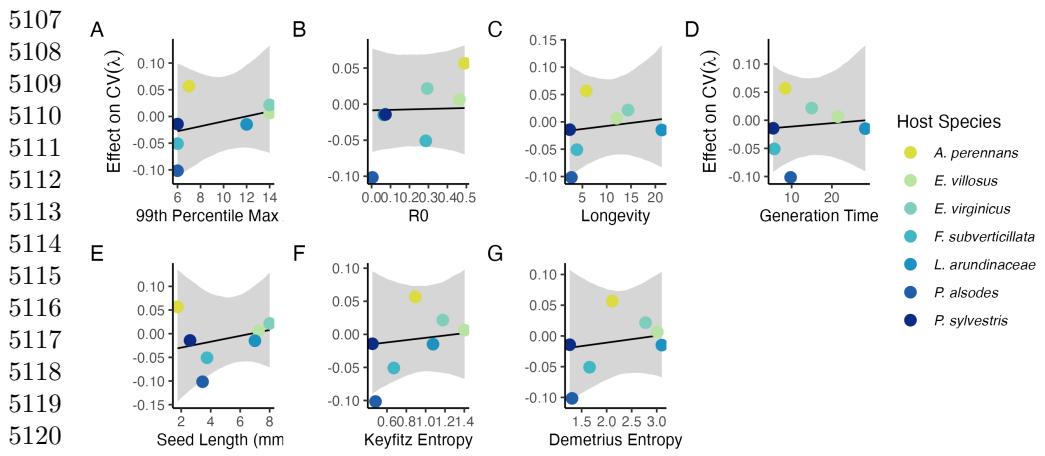


Figure S82: Vital rate decomposition of endophyte contributions to stochastic growth rates under observed and elevated variance across species. The total effect of endophytes comes from mean and variance effects across vital rates, but are primarily driver by effect on survival and growth, rather than vital rates associated with reproduction. Circles 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.



5121 Figure S83: Relationship between variance buffering and life history traits describing  
 5122 the fast-slow life history continuum accounting for phylogenetic covariance between  
 5123 grass host species. Regressions between life history traits describing the fast-slow life  
 5124 history continuum ((A) 99th percentile maximum age observed during long term cen-  
 5125 suses in years; (B) Net reproductive rate; (C) Longevity; (D) Generation time in years;  
 5126 (E) Seed size) and the effect of endophyte symbiosis on the coefficient of variation in  
 5127 population growth rate ( $\lambda$ ). Each panel shows the fitted mean relationship (line) along  
 5128 with the 95% credible interval.  
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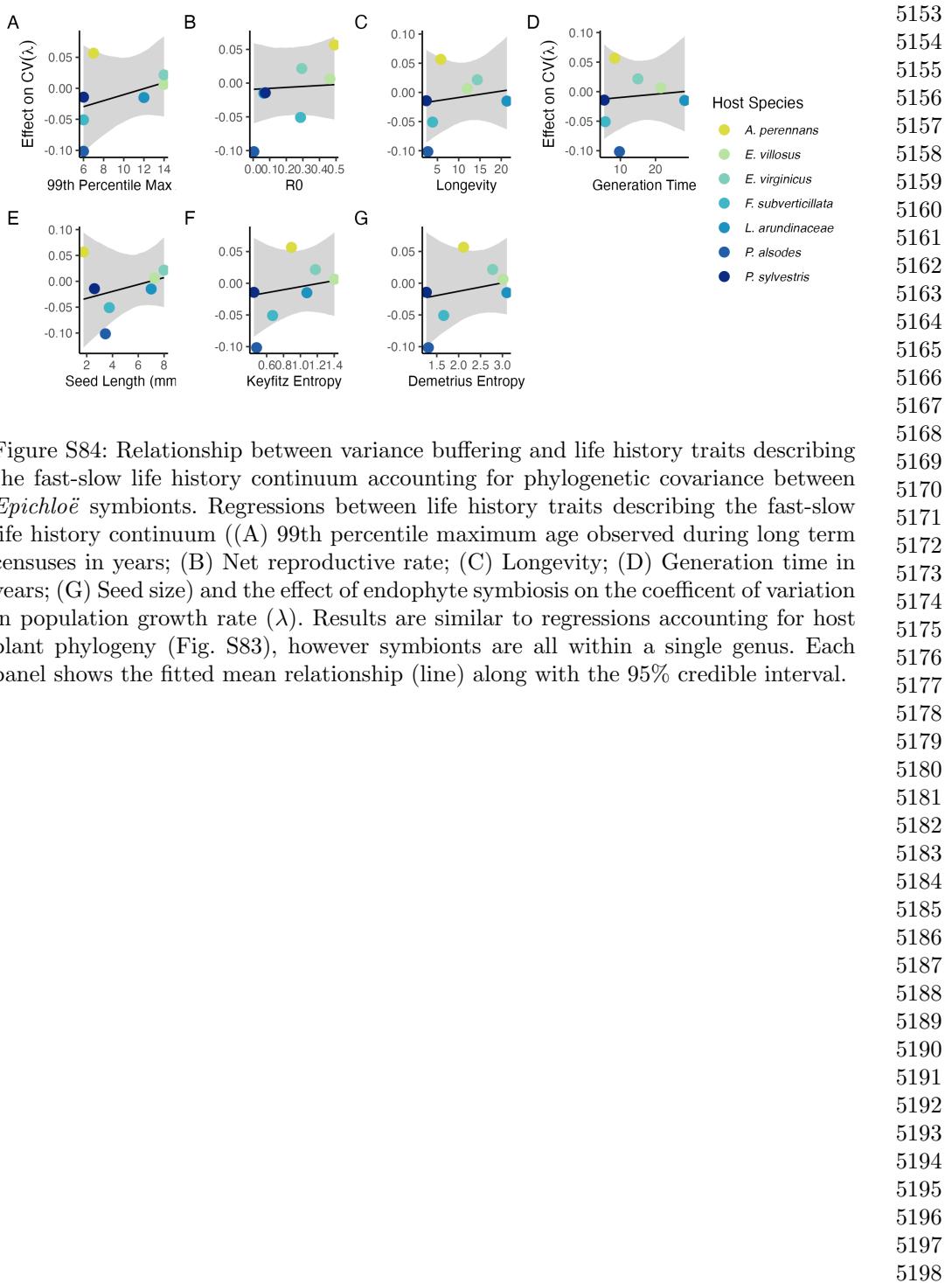
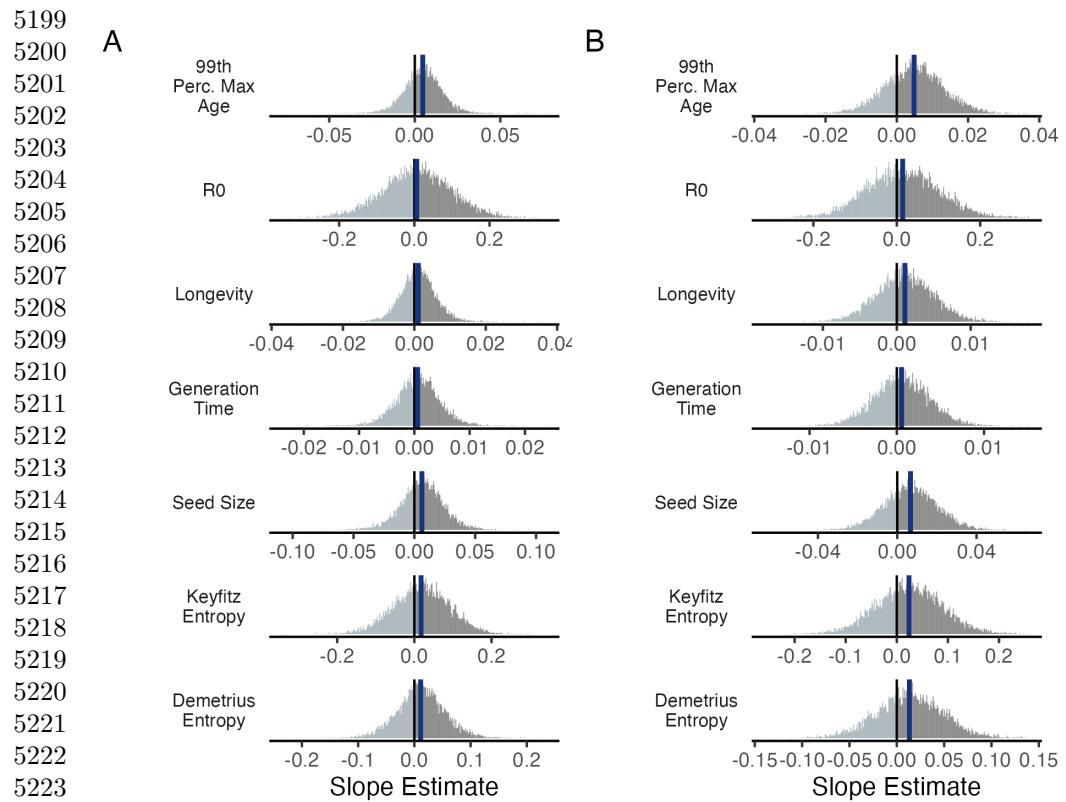


Figure S84: Relationship between variance buffering and life history traits describing the fast-slow life history continuum accounting for phylogenetic covariance between *Epichloë* symbionts. Regressions between life history traits describing the fast-slow life history continuum ((A) 99th percentile maximum age observed during long term censuses in years; (B) Net reproductive rate; (C) Longevity; (D) Generation time in years; (G) Seed size) and the effect of endophyte symbiosis on the coefficient of variation in population growth rate ( $\lambda$ ). Results are similar to regressions accounting for host plant phylogeny (Fig. S83), however symbionts are all within a single genus. Each panel shows the fitted mean relationship (line) along with the 95% credible interval.



5225 Figure S85: Posterior estimates of life history trait effects on variance buffering.  
 5226 Grey histograms show the posterior distribution of the slope parameter from models  
 5227 incorporating (A) host plant phylogenetic covariance and (B) symbiont phylogenetic  
 5228 covariance for each life history trait with blue bars showing the posterior mean.

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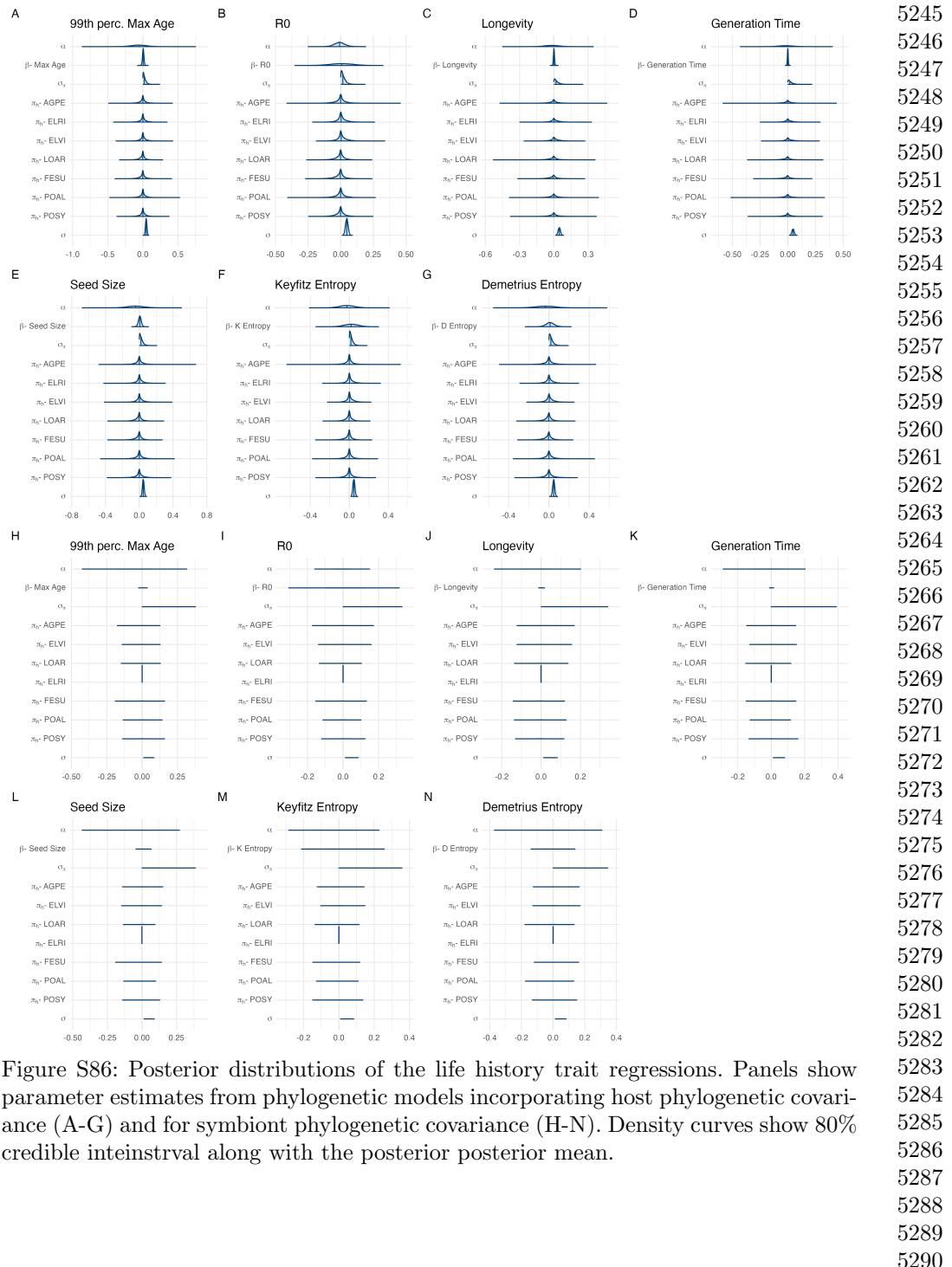
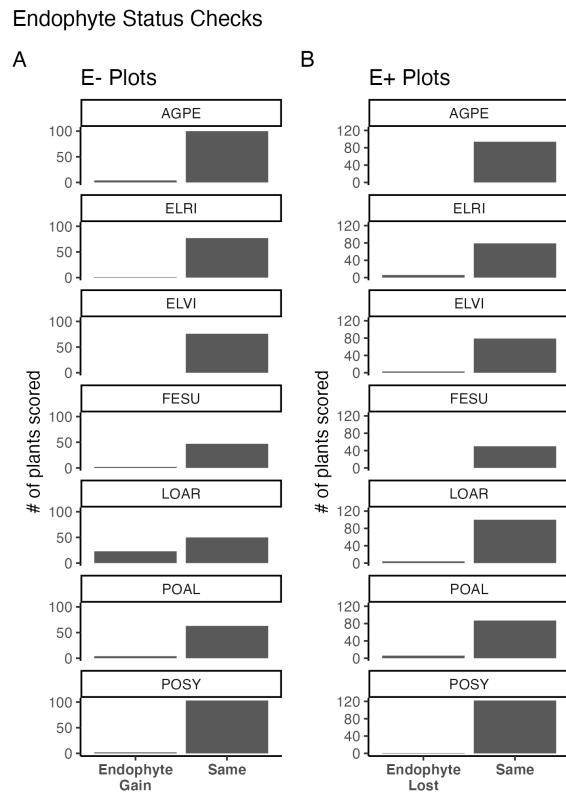


Figure S86: Posterior distributions of the life history trait regressions. Panels show parameter estimates from phylogenetic models incorporating host phylogenetic covariance (A-G) and for symbiont phylogenetic covariance (H-N). Density curves show 80% credible interval along with the posterior mean.

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5317 Figure S87: Faithfulness of experimental plots to assigned endophyte status. Counts  
5318 of plants scored with leaf peels or seed squashes to check the faithfulness of recruits  
5319 to the assigned plot-level endophyte status. (A) Endophytic plants may be gained in  
5320 initially S- plots, or (B) lost in initially S+ plots.

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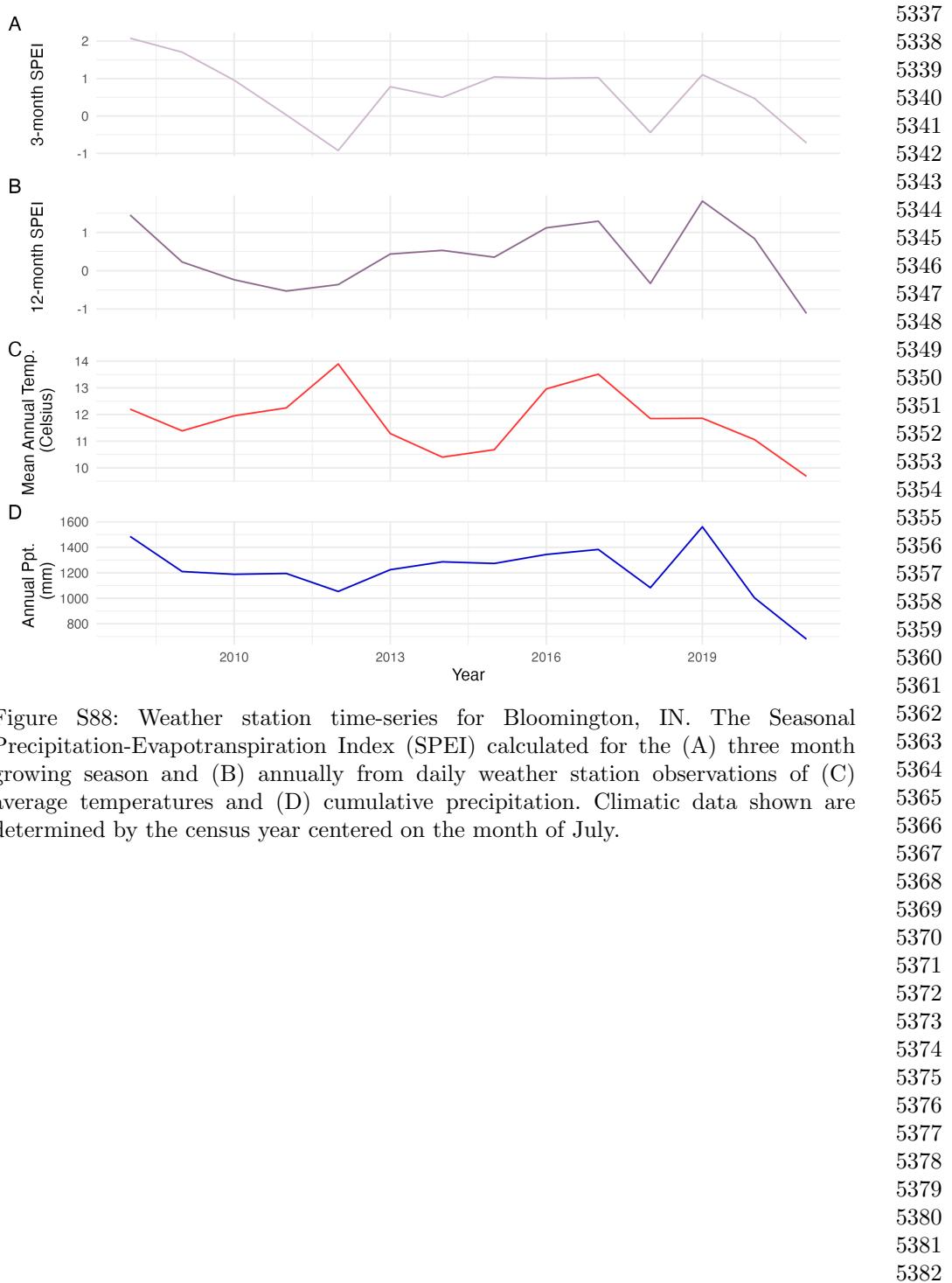
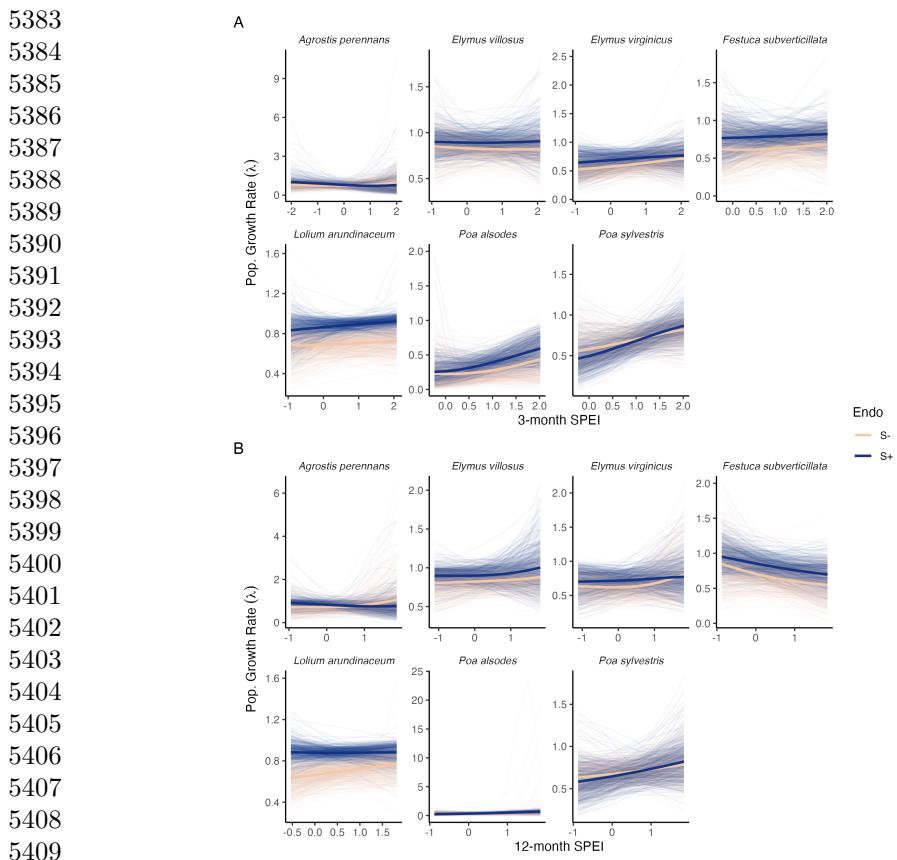


Figure S88: Weather station time-series for Bloomington, IN. The Seasonal Precipitation-Evapotranspiration Index (SPEI) calculated for the (A) three month growing season and (B) annually from daily weather station observations of (C) average temperatures and (D) cumulative precipitation. Climatic data shown are determined by the census year centered on the month of July.



5410 Figure S89: Predicted population growth rates across drought indices. Symbiotic (S+;  
 5411 blue) and symbiont-free (S-; tan) populations respond differently to climate as mea-  
 5412 sured by the (A) 3-month SPEI and (B) 12-month SPEI. Thick lines represent the  
 5413 predicted mean growth rate and thin lines show 500 posterior draws.

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<b>Supplemental Tables S1-S3</b>	
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**Table S1:** Summary of host-endophyte prorogation 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)

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	0.003	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
<b>Page's <math>\lambda</math>-host</b>	—	0.23	0.22	0.19	0.23	0.23	0.19	0.22	—	—
<b>Page's <math>\lambda</math>-host (90% CI)</b>	—	(0-0.8)	(0-0.8)	(0-0.7)	(0-0.8)	(0-0.8)	(0-0.8)	(0-0.8)	—	—
<b>Page's <math>\lambda</math>-symbiont</b>	—	0.57	0.56	0.56	0.56	0.56	0.55	0.58	—	—
<b>Page's <math>\lambda</math>-symbiont (90% CI)</b>	—	(0-0.9)	(0-0.9)	(0-0.9)	(0-0.9)	(0-0.9)	(0-0.9)	(0-0.9)	—	—

\*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>	0.0475	0.0513	-0.06	0.05	0.83	-0.05	0.119	2.34
<i>Elymus villosus</i>	0.0105	0.0710	0.00	-0.01	5.89	0.05	0.03	0.74
<i>Elymus virginicus</i>	0.031	0.0913	0.04	0.06	1.56	0.02	0.06	2.41
<i>Festuca subverticillata</i>	-0.1524	0.1386	0.02	0.03	1.15	-0.09	-0.11	1.20
<i>Lolium arundinaceum</i>	-0.0799	0.1872	0.02	0.01	0.47	-0.00	0.05	11.1.
<i>Poa alsodes</i>	-0.6859	0.1079	0.10	0.09	0.62	0.14	0.11	0.79
<i>Poa sylvestris</i>	-0.0164	-0.0211	0.18	0.12	0.64	0.09	0.06	0.64

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